# The Evolution of Empathy

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**Abstract**

Empathy—the ability to feel what another organisms feels, because that other organism feels it—is a trait that is widespread in the animal kingdom. As I make clearer in this chapter, it is plausible (though further work is needed to confirm this) that there are two distinct sources of selective pressures that led to the evolution of this trait. First, empathy can facilitate cooperation, which, in turn, can be highly adaptive (e.g. when it comes to helping offspring). However, it furthermore turns out that this cooperative empathy can be altruistically or egoistically constituted. Second, empathy can facilitate fast responding to environmental contingencies (such as predatory attacks). Considering these adaptive pressures on the evolution of empathy is useful, as they have several further implications: they provide a partial explanation for why empathy is so widely instantiated, they suggest that empathy can be inter-specific, they suggest that empathy is biased towards certain types of organisms, and they give partial support to the suggestion that empathy has less moral importance than is often supposed.

**Keywords**: empathy, evolution, altruism, egoism, cooperation, emotional contagion

# The Evolution of Empathy

There is no doubt that humans frequently empathize (though exactly how often they do so is a matter of some controversy—see e.g. Hatfield & Rapson, 1994; Hoffman, 2000; Prinz, 2011). There is also increasingly little doubt that other species do so, too: in particular, chimpanzees have been shown to display empathetic reactions (see e.g. de Waal, 2008), and something similar seems to hold for dogs (Custance & Mayer, 2012), dolphins (Frohoff, 2013), and elephants (Hakeem et al., 2009; Plotnik et al., 2006). These facts raise the question of why the ability to empathize evolved: what evolutionary pressures brought it about that the ability to empathize spread through a number of different populations of organism? In what follows, I provide a partial answer to this question.

In particular, the goal in what follows is twofold. First, I outline some of the major factors that are likely to have influenced the evolution of empathy. Second, I show why knowing something about the reasons for which the ability to empathize has evolved is useful for answering various further questions concerning this ability.

This entry is structured as follows. In section I, I make clearer what I understand by empathy, and consider some methodological issues surrounding the evolutionary biological investigation of this trait. In section II, I then lay out the major driving force that is commonly thought to underlie the evolution of empathy: namely, the facilitation of cooperation. After that, in section IV, I present another, less commonly discussed, factor that likely influenced the evolution of empathy: namely, the facilitation of the generation of non-cooperatively adaptive behavioral responses to the environment. In section V, I

consider some implications of these evolutionary biological points for the discussion surrounding the nature and moral importance of empathy. I conclude in section VI.

## I. What is Empathy and How Can It Be Evolutionary Biologically Studied?

In what follows, I take empathy to be a kind of "emotional mirroring": more specifically, organism A can be said to empathize with organism B to the extent that, upon obtaining evidence that B is feeling some emotion E, A is disposed to feel that same emotion E (Hatfield & Rapson, 1994; Hoffman, 2000; Prinz, 2011). Three points are important to note about this way of understanding empathy.

First, the view of empathy at stake here presupposes that organism B outwardly displays cues as to its emotional state. This is necessary, as only if B displays these cues is it possible for another organism A to react to B's emotional state by mirroring it. In the background here is the idea that cases of empathy should not be confused with situations in which two organisms just happen to share an emotion; rather, genuine empathizing is the *effect* of the fact that some other organism is in a relevant emotional state. Note further that this assumption of the presence of outward signs of an emotion that can be detected by other organisms is not guaranteed to be met in all populations of organisms. However, empirically, it does frequently seem to hold (Sauter et al., 2010; Ekman & Rosenberg, 1997; Prinz, 2007). For this reason, I will simply accept it here—i.e. the rest of the discussion should be seen to be restricted to populations in which this prerequisite to the evolution of empathy has already evolved. (It is possible that outward displays of cues pertaining to the emotional state of an organism coevolved with the ability to

empathize. While raising some interesting issues, nothing in this chapter hangs on this, so I will not discuss it further here.)

