# Evidential Critieria of Homology for Comparative Psychology

**Abstract:** While the homology concept has taken on importance in thinking about the nature of psychological kinds (e.g. Griffiths 1997), no one has shown how comparative psychological and behavioral evidence can distinguish between competing homology claims. I adapt the operational criteria of homology to accomplish this. I consider two competing homology claims that compare human anger with putative aggression systems of nonhuman animals, and demonstrate the effectiveness of these criteria in adjudicating between these claims.

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## 1. Introduction

Many emotion researchers and theorists have suggested that anger is an innate adaptation that may be shared with nonhuman animals (e.g. Ekman 1999; Sell, Tooby, and Cosmides 2009). This raises the question of which behaviors might be manifestations of anger in non-human animals. Given the tight link between anger and aggression in humans, some aggression researchers propose that innate patterns of aggression in nonhuman animals are manifestations of anger. In other words, they propose that the system responsible for these phenomena is homologous with human anger, meaning that these complex traits are derived from a common ancestral trait.

As plausible as this may sound, there have been two incommensurate proposals along these lines, and there has been little progress in adjudicating between them. According to the *ethological hypothesis*, a repertoire of confrontational behaviors observed in "resident", territory-holding, rats reflects "an underlying emotional state" that is a primitive version of anger (Blanchard and Blanchard 1984, 17 see also; Blanchard and Blanchard 1988; Blanchard and Blanchard 2003). This behavioral repertoire is set in opposition to avoidance behaviors observed in intruder rats, which reflect fear. Moreover, the hypothesis holds that these two distinct emotional systems provide the best way of understanding angry aggression and fearful aggression in humans. Another proposal, the *neurophysiological hypothesis* is that human experiences of anger "emerge" from a pan-mammalian brain system that produces defensive behaviors that are elicited when areas within the ventral hypothalamus (among other areas) are electrically stimulated (Panksepp and Biven 2012; Panksepp 1998; Panksepp and Zellner 2004). These behaviors are set in opposition to predatory behaviors,

which are neurally dissociable from the defensive behaviors. In other words, this hypothesis holds that there are two neural systems for aggression, and that one of them, the defensive aggression system, provides the primary neural substrate for human anger and is the proximate cause of "the feeling states and behavioral acts" (Panksepp, 1998, p. 14) distinctive of human anger. Moreover, the proponents of this hypothesis claim that we can best understand certain types of human aggression, impulsive and instrumental forms of aggression, in terms of the neural systems for defense and predation, respectively.

Importantly, these hypotheses are incompatible. Within the neurophysiological tradition, the neural dissociation between predatory and defensive aggression is the main reason to consider them fundamental, distinct categories of aggression. However, confrontation and avoidance behaviors do not exhibit this kind of clean neural dissociation (Siegel 2004, chap. 1). Moreover, the kinds of defensive aggression in rats produced by electrical brain stimulation is distinct from the aggression observed in ethological research in the sense that it lacks features that are diagnostic of these forms of aggression (e.g. Kruk 1991). In other words, the aggression phenomena identified by these different research programs are behaviorally distinct and distinct neural mechanisms are responsible for them. As a result, they make incompatible inferences about what anger is and, more specifically, about which aggression phenomena are its manifestations. The bimodal classification schemes for aggression (defensive versus predatory and confrontational versus avoidant) that distinguish these respective phenomena are incommensurate.

While proponents of these hypotheses aim to identify homologies, there has been little progress in adjudicating between them. There are two reasons for this. One is the *target*

problem: they have not carefully identified the human psychological trait that is the target of comparison. Another is the *evidence* problem: it is unclear how cross-species comparisons support homology claims. More specifically, it remains obscure how comparative evidence can play a role in adjudicating competing homology claims. While the issues pertaining to the target problem have received a good deal of attention in philosophy of biology, the evidence problem has been neither raised nor resolved. In this paper, I show a way forward by developing evidential criteria of homology and an evidential constraint on homology claims. I then apply these criteria to the case of human anger and animal aggression to make it clear how hypothesis testing can proceed.

