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Relations of homology between higher cognitive emotions and basic emotions

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Abstract In the last 10 years, several authors including Griffiths and Matthen have employed classificatory principles from biology to argue for a radical revision in the way that we individuate psychological traits. Arguing that the fundamental basis for classification of traits in biology is that of 'homology' (similarity due to common descent) rather than 'analogy', or 'shared function', and that psychological traits are a special case of biological traits, they maintain that psychological categories should be individuated primarily by relations of homology rather than in terms of shared function. This poses a direct challenge to the dominant philosophical view of how to define psychological categories, viz., 'functionalism'. Although the implications of this position extend to all psychological traits, the debate has centered around 'emotion' as an example of a psychological category ripe for reinterpretation within this new framework of classification. I address arguments by Griffiths that emotions should be divided into at least two distinct classes, basic emotions and higher cognitive emotions, and that these two classes require radically different theories to explain them. Griffiths argues that while basic emotions in humans are homologous to the corresponding states in other animals, higher cognitive emotions are dependent on mental capacities unique to humans, and are therefore not homologous to basic emotions. Using the example of shame, I argue that (a) many emotions that are commonly classified as being higher cognitive emotions actually correspond to certain basic emotions, and that (b) the "higher cognitive forms" of these emotions are best seen as being homologous to their basic forms.

Keywords Homology · Serial homology · Function · Psychological categories · Biological categories · Homology of function · Basic emotions · Higher cognitive emotions · Shame

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Introduction

In the last 10 years, a number of authors have employed classificatory principles from biology to argue for a fairly radical revision in the way that we individuate and classify psychological categories (Griffiths 1997, 2001, 2004a, b; Matthen 1998, 2000, 2002, 2007). Arguing that the fundamental basis for the classification of traits in biology is that of 'homology' (rather than, as many have suggested, 'analogy', or 'function'), and that psychological traits are a special case of biological traits, they maintain that psychological categories should be individuated primarily by relations of homology rather than in terms of shared function. These authors allege that while homologous categories share 'deep causal commonalities' at various levels (genetic, physiological, mechanistic, computational, etc.), functional categories are by comparison relatively shallow, capturing only the commonalities in terms of which they are defined. This poses a direct and serious challenge to the dominant philosophical view of how to define psychological categories, viz., 'functionalism'.[1]

Although the implications of this position potentially extend to all psychological traits, the bulk of the debate has centered around 'emotion' as an example of a psychological category ripe for reinterpretation within this new framework of classification.[2] Roughly, these authors have argued that the general category of 'emotion' contains at least two very different kinds of phenomena: 'basic emotions' (BEs), which are relatively simple, modular responses that are homologous to corresponding emotions in other species, and 'higher cognitive emotions' (HCEs), which are cognitively complex responses that are uniquely human, and thus not homologous to states in other species.[3] The view that emotions can be divided in this way is widespread among theorists of emotion, and has a long history. The authors presently under consideration, however, offer a relatively novel basis for drawing the distinction, and draw different implications from the distinction than many of their historical predecessors. In particular, they maintain that while the category of BEs groups together states that share the kinds of 'deep causal commonalities' characteristic of homologous categories, the category of HCEs is causally heterogeneous, and that HCEs can only be grouped together with BEs on the basis of broad functional similarities that lack the explanatory power of homology relations. Therefore, they have argued, general theories of 'emotion' should be eliminated from scientific psychology, to be replaced by at least two

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[1] Interestingly, given the significance of the challenge, there has been little response or acknowledgment from mainstream advocates of a functionalist account of mind. This seems due, in significant part, to the fact that the challenging view has typically been presented in books or articles ostensibly about specific psychological traits, especially emotions, rather than as a more general position in itself.

[2] Though see (Matthen 2000, 2002, 2007) for a discussion of some other psychological categories.

[3] Griffiths has since repudiated the term 'higher cognitive emotion' as misleading, choosing instead to call such emotions 'complex emotions'. I will use his old terminology in this paper, both because it better captures the distinguishing features with which I am concerned, and because it is better established and somewhat less vague than 'complex emotions' for those who are unfamiliar with Griffiths's particular, technical definition of the latter term.

separate theories corresponding to what are now called basic and higher cognitive ‘emotions’ (Griffiths 1997, 2001, 2004a, b; Matthen 1998).[4]

This view can be challenged on several fronts. Some have disputed the claim that biological categories are first and foremost homological categories. Relatedly, some have argued that functional classification is more powerful than these authors admit, and, indeed, that some biological and psychological truths can only be captured by means of functional generalizations (Neander 2002; Neander and Rosenberg 2009). While I agree that these strategies are worth pursuing (Clark 2009a), here I would like to consider another approach, one which is in fact broadly consistent with the principles invoked by these authors, but which arrives at different conclusions regarding both the application of these principles, as well as the substantive conclusions they draw concerning the psychological category of ‘emotion’.

Specifically, I want to argue that there are relations of homology among psychological categories that have so far been neglected. Given that the debate thus far has centered around emotions as a model psychological category, I will frame my arguments within emotion theory. I will argue that emerging evidence suggests that the similarities between some HCEs and BEs are deeper than these authors claim, and that we can capture some these similarities by exploring the neglected possibility that such HCEs may be homologous to their corresponding BEs in either of two possible senses of ‘homology’: ‘single-trait homology’, and ‘serial homology’. I believe that this refinement of homological thinking regarding emotions will help to clarify future debates about its application to other psychological categories.