Second, empathy as understood here involves more than just representing that another organism is in some emotional state: it involves actually being in that same state. Put differently: empathy goes beyond having a theory of another's mental states by requiring that the empathizer undergoes these mental states itself (for more on this, see e.g. Goldman, 2006; Schulz, 2011a). Relatedly, note that this view of empathy contrasts with *sympathy*—cases where an organism represents another organism as feeling some sort of (typically negative) emotion, and reacting accordingly (Prinz, 2011; Darwall, 1998). Unlike sympathy, empathy concerns cases where the same emotion—fear, disgust, joy, etc.—is *mirrored* in different organisms.

Third and finally, I here assume that a key adaptive function of many emotional reactions is to guide and initiate appropriate behavioral responses to the world. Put differently, I here assume that a key reason for why some emotions (like pain, fear, anger, or joy) have evolved is that they are highly adaptive as triggers for important behaviors—such as repair of damage, fleeing, fighting, grooming, etc. Note that I do not assume that this is true for all emotions, or that this is the only reason for why certain emotions have evolved; the claim is just that a key reason for why some emotions have evolved is that they enable the organism to better engage in adaptively appropriate behaviors. In this weak form, this is an assumption that is widely shared (Stich et al., 2010; Prinz, 2007)

Given all of this, then, the question to be answered here can be more precisely formulated as follows: why would an ability to feel what another organism feels—because this other organism feels it—spread and be maintained in a population of

organisms? Before considering two different ways in which this evolutionary psychological question can be answered, it is useful to make two methodological remarks.

First, it needs to be acknowledged that evolutionary psychology, in general, is hard to do well (Richardson, 2007; Buller, 2005). In particular, for a full account of the evolution of any trait, we would need to know—at least—the ancestral state of this trait, the extent to which it is heritable, the size and origin of the relevant selection pressures on it, the extent to which it was variable (i.e. which alternatives existed in the population), and the size and structure of the population in question (Richardson, 2007; Brandon, 1990). Needless to say, this knowledge is hard to obtain even in the best of cases—and likely to be even harder for psychological traits like the ability to empathize, whose exact distribution on the phylogenetic tree is unclear, which do not fossilize, and whose genetic basis is not well understood.

However, this should not be taken to mean that asking about the evolutionary pressures on a trait like empathy is completely valueless (as has been suggested by Lewontin, 1998; Richardson, 2007). Rather, such an analysis can be seen to provide a partial account of what drove the evolution of the trait in question (Schulz, 2011a, 2011b, 2013). Put differently, if built on sufficiently well grounded foundations, such an analysis can provide evidence— a reason—to think that a given trait evolved for a given set of reasons: while more work might be needed to fully confirm this account, this does not mean that, until this is the case, the account is completely epistemically worthless. Rather, such an account can provide a description of *some* of the major pressures on the evolution of the trait in question. As I try to make clearer in what follows, I think this is

true when it comes to empathy: that is, I think that it is possible to provide reasonably well-grounded partial accounts of some of the major evolutionary pressures that have shaped this trait.

Second, in what follows, I focus in particular on *selective* accounts of the evolution of empathy. There are two reasons for why this is plausible. On the one hand—and as will also be made clearer momentarily—it is plausible that the selective pressures on empathizing are, in some contexts, very large. This suggests that natural selection is less likely to be easily swamped by other evolutionary factors in these contexts (Gillespie, 1998). On the other hand, empathizing is a relatively complex trait: it requires a sophisticated coordination between an organism's sensory systems—which need to detect which emotions another organism is feeling—and its emotional systems—which need to be disposed to mirror the detected emotions. This is important, as it is reasonable to think that, for complex traits like this, a selective explanation has a particularly high initial plausibility (Dawkins, 1986; Godfrey-Smith, 2001; Sterelny, 2003). With this is mind, consider the major account of the evolution of empathy in the literature: the idea that empathizing can facilitate cooperation.

## II. Cooperative Selective Pressures on the Evolution of Empathy

One of the major and most widely accepted accounts of the evolution of empathy is based on the thought that empathy evolved to facilitate cooperation (de Waal, 2008; Churchland, 2011; Acebo & Thoman, 1995; Bowlby, 1958; MacLean, 1985). More specifically, the core idea behind this account can be set out as follows.

