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Intersections Between Development and Evolution in the Classification of Emotions

ABSTRACT: *In this article, I use the example of emotions to illustrate how various concepts of homology can play a role in developmental psychology by showing how developmental and evolutionary approaches to the classification of psychological traits complement and constrain one another. In order to do this I argue against the ''Standard Model'' of emotional classification according to which basic and higher cognitive emotions belong to radically different classes of emotions. Neither developmental nor evolutionary considerations support the Standard Model, and a combined ontogenetic and phylogenetic approach presents a stronger case for the revision of this model than does either of these taken alone. Recent attempts to integrate developmental and evolutionary factors in the explanation of other psychological traits can guide research in these areas. I argue that a consideration of various neglected forms of homology that are closely tied to development resolves some outstanding problems in ontogenetic and phylogenetic classification of emotion.* © *2012 Wiley Periodicals, Inc.* Dev Psychobiol 55: 67–75, 2013.

Keywords: *emotional development; evolution; homology; serial homology; basic emotions; higher cognitive emotions; shame; pride*

INTRODUCTION

Emotions have been at the center of debates about the evolution of psychological traits since Darwin (1872/1965), and have continued to be a primary test case for the application of evolutionary concepts in psychology and philosophy, among other disciplines. Many theories of emotion have drawn a sharp phylogenetic distinction between a class of evolved emotions that we share with other animals, and another class that are held to be unique to humans without any direct evolutionary precursors in other animals. I call this view the ''Standard Model'' of emotion classification. While advocates of the Standard Model often point to developmental evidence to support their claims, questions of classification have focused on phylogenetic relationships. However, emotion researchers have recently begun considering development more seriously. Here I argue that we should go beyond the generic concept of phylogenetic homology and recognize additional homology concepts that are more closely tied to developmental issues.

First, we can apply the concept of ''developmental homology'' to trace the links between earlier and later stages in the development of emotions. If two emotions share common developmental mechanisms or resources this indicates a strong continuity between earlier and later emerging capacities, and we may consider them to be developmentally homologous (Brigandt, 2003; D. Moore, this issue). Second, we can examine the developmental mechanisms underlying ancestral and derived emotions as traits in their own right to establish ''homologies of development.'' Common developmental mechanisms underlying different emotions can support claims of phylogenetic relatedness, and changes in such developmental mechanisms can illuminate the ways in which the ancestral and derived emotions have diverged. Finally, ''serial homology'' is a form of homology in which a trait is duplicated within a single organism, and which is especially closely connected to development. I will argue that the serial homology

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concept can be applied to emotions in order to establish a continuity between basic and higher cognitive forms of emotions, while accounting for the fact that earlier developing emotions seem to persist alongside emotions arising later in development. Together, these considerations undermine the Standard Model.

THE STANDARD MODEL

There are numerous articulations of the Standard Model, the most comprehensive being Griffiths (1997; see also Matthen, 1998; Panksepp, 1998, 2007; Royzman, 2011). All versions of the Standard Model distinguish two classes of emotions, which, for want of better consensus terminology, I will call ''basic emotions'' and ''higher cognitive emotions.'' Basic emotions (such as fear, joy, and anger) are seen to be evolutionarily old sets of responses involving stereotypical neural, physiological, and behavioral profiles that have evolved in response to recurrent evolutionary challenges. These patterns are held to be capable of being activated by unconditioned stimuli and lead to unconditioned, involuntary responses that cannot be easily modified by higher cognition.

On the other hand, higher cognitive emotions (such as pride, shame, and guilt) are seen as diverging from basic emotions in these respects. First, on the input side, while basic emotions can also come to be evoked by higher cognition (Le Doux, 1996), their ability to be triggered by very simple stimuli is believed to distinguish them from higher cognitive emotions. Instead, higher cognitive emotions are held to *necessarily* involve sophisticated cognitive inputs by their very nature (such as means-end, causal, and counterfactual reasoning, long-term planning, social cognition, etc.), and to lack simple noncognitive elicitors.

Second, on the output side, it is widely believed that higher cognitive emotions do not involve involuntary, stereotypical physiological, expressive, or behavioral responses, but rather involve responses that are learned or prescribed by the social environment. Thus, while there may be culture-typical patterns of higher cognitive emotional responses that have become ''automatic,'' these are dependent on local culture for their development and significance. Furthermore, the responses of higher cognitive emotions are held to be more penetrable to higher cognition, whereas even basic emotions that are triggered by higher cognitive stimuli are held to involve the same modular responses as those triggered by simple stimuli (i.e., basic emotions have more flexible inputs than they do outputs).