In the following section, I say more about homology thinking. Homology thinking is a historical mode of thinking that explains similarities by appealing to common descent. To understand what kind of evidence supports homology, I point out a range of hypotheses with which it competes and set out the kind of evidence that favors homology over and above them. The operational criteria of homology (Remane 1971) can be understood as identifying similarities that provide evidence for homology over and above these competing hypotheses. When the criteria are used in this way, I refer to them as the *evidential criteria of homology*. In section 2, I briefly address the target problem. Then I show how the evidential criteria of homology apply to the case of human anger and the aggression systems of nonhuman animals. A straightforward application of the criteria provides stronger support for the ethological hypothesis. Basic human anger has several similarities with the confrontational behaviors of resident rats, which provide some evidence that these traits are a product of common ancestry. On the other hand, there is currently no evidence that the defensive

aggression system uniquely corresponds with human anger. The similarities identified by the neurophysiological hypothesis hold not only with anger but also with other human emotions, such as fear. I conclude by highlighting the value of cross-species comparison for specifying psychological kinds.

## 2. Homology and its Competitors

Though the concept of homology is crucial to evolutionary thinking, it was conceived in the service of biological taxonomy prior to Darwin's time. Owen (1846) thought of homology as the sameness of an organ or structure in different organisms under every *form* and *function*. A common example of homology is the skeletal anatomy of the vertebrate forelimbs. The radius and ulna are bone structures that are common to bats, chimps, giraffes and manatees even though their forms and functions are dramatically different among these animals (see Figure 1). They can be more or less dense, thicker or thinner, longer or shorter, (though their spatial relationship to other bones of the forearms are preserved) and they can contribute to the different functions of swimming, flying, running and grasping in different organisms. So the radius and ulna are the same traits that occur in different animals, even though they have widely varying forms and functions within these various animals.

Now that evolutionary thinking has been integrated into biological systematics, one prominent idea about homology is that homology is a causal-historical concept (see Ereshefsky 2012 for a clarification and defense of this claim). Specifically, a homology refers to traits of various animals that derive from a trait of a common ancestor. In this way, shared ancestry is the common cause of each homologue, and this common cause explains

similarities between the homologous traits. In the words of one biologist (with some help from Darwin), homology is "…grounded in 'descent, with modification,' a process that belongs to the past." (Rieppel 2005, 24)



**Figure 1. The bones of some mammalian forelimbs. The radius (green) and ulna (red) are the same kind of bone, which takes on different forms and functions in different animals.**

As a causal-historical concept, we can identify and refer to a homology without having or requiring detailed knowledge of the developmental and hereditary mechanisms that give rise to it, just as we can refer to a disease entity, such as measles or chicken pox, without knowing about its underlying causes (Putnam 1969). Nonetheless, we learn more about each homology as we learn more about its underlying causes, just as we learn more about chicken pox as we learn more about the virus that causes it.

Given the causal-historical nature of homology, there is a vast range of evidence that could bear on whether or not one trait is homologous to another. Some of the best evidence pertaining to homology comes from cladistics. If one has an independently established phylogenetic tree, one can look at the distribution of a candidate homology, or character, on that tree. If, for instance, the existence of a homology is more parsimonious than convergent evolution on one or more occasion, then there is a strong reason to think that a trait is homologous.

Nevertheless, before we can even look at the distribution of a character on a phylogenetic tree, we need to know how to identify the character in each taxon, which becomes a tricky matter when dealing with behavioral and psychological characters. For instance, knowing that humans have anger, that rats have a confrontation system, and that cats have a defensive aggression system does not determine which of these capacities are the *same* trait or character.

One way of addressing this problem is to use the operational criteria of homology. These criteria need not function as a definition of homology but instead we can use them to establish a consistent set of methods for ascertaining homologies and by extension, identical traits. The criteria of homology attempt to identify particular kinds of similarity, the kinds that are best explained by common history over and above a range of competing hypotheses. For any given similarity across clades, there are several hypotheses in competition with homology. One is that the similarity is only by chance. Another more probable possibility is that convergent evolution explains the correspondence. When a similarity is explained purely by convergent evolution, we have a clear case of analogy. Still another possibility in the

behavioral domain is that similarity is explained by plastic developmental processes, particularly learning. In the clearest cases of plasticity, similarity can be explained entirely by convergent learning or development, perhaps shaped largely by task demands or shared developmental mechanisms.[1] The main competition is thus between hypotheses of homology, analogy, and developmental plasticity. Insofar as they function as evidence, the criteria of homology should help pick out similarites between traits that are explained by common ancestry and not convergent evolution or plastic developmental processes.

