Flegr, J. (2023). Preadaptations. In: Shackelford, T.K. (eds) Encyclopedia of Sexual Psychology and Behavior. Springer, Cham. https://doi.org/10.1007/978-3-031-08956-5_386-1

Preadaptations

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Synonyms

Anticipatory adaptations, Evolutionary precursors, Adaptive predispositions, Evolutionary potentialities
A related term with different meanings: Exaptations

Definition

Preadaptation refers to a trait, such as a structure or behavioral pattern, that initially evolved as an adaptation for one function but later enabled the evolution of another function.

1. Relations Between Adaptations, Preadaptations, and Exaptations

For historical reasons, the term 'preadaptation' is often used to describe traits that evolved from preadaptations. However, according to current evolutionary terminology, we should refer to structures evolved from preadaptations as 'exaptations' (co-opted adaptations). As per Gould and Vrba (1982), the original structures or behavioral patterns are termed 'preadaptations', while the current structures or patterns fulfilling new functions are called 'exaptations'. This terminology is widely accepted in evolutionary biology.

In the natural world, a hierarchy of adaptations, preadaptations, and exaptations can be observed. Every trait emerges by chance, typically through random mutation. These evolutionary novelties often reduce an organism's viability. However, on occasion, a mutation positively impacts the biological fitness of an individual, enhancing a specific biological function, here referred to as function A. In such cases, the new trait can be considered a preadaptation for function A. The efficacy of this function can be amplified by accruing additional mutations, leading the corresponding structure or behavioral pattern to become an adaptation for function A.

Furthermore, trait A may serve as a preadaptation for trait B, and occasionally even for traits B, C, D, and so forth. These new traits represent exaptations for various biological functions, and some may simultaneously act as preadaptations for different and distinct functions.

2. Examples of Preadaptations and Exaptations

Feathers in birds likely evolved as an adaptation for thermoregulation, either heat exclusion or retention, in certain reptile groups (Regal, 1975). The development of these structures later facilitated the evolution of wings, allowing for gliding and eventually active flight. Feathers can thus be considered a "preadaptation" for flying, as their original function was to insulate animals, but they were later modified by selection for flight. As soon as feathers started serving this new purpose, they became exaptations rather than adaptations.

Insect wings are also frequently cited as an example of preadaptation. One prevalent hypothesis suggests that insect wings evolved as adaptations from pre-wings, initially serving as structures for movement, perhaps even gliding. These pre-wings were likely outgrowths, termed paranotal lobes, that assisted insects in maintaining balance or facilitating glide during jumps or falls. However, two alternative hypotheses have been proposed, both grounded in the concept of preadaptation. The first hypothesis suggests that wings evolved from respiratory structures (Averof & Cohen, 1997). Insects possess a unique respiratory system that uses a network of tubes, known as tracheae, to deliver oxygen directly to their cells. Some researchers propose that insect wings evolved from lateral outgrowths initially designed to expand the surface area of the tracheal system, thereby enhancing gas exchange efficiency. The second alternative hypothesis postulates that wings evolved from structures initially used for thermoregulation (Kingsolver & Koehl, 1985). As ectothermic creatures, insects depend on external heat sources to regulate their body temperature. Paranota, structures found on the sides of the thorax in many insects, are believed to have originally functioned as heat sinks or radiators. Over time, these structures may have evolved into wings for flight.

Another example of preadaptation is the waxy cuticle found on the leaves and stems of plants (Kong, et al., 2020). This trait initially emerged in certain algae taxa as a preadaptation for preventing waterlogging and facilitating flotation on the water's surface. However, in terrestrial plants, the waxy cuticle serves the critical function of preventing water loss through transpiration — a crucial adaptation for survival in dry environments.

Other preadaptations for terrestrial life might include the development of roots, which anchor the plant in soil and absorb water and nutrients. These roots also contributed to the evolution of a system for transporting water and nutrients throughout the plant's tissues. In the algae class Chlorophyta, which is closely related to the ancestors of embryophytes (land plants), there are structures analogous to roots, known as rhizoids (Raven & Edwards, 2001). These rhizoids can penetrate several millimeters into sediments and are involved in nutrient uptake. However, they lack the diverse functions of roots found in land plants.