Classifying emotions: basic and higher cognitive emotions

According to Griffiths, BEs are based in evolutionarily old sets of stimulus-detection mechanisms and stereotyped physiological and behavioral response patterns rooted in dedicated neural circuits, with a genetic basis that has evolved in response to recurrent evolutionary challenges, and which we share with nonhuman mammals. These patterns are capable of being activated by unconditioned stimuli and lead to unconditioned, involuntary responses of brief durations. They are relatively modular in such a way that neither the unconditioned stimuli that evoke them, nor the resulting responses are susceptible to the influence of more newly evolved higher cognitive processes. Despite having evolved to respond to simple, unconditioned stimuli, BEs are also capable of being activated by conditioned

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[4] Griffiths appears to have softened this conclusion in his recent work (Griffiths and Scarantino 2009; Griffiths 2003, 2004a, b). Nevertheless, I will largely focus on the sharp distinction between BEs and HCEs as drawn by Griffiths in his earlier work. I emphasize this starker version of the distinction because (a) Griffiths has not explicitly disavowed the view, or directly discussed its relation to other trends in his more recent work, (b) we still find some clear assertions of the strong distinction in his recent work, and, in any case (c) the distinction has been widely taken up by others in the emotion literature, and hence has a kind of life of its own. I think that the views I offer are actually *suggested* by some strands of Griffiths’s (and Scarantino’s) recent work.

(even highly cognitive) stimuli, though their output appears to be less capable of modification.

While both BEs and HCEs are capable of responding to higher cognitive inputs, many argue that they differ more broadly in their relation to higher cognitive processes. First, on the input side, while BEs have evolved to take as input relatively unprocessed, even ‘purely sensory’ cues that require little or no learning, it is argued that HCEs do not have such inputs. Instead, HCEs are held to *necessarily* involve higher cognitive inputs by their very nature, where this includes inputs resulting from learning, acculturation, or sophisticated cognitive processing (such as means-end, causal, and counterfactual reasoning, long-term planning, social cognition, etc.). Also, the simple stimuli capable of evoking BEs have a privileged strength which makes unlearning emotional responses to them extremely difficult or impossible (as in some universally occurring phobias), whereas the stimuli that engage HCEs can be more easily modified by further learning or cognitive regulation.

Second, on the output side, it is widely believed that HCEs do not involve involuntary, stereotypical physiological, expressive, or behavioral responses, such as those we see in BEs. Rather, the outputs associated with HCEs are largely learned or prescribed by the general social environment or immediate context of occurrence, and are they are hence also directed towards social processes that themselves depend on higher cognition. Thus, while there may be culture-typical patterns of HCE response that have become ‘automatic’, these are dependent on local culture for their development and significance. Furthermore, the outputs of instances of occurrent HCEs are held to be more susceptible to contextual influences or regulation by higher cognition, and HCEs are held to be capable of enduring for much longer periods than BEs, in part due to their involvement with higher cognitive capacities for extending thought into the distant past and future. Finally, HCEs are commonly distinguished from BEs by their developmental timetable. According to the dominant view of emotional development, Cognitive Developmental Theory (Lewis 2007; Sroufe 1996; Stipek 1995), while all BEs emerge roughly during the first year of development, HCEs (here often called ‘self-conscious emotions’) develop later (between 18 months and 4 years of age), and only once the prerequisite cognitive capacities are in place. These cognitive capacities include such things as the ability recognize or internalize norms, the capacity for self-other awareness, a theory of mind, etc.[5]

According to Griffiths, it is possible to agree that the class of emotions is divided in this way, while still maintaining that it is a unified natural kind, by arguing that HCEs and BEs are united by their shared functional roles. Griffiths, however, goes on to argue that these two classes of emotion do not belong to a single, maximally robust natural kind. This argument is based on his view of natural kinds in biology. According to this view, there are (crudely put) two main types of biological categories—homologies and analogies. *Homologies* are traits that organisms share in common as a result of descent from organisms with similar traits. These traits

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[5] I challenge the developmental basis for a sharp BE/HCE distinction, as articulated in Cognitive Developmental Theory, in a separate paper (Clark 2009b).

must all occur within a continuous line of descent, but they cut across species and functional lines, so that, e.g., dolphin flippers and human hands are homologous. *Analogies* are traits occurring in different evolutionary lineages which share a common function, but not a shared path of descent; e.g., the eyes of an octopus and the eyes of humans are analogues of one another.

Griffiths argues that classification by homology better supports the kind of generalization required and practiced in biology and, by extension, biologically oriented empirical psychology. In virtue of their shared line of inheritance, homologous traits are likely to share various ‘deep’ commonalities in their underlying mechanisms at various levels of organization, including the genetic, ontogenetic, physiological, behavioral, computational and other levels. On the other hand, analogous traits typically do not share these ‘deep’ features; e.g., while the wings of birds and bats share some broad functional features, their underlying mechanisms and structure are very different. Griffiths argues that the ‘deep’ features captured by homology provide a much stronger basis for the explanation of traits within biology and psychology, and for drawing cross-species inferences about traits. With regard to emotions, he argues that while BEs in humans are homologous to their correlates in other species, HCEs are uniquely human and, due to their differences from BEs, are not homologous with emotions in other species. Therefore, the only sense in which HCEs and BEs can be grouped together under the general rubric of ‘emotion’ is as analogous, a theoretically inferior classification. Therefore, he argues that (at least for the purposes of empirical psychology) it is more sound to renounce general theories of ‘emotion’, and to treat HCEs and BEs as separate phenomena, requiring largely independent theories.[6]