Finally, higher cognitive emotions are commonly distinguished from basic emotions by their later developmental emergence. According to the dominant view of emotional development, Cognitive Developmental Theory (e.g., Lewis, 2007; Sroufe, 1996; Stipek, 1995), all basic emotions emerge roughly during the first year of development, while higher cognitive emotions such as shame and pride emerge later (between 18 months and 4 years of age), and only once certain 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. While these emotions continue to develop beyond this point, and while there may be some higher cognitive emotions that do not emerge until later, the focus here is on emotions that emerge at this time, viz. shame and pride.

The Standard Model interprets such evidence as indicating that basic emotions and higher cognitive emotions belong to radically different classes, and arise via different developmental origins rather than via elaboration of more basic evolved affective abilities (though, as we shall see, this conclusion is not supported by a closer look at Cognitive Developmental Theory itself). Based on these evolutionary and developmental differences Griffiths and the authors cited above (Griffiths, 1997; Matthen, 1998; Panksepp, 1998, 2007; Royzman, 2011) have argued that it is a mistake to subsume both basic emotions and higher cognitive emotions under a general category of ''emotion,'' holding that there is simply not enough overlap between the two in developmental or evolutionary origins to make ''emotion'' a useful theoretical concept.

Evolutionary considerations have dominated the classification of emotion, with less attention paid to development. In several recent articles I have argued that the evolutionary picture presented by the Standard Model is incorrect **(Clark, in press, 2010a, 2010b). Instead, there are deep similarities between emotions such as pride and shame in humans and status-related emotions concerning dominance and submission in other mammals, and the former bear clear marks of having evolved from the latter, including the retention of many features denied to them by the Standard Model such as characteristic expressions, neural basis, etc. Such a picture also characterizes the relations between paradigmatic basic emotions and their higher cognitive forms (Clark, 2010a) (e.g., basic and moral disgust), whereas on the Standard Model, purported higher cognitive forms of paradigmatic basic emotions are held to be mere metaphors, rather than more complex stages in the evolution of basic emotions (Panksepp, 2007).

I return to these arguments briefly below, but first I want to focus on the way in which developmental research has been used to support the Standard Model.

Evolutionary and developmental classifications are tightly intertwined, and therefore the argument for abandoning the Standard Model must also consider the developmental evidence. In considering the developmental classification of emotions advanced by the Standard Model, the comparisons are primarily internal to the developmental process—we want to understand how basic emotions and higher cognitive emotions are related to one another in developmental processes, and in particular, whether they show radically different developmental origins or mechanisms. Such an internal investigation requires no reference to evolution, though as we shall see evolution lurks in the background in numerous ways.

While I argue against the Standard Model on these grounds, as we shall see, there is a sense in which the basic/higher cognitive distinction holds true: Adult human forms of pride and shame and other higher cognitive emotions are indeed more complex and tightly integrated with higher cognitive capacities than are more basic emotions. But the overall picture is quite different.

DEVELOPMENTAL CLASSIFICATION OF EMOTIONS

Recently, a number of theorists have offered accounts of emotional development that clearly and explicitly challenge the Standard Model (e.g., Parkinson, Fischer, & Manstead, 2005; Reddy, 2005; see Draghi-Lorenz, Reddy, & Costall, 2001 for extended discussion of such theories). They argue that all emotions can be observed in primitive form in infants and toddlers, prior to the development of the higher cognitive capacities that are usually taken to be definitive of them. While these primitive emotions do become more complex as they are integrated with higher cognitive capacities, they maintain that presence of these earlier forms contradicts the idea that these emotions emerge de novo at a certain point in cognitive development, and it puts these emotions on a developmental par with paradigmatic basic emotions.

I do not have the space in this article to investigate such theories in any depth. Instead I will examine the mainstream view of emotional development that underlies most presentations of the Standard Model—Cognitive Developmental Theory. I will argue that (i) even this account does not support the Standard Model (especially when it is situated in an evolutionary context), (ii) that advocates of the Standard Model that rely on Cognitive Developmental Theory to support their views depend on semantically ambiguous superficial readings of Cognitive Developmental Theorists' conclusions, and thus that (iii) Cognitive Developmental Theory itself supports a revision of the Standard Model.