Behavioral preadaptations represent another category of preadaptations, with the use of tools by primates serving as an example. It is proposed that the preadaptation for the use of tools was the development of complex motor skills necessary for climbing trees and manipulating objects (Dunkel, 2019). Additionally, some suggest that the development of tool use may have been a preadaptation for the evolution of verbal language in humans (Steele, Ferrari, & Fogassi, 2012; Stout & Chaminade, 2012). This is due to the similarities in the motor skills and cognitive abilities required for both tool use and language production.

3. Why to Discriminate Between Adaptations and Exaptations

Taken to the extreme, all adaptations are exaptations since evolution does not begin from scratch. It modifies pre-existing structures or functions (Dennett, 1995). Nonetheless, the term and concept of exaptation are valuable in the analysis of the evolution of specific traits and in identifying developmental constraints that played a role in their formation.

In many contexts, it is important to discriminate between adaptations and exaptations. Especially, it is necessary to keep in mind that the traits that evolved from preadaptation are not specifically designed for their current function. Therefore, many, and possibly all, traits carry traces of selection for their present function as well as vestiges of their past function(s), and often must fulfill both old and new functions. This results in a trade-off between optimizing for old and new functions, which can lead to suboptimal structure, or suboptimal nature of some behavioral patterns, in the context of their current biological function. For example, the feather best suited for thermoregulation differs from the feather best suited for flying. Similarly, the structure of the seal paw cannot be optimal for both swimming and walking. In some cases, such as feathers, the two functions can separate with further evolution. In other cases, such as seal paws, the separation is complex or even unattainable, leading to a prolonged state of suboptimal exaptation.

The concept of preadaptation is essential in analyzing the evolution of specific traits and identifying evolutionary constraints that played a role in their formation. Some of these constraints are developmental (being caused by the mechanism of the embryology of a given trait) or external (being caused by laws of physics or chemistry), however, many of them are historical, being caused by the fact that the trait is an exaptation, not an adaptation.

4. Role of Baldwin Effect in the Origin of Adaptations and Exaptations

The transformation of a preadaptation, spandrel, or nonadaptive trait that originated from a random mutation into an adaptation often involves the Baldwin effect (Baldwin, 1896). While the Baldwin effect is often discussed in relation to the evolution of certain behavioral patterns, its role is more universal and can also apply to the evolution of morphological or physiological traits. The Baldwin effect emphasizes the role of learning in evolution and suggests that a change in behavior may occur before a change in gene frequency.

In simple terms, the Baldwin hypothesis states that an animal "cannot evolve fins without first starting to swim." Initially, the animal must start swimming, using limbs (designed by selection for walking) for moving in water, to allow for selection and accumulation of mutations that modify the limb structure, increasing swimming efficiency and eventually leading to the transformation of terrestrial animal feet into aquatic animal fins. Some mutations also modify the animal's neural system, causing the behavioral patterns required for swimming with the new morphological traits to become instinctive, despite having been originally learned and transmitted culturally from generation to generation. Though J.M. Baldwin was a psychologist with a primary interest in the genetic assimilation of learned behavior, this principle—often referred to as organic selection in this context—is almost universal and can occur in some form in the evolution of any phenotypic trait.

Animals can start to use the same structure in many different ways. Therefore, due to the Baldwin effect, the same structure can function as preadaptation to many different biological functions and can result in origin of many different organs. The prototypical example is the limb of terrestrial tetrapods. They originated as exaptation from the fins of fish that served as organ of swimming. However, the ancestors of various taxa of tetrapods started to use the same organ in a different way, for running, digging, swimming, jumping, gliding and later flying. With the help of the Baldwin effect, the same trait, the same preadaptation, evolved into many exaptations for many different functions.

5. Not All Preadaptations Arose as Products of Selection

It should be noted that the preadaptations do not always emerge as products of selection. They could sometimes emerge as biological spandrels – traits or features in organisms that are not directly evolved for any use or purpose but rather emerge as byproducts of non-biological factors such as topological, physical, or chemical natural laws. S.J. Gould introduced the concept of spandrels into biology in his fight against panselectionism that prevailed in biology in 1970s (Gould & Lewontin, 1979). He borrowed this term from architecture, where it was used for architectural elements that arose not by the intention of the architect, but out of necessity, usually due to topological laws. In architecture, this refers, for example, to triangular shapes at the ceiling of a hallway formed by a column arrangement, whose ceiling is supported by arches. Another type of architectural spandrel are pendentives, triangular shapes in the upper corners of a square room covered, for example, by a dome. Sometimes, spandrels might be very complicated structures that are difficult to believe to have no biological function.

