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Pattern and Process in Evolution: Unfolding Nature's Origami

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Pattern and process are central concepts to understanding the evolution of behavioral traits for comparative psychologists. Origami is an art form which involves application of pattern and process to produce a wide array of objects using paper. Because of origami's parallels with evolution, both of morphology and behavior, it can serve as a concrete and accessible analogy for students of comparative psychology. Origami's processes can be reversed by unfolding the paper, thereby revealing patterns common across designs. Likewise, by studying pattern and process in evolution, scientists unfold nature's origami. Application to comparative psychology and pedagogy are discussed.

Keywords: cladistics, evolution, origami, pattern and process, teaching

Despite the centrality of the interplay of pattern and process to the foundations of evolutionary history and phylogenetic change, few teaching tools are available that focus on pattern and process. The goal of the present teaching exercise is to provide an overview of the concepts of evolutionary pattern and process and their importance to comparative psychology. This will allow educators to demonstrate to students how pattern and process work together to produce evolutionary change using a fun and simple, low-cost demonstration which would be suitable for classrooms especially in countries that are in need of stronger comparative psychology education. I have used this demonstration at institutions which serve low-income, high-risk college students, many of whom have little or no exposure to evolution prior to enrollment in the comparative psychology course. After completing this exercise, students will be able to identify patterns across phyla, the processes that acted upon them to produce phenotypic change, classify organisms based upon the patterns observed, and apply their knowledge to morphological and behavioral traits.

Origami is the art of paper folding, which likely had its origins in China and was popularized in Japan around the 9th century (McArthur & Lang, 2013). Comparisons of 19th century origami examples from both Europe and Asia suggest that the art was most likely developed independently in different parts of the world, the confluence of which produced modern origami through cultural exchanges in the late 19th century (Hatori, 2011). Today, origami is practiced around the world as an art form but also has influences in engineering and materials science (e.g., Faber et al., 2018; Turner et al., 2016). Traditionally, origami is made by folding a single square sheet of paper with no cutting or gluing. From a small square sheet of paper, a wide variety of plants, animals, and everyday objects can be represented. Folding diagrams and step-by-step instructions allow beginners to quickly learn the basic techniques and produce good results. It is a low-cost and easy-to-learn activity and has been successfully employed in a number of educational settings, such as middle school math education (Boakes, 2009; Robichaux & Rodrigue, 2003), language-communication (Foreman-Takano, 1998), and spatial problem solving (Taylor & Tenbrink, 2013).

Pattern and *process* are terms that have a specific meaning in the context of evolution. Evolution is the result of the interaction between patterns, the raw material for change, and processes that act upon the pattern to produce change. Examples of processes in the evolutionary context are forces that produce change, such as natural selection, mutation, and genetic drift. However, it is equally important to consider the influence

of evolutionary patterns, or the precursors to change that limit the possibilities for evolutionary change. New characteristics do not arise spontaneously; rather, they are derived from existing characteristics. The mythical Pegasus, the horse with four legs and two wings, does not make sense as a bird nor as a mammal with its six appendages. All birds and mammals evolved from tetrapods with a common four-limbed body plan, and in all cases that favored the evolution of wings, wings were co-opted from the existing four limbs. Evolution works through modification of an existing trait, or pattern. Evolution is a continuously iterative process, such that the patterns and processes are dynamically changing and interacting as time progresses. Through patterns, the conserved phylogenetic history of organisms can be traced, while the diversity of characteristics produced by these patterns reflects the processes that have shaped them.

A good morphological example is the four-limbed vertebrate body plan. The bones of the forelimbs are identifiable in humans, bats, and cetateans, though the shape and function are dramatically different. Additionally, pattern and process allow us to distinguish *homology*, similarity due to common ancestry, from *homoplasy*, similarity based upon similar selective pressures. The wings of a pigeon and the wings of a honey bee share a similar function but are not derived from a common pattern from common ancestry and are thus homoplasious. *Divergence* is when characters are dissimilar but share common ancestry.

