Definitions and Levels of Analysis

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Although Buss, Haselton Shackelford, Bleske, and Wakefield (1998) presented a topic that deserves mainstream attention in psychology, I am concerned about their article on several grounds. My main concern is with their interpretations of Gould's (1987 1991, 1997) writings. Buss et al. suggested that Gould (1991) was inconsistent in his usage of the term *exaptation*, and that his "stated definitions seem to require that these effects and culturally useful features (exaptations) must contribute to fitness and have *specifiable biological functions* [italics added] to qualify as exaptations" *(p.541).* Yet nowhere in Gould's (1987 1991, 1997) writings did he suggest that the function performed by an exaptation needs to be biological. As Buss et al. reported, Gould (1991) offered two definitions of exaptation: "a feature, now useful to an organism, that did not arise as an adaptation for its present role, but was subsequently coopted for its current function" (p.43) and "features that now enhance fitness, but were not built by natural selection for their current role" (p.47). Thus, although exaptations *always* provide a current function, that function need not be biological. In fact, Gould's (1991) thesis is geared toward exapted functions performed by the brain to serve psychological rather than biological functions.

Additionally, Buss et al. (1998) suggested that Gould (1991) used the term exaptation "to cover novel but functionless uses or consequences of existing characteristics" (p. 539) My reading of Gould (1987, 1991, 1997) suggests otherwise: Structures or characteristics for which there are no identifiable functions, either current or historical, are always spandrels. Thus, the term *spandrel* subsumes what Buss et al. referred to as functionless by-products. When a spandrel is coopted (exapted) for a function, it becomes an exaptation; there is no need to differentiate between spandrels and functionless byproducts. Ironically, Gould (1991) coined the terms exaptation and spandrel to avoid this sort of confusion.

Additionally, although Buss et al. (1998) sought to outline the usefulness of the terms adaptation, exaptation, and spandrel for the science of psychology, most of their discussion was restricted to structural rather than psychological levels of analysis. Although understandable given their strictly biological interpretation of exaptations, this approach is problematic because the authors sought to apply their standards of evidence to the list of exaptations proposed by Gould (1991), namely language, religion, principles of commerce, warfare, reading, writing, and the fine arts. All of the items on this list are psychological phenomena borne of a structural complexity (i.e.. the human brain) that is not well understood and that was not sufficiently considered by the authors. Here again. Buss et al. may have misinterpreted Gould, who did not use human brain size merely as an "example of an exaptation" (p. 539), as the authors stated. Rather, Gould suggested that the human brain, by virtue of both complexity and flexibility, is "the best available case for predominant exaptation--in other words, for a near certainty that exaptations must greatly exceed adaptations in number and importance" (p. 55). Gould offered the practice of religion as an example and suggested that our enlarged brains force us to confront our own mortality. Because it is quite unlikely that brain enlargement evolved to serve this end, the practice of religion performs an exapted function by moderating, through a variety of themes, our evolutionarily functional fear of death. Thus, recognition of our own mortality is a spandrel, and the practice of religion is an exaptation.

Moreover, it is *a priori* unlikely that such complex psychological phenomena can meet the standards of evidence proposed by Buss et al. (1998). Specifically, they suggested that evidence of special design for a hypothesized function be demonstrated before concluding that any structure or behavior is adaptive. As an example, they presented the hypothesis that female orgasm serves the adaptive function of facilitating sperm transport, for which evidence is reportedly lacking. It is thus concluded that female orgasm does not serve the hypothesized adaptive function. Although instructive, this example trivializes the difficulty of falsifying, at the phenotypic level, hypotheses about exapted psychological functions, such as the practice of religion. There are at least two reasons for this. First, as outlined by Buss et al., exaptations "carry the additional evidentiary burdens of documenting both later co-opted functionality, and a distinctive original adaptational functionality" (p. 546). Thus, to confirm the exapted function of religious practice, one would be required to demonstrate (a) that enlarged brains were naturally selected for reasons independent of religious practice, (b) that such brain enlargement resulted in the capacity to practice religion, and (c) that religious practices function to assuage the fear of death (which would itself be required to meet the evidentiary standards of a spandrel). Although the first two of these conjectures may be true, they can at best be confirmed only at the pseudoempirical level. Gould (1991) recognized this and suggested that the term *aptation* be applied to cases where a lack of historical evidence precludes the determination of whether a characteristic is an *ad*aptation or an *ex*aptation. Furthermore, confirming or disconfirming the third conjecture is far more difficult than establishing the utility of female orgasm as a sperm transport mechanism, because the functional level of analysis is psychological, not structural.

All of the proposed exaptations listed by Gould (1991), because they are specified at the psychological level, are similarly precluded from meeting the strict evidentiary standards set forth by Buss et al. (1998). Yet, it would be unfortunate indeed if psychologists, in an effort to meet such standards, were to reject Gould's distinctions and continue in adaptationist practices. We should recognize the error in logic of inferring evolutionary cause from current consequence, whether or not we can empirically demonstrate the existence of psychological exaptations.

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