Very often, preadaptations arise not as the main product of selection that optimizes a particular biological function, but as a side "unintended" product of such selection. It is likely that the enlargement of a cluster of nerve ganglia at the anterior end of the nerve cord in chordates necessarily forced the development of the skull, which could begin to perform a variety of other functions, including those related to hunting and processing prey. These secondary functions of the skull later proved to be more important during the evolution of jawed vertebrates than the original function of the skull as a protection for the brain. Similarly, the belly button, now occasionally utilized as an entry point for laparoscopic surgery or other medical procedures, was likely nonfunctional in the past and arose as a byproduct of umbilical cord development, which supplies the fetus with nutrients (Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998). It is, of course, disputable whether structures that retained not a biological function in a process of biological evolution but due to cultural, namely technical evolution could and should be classified as exaptations.

In some taxa these traits may currently serve to its original function and therefore could be recognised as preadaptations. However, sometimes no extant species exist in which the trait fulfil its original function and therefore their original biological function is often at least subject to doubt. Probably, many such traits originated as spandrels, which originally fulfilled no biological function. It is sometimes practical to discriminate between two types of exaptations (Buss, et al., 1998). The type one represent exaptations that originated by co-option of and adaptation, while type two represents those exaptations that originated by co-option of a spandrel.

6. Le Charme Discret de la Adaptations

Scientists, and particularly scientific journal editors, tend to favor adaptations. This creates a temptation for authors to attribute some function to the trait they are studying. To prove or disprove the adaptiveness of existing traits is difficult and to prove or disprove the adaptiveness of traits in extinct species is even more difficult and sometimes even impossible. Evolutionary biologists are often (and sometimes rightly) accused of telling just-so stories instead of practicing an exact science. Such a risk is naturally much greater when evolutionary biologists consider the biological functions of preadaptations. Therefore, maximum caution is required when assessing hypotheses regarding preadaptations. It is always necessary to ask not how clever and interesting the story is, but what the real evidence is for its truthfulness.

6.1. A Case of Host Behavior Manipulation by *Toxoplasma* parasite

While the attribution of biological function to adaptations or preadaptations may be correct in many cases, in some cases even very popular attribution of adaptiveness to a structure or behavioral pattern can also be incorrect. For instance, there exist tens and maybe hundreds of papers showing the behavioral effects of latent *Toxoplasma* infection on intermediate hosts, including humans. These effects are primarily thought to be the product of the parasite's manipulative activity aimed at increasing transmission efficiency from infected intermediate hosts (any warm-blooded animal) to a definitive host (a cat) by predation, i.e. they are classified as a biological adaptation of *Toxoplasma*.

Specific effects, such as the change from fear associated with a cat's smell to attraction to this smell in infected rodents (Berdoy, Webster, & Macdonald, 1995, 2000), chimpanzees (Poirotte, et al., 2016), and possibly even humans (Flegr, Lenochová, Hodný, & Vondrová, 2011; Flegr, et al., 2018), have a high probability of being the product of parasite manipulation. However, some effects are less specific and may therefore be the byproduct of other parasite activities or the product or byproduct of adaptive or maladaptive host reactions to the infection.