Assume that it is adaptive for organism A to cooperate with organism B: for example, assume that B is A's offspring, or that cooperating with B enables A to reclaim that help in the future when it (i.e. A) is in need of help. (I return to the adaptiveness of this and other kinds of cooperation momentarily). Given this, emotional mirroring between A and B can make it easier for this cooperation to come about. In particular, the fact that the helping organism and the one in need of help share the same emotional state can make the need for help more salient to the helping organism.

More specifically, empathizing can make it more likely that a given organism provides (by assumption adaptive) help to another organism, as the helping organism does not just represent the other organism as in need of help—it *feels* the need for help. Given the fact (noted earlier) that many emotional states are known to be closely connected to certain behavioral outcomes, this thus makes it more likely that the helping organism will in fact cooperate with the organism in need (Damasio, 1994; Prinz, 2007). Put differently, the fact that organism A literally *feels* B's need for help plausibly functions as a reliable trigger for A to in fact help B.

In short: on this account, we should see empathy as a tool that has evolved so as to aid in the reliable establishment of cooperative interactions. Two further points about this account of the evolution of empathy need to be noted.

First, as should be quite obvious, this account of the evolution of empathy is tied to the evolution of cooperation: on this picture, empathizing is only adaptive when cooperating is, too. Fortunately, there are a number of cases where the latter is true—in fact, cooperation can be *highly* adaptive in some contexts. One of the most straightforward examples of this sort of situation concerns parent-offspring interactions: for many

organisms, it is true that their own fitness is inextricably linked to that of their offspring (Sober, 2001; but see also Trivers, 1974). Indeed, parent-offspring can make for the major adaptive pressures for both members of the interaction (see e.g. Thometz et al., 2014). However, while this is one of the major cases in which cooperation—and thus, empathy—can be highly adaptive, it is not the only case: other examples include interactions among kin more generally (Griffin et al., 2004; Gardner & West, 2010; Griffin & West, 2002), reciprocal helping interactions (see e.g. Sachs et al., 2004; Carter & Wilkinson, 2013; Skyrms, 1996, 2004), and membership in cooperative groups (Sober & Wilson, 1998)—all of which can also provide major adaptive advantages to an organism (Sachs et al., 2004; Skyrms, 1996, 2004).

That said, it also needs to be acknowledged that, in many situations, the benefits from cooperation are small or cooperation is unlikely to evolve for other reasons (such as the fact that it has very demanding psychological or other prerequisites—see e.g. Hammerstein, 2003). For this reason, the evolution of empathy needs to be seen to be inherently limited on this account: in particular, the tether to the evolution of cooperation implies that, on this account, empathy will not be adaptive in all populations all of the time. This is important to note for what follows below.

The second point worth noting concerning this account of the evolution of empathy is that the latter is compatible with a number of different theories concerning the psychological role of empathy in the generation of helping behavior. To see this, note that, in general, organisms that are committed to cooperating with other organisms can be either altruists or egoists. (It is also possible that organisms cooperate for reasons that are neither altruistic nor egoistic; however, this is not so relevant here. See also Schulz,

2016.) Altruistic cooperators are organisms whose help is directly driven by concerns for the other organism (Sober & Wilson, 1998; Stich et al., 2010): psychologically, they cooperate because they aim to help the organism in need—while this help may also favor themselves biologically, this is not the psychological reason for their helping. By contrast, egoistic cooperators are organisms that help precisely because they think that helping is in their own best interest. This is important to note, as empathetic organisms, too, can be either psychological altruists or egoists.

To see this, note that an organism A will be altruistically empathetic if the mirrored emotion that drives its helping behavior makes a standing desire to help B more salient or directive—without though altering the content of that desire (see also de Waal, 2008). In turn, this implies that, for altruistic helpers, empathizing is adaptive for making the commitment to help *more vivid or clearer*. Organisms are bound to have many commitments (including to themselves) and thus need to be able to decide which of these commitments to act on in a given situation. Here, an empathetic emphasis on the commitment to help can be highly useful in ensuring that the organism acts on this—by assumption—adaptive commitment. Put differently, empathizing can be useful for psychological altruists, as, by *emphasizing* their existing disposition to help B, it makes them more reliable in their helping behavior.