The most prominent criteria for homology were developed by Adolf Remane (1971) and can be deployed for this purpose. Consider first the criterion of *position*. The criterion applies to the radius and ulna because even with different forms and functions across different organisms, they retain their relative position to other bones of vertebrate forelimbs (humerus and the bones of the wrist). It would be highly unlikely for these characters to have evolved de novo in each of the different animals that possess it and yet to have the same relative position to other structures. Moreover, there is no shared function across the different animals which possess this character that would explain the correspondence. While corresponding position sounds like a spatial property, it is actually topological, and can include corresponding positions in temporal sequence or corresponding positions across cognitive architectures (e.g. "boxologies").

The criterion of *special quality* concerns "…shared features [that] cannot be explained by the role of a part in the life of the organism. The fact that in the vertebrate eye the blood supply to the retina lies between the retina and the source of light is a famous

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[1] See Brown (2013) for a detailed discussion of the difficulties (e.g. due to the plasticity and transformability of behavior) in applying the criteria of homology to behavior.

example of a 'special quality'." (Griffiths 2007, 648) The more complex a shared quality is, the less likely that they would have evolved independently. The location of blood supply to the vertebrate retina is both complex and non-essential (and even slightly counterproductive) given the functional role of the retina (what it is used for in the organism), so it identifies a correspondence that provides strong evidence that the various instances of this character derive from common descent.

Finally, the criterion of *intermediate forms* allows identification of homologous forms, A and C, because of the existence of one or more transitional states, $B_1...B_n$, between the two forms. In many cases, the homology between transitional forms, say between A and $B_1$ or between $B_1$ and $B_2$, is determined by applying the other two criteria. For instance, there are transition states between the bones of the mammalian inner ear and the bones of the reptilian jaw. We know this because the bones of the reptilian jaw share the same *position* (relative to other bones of the jaw) as the bones of several intermediate forms, some of which share the same position as the bones of the mammalian inner ear.

For my purposes, an important constraint on homology claims derives from the fact that some homologies are nested within other homologies. For instance, the class of tetrapod forelimbs is nested within the class of paired appendages. Thus, the forelimbs of reptiles, amphibians, mammals and avians are members of the homology class of tetrapod forelimbs, but they are also members of the more inclusive homology class of paired appendages, which also includes the pectoral fins of sharks and teleosts. While pectoral fins are homologous with instances of tetrapod forelimbs *as paired appendages*, the similarities between pectoral fins and tetrapod forelimbs do not provide evidence for homology at the less inclusive level

of tetrapod forelimbs. Inclusion in this more specific class is indicated by bone structures that are absent in pectoral fins. These structures are due to modifications that occured subsequent to the divergence of tetrapods from teleosts, and that is why teleost pectoral fins are not included in this homology class.

As a result, some similarities only indicate inclusion in a broader homology class (e.g. paired appendages), whereas other similarities indicate inclusion in narrower homology classes (e.g. tetrapod forelimbs). In other words, some similarities (e.g. those between pectoral fins and forelimbs) only provide *evidence* for inclusion in broader homology classes (e.g. paired appendages rather than tetrapod forelimbs). It follows that, when evaluating similarities between traits, it is sometimes necessary to consider which homology class a similarity indicates.

From these considerations, we can derive an evidential constraint on homology claims. To see this, consider the correspondences between a human forelimb and a feline *hind limb*. The criterion of position is satisfied, because there are similarities between the parts (e.g. between humerus and femur). There *are* relations of homology between these traits. They are homologous as mammalian extremities and tetrapod extremities. Nevertheless, if we were to specify the homology class as one that includes human forelimbs but excludes human hind limbs, the similarity in question does not provide evidence for homology at this level.[2] This is because there are no similarities between the human forelimb and cat hind limb that *are not also shared between the human forelimb and hind limb*. Thus, to provide evidence for relations of homology at the level of some homology class G (in this

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[2] For similar reasons, we also do not have evidence here for a relation of homology that would include feline hindlimbs but not feline forelimbs.

case, the homology class that includes forelimbs but excludes hindlimbs) *as opposed to the more inclusive class,* H (in this case, homology classes that includes forelimbs and hindlimbs), requires that some similarities between relata are not shared by traits in the more inclusive class, H. I call this an "evidential constraint" on homology claims.