Again for reasons of space, I will here use Michael Lewis's theory as a representative of Cognitive Developmental Theory more generally (Lewis, 1992, 2007). I will focus on his account of three stages of early emotional development, though importantly there are many further stages. While many Cognitive Developmental theorists disagree with Lewis on the particulars of his account, here I am primarily interested in some structural features of Lewis's theory that are inconsistent with the Standard Model, and which are broadly shared in Cognitive Developmental Theory.

According to Cognitive Developmental Theory the classificatory basis for emotional development is essentially based on various milestones in cognitive development, and emotions are classified with respect to these milestones. As various cognitive capacities come on-line, this allows for the development of new forms of emotionality, which are classified in terms of the cognitions in question. There are many cognitive capacities whose development is relevant to this progression, but Lewis focuses primarily on self-awareness and the ability to grasp and evaluate oneself according to external norms. As a result of this, Lewis focuses on ''self-conscious emotions,'' a particular type of higher cognitive emotion defined in terms of self-awareness and related capacities. Following most authors, Lewis holds that basic emotions emerge during the first year. After that, self-conscious emotions emerge in two steps. Between 15 and 24 months, the ''self-exposed'' emotions appear as a result of the development of a simple form of implicit self-consciousness of the self as an object. These include emotions such as empathy and envy. Sometime between 2 and 4 years, children develop a more sophisticated sense of self and other (roughly, a theory of mind), and become capable of internalizing norms and evaluating their behavior with respect to them. This gives rise to a third set of emotions—the ''self-evaluative emotions''—that require cognition about the self as an object that can be evaluated according to both external and internalized normative standards. These emotions include guilt, shame, and pride.

Prior to this point, while the child may be, for example, capable of responding in positive ways to success, and while some of these responses share features in common with adult pride displays, according to Cognitive Developmental Theory they do not constitute ''genuine pride'' because they occur in the absence of the required cognitions. For example, pleasure in success or achievement or in response to praise from adults is a common finding in studies of infants within the first year (Reddy, 2005).

Authors in the Cognitive Developmental Theory tradition, however, usually avoid labeling such displays as ''pride,'' but rather call them, for example, ''mastery motivation,'' ''pleasure in efficacy,'' etc. (Dunn, 1994; Heckhausen, 1988; Piaget, 1952; Sroufe, 1996; Stipek, 1995; Stipek, Recchia, McClintic, & Lewis, 1992). Crucially, most Cognitive Developmental theorists *do* maintain that these early affective states are necessary precursors for the emergence of pride, but they nevertheless adhere to the Cognitive Developmental Theory thesis that these emotions cannot be said to ''properly'' emerge until the requisite cognitive capacities are in place.

From the fact that Cognitive Developmental Theory theorists say (a) that pride and shame do not emerge until later in development than basic emotions, and (b) that these later forms essentially depend on higher-cognition unique to humans, it is easy to conclude that basic and higher cognitive emotions are radically distinct as described in the Standard Model Section. But this conclusion is facile and reflects botha misunderstanding of what Cognitive Developmental Theory theorists mean when they assert these claims, and a neglect of other aspects of their theories. I believe that such claims are best interpreted as urging a semantic policy for the use of ''shame'' and ''pride'' in order to mark off distinct stages in a more continuous development of higher cognitive emotions.

In any case, however, these semantic distinctions are not sharp distinctions in the manner asserted by the Standard Model, for a variety of reasons. First, Lewis, like other Cognitive Developmental theorists strongly affirms the idea that later emotions are closely linked to and dependent upon earlier ones, and he offers an account of the developmental progression from the exposed self-conscious emotions to the evaluative self-conscious emotions according to which the exposed self-conscious emotions interact with and incorporate standards, rules and goals and the newly emerging objective self-awareness, leading to the emergence of evaluative self-conscious emotions from exposed self-conscious emotions. Given that early and later forms of these emotions share common developmental mechanisms and resources, including the exploitation of the resources of earlier stages by later emerging emotions, it would appear that these forms are developmental homologues of one another. Importantly, this does not involve the complete transformation of earlier forms into later forms. Rather, Lewis holds that the earlier forms of these emotions persist alongside the later forms and can function independently to some degree (see the discussion of the ''persistence problem'' below).