There are at least two broad (potentially complementary) approaches to distinguishing BEs from HCEs. The first approach divides existing emotion-types into those that are BEs and those that are ‘pure’ HCEs. Thus, e.g., emotion-types such as anger, joy, sadness, fear and disgust are widely considered to be BEs, while emotion-types such as guilt, shame, jealousy, and envy are widely believed to be ‘pure’ HCE-types without BE forms. Second, some authors (including Griffiths) also maintain that many emotions that are labeled using terms associated with BEs are actually HCEs that bear only a relatively superficial similarity to the corresponding BEs; e.g., there are instances of ‘anger’ that are BEs (BEanger), but there are also instances of ‘anger’ that are HCEs (HCEanger) (Griffiths 1997; Griffiths and Scarantino 2009). For example, we often label as ‘anger’ both the emotion we experience when someone physically attacks us, and the emotion we feel towards social injustices like racism. According to Griffiths, the second kind of

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[6] Two caveats about this conclusion: First, Griffiths explicitly presents his analysis as ‘interest relative’ and does allow that it may be more useful and appropriate (perhaps even essential) to group BEs and HCEs together for the purposes of theories other than empirical psychology (e.g., moral or aesthetic theories). Nevertheless, the distinction that he draws does have implications for the way that emotions are treated in these other types of theory. Second, as noted above, while the early Griffiths more strongly downplayed the scientific value of general functional or ecological theories, in his more recent work he seems to have offered such theories himself, explicitly presenting them as a means of capturing some of the commonalities between BEs and HCEs. Here he seems to focus more on the complementary relations between functional and homological classification than in earlier work, though he doesn’t specifically address this issue.

emotion has a number of features of HCEs that radically distinguish it from the former, and the similarities between basic and higher cognitive instances of these emotion-types are relatively superficial, masking the fact that these HCE instances are as different from their basic correlates as any other pair of BEs and HCEs.

Thus there appears to be a subclass of putative HCEs which are homonymous with their respective BEs. I will call these 'correlates' of one another. While Griffiths argues that the significant differences between these correlates are belied by the fact that they share the same name, and that they are different enough from one another that it is better to approach them from different theoretical perspectives, I maintain that empirical evidence indicates a deeper commonality between these classes of emotions. Griffiths is aware of this evidence (e.g., Griffiths and Scarantino 2009) and cites its authors with apparent approval, but has not, I think, fully properly appreciated its implications or potential for his theory.

Shame: a case study

If some emotions can be shown to have BE and HCE forms that are in some sense(s) homologous to one another, this will provide a strong counterexample to the sharp division between BEs and HCEs. Furthermore, since this division is perhaps *the* paradigmatic example in the literature of how to apply the homology-based strategy for the classification of psychological traits, such a demonstration will provide a reason for reconsidering the manner in which this strategy has been employed. Nevertheless, undercutting this paradigmatic example of the strategy does provide a degree of vindication for the general program of classification, and suggests what I believe to be a natural extension of it.

Shame as a basic emotion

For reasons of space, I will largely restrict my attention to evidence concerning a single representative case of such emotion-types, shame. Shame actually serves as a counterexample to both of the strategies described above for dividing such emotions along the BE/HCE line, since, I will argue, it (a) has a basic form, and is thus not a pure HCE, and (b) displays the kind of deep commonalities between its basic and higher cognitive forms necessary for grouping them together as homologous. Furthermore, an examination of shame highlights the fact that many emotions classified as HCEs do in fact possess many of the features denied to them by Griffiths and others, such as stereotypical physiological, behavioral and expressive characteristics.

Shame in its present human form appears to have emerged from a rank-related emotion in nonhuman mammals, in which its primary function was to signal subordinance to a dominant in order to appease them (Fessler 1999, 2001, 2004, 2007; Gilbert et al. 2002; Sloman et al. 2003; Gilbert 2007). This primitive form of the emotion may be evoked in a subordinant simply by being in the presence of a higher-ranking individual. It has characteristic expressive and behavioral features (across both species and cultures), which include (where applicable) shrinking posture, gaze aversion, flight, bent kneed gait, avoiding social contact, hiding (Fessler 2004; Gilbert 1997, 2007; Keltner and Buswell 1996; Keltner et al. 1997), and possibly a distinctive facial expression. It also involves patterned physiological activity within the HPA axis and immune system, among other areas (Gruenewald et al. 2007), and a small but growing literature also suggests that shame involves characteristic patterns of neural activity (Beer 2007; Berthoz et al. 2002; Takahashi et al. 2004), distinctive affective and cognitive sequalae, and phenomenological qualities such as feeling small, and wishing to avoid being seen by others. The aversive nature of shame also appears to generate an internal hedonic motivation to attain higher rank and avoid loss of rank (Fessler 1999, 2004). Contrary to the opinion that shame is a pure HCE, the features of shame described above are good reason for regarding the primitive form of shame as a BE, and a number of authors (including Griffiths, and notably, (Ekman 1999; Griffiths and Scarantino 2009) have added shame to their list of BEs. I will follow these authors and call this form of shame BEshame.

Shame as a higher cognitive emotion

Many characteristics and functions of BEshame are directly retained in human forms of shame, to the extent that dominance hierarchies still play a role in human life (Fessler 1999, 2004). However, in humans the functional breadth of shame has expanded in at least two ways. First, while the dynamics of dominance hierarchies continue to play a role in human culture, the primary basis for the establishment of human social hierarchies has largely shifted from dominance (coercive power) to 'prestige competitions' (involving the attraction of positive social attention, and the possession of socially valued traits or materials), and shame has also come to be associated with loss in such prestige competitions. Second, shame has acquired the function of facilitating cooperation and conformity, by signaling our awareness of our violations of collective norms, as well as our desire to adhere to them. We thereby communicate to others that we are reliable partners for cooperative ventures, which facilitates cooperation with other members, and enhances social reincorporation when we have violated these norms (Fessler 1999, 2004; Gilbert and Andrews 1998; Sloman and Gilbert 2000). Despite the expanded functions of shame in humans, its physiological, expressive, behavioral, and perhaps some affective/cognitive effects have been largely conserved. For example, individuals in situations involving prestige- or cooperation/conformity shame still display the expressive and behavioral displays characteristic of BEshame.

