Spotlight

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Exapting exaptation

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The term exaptation was introduced to encourage biologists to consider alternatives to adaptation to explain the origins of traits. Here, we discuss why exaptation has proved more successful in technological than biological contexts, and propose a revised definition of exaptation applicable to both genetic and cultural evolution.

The rise and fall of biological exaptation

Last year marked a decade since the death of Stephen Jay Gould, and 30 years since the publication of one of his most provocative challenges to orthodox evolutionary theory [1,2]. Concerned about a perceived lack of rigour, Gould, together with Elizabeth Vrba, introduced a vocabulary intended to undermine the primacy of adaptation for explaining the evolution of biological traits [1]. Chief among the new terms was exaptation. According to Gould and Vrba, exapted traits arose as by-products of other evolutionary processes, or were initially selected for some function unrelated to their apparent use [1]. Exaptation was therefore introduced to encourage evolutionary biologists to avoid conflating a trait's current utility with its historical origin.

It has been claimed that exaptation can be found at every level of biological organisation. For example, cell signalling might be an exaptation of machinery originally designed to pump calcium out of the cell [2]. Calcified skeletal support might be a by-product of a mechanism to store calcium phosphate that evolved to compensate for seasonal fluctuations in oceanic phosphate availability [1], and the warning colours of aposematic organisms might originally have evolved in the context of sexual signalling [3].

In spite of the apparently widespread relevance of the term exaptation, it has not become widely used in the biological sciences (Figure 1). We contend that the principal reason for this is that although the general meaning of the term is clear, exaptation lacks a formal definition that distinguishes it from adaptation. Most traits are under multiple selective pressures and the relative importance of those pressures can shift dynamically in both space and time, not always demonstrating a neat switch from one to another in the way implied by exaptation. This makes it difficult to say at what point a trait became exapted, or to relate functions and effects to the multiple selective pressures. Moreover, in some sense, every trait is likely to have been modified from pre-existing versions that, at some time point, were not used in the way that they are now. As a result, all adaptations can also be said to be exaptations, thus rendering the term redundant [4].

Technology and the exaptation of exaptation

Despite failing to catch on in evolutionary biology, exaptation has been adopted with considerable success in studies of the history of technology [5]. Technological innovations frequently involve the use of a process or artefact in a new context [6]. A classic example is microwave radiation, which was originally used in the radar magnetron to intercept and reflect off target objects, and was subsequently exapted as a means to heat food. Similarly, technologies that were initially developed as part of NASA's space research program were later exploited for new commercial uses. For instance, organic recycling agents designed for long space missions are now used as microalgae-enriched food supplements. Many low-tech, local-level innovations also involve co-opting existing tools for new functions. The Trinidadian steel drum, for example, was improvised from 55-gallon oil containers by carnival performers in the mid-twentieth century. One of the authors (RL) observed that when the tractor replaced the horse and ox in French farms in the 1960s, discarded horseshoes were used as gate closures and hubs of wooden cartwheels were mounted horizontally to form the centre of a rotating stile.

Differentiating exaptation from adaptation

In light of the examples above, we suggest that the contrasting fortunes of the term exaptation in biology and the history of technology reflect broad differences in the evolutionary processes associated with (but not limited to) these domains. Typically, in biological evolution, selection is blind, acting on pre-existing traits that are often under multiple environmental pressures. Technological evolution, however, is often directed by an element of foresight, or guided variation [7], which is inherently teleological. Thus, it is far easier to discriminate between the original function of a phenotype, i.e., what it was originally selected for, and its current effect, i.e., why selection maintains it.

We emphasise that the distinction between "blind adaptation" and "guided exaptation" does not map simplistically onto the division between genetic and cultural inheritance systems. Firstly, cultural evolution is not driven exclusively by guided variation: stochastic forces (such as learning error) and ecological adaptation also play important roles [8]. Secondly, in some cases, cultural traits can acquire new functions without intentional or goal-directed effort. For example, linguists have demonstrated that, as languages evolve, some of their grammatical

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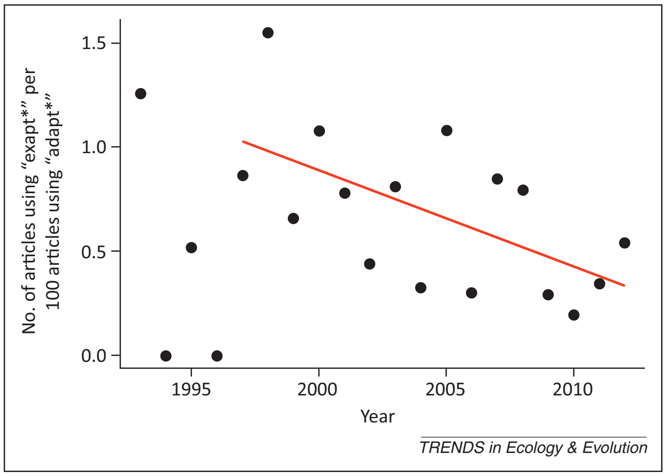

Figure 1. The relative indifference of biologists to the term expatation is illustrated by the term's usage between January 1993 and December 2012. Only articles categorized as ''Evolutionary biology'' by ISI Web of Science are considered here. Black circles show the relative number of published articles that refer to ''exapt*'' per 100 articles in each year that refer to ''adapt*'' (specific search terms are WC = Evolutionary biology AND TS = exapt*; or WC = Evolutionary biology AND TS = adapt*). ''exapt*'' was used sporadically until 1997 and has been declining in relative use since (the red line depicts a linear regression from 1997 – 2012: $R^2 = 0.36$, $p = 0.015$). The failure of the term exaptation to gain a foothold in biological sciences has most likely resulted from a lack of a formal definition that clearly differentiates it from adaptation.

features can be rendered defunct. While many of these features subsequently become extinct, others can persist for generations as linguistic "junk", during which time they are applied inconsistently before eventually finding a new communicative function [9].

Genetic evolution can also be driven by guided variation. For instance, a recent study of allelic variation in the coat colour gene *MC1R* in both wild boar and domestic pigs demonstrated that while purifying selection maintains camouflaged coat colours in the wild, positive artificial selection has resulted in the fixation of multiple non-synonymous mutations, leading to a wide variety of domestic coat colours [10]. Selective breeding within domestic species often targets previously non-adaptive traits, exapting them specifically for exploitation by humans.

Owing to its historical and confusing overlap with adaptation (which almost always involves shifts in emphasis between functions), we believe that exaptation and adaptation should be used in explicit contexts. Specifically, all forms of both biological and cultural evolution that result from blind selection should be referred to as adaptation, while only evolution that results from an unambiguous reassignment of function, exclusively as a product of intentionality (guided variation), should be referred to as exaptation. While not all instances of evolution will fit easily into this dichotomy, our definition encourages critical consideration of the degree to which intentionality plays a role in the underlying selective processes.

Concluding remarks

The ironies of this narrative are manifold. The co-option of the term by those outside of biological evolution epitomises the very process that exaptation was coined to describe. Furthermore, Gould and Vrba invented the term to replace pre-adaptation in evolutionary narratives and the teleological inference inherent in that term. Yet, as we have argued here, it is impossible to differentiate exaptation from adaptation unless we interpret the term teleologically. For this reason, most evolutionary biologists have abandoned exaptation. However, there are domains of both cultural and genetic evolution where processes of variation and selection are not blind, but directed by a degree of foresight, such as artificial selection and technological innovation. We contend that in these areas, teleological explanations are not only legitimate but necessary, and provide a wide remit for a renewed exaptationist program.

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