For example, Lewis (1992) argues that shame (a self-evaluative emotion) arises out of a simpler form of embarrassment (a self-exposed emotion). He distinguishes between two forms of embarrassment. ''Non-evaluative embarrassment'' is a self-exposed emotion, and hence a relatively simpler reaction, occurring when the individual becomes aware of being the center of attention (whether positive or negative), and requires only a basic awareness of the self as an object of attention. ''Evaluative embarrassment'' is a self-evaluative emotion, and thus requires more sophisticated forms of cognition, such that the individual be aware that others are evaluating the self or its actions, that these norms are internalized, etc. Shame, in turn, is seen as growing out of evaluative embarrassment. Nor does Lewis construe the emergence of later forms of emotions as a unidirectional process driven solely by the emergence of cognitive capacities, but instead sees it as involving reciprocal interactions between emotion and cognition, each of which bootstraps the other, such that ''... emotion gives rise to thoughts about emotions that, in turn, give rise to the objectification of the self, and to the new self-conscious emotions'' (Lewis, 1992, p. 97).

In addition, while the stages of emotional development are *classified* by their cognitive components within Cognitive Developmental Theory, and the *specific* standards, rules and goals to which they are calibrated are partly determined by local culture, they are not exclusively cognitive in *nature*, nor are they in any obvious sense less ''biological,'' or ''purely cultural,'' despite a broad reliance on social scaffolding for their development. For example, Cognitive Developmental Theory generally recognizes that emotions like pride and shame also have characteristic expressive, behavioral, and physiological features (e.g., blushing) and are thus ''genuine affects'' rather than merely forms of cognitive assessment (Miller, 2007). Note that while blushing does indeed appear to be an evolutionary novelty in humans (Darwin, 1872/1965), it is not the kind of novelty one would expect to find if the Standard Model were true. Blushing is an example of the kind of affective physiological reaction that Standard Model advocates would attribute to basic emotions and deny to higher cognitive emotions, for example, it is not constituted by higher cognition, despite the fact that it emerges relatively late in evolution and development. Here, Lewis also correctly resists classifying emotions as biological or not depending on any simple division into early and late because ''there is no reason to assume that because something emerges later it is less biologically central than something that emerges early'' (Lewis, 1992, p. 19).

Furthermore, despite their later emergence, these emotions nevertheless emerge according to a consistent developmental timetable that is robust in the face of environmental perturbations. These are features that are characteristics of evolved (or at least strongly developmentally canalized) traits, suggesting that their development is an inherited process. Thus, Lewisacknowledges that ''the evaluation of our behavior in terms of our standards is a natural process independent of the nature of the standards themselves'' (Lewis, 1992, p. 68); that is, that at a broader level of description the input features associated with such emotions are universal, and that ''[I]t is difficult to imagine that we 'learn' shame. While we may learn about the elicitors of these emotions or about what responses are culturally appropriate, the emotion itself is not learned'' (Lewis, 2007, p. 145). Thus the developmental programs underlying emotions appear to have evolved themselves, and are not solely the products of cultural learning in the way that, say, reading and writing are. Finally, Lewis situates higher cognitive emotions within an evolutionary framework in a way that is inconsistent with the Standard Model. He acknowledges that at least some of the relevant higher cognitive capacities, and the emotions associated with them, have parallels in great apes saying that ''the ontogenetic difference is supported by a phylogenetic difference'' (1992, p. 19) according to which apes (at least) are capable of self-exposed emotions, from which the self-evaluative emotions evolve in humans.

In sum, it is a caricature of Cognitive Developmental Theory to see it as holding the overly simple idea that while basic emotions are biologically rooted responses, higher cognitive emotions like pride emerge de novo in late development, and are primarily cognitive or ''cultural'' in nature, or not genuine ''affects'' in the full blown sense. If the Standard Model were correct it is likely that we would find that basic emotions and higher cognitive emotions arise through different developmental mechanisms with sharply distinct origins. This is not what we find in Lewis's (1992, 2007) account. Instead, we find developmental continuity between more basic affective states and more complex ones. Complex emotions inherit many of the features of their more simple forms, including ''special qualities'' such as display features. The emergence of higher cognitive emotions is not driven solely by the emergence of higher cognitive capacities, but rather involves an interplay between affect and cognition. Nor are higher cognitive emotions constituted solely by higher cognitive capacities. Rather, these emotions are genuine emotions in the same sense that canonical basic emotions are genuine, that is, they possess many of the paradigmatic features usually used to dissociate basic emotions from higher cognitive emotions.