However, an organism A can also be egoistically empathetic. This will be so if it is the tokening of the mirrored emotion in A itself that drives the helping behavior: here, an organism helps another organism only to alleviate its own emotional state. So, if A helps B because (a) the perception of sadness on B's face makes A feel sad as well, (b) A is driven to reduce its own feelings of sadness, and (c) A thinks that the best way to reduce

its own feeling of sadness is to make B happy, then A is an egoistic helper. In turn, this implies that, for psychological egoists, empathizing is adaptive, not for emphasizing an existing disposition to help, but for ensuring that they *in fact engage in* the—by assumption—adaptive helping behavior. Put differently: empathizing can be useful for egoistic helpers as, by *generating* a disposition to help B, it makes them more reliable in their helping behavior. (Note that while here is some controversy over whether we should expect the egoistic solution to be less reliable at motivating cooperative behavior than the altruistic one—see Sober & Wilson, 1998; Stich et al., 2010; Schulz, 2011b; 2016—for present purposes, it is not necessary to discuss this further: what matters here is not the question of whether altruism is more reliable at causing cooperative behavior than egoism, but rather whether empathetic egoism is more reliable than non-empathetic egoism.)

Summing up, therefore: the key idea of the cooperative account of the evolution of empathy is that empathy is a tool to altruistically or egoistically facilitate the generation and maintenance of cooperative behavior. However, there is also another quite different—non-cooperative—perspective on the evolution of empathy. Bringing this out is the aim of the next section.

## III. Non-Cooperative Selective Pressures on the Evolution of Empathy

The non-cooperative perspective on the evolution of empathy focuses on the fact that emotional mirroring can be beneficial even in non-cooperative settings, provided that there is a correlation between the biological advantageousness of one organism feeling a

particular emotion and another organism doing so. In a bit more detail, the core idea behind this account can be laid out as follows.

Assume that two organisms A and B live in close spatial proximity—perhaps because they are members of a large herd of zebras, or because they are members of a small family of chimpanzees. Further, assume that the organisms are often subject to a kind of collective attack: a predator charges both A and B (and perhaps the rest of the herd or family group as well), and tries to grab whoever it can reach. Finally, assume that flight responses in these organisms are at least sometimes mediated by emotional states—for example, assume that the organisms flee when becoming afraid, nervous, panicked, or anxious.

If these emotional reactions come with distinctive outer signs (as is assumed here), it can then be adaptive for A to react with fear to the sight of B's fear: for if B is afraid, there is good reason that a predator is near—which also is a good reason for A to be afraid (even if A has not yet spotted this predator). In turn, this is due to the fact that reacting with fear to B's fear gives A valuable time to initiate its own fleeing behavior: it does not have to wait until it has spotted the predator, but can engage in flight nearly simultaneously with those organisms that have spotted the predator. Here, then, empathy evolves not as a tool to enable cooperation, but as a way to exploit correlations in the adaptive behaviors of different organisms: if it is adaptive for A to feel X, then it is often also adaptive for B to feel X, simply because A and B are subject to the same sorts of environmental contingencies. (In fact, one could see this case of empathy as a special case of the evolution of signaling more generally: see e.g. Skyrms, 2010.) Three further remarks about this account of the evolution of empathy are useful to make here.

First, it is important to realize that, also in this context, the ability to empathize can allow for major adaptive advantages. As suggested in the above example of the predator attack, given that even a fraction of second's delay in responding to an attack can make the difference between escaping unharmed and being majorly injured or even killed, the time savings brought about by empathizing can be adaptively highly important. Moreover, this fleeing-focused case is not the only sort of case that makes non-cooperative empathizing adaptive. For example, it can be adaptive for a bird to react with excitement upon observing the excitement of another bird, as this can lead to faster generation of "mobbing" behavior—which can be highly adaptive (Hurd, 1996). Similarly, it can be adaptive to react with anger to the detection of anger in another organism: this can ready an organism for fighting behavior, which again can prevent major injury or death and can even lead to significant gains (e.g. in interspecific fights to gain access to mates: Plavcan & van Schaik, 1992; Fessler, 2010; Campbell, 2004). In short: since, for many animals, time is often of the essence, mirroring others' emotional states can be highly advantageous.