Pattern and process are critical to comparative psychology, which is devoted to understanding the development and evolution of behavior. The word *comparative* in comparative psychology suggests a search for similarities and differences in behaviors between species. How do we know if a behavior that is similar between two species is homologous or homoplasious? The answer to this question requires comparisons of mechanisms of behavior across species in search of evolutionary patterns. Like morphological traits, processes that produce behavioral traits are bound by the patterns that preceded them. For example, for "fear" that is induced by fear conditioning to be considered homologous between birds and mice, it is expected that the behavior would rely upon homologous brain circuitry, neurotransmitter systems, and cell molecular processes (Papini, 2002). Comparative psychologists are also concerned with how existing mechanisms are co-opted to new functions. For example, the evolution of spoken language in humans is of considerable interest but remains an open question. Some of the best evidence at present examines the intersection between gestural communication in nonhuman primates, along with overlapping genes and brain areas that are important for both spoken and gestural language (Corballis, 2009). The patterns lie in the mechanisms of the behavior, which are the traces of its phylogenetic origins shaped by evolutionary processes to produce new behaviors.

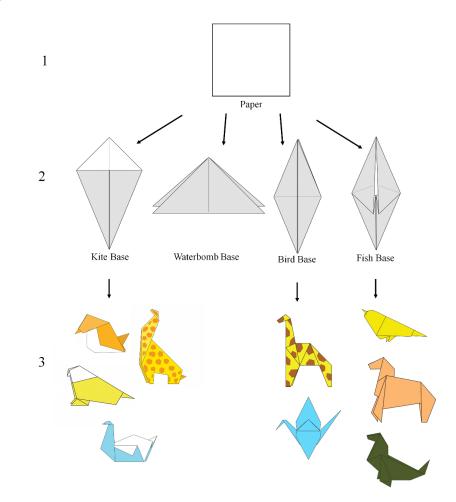
Because phylogenetic relationships between species are central to the comparative psychology discipline, an overview of basic evolutionary concepts early in a comparative psychology course is important. Many students have misconceptions about evolution even after initial instruction, especially in relation to the derivation of new characteristics (Anderson et al., 2002; Champagne Queloz et al., 2017; Coley & Tanner, 2012; Perez et al., 2013). It is easy to emphasize processes, such as natural selection, when teaching evolution, but it is equally critical to consider the interaction of both pattern and process to fully understand evolution and the key element of shared phylogenetic history. In my experience, students are initially more comfortable with thinking of morphological (rather than behavioral) characteristics as evolved traits. I usually begin with morphological examples and transition to behavioral characteristics. After all, morphological changes often suggest earlier changes in behavior; spending more time in water is a behavior that might create selective pressures that favor webbing between the toes. Once they are more comfortable with the central role of behavior in evolution, the adaptive significance of cognitive capacities, emotions, or social relationships can be discussed. Sexual selection and secondary sexual characteristics are a good transitional topic, since mate choice behaviors have direct consequences on reproductive success. Students can easily grasp the adaptive significance of the high salience an infant's cry and consider the implications for fitness if the cry were not salient. The important overall concept is to show that evolutionary patterns reflect the phylogenetic history of organisms, evolutionary processes can shape patterns for different outcomes, and that this is evident in both morphology and behavior.

Origami has specific features that make it suitable to demonstrating pattern and process. First, all origami starts from a square sheet of paper. This is the common pattern that unites all origami creations.

Second, the process of producing origami frequently has an intermediate step called a "base," which many designs may utilize. The bases are a commonly used set of useful patterns that serve as a platform for different kinds of designs. The water-bomb base and the bird base, for example, both feature four flaps of paper, which lends them to the creation of four-limbed model creatures (Figure 1). Models that share the same base are analogous to phylogenetic *clades*, or monophyletic groups that include a common ancestor and all of its descendants. Because these bases are commonly used, pattern and process can be analyzed at three points: the starting sheet of paper, the base, and the final product. By unfolding the final product, the relationships between similar and dissimilar models becomes apparent.

Figure 1

The Creation of Origami Figures Mirrors the Pattern and Process in the Evolution of Derived Characteristics



Note. From a sheet of paper (pattern), different folds (processes) produce a variety of bases (patterns). The bases then undergo further folding (process) to produce a wide variety of different outcomes. A base that produces several creatures is analogous to a common ancestor (homology), even though they may be different from each other (divergence). Some creatures have similar features but are derived from different bases (homoplasy). Note, this figure illustrates only the transitions from paper to base and to the finished products. Step-by-step folding directions for these figures can be found free online at <u>www.Origami.me</u>.