Of particular importance in considering the usual division of emotions into BEs and HCEs, the newly developed forms of human shame appear to involve characteristic physiological responses which resemble those seen in BEshame. This is important because the common characterization of HCEs as 'more cognitive' is typically associated with the claim that they are somehow 'more cerebral' and less connected to 'bodily processes'. The view that HCEs do not have any distinct neural, physiological, expressive, or behavioral characteristics is widely held, but poorly supported. Indeed, until very recently, the same was widely believed even of basic emotions. I would argue that many otherwise rigorous, biologically oriented researchers have prematurely ceded the territory of 'higher' emotions to those who maintain that such emotions are largely 'socially constructed' or primarily dependent upon higher cognitive capacities and socialization.

One reason for inferring that HCEs do not have a specialized neurophysiological basis might be that whereas HCEs can persist for weeks or months, the kinds of physiological signatures that are typically associated with (basic) emotions are rapid autonomic responses which are necessarily of a short duration.[7] My response to this is two-fold. First, while things like spikes in skin conductance are not the kinds of things that can last for weeks or months, nevertheless (1) alterations in the thresholds or cyclical patterns of such transient patterns can last for longer periods of time (e.g., we can be 'on the verge of tears' for long periods of time, with only relatively short bursts of actual crying), and (2) there are other physiological elements of emotional responses that are the kinds of things that can persist over long periods of time, such as alterations in hormonal or neurotransmitter levels. Several of the physiological responses associated with HCEshame that I cite below are such kinds of responses. Second, as I argue elsewhere, I think that the appeal to differences in duration to distinguish between BEs and HCEs (and moods for that matter) is a bit of a red herring. While they may typically be short-term responses, I believe that BEs can endure for much longer periods of time than is generally thought, and that they are accompanied by prolonged physiological responses.[8]

Whatever the reasons for accepting this conclusion, it is, in any case, not based on any solid evidence concerning the *lack* of a neurophysiological basis for HCEs. Most scientific research on emotions thus far has focused on such simple cases of emotion, which are easier to induce and measure, and only a few studies have directly looked for physiological correlates of HCEs. Given this lack of attention it is really no surprise that there is not much evidence supporting the idea that HCEs have distinct physiological correlates—but to infer their absence from lack of research is in itself misguided, and (as the evidence that *has* so far accumulated suggests) the claim is probably false.

For example, shame responses under conditions of social-evaluative threat (a relatively cognitively complex, culture-based form of threat), are especially potent activators of the HPA axis and proinflammatory immune system responses (Dickerson and Kemeny 2004; Dickerson et al. 2004; Gilbert and McGuire 1998; Gold and Chrousos 2002; Gold et al. 2002; Gruenewald et al. 2004, 2007) Activity of the HPA axis and inflammatory cytokines serves basic physiological protective and reparative functions in response to physical injury, mobilizing immune responses to fighting infection and promote the healing of damaged tissue. However, they are also associated with affective and motivational states that are adaptive[9] under conditions of threat and injury. For example, they underlie the

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[7] I thank an anonymous reviewer for pressing this point.

[8] I will not argue directly for this more general claim here, though I do take it up elsewhere (Clark 2009a, b). For present purposes, I merely present the evidence for a physiological component to HCEshame as a possible counterexample to the dominant view.

[9] Except where context indicates otherwise, I will use the word 'adaptive' in this paper to include both traits that have evolved by natural selection as well as traits that currently play a positive role in the survival and reproduction of an organism (e.g., exaptations), but have not (yet) been selected for as

induction of ‘sickness behavior’, which involves reductions in eating, grooming, social exploration and interaction, aggressive displays, sexual behavior, and pleasure felt in response to social and physical stimuli.

Such physiological reactions are not only adaptive as a response to physical threat and injury, but also appear to be adaptive with respect to threat or injury to one’s ‘social’ or ‘psychological self’ in situations involving dominance and submission, and other social hierarchical contexts. Activation of the HPA axis and/or levels of hormones and neurotransmitters (such as 5-HT) involved in this response are associated with dominance and submission behavior in a wide range of animals including rats, mice, monkeys, baboons, tree shrews, fish and humans. Corticosteroid and ACTH levels transiently increase in losers following social dominance contests, and subordinate animals tend to have higher levels of basal corticosteroids than their dominant peers, as well as enhanced proinflammatory immune activity. This constellation of responses is believed to have adaptive value by allowing organisms to recover from any injuries suffered during dominance contests, as well as to avoid any further aggression.

Thus, the conserved aspects of BEshame (at the physiological, expressive, behavioral, and other levels) appear to also play an adaptive role in the newly emerging prestige and cooperation/conformity instances of shame, although their functional role in these contexts is somewhat different. Importantly, however, within the context of ‘prestige-competition shame’, the conserved display features may actually be counterproductive, since signaling weakness or subordinance in the context of a prestige-competition may run contrary to the interests of the losing agent. In this context the shame display may be considered dysfunctional, since the deterrence of aggression is no longer necessary, and the display actually reduces the social desirability of the actor. It may therefore be best classified as vestigial in these contexts (Fessler 2007; Gilbert and McGuire 1998). The physiological responses described above also have the potential to be dysfunctional when they are chronic and long-term. Chronic occupation of low social status in humans and nonhuman animals often leads to depression or anxiety, and both shame and social anxiety are thought to be key components of depression and other forms of psychopathology in humans and nonhuman models of depression. Shame-related physiological responses also appear to have negative consequences for physical health when they are chronic or prolonged, a condition that is made more likely by humans’ abilities to extend emotional episodes in time via longer lasting cognitive responses.[10] I discuss the significance of the dysfunctional retention of these responses below.