While the examples so far deal straightforwardly with morphology or body structure, all three of Remane's criteria have also been applied to behavioral and psychological traits by ethologists (for overviews, see Ereshefsky 2007; Wenzel 1992). I suspect that what seems obvious concerning morphology might be easily confused concerning behavior or psychology. As a result, one could find evidence that psychological traits are homologous, but misidentify the homology class that this evidence supports. One way of doing so is to violate the evidential constraint above. I will argue that the neurophysiological hypothesis is an instance of this mistake. As yet, there is no evidence that the defensive aggression system identified by neurophysiological research is a member of the homology class that includes anger but excludes other human emotions. This is because the hypothesis does not identify any similarities that are not shared with other human emotions. I spell out the details of this argument in the following section.

In summary, homology is a causal-historical concept, and homology thinking is a way of providing historical explanations for observed similarities between biological traits (or characters). The evidential criteria for homology can isolate evidence pertaining to this kind of historical explanation. In the following section, I show how the evidential criteria can discriminate between the two hypotheses laid out in section 2.

### 3. Which Kinds of Aggression are Manifestations of Anger?

Before I apply the criteria to the two comparative hypotheses, I will first say something about the target problem, the problem of specifying the psychological trait that is the target of comparison. For the sake of space, I assume that the appropriate target of the ethological and neurophysiological hypotheses is *basic human anger*, the cluster of properties associated with involuntary facial expressions of human anger (Ekman 1999; Griffiths 1997). To briefly defend this choice, this is the most closely studied set of "anger" phenomena the structure of which is likely explained by inheritance, therefore it is the most plausible target for homology claims. This is because homology claims identify traits across taxa that are inherited from a common ancestor. One might say that inheritance is one of the causal homeostatic mechanisms that preserve the structure of homologous traits across lineages (cf. Assis and Brigandt 2009; Brigandt 2009). Thus, if there is something like anger in non-human animals, then it is most likely to correspond with phenomena in humans that are explainable by inheritance, namely basic human anger.

Now we are in a position to evaluate the two hypotheses. Recall that the two hypotheses focus on different sets of phenomena. The ethological hypothesis focuses on patterns of confrontational behavior of territory-holding, "resident" rats, whereas the neurophysiological hypothesis focuses on patterns of defensive behavior elicited by electrical brain stimulation. The ethological hypothesis lumps its phenomena together according to contrasting motives of behavior (confrontation versus defense), whereas the neurophysiological hypothesis lumps its phenomena together according to dissociable neural

substrates of behavior (regions of the hypothalamus that elicit defense behavior versus distinct regions that elicit predation behavior).

First, consider the ethological hypothesis. The strongest pieces of evidence for homology is a special quality that is shared by rats and stumptail macaques. Adams and Shoel (1981) note that dominant macaques and resident rats both implement strategies aimed at accessing the back and biting it. In macaques, this behavior seems arbitrary with respect to the (probable) function of inflicting non-lethal damage on the subordinate. Macaques have a much larger repertoire of bodily movements than rats, many of which could serve the function of inflicting non-lethal harm (pushing, kicking, scratching, slapping, holding etc.). Thus, back-biting is a *special quality*, and the best explanation of this behavior may appeal to products of common ancestry. In other words, the reason that the attacks of both rats and macaques are aimed at biting the neck and back may be that they share a common ancestor with a corresponding aggressive strategy and perhaps similar motivational mechanisms for negotiating intraspecific conflict.[3] There is some evidence that human anger includes an impulse to approach and attack, but no one has demonstrated that the impulse is pan-cultural or species-typical.[4]

While Adams and Schoel did observe several facial expressions of subordinate macaques, they did not note any facial expressions that uniquely accompanied the attacks of a dominant macaque. However, in more ecologically valid studies of macaque behavior, macaques with higher dominance status do display facial expressions toward lower ranking

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[3] Adams and Schoel argue for homology by considering similarity in the dynamic of attack and submission across both species.