Procedure

Materials

Plain paper can be cut into squares and used, but specially designed origami paper is affordable, colorful, and is of a weight and texture that is more suited to the paper layering and creasing required while doing origami. At the time of writing, packages of 500 sheets of origami paper ranged from \$6-20 USD depending on size and print patterns (Amazon.com). A standard size is 15 cm × 15 cm. Some models may ask for scissors to make simple cuts, so having a pair handy is recommended.

Choosing Origami Models

For this demonstration, you will ideally want to choose models that have the following features: A variety of different bases, a variety of models that use the same base but look different, and a variety of models that have similar end products that use different bases. For example, the web site Origami.me (https://www.origami.me/) has instructions for two giraffes, one which uses a kite base and another which uses a crane base. The traditional origami swan uses a kite base as well, but the outcome is dramatically different. The "easy origami sparrow" uses a fish base but has features (a beak, for example) that are shared with the swan (Figure 1). Look for patterns specified as "easy" or for beginners because this will maximize success on the first try. Aside from free online patterns, a variety of books are available with step-by-step folding diagrams (e.g., Kasahara, 1973; Montroll, 2014).

Folding

Provide each student with a folding diagram for their creature and a few pieces of origami paper and ask them to make the model. It is useful to have multiple students working on the same model so they can assist each other. Due to time constraints the folding can be done outside of the classroom, but, for many students, it will be their first experience folding paper in this way and may need the hands-on help. Once the models are finished, they are ready for the analysis portion of the exercise.

Analysis 1

Once the creatures have been folded, ask students to show each other the models they have created. The next step is to try and classify the organisms based upon the final outcome. They should try to create a phylogenetic tree based upon the creatures. Which creatures are more closely related? Which creatures are distantly related? Which features did they use to classify them? They may place them in groups on a large table at the front of the room in order of relationship.

Discussion of Pattern and Process

The instructor should now introduce the ideas of pattern and process. In the case of origami, talk about the different bases and show an example of each. The bases represent patterns, whereas the subsequent folds represent processes acting upon those patterns to produce change. Homologous features are those which share common patterns (bases), and homoplasious features are those which look similar but come from different bases. Divergence is indicated by character dissimilarity derived from a common base.

Analysis 2

Have the students take the models, analyze them, unfold and refold them, and discuss with each other the pattern and processes used to make them. Then, have them try and reclassify the creatures based upon this new information. Which creatures are more closely related? Which creatures are distantly related? How did the relationships change from the first time they were classified without paying attention to the pattern? A fun variation might be to include an unknown model and have them try to classify it.

Class Discussion

Now, students should be ready to discuss the interaction of pattern and process to produce change. Discussion concepts should include basic ideas of pattern and process, homology, homoplasy, divergence, common ancestry, and so on. A list of suggested discussion questions is included in Table 1.

Table 1

Sample Discussion Questions After Completing the Origami Models

Discussion Question	Key Concept
Which, if any, models are similar and share the same base?	Homology
Which, if any, models look similar but are derived from different bases?	Homoplasy
Which, if any, models share the same base but look very different from each other?	Divergence
How did the starting base limit the features of the finished model?	Constraints imposed by patterns
What happened to make models with the same base different from each other?	Change caused by processes
What do all of the models have in common?	Common ancestry
How similar were the models before we started folding them? How about after?	Evolution can produce diversity
Could we keep folding and create new models from our existing ones?	Evolution is ongoing

