



# Primate empathy: three factors and their combinations for empathy-related phenomena

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## Article type: Opinion

**Article title:** Primate Empathy: three factors and their combinations for empathy-related phenomena

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## Abstract

Empathy as a research topic is receiving increasing attention, although there seems some confusion on the definition of empathy across different fields. Frans de Waal<sup>1</sup> used *empathy* as an umbrella term and proposed a comprehensive model for the evolution of empathy with some of its basic elements in nonhuman animals. In de Waal's model, empathy consists of several layers distinguished by required cognitive levels; the perception-action mechanism plays the core role for connecting ourself and others. Then, human-like empathy such as perspective-taking develops in outer layers according to cognitive sophistication, leading to prosocial acts such as targeted helping. I agree that animals demonstrate many empathy-related phenomena; however, the species differences and the level of cognitive sophistication of the phenomena might be interpreted in another way than this simple linearly developing model. Our recent studies with chimpanzees showed that their perspective-taking ability does not necessarily lead to proactive helping behavior. Herein, as a springboard for further studies, I reorganize the empathy-related phenomena by proposing a combination model instead of the linear development model. This combination model is composed of three organizing factors: matching with others, understanding of others, and prosociality. With these three factors and their combinations, most empathy-related matters can be categorized and mapped to appropriate context; this may be a good first step to discuss the evolution of empathy in relation to the neural connections in human and nonhuman animal brains. I would like to propose further comparative studies, especially from the viewpoint of *Homo-Pan* (chimpanzee and bonobo) comparison.

## Sidebar title: Primate Empathy

### What is empathy?

Empathy as a research topic has gained increasing attention from social scientists, and its evolution has become one of the hottest topics in comparative cognitive science. However, there does not seem to be consensus on the definition of the concept of empathy. Daniel Batson<sup>2</sup> categorized eight related, but distinct, phenomena called empathy in human social science. Previous studies seem to have individually sought different cognitive, emotional, and behavioral aspects of empathy without well organizing these various facets at different levels. When studying empathy, some researchers may ask “How can we understand the other’s mental state?” Meanwhile, other researchers may develop studies from another question: “How sensitive are we to others’ emotions?” The former question normally involves “theory of mind,” and the latter is highly related to prosociality and altruism. These questions and their underlying theories may be related, but they are not the same, although the same term, *empathy*, is often used for them. Vasconcelos and his colleagues<sup>3</sup> voiced a typical criticism of the usage of *empathy*. They critically compared two recent studies that reported similar phenomena of rescuing behavior in nonhuman animals, which was interpreted very differently by the respective authors. Bartal et al.<sup>4</sup> interpreted rescue behavior in rats as providing evidence for empathy, whereas Nowbahari et al.<sup>5</sup> interpreted rescue behavior in ants without referring to shared emotions. This type of confusion can often be found in studies on “empathy.”

One way to resolve this confusion may be to avoid using the term *empathy*, unless the phenomenon meets strict criteria, i.e., actor individuals possess a representation of the receiver’s emotional state and are driven by the psychological goal of improving the receiver’s well-being.<sup>3</sup> However, when this strict definition is adopted, only a limited number of phenomena can fall into empathy in humans, and, needless to say, nonhuman animals. This might not be constructive when investigating the evolution of empathy from comparative viewpoints. Instead, some comparative cognitive scientists are trying to dissolve empathy as an aggregation at different levels of phenomena and to find evidence, or evolutionary bases, of each phenomenon in nonhuman animals.<sup>6,7,8</sup> I would like to follow this approach. In this opinion paper, I do not plan to discuss empathy’s definition. More frankly, I do not feel a strong need for the term *empathy* to label a specific phenomenon since each of the related phenomena has already been labeled with scientific terms other than *empathy*.<sup>2</sup> Thus, using *empathy* as an umbrella term that covers wide-ranging phenomena rather than one specific item would be appropriate. Consistent with this approach, investigating what factors underpin empathy would be fruitful, as would discussing how the factors work and connect to one another for empathy’s occurrence, rather than arguing in a circle what empathy itself is. My main purpose in writing this opinion piece is to propose a novel method of reorganizing empathy-related factors and discussing their evolution from the viewpoint of comparative cognitive sciences.