Footnote 9 continued
primary or secondary adaptations in the strong sense. For many of the traits I discuss, it is not empirically clear whether they have been selected for or not, and I want to leave the question open. This usage might be better captured by Gould and Vrba’s term ‘aptive’ (Gould and Vrba 1982), but since their terminology has not achieved widespread use, I will stick to the loose sense of ‘adaptive’.

[10] Many of these shame-related physiological responses are also associated with “stress” more generally, and one might object that they are merely a general response to “threat”, of which shame is only a particular instance. There is, however, evidence that some of these effects are selective to shame. Even as general markers of stress, however, their co-option by the shame response appears to be a herterochronic insertion of an earlier physiological response to injury into a socioemotional context, which casts them in a different light (see below).

Whereas the primitive form of shame requires only the ability to assess one's relative position in a hierarchy (a cognitively simple capacity), the more recently developed forms of shame appear to require higher cognitive capacities, such as enhanced awareness of the self and the minds of others, and their reactions to oneself. These higher cognitive aspects of shame are typically what theorists have in mind when they classify shame as a HCE (Tracy and Robins 2007a, b). However, while the HCE form of human shame does require higher cognitive abilities, there is reason to believe that these aspects did not emerge de novo as an entirely different emotion (as is suggested by those who want to classify them separately as HCEshame), but rather arose via modification of existing affective structures, made possible by the increasing socio-cognitive complexity of humans, thus producing "an evolved psychological mechanism that makes us exquisitely sensitive to the extent to which others view us unfavorably" (Fessler 2004, p. 242), which in turn enabled these forms of shame to acquire new functions:

The case for homologizing basic and higher cognitive emotions

The evidence that HCEshame is systematically related to BEshame suggests that the relation between these categories is deeper than mere nominal similarity. In fact, there is good reason to believe that HCEshame is homologous to BEshame, in some sense(s), and on at least some levels, including some 'higher' organizational levels, e.g., behavioral, psychological, or functional.[11] The concept of homology was originally developed to apply to anatomical structures (Owen 1843). The operational criteria for homologizing traits at higher levels of organization have been developed by analogy with classical criteria for the establishment of structural homologies, such as Remane's criteria (Remane 1952). Analogous to Remane's criteria for structural homology, we can formulate operational criteria for identifying and testing homologies of higher-level traits (Ereshefsky 2007; Love 2007):

1. *Position*: the spatio-temporal position or functional role of a trait within a more general pattern of organization.
2. *Special Quality*: the complexity, distinctiveness, or specialization of the trait.
3. *Continuity*: Identifying an evolutionary continuum of properties, from a simpler and more primitive state to a more complex and derived state of the trait.

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[11] Regarding the paradoxical sounding "homologies of function", a number of authors have convincingly argued that in order to avoid conflating homological and analogical (functional) reasoning in discussing such relationships, "function" must be construed either in the sense of "activity function" or as "causal-role function", rather than as adaptive function (in any of several senses) (Ereshefsky 2007; Love 2007). In what follows, I intend my use "function" to be read in this way. This includes the relevant social functions, so that in describing the social functions of shame, I am simply recounting the roles that it plays in a social "economy" or "system", whether these be adaptive or not. Despite the fact that I and the authors cited above have clearly discussed shame in terms of its purported adaptive functions, this claim is not necessary for my argument, and would just cloud the issues. Many of these functions are likely to *also* be adaptive functions of one sort or another, but that is another argument.

Applying these insights to the characteristics of shame detailed above, a strong case for homologizing BEshame with HCEshame emerges. The characteristic features of BEshame are conserved in HCEshame. These features are complex, as well as distinct and specialized to shame; i.e., they possess *special qualities*. They also play (broadly) similar functional roles in HCEshame at each of their respective organizational levels, and in relation to one another, supporting a claim of '*positional*' or functional similarity. While the functional roles of HCEshame are different from those of BEshame, these functions remain centered around the same themes at a more general level of description, and have altered to the extent and in the direction that these themes have developed in humans. Furthermore, the integration of BEshame with newly evolved cognitive abilities appears not to have happened all at once in humans, but rather to the degree that a given species possesses these capacities. Higher primates, e.g., possess more sophisticated cognitive abilities than rats (including at least a rudimentary TOM), and these abilities are reflected in the increased range and complexity of their affective responses, pointing to an evolutionary *continuity* between BEshame and HCEshame (Bekoff 2002; Byrne and Whiten 1988; de Waal et al. 2006).

It should be noted that *non*-functional resemblances can also be crucial to diagnosing homologies (Griffiths 1997), and the fact that, e.g., the shame display may play a vestigial function in prestige-competition shame which results in functional consequences contrary to the interest of the agent, actually constitutes evidence in favor of construing them as homologous. This highlights the possibility of divergence among different levels of homology—in this case, some BEshame responses may have come to play functional roles facilitating the maintenance of social status in a new context, while others just came 'along for the ride' without facilitating (or even hindering) the newly emerging functional roles. It is now well recognized that traits which are homologous at one level of organization may not be homologous at other levels. The idea that we must consider different possible levels of homology for a trait has recently become a more central topic in discussions of homology (Abouheif 1997; Abouheif et al. 1997; Love and Raff 2006).