[4] See e.g. Carver and Harmon-Jones (2009); Baron (1971); Berkowitz et al (1981); and Pedersen et al (2011).

macaques in aggressive encounters, expressions that resemble anger expressions in humans (Chevalier-Skolnikoff 1974).[5] Chevalier-Skolnikoff (1973) argues that two of these expressions are similar (utilizing homologous action units) across macaques, chimps, and humans. Some confirmation of these comparisons has been attained by comparison using a facial action coding system to quantify chimpanzee facial expressions (Parr et al. 2007). Thus, there is *continuity across the intermediates* for some components of putative aggression systems across the common ancestors of these species.

Now consider the neurophysiological hypothesis. The problem is that the case for homology is incomplete. First, there is some evidence for correspondence that has *continuity across intermediates*: stimulation of the hypothalamus of cats, possums, rats and marmoset monkeys leads to similar forms of attack (Roberts, Steinberg, and Means 1967; Bergquist 1970; Panksepp 1971; Woodworth 1971; cited in Lipp and Hunsperger 1978).[6] However, ethical and practical considerations make it nearly impossible to obtain evidence concerning the effects of hypothalamus stimulation in humans. It remains uncertain whether it would leads to attack or to any of the other concomitants of human anger (e.g. experiences of anger, facial expressions of anger, or physiological changes associated with anger, as distinct from fear). Nor have any of these studies observed distinctive facial expressions that indicate continuity with human anger.[7]

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[5] Chevalier-Skolnikoff calls these expressions "stare", "round-mouthed stare" and "open-mouthed stare".
[6] Delgado (1968) produced aggressive behaviors with electrical stimulation of the thalamus and cerebellum of chimpanzees and macaques. However, these brain structures are notably absent from the neurophysiological hypothesis and its descriptions of brain structures involved in aggression. Moreover, Delgado and colleagues did evaluate facial expressions. However, these facial expressions were not analyzed.
[7] It is compelling that in macaques, stimulation only results in attack under certain conditions (Alexander and Perachio 1973), some of which depend on whether the electrical stimulation occurs in the presence of a higher or lower ranking conspecific (attack being more likely in the latter case). Nevertheless, one cannot conclude from

There is some evidence that amygdala stimulation can produce feelings of anger (e.g. Hitchcock and Cairns 1973). This evidence is even bolstered by the fact that stimulation of the medial amygdala in cats can potentiate defensive behaviors elicited by electrical stimulation of the hypothalamus (e.g. Shaikh, Steinberg, and Siegel 1993). However, several other emotional experiences beside anger have also been reported as a result of amygdala stimulation in humans, including anxiety, guilt, embarrassment, jealousy, and a "desire for flight or escape" (which is more strongly associated with human fear, see Frijda, Kuipers, and ter Schure 1989). It seems that current evidence does not support a distinct localization of anger-like and fear-like feelings or behaviors within the HAA or in the other brain structures that make up the defensive aggression system (in cats or otherwise). Thus, the evidence from brain stimulation does not reveal a unique correspondence with human anger; one that is not also shared with other human emotions.

Second, consider the criterion of position. As with the offensive attack observed in ethological work, physiological arousal and threat signals do occur prior to defensive attacks elicited by electrical brain stimulation. However, no evidence has been presented that either the signals or physiological arousal involved in these attacks are homologous with these

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this that this form of aggression is of a piece with the aggressive syndrome which includes angry facial expression. It is quite possible that there are several forms of impulsive aggression that an animal might inflict only upon lower ranking conspecifics, including pain induced aggression, fear induced aggression or perhaps even disgust induced aggression. Neither is it obvious that any of these forms of aggression are of the same kind as angry aggression. By contrast, the work of Adams and Schoel (1981), and Chevalier-Skolnikoff (1973) describes a certain kind of offensive or dominance-related aggression *with which angry facial expressions are associated.* The same is not true of aggression elicited by electrical brain stimulation. The connection with angry facial expressions has not been made, nor has the behavioral syndrome been carefully circumscribed in ecologically valid conditions in most of the organisms in which it has been observed. Leyhausen (1979) has done this work concerning defensive aggression in cats, but he distinguishes this form of aggression from an offensive form of aggression that includes a back-biting attack. I suspect that this latter form of aggression is more comparable to the confrontation system in rats (cf. Blanchard and Blanchard 1984).

components of human anger as opposed to human fear. Moreover, it seems unlikely that any such evidence will materialize.