### Three factors and their combinations

Here, I use *empathy* as an umbrella term, and I propose to distinguish three component factors of empathy: “matching with others,” “understanding of others,” and “prosociality,” so that we can categorize a broad spectrum of psychological phenomena such as emotional contagion, preconcert, consolation, perspective-taking, and so on. “Matching with others” is a process whereby an individual either intentionally or unintentionally matches his/her mental, behavioral, and/or environmental states with another’s. Meanwhile, the term “understanding of others” in this study means appreciation of others’ states based on the cognitive ability of self-other distinction. This distinction between matching with others and understanding of others might appear to resemble the distinction between “emotional empathy” and “cognitive empathy”; however, my terms here (“matching with others” and “understanding of others”) represent factors or mechanisms of empathetic phenomena, whereas “emotional empathy” and “cognitive empathy” represent empathetic phenomena themselves. My terms are also more inclusive. For example, “understanding of others” can involve phenomena such as Machiavellian intelligence and *schadenfreude*, which are selfishly motivated (thus “understanding of others” is not empathy itself). It is important to note that in this model the two factors are not mutually exclusive, but can overlap in part. Prosociality, the third factor, is defined as a psychological and/or behavioral tendency to benefit others. Prosociality is often considered as a result of an affective response that stems from the apprehension or comprehension of another’s emotional state. However, in this study, I treat this aspect as one of the three independent factors or mechanisms of empathetic phenomena, and not as a result of the other two.

These three factors have been blended into the concept of empathy in many previous studies, in which empathy has often been defined as an affective response that stems from the apprehension or comprehension of another’s emotional state and is similar to what the other person is feeling or would be expected to feel<sup>9,10,11</sup>; however, this may have caused confusion. I distinguish these three as components because some empathy-related phenomena belong to one or two of the three factors, but are excluded from the other(s). These factors sometimes overlap, but can be conceptually separated. For example, behavioral synchrony is one way of matching with others, but it does not necessarily require a self-other distinction that leads to understanding others as “others.” On the other hand, perspective-taking is one of the most sophisticated ways of understanding others, but can be experienced without matching with others. People may feel happy when they see others, such as their opponents, suffer (“*schadenfreude*”). Psychopaths, who understand others’ emotions but never feel others’ suffering as their own, are a good example for the distinction between the two factors. Similarly, it is possible to consider prosociality without “matching with others” nor “understanding of others.” Thus, considering these as separate mechanisms seems a better approach. Later, in the next section, I address each of the factors and their combinations in more detail.

Here, let me explain more why I think this separation of three factors is appropriate and constructive, and what distinguishes this model from de Waal’s Russian Doll Model, one of the most famous, prevailing models of the evolution of empathy in the comparative cognitive research field.<sup>7</sup> In de Waal’s model, empathy develops on the basis of emotional contagion, and at the core of

emotional contagion is the perception-action mechanism, i.e., automatically and unconsciously activated neural representations of states in the subject similar to those perceived in the object.<sup>6</sup> The outer layers, beginning with preconcert and followed by sympathetic concern and targeted helping, accrue around the core mechanism. I agree with de Waal's idea that empathy's beginnings should be so simple that we can find them in nonhuman animals. In his model, however, there seems to be a presupposition of a simple, linear, developmental schema of empathy-related cognition, that is, from lower cognitive processes toward higher, cognitively demanding abilities. That is, this model seems based on the assumption that primitive traits gradually evolved toward human-like empathy positioned at the peak of development. Based on the perception-action mechanism, the ability to understand others matures into perspective-taking as the self-other distinction increases. Accordingly, emergence of highly sophisticated prosocial behavior, such as targeted helping, is assumed. However, how empathy emerges is not so clear, nor is how it incorporates different factors such as understanding others' affections and prosocial tendencies.