This calls into question the traditional idea that homology judgments trace the modification of a single trait, and arrive at a 'yes or no', 'all or none' answer to questions about whether modified forms of the trait are homologous to earlier forms. While the fact that relations of homology at different levels can be dissociated does not undercut the claim that homologous traits are *likely* to share various 'deep' causal commonalities of the sort cited by Griffiths, it does make such judgments significantly more complicated, since it entails that the different components (or perhaps 'constituent traits') of a complex trait must be examined separately in order to determine relations of homology at the level of complex traits, and this leaves open the possibility that such traits may exhibit 'partial' or 'mixed' homology (West-Eberhard 2003, pp. 485–491).

With respect to the present arguments, this implies that for highly complex psychological traits (like 'emotions'), we may not be able to classify them simply as 'homologous' or 'not homologous'. While we might still arrive at such a summary judgment after a broad consideration of the relations among various facets of complex psychological traits, such judgments need to be recognized for what they are—highly general and complicated assessments of 'overall' similarity with respect to evolutionary origins. As with all homologies, it may suit some purposes to treat BE- and HCEshame as homologous *simpliciter*, while for other purposes we might wish to make finer distinctions between BE- and HCEshame, or their several components.[12] This is related to the more general 'hierarchical nature' of homology, according to which traits can be 'simultaneously' homologous and not homologous, depending on the level of analysis and the interests behind the classification. As Brian Hall has said, traits should not be classified as 'homologous' but only 'homologous as…' (Hall 1994). In what follows, I will generally speak simply of BEs and HCEs as being 'homologous' (making some finer distinctions where necessary), but these general features of homological reasoning should be borne in mind.

'Single-trait' homology and serial homology

There are at least two ways or senses in which traits may be homologous to one another, and hence, two ways in which HCEshame (or its components) might be homologous to BEshame (or its components). I will sketch these two possibilities without offering a conclusive opinion about which one is the 'correct' analysis, largely because any answer would be underdetermined by the present evidence. First, BEshame and HCEshame may be 'single-trait homologous'; i.e., the emotion of shame may have undergone an evolutionary transformation as a 'single' trait, from BEshame to HCEshame. This is the way in which the relation of homology is most commonly conceived. According to this view, humans *would not possess two distinct forms of shame—BEshame and HCEshame—but rather, the emotion of shame as we have inherited it from ancestral species has developed into something more complex*. If this were the case, then categorizing the prestige-competition and cooperation-conformity forms of shame as a separate class or trait (as 'HCEshame') would be a mistake, for while BEshame would be a distinct form of shame in nonhumans, it would not be present in humans as a distinct emotion, acting alongside separate, HCE forms of shame, but would rather have been incorporated and modified into a single, more elaborate kind of emotional response.

Second, BE-and HCEshame might be serial homologues of one another.[13] Serial homologues are duplications or repetitions of some preexisting trait in an organism, e.g., spinal vertebrae. That two traits are serial homologues of one another does not imply that they are exact duplicates of one another. Duplicated traits occur in different spatial, temporal, or functional contexts than the original trait, a feature referred to as 'heterotropy' or 'heterochrony' which facilitates evolutionary novelty or innovation by allowing selection to operate differentially on the two kinds of 'duplicates', as in, e.g., arthropod body segments.

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[12] Component theories of emotion may be better equipped to deal with such divergences of levels and constituent parts than are discrete emotion theories. Component theorists argue that rather than trying to identify sets of discrete emotions, we should instead focus on the dissociable components and subcomponents that go into the construction of emotion, and the ways in which these components can recombine to form distinct affective states (Scherer et al. 2001).

[13] I owe the suggestion that I explore the possibility of serial homology in this context to Alan Love.

The concept of serial homology was also originally developed to apply to anatomical structures, but its breadth of application has also widened to include traits at other levels of organization. Serial behavioral homologues, for example, are especially common in social displays, such as the ritualized displays involved in courtship and dominance/subordinance behaviors. These often involve what West-Eberhard calls “sensory traps”—the novel use of a behavior that elicits preexisting responses from its recipient in other preestablished contexts. So, e.g., the courtship displays of many male birds involve food-pecking movements which have earlier and independently evolved to elicit approach behavior by females in anticipation of acquiring food. Note that here, as is often the case, the complex behavior in question is actually several degrees or levels removed from the original behavior: pecking originally served as a means of obtaining food, then as a means of ‘broadcasting’ a male’s foraging abilities to attract females when food is found, and finally, as a courtship display entirely removed from a foraging context. Thus, the same behavior may play several functional roles, each of which is layered and dependent upon (exapted from) previous functional roles.

There are several reasons to think that some BEs and HCEs might be serial homologues of one another. First, emotions like BEshame fall into a class of behaviors where robust serial behavioral homologies have already been established, i.e., that of social displays related to dominance/subordinance. Second, while HCEshame involves more sophisticated socio-cognitive elements, many of the core aspects of BEshame are retained in HCEshame as ‘marks of its past history’. It is worth noting here that the physiological responses associated with BEshame may themselves be heterochronic redeployments in a social context of a response to a yet more basic form of threat—physical threat—in which case their function in HCEshame would be a tertiary function of such responses. Third, while HCEshame occurs in contexts that are functionally distinct from those in which BEshame occurs, these types of contexts are nevertheless closely related to one another. Thus the preestablished functions of behaviors and other responses in primitive dominance-related contexts are well suited to heterochronic redeployment (a kind of ‘sensory trap’) in the cooperative and competitive contexts in which HCEshame occurs. Finally, if the HCEs in question are serial homologues, it might help to explain their greater involvement with higher cognition since their ‘positional’ relations with other psychological traits could vary from those of their BEcorrelates, allowing them to develop different relationships with, and be transformed by interactions with those other traits.