For example, it is highly probable that certain personality changes associated with latent toxoplasmosis are byproducts of impaired health in infected individuals. For instance, studies have found that both men and women with *Toxoplasma* infection score lower on the personality trait novelty seeking compared to uninfected individuals (Flegr, et al., 2003; Novotná, et al., 2005). This trait is linked to higher levels of the neurotransmitter dopamine (Cloninger, 1998), It was initially suggested that dopamine is produced by activated leukocytes in inflammation sites in the infected brain (Flegr, et al., 2003). However, later studies identified genes for two enzymes essential for dopamine synthesis in the genome of *Toxoplasma gondii* (Gaskell, Smith, Pinney, Westhead, & McConkey, 2009) and observed high levels of dopamine production in cysts of *Toxoplasma* in the infected brain tissue (Prandovszky, et al., 2011). It is thus plausible that increased dopamine production and resulting behavioral changes were originally byproducts of pathological processes in the infected brain, which were later reinforced by acquiring corresponding genes, possibly through horizontal transfer, and dopamine production in infected cells. It should be noted that increased levels of dopamine are considered responsible for the positive symptoms of schizophrenia – most schizophrenia medications reduce dopamine levels or block its receptors. Increased dopamine levels might explain why individuals infected with *Toxoplasma* have a 2.7 times higher risk of schizophrenia than uninfected individuals (Torrey, Bartko, Lun, & Yolken, 2007; Torrey, Bartko, & Yolken, 2012) and why infected schizophrenics exhibit more severe symptoms of the disease (Holub, et al., 2013).

Similarly, many behavioral changes observed in animals and humans infected with toxoplasmosis may be more of a side effect of the infection, such as the worsened health status of infected individuals, rather than a direct or indirect effect of the parasite's manipulative activity. In humans, infected individuals have been observed to undergo a number of changes in their psychological profile, with opposite directions of change between men and women. These are psychological traits that typically change in people experiencing chronic stress. The direction of these stress-associated changes differs between men and women, essentially mirroring the changes observed in individuals with toxoplasmosis. Some of these changes are also observed in individuals infected with other parasites or pathogens, even those that are not transmitted by predation like *Toxoplasma* (Novotná, et al., 2005). It is therefore likely that a large part of the psychological changes originally described as manifestations of *Toxoplasma*'s manipulative activity are rather a manifestation of chronic stress or a psychological reaction to this stress.

However, it is almost certain that this does not apply to all observed changes. For example, a number of changes, such as novelty-seeking and conscientiousness, occur in the same direction in both men and women, and the relevant psychological traits are not related to the stress-coping mechanism. A recent study using path analysis techniques has shown that infection affects certain psychological traits and cognitive test performance directly, not just indirectly through worsened physical health (Flegr, Hlaváčová, & Toman, 2023).

Conclusions

The concepts of adaptations, preadaptations, and exaptations are crucial frameworks for understanding the evolutionary history and present-day functionality of various traits in organisms. Adaptations refer to traits shaped by natural selection for their present use, whereas preadaptations denote traits that initially served different functions but later provided a foundation for new adaptations. These newly adapted functions are termed as exaptations.

It is essential to differentiate between adaptations and exaptations, as this understanding provides a nuanced perspective on the evolution of specific traits. Traits evolved from preadaptations are not specifically designed for their current function and often retain vestiges of their past function(s). This circumstance can lead to trade-offs between optimizing for old and new functions, potentially resulting in suboptimal structures or behavioral patterns in the context of their present biological function. These trade-offs can illuminate peculiarities of biological structures, including their suboptimality, which in humans can have adverse health impacts.

The Baldwin effect, or organic selection, plays a significant role in converting a preadaptation into an adaptation. This principle underscores the role of learning and behavioral change, often taking place before a shift in gene frequency. This mechanism implies that the same structure can serve as a preadaptation for many different biological functions, potentially resulting in the genesis of various organs. As accurately predicted 120 years ago, organic selection plays a pivotal, albeit often underestimated, role in the evolution of adaptive structures, particularly in the transformation of preadaptations into exaptations.

It's also worth noting that not all preadaptations emerge as products of selection. Some may surface as biological spandrels, traits, or features that manifest as byproducts of non-biological factors. These spandrels can later assume different functions, evolving into exaptations. Spandrels, it appears, likely play a crucial role in the evolution of complex adaptive structures.

In conclusion, the concepts of adaptations, preadaptations, and exaptations offer a comprehensive framework for understanding the dynamic and complex nature of evolution. When studying adaptive biological structures and complex behavioral patterns, one should bear in mind that not all adaptive phenomena stem from a simple Darwinian process that involves the unidirectional influence of a specific selection pressure. Discontinuities in the application of selection pressure, varying in intensity and sometimes direction, often play a critical role in adaptive evolution.

Cross-References

Adaptation, Exaptation, Spandrels, Baldwin effect.

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