A higher level of understanding others, such as perspective-taking, is a prerequisite for targeted helping by definition, but is not a sufficient condition for it. Our chimpanzee studies showed this relationship. Chimpanzees are known to demonstrate highly prosocial and cooperative tendencies in their helping,<sup>12,13,14</sup> collaborative activities,<sup>15,16,17</sup> food sharing,<sup>18</sup> and in many other contexts. However, most of these prosocial behaviors occur not proactively, but reactively to recipients' begging or requests (for a review, see 19). In our studies with captive chimpanzees in the Primate Research Institute, Kyoto University, Japan (for recent projects here, see 20), we found that they handed a tool, predominantly upon request, to a conspecific partner who needed one in order to drink juice.<sup>13</sup> In subsequent advanced tests, we confirmed that the chimpanzees selected an appropriate tool from a set of seven objects, according to the partner's situation<sup>14</sup> (see Figure 1). They seemed to understand the partner's need by just visually inspecting the situation. These results have two important implications. First, chimpanzees demonstrate flexible targeted helping according to the partner's situation. Second, and closely related to the point raised above, chimpanzees can understand the partner's need; nonetheless, they seldom help proactively. Thus, the perspective-taking ability does not automatically lead to prosocial behavior. This finding has been replicated by another research team.<sup>21</sup> This is also true, at least in part, with humans. We sometimes feel compassion for others when we know they are in need, but we might also feel *schadenfreude* or sadism, and sometimes, unfortunately, torture others precisely because of our ability to know their suffering.

<<< Figure 1 around here >>>

These points make the linearly developing model seem too simple to investigate the evolution of empathy. To stimulate discussion on primate empathy, I would like to propose another perspective, i.e., a combination model, in which the three factors are laid out horizontally and in parallel, and consequently, empathy's complexity can be represented as combinations of elements.

## **Primate evidence and the three-factor model**

With reference to Figure 2, let me introduce each of the three factors and their combinations and briefly list some evidence for each of them in nonhuman animals.

<<< Figure 2 around here>>>

### ***(a) Matching with others***

Phenomena in this category are considered the most fundamental of empathy — sometimes called emotional empathy — and can be accomplished through the process of matching one's mental, behavioral, and/or environmental states with another's. Matching with others might work as a lower mechanism that underlies understanding others and prosociality;<sup>6</sup> however, I would like to separate this from the other two factors, because it is not necessarily a prerequisite for them. Synchrony, mimicry, social facilitation, automatic gaze following, and emotional contagion without cognitively understanding another's feelings is typical in this category. These phenomena can be found in a variety of animal species, not only in primates, but also in non-primate mammals and other animals.<sup>1</sup>

### ***(b) Understanding of others***

Perspective-taking is typical in this category. It was previously considered unique to humans, but experimental studies have revealed its existence in chimpanzees.<sup>14,22</sup> When this category is broadened to include Machiavellian intelligence in general, i.e., understanding and/or expecting what others are doing and/or will do, a much wider range of primate species, as well as some other mammals and birds, can demonstrate this phenomenon quite well.<sup>23,24</sup> This does not necessarily lead to prosociality, nor does it stem from matching with others. As discussed above, chimpanzees can understand another's need, but this does not automatically provoke their helping behavior. Machiavellian intelligence is often exerted in conflictual contexts, in which situations it is beneficial for animals to understand others' behavior or mental states without matching their states to others'. Schadenfreude is also a typical example of understanding others without matching with others.

### ***(c) Prosociality***

As described in the definition above, I treat "prosociality" as a basic tendency toward altruism and mutualism, which can be found in many animals such as rats<sup>4</sup> and ants<sup>5</sup> as noted earlier in this article. In primates, food sharing is one of the most conspicuous behaviors in this category. It can be found broadly in the animal kingdom, not only in primates, but also in non-primate animals in their natural habitats. Prosociality is believed to stem from parental care, which is widespread in mammals and birds.<sup>25</sup> Jaeggi and van Schaik<sup>26</sup> showed that primate species that share food among non-kin individuals inevitably demonstrate parent-offspring food sharing. Recent development of the "prosocial choice" experimental paradigm<sup>27</sup> has provided a good way to examine animals'

prosociality, i.e., preferring the mutual option that rewards both self and partner over the selfish option that delivers reward only to the self. In this prosocial choice, there is no explicit need to assume any emotional matching or cognitive understanding of others' affections or needs. We now know that this type of prosociality is widespread in various species of apes, Old-world Monkeys, and New-world Monkeys (for a review, see 28).