Conceiving of BE- and HCEshame as serial homologues would enable us to view the two forms as existing and functioning relatively independently, since HCEshame could have undergone modification while leaving BEshame mechanisms relatively intact. Most authors maintain that BEs continue to exist as such in humans (regardless of what other emotions we may have, and what their relations with HCEs may be). One reason to believe that BEs are retained in humans is the advantage associated with having rapid, simple modular responses to basic life challenges. Construing the relation between BEs and HCEs as serial homology would preserve this function of the BEs, while still allowing HCEs to vary more widely in their inputs and responses, and thus capture the common intuition that

BEs continue to exist separately in humans. Note that this independence of BEs would *not* be preserved by construing the homology relation as the modification of a 'single trait', though the 'single-trait view' might nevertheless accommodate such 'quick fuse' responses as being at one end of a graded response continuum, whereby certain kinds of stimuli have weighted or privileged effects on response timing, intensity, learning, etc.[14]

To my knowledge, no one has explicitly proposed a relation of serial homology between psychological traits as such. Such claims are certainly implicit in many assertions of behavioral homologies, but are not discussed directly at the psychological level. As with other forms of homology, the issue of 'levels' arises for claims of serial homology. Serial homologues may be homologous with one another (or not) at a number of dissociable levels. With respect to BE- and HCEshame, the evidence in favor of construing them as homologous clearly seems to indicate homologies at the behavioral and expressive levels, as well as the physiological level at which HPA responses occur. Beyond this, the situation becomes more difficult. Whether BE- and HCEshame are homologous in their social functions depends on how finely one defines these functions; e.g., both serve similar functions related to social status, but HCEshame is clearly related to different means of achieving and types of social status.

It is still more difficult at the neural or psychological level, though identifying instances of 'encephalization' may provide some support for claims of relations of serial homology at the neural and psychological levels. In encephalization, functions originally performed by 'lower' brain regions gradually migrate to 'higher', more newly evolved ones. In some cases this results in the loss of that function in the lower region, while in other cases the higher region comes to govern or regulate the lower region, sometimes resulting in a 'rewiring' of the lower area. In any case, the function in question typically becomes more complex and flexible as it migrates, and this occurs via a transitional process that does not result in a disruption of the original function, a pattern common to serial homology. Encephalization appears to have occurred in several key brain regions responsible for emotion (see, e.g., Rolls 1999, 2005).

The plasticity of emotions

Despite the similarities in BEshame across species, and the similarities in both BE- and HCEshame across human cultures, there is nevertheless significant variation among species and cultures along many dimensions of the shame response, especially as these apply to HCEshame in humans. Any account of the two kinds of emotion as homologous must offer some explanation of this variation. I believe that this variation can be explained as a result of developmental (and other forms of)

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[14] As noted by an anonymous reviewer, the fact that the serial homology approach would preserve the distinction between BEs and HCEs raises the question of whether this would in the end amount to the same thing as Griffiths's disunity thesis, i.e., that there are two distinct shame mechanisms that function independently. My response is that while this might support *a* disunity thesis, it would not be *Griffiths's* disunity thesis. The distinction would be between two homologues (and not between, say, two analogous traits), which would license defeasible inferences to all sorts of deep commonalities between them.

plasticity. Emotions are extremely complex responses to extremely complex environments, and as environments (especially social environments) become more complex and variable through evolution and development, emotions must keep pace. Simply possessing a set of stereotyped responses to a limited range of stimuli (while still essential in some situations) is no longer a feasible option. Nor is it feasible to evolve specialized responses to every conceivable variation in the environment. While there are broad themes within species- or taxon-typical social organizations which remain relatively constant (e.g., the existence of dominance hierarchies or social status), in general, complex social environments are simply too unstable and variable for phenotypic fixation to occur, much less be adaptive. Consequently, emotions have become highly plastic traits, and appear to have been *selected for* such plasticity. Such selection for plasticity is a common response to environmental complexity (West-Eberhard 2003, p. 178).

To some extent this plasticity can be found even in ‘core’ BEs—as species’ abilities to respond to more abstract features of the environment increase, so does the range of stimuli that are capable of triggering BEs. While organisms may be ‘prepared’ to respond to certain fixed stimuli with fear (e.g., heights or snakes), the range of stimuli to which fear is an appropriate response is much wider, and the mechanisms of assessment determining which stimuli elicit BEfear have evolved to be about as plastic as an animal’s ability to learn will allow. In humans, both the complexity of our social environment and our ability to learn are unparalleled. So while there remain general themes around which human emotional life is structured, it is to be expected that there will be considerable variation in the ways in which individuals and cultures have organized themselves around these themes. Such variation can be seen as a form of plasticity that is ‘built-in’ to the developmental and learning mechanisms associated with human emotions, rather than as evidence that HCEs are a fundamentally different kind of psychological state.

Conclusion

The application of ‘homology thinking’ to the problem of characterizing mental categories like ‘emotion’ within empirical psychology has posed a significant challenge to mainstream functionalist views of how to individuate such categories. One particularly important theoretical consequence of this challenge is the splitting of categories previously considered ‘unified’ or ‘general’ into collections of separate categories that bear only more superficial relations to one another; e.g., to split the general concept of ‘emotion’ into the relatively unintegrated classes of BEs and HCEs. Given that a theory’s explanatory power is partly determined by the degree of unification or generality it is able to achieve, this splitting would significantly reduce the explanatory power of many empirical theories of psychological traits. Advocates of this strategy argue that this reduction in explanatory generality is the price we must pay for the more detailed causal-mechanistic explanations offered by homologous categories, and that the trade-off is worth making.