PHYLOGENETIC CLASSIFICATION OF EMOTIONS

An increasing number of authors are converging on the conclusion that such higher cognitive emotions are homologous to more basic forms of these emotions in other animals (see in press, 2010a, for discussion and references). For example, both pride and shame appear to have characteristic, universal whole body expressions, distinctive physiological and neural correlates, distinct behavioral patterns, and deeply rooted, evolved social functions centered around status hierarchies. These features also characterize related emotions in other animals that are concerned with hierarchical dynamics, such that, for example, displays of dominance status in animals strongly resemble pride displays in humans, while appeasement displays strongly resemble shame. Status in other animals is determined primarily by coercive dominance. In humans, however, status dynamics have changed considerably as a result of the emergence of a variety of uniquely human social, emotional, and cognitive capacities, including explicit norms, conformity and cooperation, higher-order punishment, and prestige (Fessler, 1999; Henrich & Gil-White, 2001). While coercive dominance-based hierarchies remain present in humans, and shame and pride continue to play a role in these contexts similar to that found in other primates, coercive dominance is no longer the primary factor underlying the achievement of status, and the emotions associated with status have been co-opted and modified for these newer contexts. Importantly, however, dominance-based pride persists in humans alongside prestige-based pride.

For example, consider the ways in which prestige has changed the functions of pride. Henrich and Gil-White (2001) define prestige as a form of status resulting from freely conferred deference, which evolved in order to facilitate the cultural transmission of information. Prestige is a form of nonagonistic exchange between individuals with differing assets, skills, or resources in which social learners show deference towards successful, skillful individuals in order to gain proximity and the opportunity to imitate them and acquire information relevant to their success. In such contexts, status is associated with high performance relative to social norms, and pride is elicited in situations in which the actor succeeds in the performance of socially valued activities, or in acquiring socially valued goods and traits, whereas shame results from failures in prestige contexts, and also as an

appeasement gesture involved in showing deference to the prestigious.

Henrich and Gil-White (2001) note two specific precursor capacities that are antecedently well suited for prestige processes, and which are present in other animals: (1) skill ranking of conspecifics, and (2) discriminatory deference. Macaques, for example, are able to rank conspecifics in terms of foraging success and both maintain proximity and show discriminatory deference to them (e.g., by preferential grooming) in return for food opportunities (Stammbach, 1988). However, prestige hierarchies as Henrich and Gil-White define them can only arise once certain uniquely human higher cognitive capacities are in place that permit the direct learning and transmission of cultural knowledge from skilled to less skilled individuals.

For example, ''true imitation'' requires mirroring of both the model's goals as well as the model's specific motor actions. Other animals are capable of understanding and imitating a model's goals, but not their specific motor strategies for achieving them, whereas even very small children are capable of imitating the particular motor patterns of the model, even when these are clearly nonfunctional (Horner & Whiten, 2005). The ability to imitate prestigious individuals' specific techniques (and not merely their goals) is a prerequisite the accumulation and refinement of cultural knowledge and practices that are transmitted in prestige-based learning, and in terms of which it is defined.

For example, by observing others, chimpanzees can learn that reeds may be used to gather termites, and based on individual learning they can refine these techniques to, for example, use particular size reeds under different conditions. However, the initial learning does not involve direct social transmission (even mothers do not ''teach'' their infants to use reeds), and is also limited to imitating goals rather than specific techniques, so that the refinements that occur as a result of individual learning are not directly transmitted. Therefore, each individual must learn these refinements on their own, and there is little to no accumulation and transmission of social knowledge between generations (Tomasello, 1990, 1999).

Pride evoked as a result of prestige-based attainment of status shares expressive, behavioral, physiological, neural, etc., features in common with dominance-based forms of pride, and in prestige contexts, pride serves functions which overlap with its dominance-based forms at a higher level of generality (e.g., achieving status in hierarchies). These similarities are sufficient to ground a prima facie case for phylogenetic homologies between the basic and more complex forms of these emotions. However, unlike dominance-based status, prestige is granted to the actor by the observer rather than being attained through force. Thus the task demands surrounding dominance- and prestige-based status are quite different and in many ways inconsistent insofar as, for example, subordinates seek closer contact with those who have attained prestige-based status, rather than trying to avoid them, as they do towards individuals who hold dominance-based status. All of this strongly suggests that the Standard Model's picture of a sharp evolutionary difference between basic and higher cognitive emotions and/or differences in their possession of various ''core'' features of genuine emotions, such as expressive, physiological, etc. qualities, is mistaken.