As mentioned above, when comparing the exercise to biological examples, it is easier to start with morphological examples before moving on to behavior. I suggest starting with the skeletal anatomy of vertebrate limbs. When discussing behavioral traits, I refer to the reward downshift literature as an example because frustration has been explored behaviorally in many species (Papini, 2003) and there are underlying mechanisms that suggest its evolutionary origins in the pain and fear circuitry (Papini, 2009). To summarize these lines of research, frustration is frequently observed among mammals, even in didelphid marsupials, which diverged from the other lineages early in mammalian evolution. Outside of mammals, instances of frustration are rare, scattered across phyla in a nonsystematic way. This can be interpreted as evidence for frustration as a homologous behavioral trait among mammals. In nonmammals, frustration is considered homoplasious, evolving independently due to similar selective pressures rather than common ancestry. Further research has shown that many of the same mechanisms used for fear conditioning, which is general to vertebrates, are also important for the expression of frustration in mammals. For example, administration of the opioid agonist morphine reduces both pain and frustration in rats, and both are enhanced by opioid blockade by the opioid antagonist naloxone. These results suggest that the pain-fear system in vertebrates was co-opted to also be engaged during surprising reward loss situations early in mammalian evolution. A capacity for learning is common to all vertebrates and most if not all invertebrates, which was then co-opted to be used for fear conditioning among vertebrates and further adapted for frustration in mammals. Table 2 compares origami, vertebrate limb morphology, and frustration at three time points, beginning with a starting point common to all members of the group (Level 1), which is then acted upon by processes to produce divergence into related groups with shared ancestry (Level 2). These related groups are further acted upon by processes to produce more divergence that is constrained by the pattern from Level 2 (Level 3). Even though the end results are different because they are shaped by processes, we can see evidence of the patterns and relationships between the creatures. Levels 2 and 3 both involve development of derived characteristics from modification of an ancestral trait. Students can brainstorm other examples and make predictions about unknown behaviors. In this case, it helps to start at the end point (Level 3), work backward, and ask which relevant behavioral capacities were required to generate behavior at this level.

Table 2

	Origami	Morphological Trait	Behavioral Trait
Level 1:	Paper. Common to all	Central nervous system.	Learning. The ability to
Common starting point	designs.	Common to all	learn and remember
		vertebrates.	information about stimuli is general to vertebrates and invertebrates.
Level 2:	Base. Different bases	Tetrapods. Land	Fear Conditioning.
Divergence into related groups with shared patterns	have features that influence the finished product and mark the relationship between designs.	vertebrates have common body plan limited to four limbs.	Pairing a neutral CS with a painful US leads to behavioral changes, which are modulated by opioid mechanisms in vertebrates.
Level 3:	Finished model.	Limbs. Morphology	Frustrative Nonreward.
Further divergence is constrained by pattern at Level 2 to show interaction between pattern and process	Patterns vary depending upon processes that produced them.	varies according to function, shaped by selection (e.g., flippers, hands, bat wings, bird wings).	In mammals, the opioid system used for fear has been co-opted to cause similar changes in behavior in situations involving reward loss. This new emotion is called frustration.

Example Comparisons Between Origami and Morphological and Behavioral Traits

Concluding Remarks

This article has outlined a teaching tool to familiarize students with the basic concepts of pattern and process, homology, homoplasy, and divergence. I have been developing this idea over the past 9 years to maximize the time investment versus depth of understanding. The discussion phase tends to be socratic, such that I can scaffold my comments to their level of understanding, providing a more cohesive and layered understanding of how the key concepts are interrelated. It is a memorable activity, as I have had students remark upon the experience years later—a standard my traditional lectures rarely achieve. I usually plan for 20-30 minutes of time for folding and another 20 minutes of discussion. Students occasionally have difficulty understanding a fold on the diagram and need help, but, once one or two grasp the concept, they can help others. For an online version of the exercise, it would be useful to give a single student a few models with the same base to construct so they can see the similarity of the pattern but perhaps provide video instructions with each model to help overcome any difficulties. Overall student reception has been positive, and they leave the classroom with a new skill and a souvenir to remind them of their new appreciation for evolutionary pattern and process.

After completing the exercise, students should be able to identify pattern and process at work in origami, and identify which models are "related" based upon their common base. This gives them a framework for understanding pattern and process in evolution, and the idea can be extended to the adaptive significance and evolution of behavior as studied in comparative psychology. The educational advantage of this

demonstration is that origami has a clear pattern and process and intermediate stages that can be compared across many different models. This demonstration is aimed at introducing college level students to these concepts, allowing them to make hands-on and concrete observations about pattern and process. The concepts described here can be embedded in a larger context of evolutionary ideas related to common ancestry, taxonomy, cladistics, and as a launch point for evolutionary processes such as natural selection and genetic drift. It can also be important to discuss evidence of pattern and process at different levels of analysis (e.g., behavioral, neuroanatomical, neurochemical, cell molecular). The abstract ideas of pattern and process are not limited to evolution and may apply to other disciplines such as ecology and environmental science.

By unfolding origami, we trace the patterns and processes that produced it. Exploring the comparative mechanisms of behavior to understand the interplay of pattern and process in evolution allows us to unfold nature's origami.

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