Responses to this challenge have so far focused on arguing that functional classification yields deeper and more similarities among traits than the challengers allege. I agree, and have offered my own arguments to this effect elsewhere. These responses, however, have taken the challengers' characterizations of homological classification and its consequences for particular psychological categories for granted. They have so far failed to adequately explore the possibility that 'homology thinking' itself might provide the basis for a greater degree of unification or generality than their challengers have asserted, and therefore that the trade-offs among theoretical values might not be as stark as they have been presented to be. Why has this possibility been under explored? It is certainly *not* because the possibility of homologizing the traits in question hasn't occurred to anyone—it is perhaps the most obvious response to the challenge. Rather, I believe that both challengers and defenders of classification by homology have ignored the full range of possibilities available within homological reasoning.

With respect to the particular case of emotion, I believe that both sides have also too readily accepted the presuppositions involved in traditional debates about emotion, in particular, that HCEs are too 'social' or 'cognitive' to be grouped together with BEs, and that HCEs lack many of the distinguishing features of BEs, such as characteristic expressive, behavioral or physiological responses.[15] Many advocates of biologically based theories of emotion have argued that rigorous studies of BEs from a biological perspective have uprooted traditional or vernacular ideas about their nature. Nevertheless, they have failed to fully recognize the possibility that a rigorous study of HCEs might produce a similar transformation in our thinking about them, and have consequently accepted this traditional view of HCEs too quickly, in the absence of the kind of evidence that would be required to properly decide the question.

In this paper I have argued that the application of the full range of homological reasoning to the emotion of shame, together with evidence challenging the traditional view of HCEs, gives us reason to believe that these emotions have deep roots in our biology, and that the higher cognitive forms of these emotions develop continuously from these roots. I believe that same relation obtains between 'core' BEs and their 'HCE versions' (such as BEanger and HCEanger), where, I think, the artificial nature of the distinction is even more apparent. A growing literature also suggests that similar explanations may be given of other so-called HCEs, such as pride, aesthetic pleasure, guilt, jealousy, and moral disgust, among others (Aharon et al. 2001; Beer 2007; Berthoz et al. 2002; Blood and Zatorre 2001; Britton et al. 2006; Greene and Haidt 2002; Haidt et al. 1997; Haidt 2001, 2003a, b; Rozin et al. 1993, 1994, 1999, 2000; Rozin 1997, 1999, 2000; Royzman and Rozin 2006; Tracy

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[15] Interestingly, in their latest work on emotions, Griffiths and colleagues have attempted to narrow the divide between BEs and more complex emotions with respect to their degree of sociality, by construing (at least the expression of) both kinds of emotions as involving inter-personal 'Machiavellian', or 'transactional' aspects which are highly sensitive to social contextual cues, in both humans and nonhuman animals (Griffiths and Scarantino 2009; Griffiths 2003, 2004a, b). In part this is an argument that many of the social processes associated with HCEs may not be as complex (and hence not require as much 'higher cognition') as has been assumed.

and Robins 2004, 2007a, b; Takahashi et al. 2004, 2008; Vartanian and Goel 2004).[16] Ultimately, it will be necessary to establish such claims on an emotion-by-emotion basis, and it is virtually certain that there are many things falling under the vernacular category of emotion which fall outside this pattern. Nevertheless, I believe that establishing such relations for shame provides a starting point and template for a more general (though still less than fully comprehensive!) theory of emotion, and that the lessons learned by this consideration of emotion should be carried forward into the analysis of other psychological traits in terms of relations of homology.

Such a project could yield many theoretical benefits, in a wide range of sciences that deal with mind and behavior, and it is precisely these benefits that motivate Griffiths's emphasis on the value of classification by homology. In addition to the benefits that basic conceptual clarity could bring to debates about emotion, recognizing the continuities and differences between BEs and HCEs can (as Fessler has shown) guide research in anthropology into the phylogenetic origins of these emotions, and (given the importance of emotions to social relations), into the evolution of social structure and morality. It could also help to clarify, resolve, and guide research in developmental psychology, where the (often unclear) division between BEs and HCEs plays a prominent role in many developmental theories. Similarly, an understanding of the relations between BEs and HCEs could guide research into the neural and computational basis of these emotions, as well the genetic components that might influence their expression or development, leading not only to a better understanding of them, but also, potentially, the development of pharmaceutical interventions to treat disturbances within them.

Within clinical psychology more broadly, it could lead to the development of different treatments for different pathological disturbances (e.g., one might predict that more cognitive forms of therapy are less effective for syndromes primarily involving BEshame, whereas they are essential for those involving HCEshame). Indeed, many of the ideas regarding the interconnections between BEshame and HCEshame have been developed by clinical psychologists, such as Gilbert, Haidt and Rozin. Speaking more generally, most of the research cited in this paper has not been conducted with the aim of clarifying issues in the philosophy of mind or biology, but rather with the development of models of emotion that can facilitate research or treatment interests within particular empirical disciplines. Of course, that research turns out to be of enormous importance to philosophical concerns. It is my hope that by drawing the philosophical implications of this research together, philosophy can begin to return the favor.

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[16] If this is indeed the case, what are we to make of the fact that multiple BEs have developed intoHCEforms? This suggests a common systematic mechanism underlying these instances, such as modification resulting from integration within higher cognitive functions, rather than a collection of independently emerging modifications, a possibility which deserves further investigation.

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