A crucial missing piece of the puzzle of the classification of emotions is a comparative study of emotional development in primates and humans. Surprisingly, in the case of emotions, we have almost no comparative developmental evidence. While there is at least limited evidence on the development of basic emotions in other primates (Bard, 2005), there is virtually nothing on the development of status-related behaviors or emotions. Such studies are important because we may also compare and homologize developmental mechanisms *as traits in themselves*, and such ''homologies of development'' can provide insight into the phylogenetic relationships between the terminal traits under consideration. Various shifts in developmental timing or context, for example, are a common way to produce differences between the ancestral and derived traits. These include heterotopy, the deployment of a trait into different structural or functional contexts, and heterochrony, the insertion of a trait into different temporal contexts. Changes in ''context'' here may occur at all levels, including neural, physiological, behavioral, cognitive, social, etc. These processes deserve greater attention in future work (see Langer, 2006; Wobber, Wrangham, & Hare, 2010; Wobber, Hare, & Wrangham, 2010, for application of these ideas to cognitive and socioemotional traits; for an example of anatomical paedomorphosis, see Bhullar et al., 2012).

Serial Homology

Still another way in which homology can be applied in developmental psychology concerns the phenomenon of serial homology (D. Moore, this issue; West-Eberhard, 2003). Specifically, evidence of common evolutionary and developmental pathways for two traits *within the same organism*, where both the original and the duplicate remain present, suggests that the differences and similarities between basic and higher cognitive emotions reflect a particular form of homology between them—''serial homology.'' Serial homology refers to the duplication of a trait within single organisms from

a given species. Such duplications lead to either the augmentation of the original trait's function, or to variation between the original and the duplicate. For example, leaves are serial homologues of one another, where a multiplicity of leaves augments the various functions of leaves; but flower petals are also serial homologues of leaves where the duplicates have been allowed to vary in their structure and functions. Duplication can occur at any level of organization, from genes to (I will argue) psychological traits, and all levels in between. Serial homology is especially closely connected to development given that many serial homologies first emerge through accidental developmental duplications, and developmental duplication often (though not necessarily) remains the proximate mechanism by which the serial homologues are generated. This means that the duplicates will often share the same developmental mechanisms and resources, and so serial homologues are frequently instances of developmental homology, which is defined in terms of such similarities.

Serial homology is one of the primary mechanisms for the generation of evolutionary novelty. Duplicated traits occur in different spatial, temporal, or functional contexts than the original trait. These differences in context can result in divergent developmental and evolutionary paths for the original trait and the duplicate; for example, the body and head segments of many arthropods are serial homologues of one another, yet radical differences between them have arisen as a result of their different spatial, biochemical, and other contexts of development, which has in turn allowed selection to operate differentially on the two duplicates.

Serial behavioral homologues are especially common in the origin and evolution of social displays, such as the ritualized displays involved in courtship and dominance/subordinance behaviors. These often involve what West-Eberhard (2003) calls ''sensory traps''—the novel use of a behavior that is pre-apted (or antecedently well-suited) for the secondary function; for example, the courtship displays of many male birds involve food-pecking movements that have earlier and independently evolved (or had the adaptive side-effect) of eliciting approach behavior by females in anticipation of acquiring food.

In both evolutionary and developmental contexts, emotions appear to face the kinds of pressures that produce serial homologies. Developmentally, a great many theorists maintain that earlier forms of emotions continue to exist independently alongside their later emerging forms, and most accounts of their development face a problem that I have labeled ''the persistence problem'' (Clark, 2010b), and for which serial homology is a potential solution. For example, recall that Lewis argues that in emotional development ''[t]his transformational process uses the exposure emotions, but in the developmental process these emotions are not destroyed. This material transformation allows for the material of early structures to be utilized but not converted in theprocess. In this way, *both* exposure and evaluative emotions appear at the next level ... In such a transformation, embarrassment becomes the material for shame ...'' (1992, 96).