This becomes apparent when we look closely at the work of Siegel and others on the HAA, which is cited as support for the neurophysiological hypothesis (Panksepp 1998, 2012). In fact, Siegel does not advocate the neurophysiological hypothesis, and in many cases makes claims that constitute evidence against it. In several places (including Siegel 2004) Siegel compares defensive behaviors with a disorder known as Episodic Discontrol, which is marked by "...decreased impulse control – a characteristic common to defensive behavior – and altered perceptual states following stimuli evoking *anger, fear or rage*." (Siegel and Victoroff 2009, 213 emphasis mine) Indeed, many of the similarities that are noted between defensive behaviors and these forms of human aggression are characteristics of affectively driven behavior in general. Impulsivity is a characteristic of many kinds of emotion expression (see e.g. Frijda 1986), including fear, anger, sadness, and joy. Thus, the position criterion is not satisfied in a way that provides evidence for a homology between the defensive aggression system and anger that is not also shared between human anger and human fear.

By contrast, manifestations of the confrontation and avoidance systems in rats can be distinguished by quantifiable differences in the facial expressions of residents and intruders (Defensor et al. 2012), just as manifestations of anger and fear in humans can be distinguished by their distinctive facial expressions (e.g. Ekman and Friesen 1971). Moreover, resident and intruder rats have distinct forms of attack with distinct target sites. Thus, it is possible to distinguish *within rats* at least two different patterns of impulsive

behaviors accompanied by distinct facial expressions. Moreover, some of the similarities between confrontation behaviors and angry behaviors in humans are not shared with fearful behaviors in humans or avoidance behaviors in rats. In other words, human anger and the confrontation system in rats do not violate the evidential constraint on homology claims (relativized to a homology class that only includes the emotion of anger) because they satisfy the evidential criteria of homology in ways that are not also satisfied by other emotions like fear. A related virtue of the ethological hypothesis is that it can distinguish angry aggression from the widely acknowledged category of *fear-induced* aggression (see esp. Moyer 1976). The same cannot be said for the neurophysiological hypothesis. I suspect that at least some of the phenomena identified by the neurophysiological hypothesis reflect behavioral outcomes of fear, rather than (or perhaps in addition to) anger.

In sum, the case for homology between the defensive aggression system and anger (with respect to a category that includes anger but not other human emotions) may be similar to the case for homology between the cat hind limb and the human forelimb (with respect to a category that includes human forelimbs but not human hind limbs). The similarities so far observed do not evince a homology relation that excludes other emotions (especially fear), whereas the case for homology between the offensive attack system and anger does evince such a relation.

### 4. Conclusion

I have argued that the available evidence supports a homology between human anger and the confrontational attack system and not between human anger and the defensive

aggression system. However, this case study has larger implications for the scientific study of psychological kinds. The lesson is this: homology thinking can provide independent criteria for evaluating substantive disagreements on – and for eliminating confusion about – the nature of psychological kinds. In absence of homology thinking, it is difficult to see how further knowledge about the defensive aggression system or the offensive attack system would serve to determine which aggression systems in non-human animals are most like human anger. Indeed, this is probably one of the reasons why there has been little productive discussion between the advocates of the two hypotheses. Homology thinking in this case provides a set of independent theoretical constraints for identifying corresponding traits across taxa. In the service of this demonstration, I further developed some of the methods of homology thinking (Ereshefsky, 2007, 2012) as it applies to psychological kinds. This account helps to specify what kind of evidence supports homology claims, namely, identification of *unique* correspondences *at the appropriate level* between traits; correspondences that provide evidence for common ancestry as opposed to common selective pressures (whether developmental or ancestral).

Though counterintuitive from some perspectives, the concept of homology helps to clarify what counts as evidence for claims of trait identity. Note that identical traits can have different states. For example, a human arm and whale fin are identical traits, because they are both instances of the tetrapod forelimb. Nevertheless, they are different states of that trait, because they represent different forms that this trait can take. Homology thinking allows the identification of traits that take shape in dramatically different states; it enables us to identify evolved characters that walk in the guise of dramatically different forms and functions.

Anger is one such character.

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