Second, note that it is plausible to think that this route towards the evolution of empathy is instantiated in quite different circumstances than the one based on cooperation. As noted earlier, the adaptiveness of cooperation—and thus, of cooperation-focused empathy—depends on the fact that a narrow set of particular conditions obtains. Here, by contrast, empathy is adaptive even if these conditions do not obtain (i.e. even if the organisms in question are not cooperative). However, this is does not mean that there are no restrictions on the adaptiveness of empathy in non-cooperative settings whatsoever. In particular, as also noted earlier, for empathy to be adaptive on this

account, a strong correlation in adaptive responses across individuals is needed. This, though, will not be the case in all contexts either. For example, if organisms are differentially robust, so that the dangers posed to them by predatory attacks are differentially great, then it is less adaptive for some of these organisms to be empathetic: there is little reason for A to be afraid when B is afraid if the sources of B's fear generally pose little thread to A. This is important, as it might be true across generations: for many organisms, it is true that, much of what infants are adaptively afraid of (say) is not something that adults need to be afraid of (e.g. as the two groups are very differently physically robust). If so, though, then on the present account, we would not expect there to be much empathy across generations (though we might do so on the cooperative account).

Third and finally, on the present account of empathy, the direct adaptiveness of empathy is restricted to emotions signaling environmental conditions to which a speedy reaction is adaptive—emotions such as fear, anger, panic, anxiety, or excitement. This implies that, at least on the face of it, this account does not predict empathizing when it comes to emotions like joy or sadness: there is little to be gained for organism A to react to organism B's joy with joy (other than perhaps a few extra seconds of joy), and, similarly, there is little to be gained for organism A to react to organism B's sadness with sadness. Put differently: since empathy, on the present account, is adaptive because it mediates faster adaptive behavioral responses, it follows that in situations where fast adaptive responses are not required, empathy is not required either. Of course, it is possible that, for neurological or other reasons, organisms need to either be empathetic for all emotions or for none, so that an emotional specificity in empathizing cannot

evolve. Still, it remains true that the situation here contrasts with the one at the heart of the cooperative account: there, the speed with which a behavioral response needs to be decided on is not greatly important to the adaptiveness of empathy, thus widening the range of emotions for which empathizing is directly adaptive. For non-cooperatively-driven empathizing, by contrast, there are such decision making speed constraints, so that empathizing is more narrowly adaptive only.

All in all, therefore: on the non-cooperative account of the evolution of empathy, empathy is adaptive for allowing organisms to react more quickly to time-sensitive environmental conditions. Instead of just reacting to the detection of the threat itself with the appropriate emotional state, empathetic organisms can react to the effects of this detection in other organisms—i.e. the outward display of their emotional states.

## IV. Implications

There is no doubt that an understanding of the evolution of empathy is interesting in its own right: as noted above, the ability to empathize is a complex and relatively widespread trait about which we want to know more—and the reasons for its evolution are part of this. However, considering the above accounts of the evolution of empathy is important beyond this. This is due to the fact that these accounts have several implications that should be taken into account when developing a general theory of empathy.

First, considering the two accounts of the evolution of empathy—the cooperative and the non-cooperative one—together suggests that many organisms might find some form empathy adaptive. This comes out clearly from noting that these two accounts are

complementary to each other: a number of the cases in which the cooperative account does not apply (e.g. because they do not feature the adaptiveness of cooperation) are cases where empathy is adaptive for non-cooperative reasons—and the reverse. For example, while direct cooperation might not be adaptive in a herd of zebras, non-cooperative forms of empathy might be quite adaptive there, and while non-cooperative forms of empathy might not be adaptive across generations, cooperative ones might be. Of course, this does not mean that empathizing is always adaptive: even together, the two accounts do not cover all cases, as there are situations that feature neither adaptive cooperative interactions nor the needed correlations in time-sensitive responses to the environment. However, it does mean that empathizing is relatively frequently adaptive. This is important to note, as it provides a part of the explanation of why empathizing is widespread in the biological world: in fact, given the frequent adaptiveness of empathy, the two accounts of the evolution of empathy laid out above predict that future investigations will find evidence for empathetic abilities in even more species than what has been true thus far.