Evolutionary accounts of emotions also face this problem. Many authors arguing for an evolutionary continuity between pride and shame in humans and status-related emotions in other animals note that the evolutionarily earlier forms of these emotions continue to persist as distinct emotions despite the appearance of later more complex forms. For example Fessler (1999, 2007) notes that more primitive forms of shame persist alongside more complex forms, and Tracy, Shariff, and Cheng (2010) argue that dominance-based forms of pride are retained alongside prestige-based forms. This retention makes sense insofar as the dominance-based hierarchical dynamics associated with the ancestral emotion continue to characterize human life. However, many of the task demands of the simpler and more complex forms are inconsistent. Tracy et al. (2010) note at least five ways in which dominance-based and prestige-based pride are inconsistent, despite all their similarities. Their solution is to construe pride as a single emotion with two diverging ''facets,'' but the notion of a facet is not entirely clear, and sits uncomfortably between the claim that prestige-based pride and dominance-based pride constitute a single trait, and the claim that they are two separate traits. They are ''the same but different'' (Clark, 2010b; Shariff, Tracy, Cheng, & Henrich, 2010).

The persistence and relatively independent functioning of different forms of the same emotion is a problem for the usual approach to the evolution of psychological traits, which typically employs the standard notion of ''transformational homology,'' in which a single ancestral trait undergoes a transformation into a single derived trait (e.g., the evolution of bat wings from the general tetrapod forelimb). Here the ancestral trait is not retained independently. Rather the ancestral trait *becomes* the derived trait. With respect to emotions, this account usually asserts an expansion of the elicitors and outcomes of ancestral emotions, resulting in a single expanded derived trait. Such a solution cannot be ruled out at this point, but we should also consider the serial homology approach. If we construe later forms of these emotions as serial homologues of their earlier forms, then we can provide an account of their sameness: they are duplicates, and so share many properties in common. However, the duplicate higher cognitive emotion can vary in response to different selective or

developmental pressures, accounting for the differences. The features that are duplicated may in principle range from the expression alone to the duplication of the total integrated response, and every piecemeal possibility in between.

The serial homology approach towards emotions has been in use at least since Darwin (1872/1965), though it is almost never labeled as such. Darwin's account of the successive co-optation of emotional expressions (e.g., from biting responses in physical conflicts to bared-tooth expressions of anger) is essentially a serial homology account, given that the original functions of such expressions remain intact (e.g., organisms still bare their teeth to attack) despite the acquisition of new communicative functions. The application of the concept of serial homology to emotions considered as *psychological traits* (rather than, ''merely'' behavioral traits) is novel, and faces a number of challenges, primary among which is how such duplication and modification is realized in neural structures.

Due to major constraints on human brain size, among other reasons, we should not expect serial homologies of psychological traits to involve literal duplication of brain structures. Instead they are most likely to involve ''neural reuse'' rather than anatomical duplication (Anderson, 2010; Moore & Moore, 2010). In neural reuse, brain circuits originally established for one purpose are co-opted to serve additional functions without losing their original functions, for example, the use of motor sequencing regions for language. Anderson focuses largely on the reuse of the computational features of small-scale circuits. I believe that these are best seen as serial homologies, though their lack of complexity makes it uncertain whether we should consider them to be serial homologies of *psychological* traits, or serial homologies at some lower level of organization. In any case, in order to speak robustly of serial homologies of psychological states, both the original and duplicate should be psychological traits in their own right, and Anderson's model would need to be extended to include circuits at large enough scales to ground psychological states proper.

CONCLUSION

In summary, both developmental and evolutionary considerations fail to support the Standard Model. Instead of two radically separate classes of emotion, we have a more unified picture in which early basic forms of emotion give rise to more complex forms that share both developmental and evolutionary origins and mechanisms, and can thus be considered both developmental and phylogenetic homologues. Many if not all emotions have both basic and higher cognitive forms that share all of the paradigmatic features of emotions. While higher cognitive and basic forms do indeed differ in important ways, they can nevertheless be situated in a common evolutionary and developmental framework. In arguing this, I hope to have shown how various concepts of homology can play a role in developmental psychology, and how developmental and evolutionary approaches can complement one another in the classification of psychological traits. While ontogenetic and phylogenetic bases for the classification of emotion have independent validity, traits that share common developmental mechanisms are also likely to show close evolutionary relationships, and thus developmental evidence can be used as evidence for homology judgments. Similarly, traits with common evolutionary origins are likely to share developmental mechanisms, allowing the use of evolutionary evidence to draw defeasible inferences about what developmental patterns to expect. Finally, the concept of serial homology is well suited to explain some conceptual puzzles that arise in trying to characterize the relationships between earlier emerging (in both the phylogenetic and ontogenetic senses) and later emerging traits, where the earlier traits appear to persist alongside the later emerging forms.

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