Second, both of these accounts suggest that empathy can reach across species boundaries—as long as the different organisms share similar enough emotional states so that some kind of emotional mirroring is possible. For example, since interspecies cooperation—e.g. in cases of mutualism—can be adaptive, it can also be adaptive for an organism of one species to empathize with an organism of another. Similarly, since different types of organisms often live in close spatial proximity, their adaptive responses can be correlated—again making empathizing adaptive. So, for example, it can be

adaptive for a zebra to react with a given emotion—fear, say—if it sees a nearby wildebeest feel a closely related emotion—the Wildebeest equivalent of zebra fear, say.

That said, it is also true that, third, both of the above accounts of the evolution of empathy support the idea that empathy is likely to be biased towards certain organisms. Specifically, organisms are more likely to empathize with others (a) that they are in cooperative relationships with, or (b) whose behavioral responses to the environment are sensitive to the same sort of factors that their own behavioral responses are sensitive to. In turn, this suggests that organisms (humans included) are unlikely to empathize well with organisms that live in distant places or times—which both makes cooperation harder and implies that the correlation in behavioral responses to the environment is likely to be weak—or which are removed from them in other ways—e.g. socially. This turns out to be empirically very plausible (de Vignemont & Singer, 2006; Langford et al., 2006; Singer et al., 2006; Lanzetta & Englis, 1989; Preston & de Waal, 2002).

Fourth, the above accounts of the evolution of empathy also bring out that, in many cases, empathy need not lead to or be based on psychological altruism, but can be inherently selfish (this thus contradicts the conclusion in de Waal, 2008). That is, empathizing organisms should not necessarily be thought to be altruists, since the reasons for why empathizing might have evolved need not have been to support existing altruistic desires. Instead, they might have evolved to support existing egoistic dispositions of one kind or another. Put differently: short of knowing more about the details of the conditions in which the ability to empathize has evolved—whether it concerned cooperative or non-cooperative situations, and if the former, what the particular nature of the disposition to

cooperate was like—knowing that an organism has the ability to empathize does not tell one anything about whether it is also an altruist.

These last two points—viz. the biased nature of empathy and its lack of an essential connection to altruism—are worthwhile to note also because they bring out a fifth implication of the above discussion. In particular, these two points make clear that the moral value of empathy is not straightforward to assess. More specifically, to the extent that morality is seen as something that is inherently unbiased and other-directed—a relatively common view of morality (see e.g. Gill, 2007)—the fact that empathy is likely to be biased in its target and not necessarily altruistically oriented implies that empathy is unlikely to make, at least by itself, a universally good foundation for morality. This matters, as this supports a conclusion that others have reached as well. For example, Prinz (2011) argues on the basis of a number of social psychological and philosophical results that empathy should not be seen as the cornerstone of morality. The present evolutionary biological perspective can thus be seen to give some further partial support for Prinz's conclusion: while it is possible that empathy is altruistically based, it is also possible—and indeed plausible—that it frequently is not.

## V. Conclusion

Empathy—i.e. the ability to mirror an emotional state upon detecting evidence of that emotional state in others—is a complex psychological trait whose evolution is likely to have been shaped by a number of different, though complementary, selective pressures. In particular, empathizing can facilitate the generation and maintenance of altruistic or egoistic cooperative interactions, and it can aid organisms in streamlining their behavioral

responses to the environment by seeing the outward signs of others' emotional states as signals of the appropriate behaviors to engage in for themselves. While these points cannot be considered as having provided a complete and fully corroborated account of the evolution of empathy, they do provide a partial account of this evolution that is evidentially reasonably well grounded.

Apart from its inherent interest, this picture of the evolution of empathy is also worthwhile for its implications for a number of other issues. In particular, this picture suggests that (i) empathy is a trait that is likely to be relatively widespread among many different kinds of animals, (ii) it can be inter-specific, but (iii) it is biased in terms of the kinds of individuals it targets, (iv) it need not be altruistic in origin, and (v) it therefore is unlikely to make for a plausible basis for a universalist morality all by itself.

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