***(d) Matching with others and prosociality***

This combination drives animals to approach, but not escape, and provide comfort to others in pain or distress in order to eliminate their own negative feeling that is matched with the other's. This automatic response is labeled *preconcern*,<sup>8</sup> as the next step toward sensitivity to others' affections. With this definition, *preconcern* is blind attraction, in that animals and young children often seek out distressed parties without any indication that they know what is going on. Therefore, cognitive understanding of others' situations is not required. There are few well documented empirical studies on this behavior in nonhuman animals, but some researchers think it might be widespread in primates<sup>29,8</sup> and certain animals such as household pets.<sup>30</sup> The *chameleon effect* is also closely related to this category. Humans are known to demonstrate automatic and unconscious mimicry of body postures, gestures, and mannerisms of our social-interaction partners, which increases shared rapport and liking; further, it is likely to promote imitated partners' prosocial behaviors.<sup>31,32</sup> Recently, this effect has been partially found in capuchin monkeys that display affiliation toward human imitators over non-imitators.<sup>33</sup> This link between matching and prosociality also potentially leads to collaboration between two individuals. When animals collaborate, an individual needs to coordinate movement and timing with the partner in order to achieve their mutual goals. This is realized consciously as well as unconsciously. Recent empirical studies have revealed substantial evidence for this collaboration in some highly socialized animals such as chimpanzees,<sup>15,16</sup> bonobos,<sup>34</sup> capuchins,<sup>35</sup> tamarins,<sup>36</sup> elephants,<sup>37</sup> hyaenas,<sup>38</sup> and corvids.<sup>39</sup>

***(e) Matching with and understanding of others***

In this category, cognitive contagion or cognitive empathy is considered a main phenomenon. This is a process of knowing another's affections, or some other mental states, and differs from emotional contagion, which is a more automatic, unconscious process of feeling what another is feeling. In this stage, animals can achieve a self-other distinction not only in emotion but also, at times, in more cognitive acknowledgement of situations and status. This combination of the two factors leads animals not only to match with others, but also engage in social comparison with others, which sometimes evokes emotional responses such as envy, i.e., an individual detects a difference between the self and others and desires the others' status. This has been investigated in non-human animals as a form of *inequity aversion* (in particular, negative responses to an inequitable situation in which an animal has concern about having less of a commodity than others: disadvantageous inequity aversion). Disadvantageous inequity aversion is found in some primate species such as chimpanzees, bonobos, long-tailed macaques, capuchins, and cotton-top tamarins (for reviews, see 28, 40, 41) and also in highly socialized animals such as dogs.<sup>42</sup>

***(f) Understanding of others and prosociality***

With this combination, animals demonstrate targeted helping, i.e., helping directed at an individual with a specific need. This type of helping behavior has been empirically confirmed in only a limited number of animals other than humans, although there have not yet been many studies with non-human animals. As mentioned above, chimpanzees show this trait.<sup>12,13,14,21</sup> Although capuchin monkeys demonstrate prosociality in prosocial choice tests,<sup>43,44,45</sup> their helping behavior is much less frequent than that of chimpanzees and does not seem to be directed according to a partner's specific goal.<sup>46</sup> This is probably because the capuchins lack an ability, such as perspective-taking.<sup>47</sup>

***(g) The three factors combined***

Finally, there is the combination of all three factors. Animals might feel the same feeling as another individual, but know this feeling comes externally from the partner and not from their internal response to their own situation by examining the partner's situation; they may then behave prosocially toward the partner. This combination leads an individual to show sympathetic concern, or consolation, which is defined as reassurance provided by an uninvolved bystander to one of the combatants in a previous aggressive incident.<sup>48</sup> Consolation can be found in apes and humans, but not in monkeys.<sup>1</sup> de Waal and Aurelli<sup>49</sup> observed captive groups of chimpanzees and rhesus monkeys with strictly identical protocols and found evidence of consolation only in chimpanzees. Subsequent studies with wild animals have also confirmed this (e.g., chimpanzees<sup>50</sup>; Japanese monkeys<sup>51</sup>). This combination might enable some other phenomena closely related to cooperation, such as calculated reciprocity and advantageous inequity aversion (aversive response to a situation in which the responder inequitably has something better than another, which leads to proactive prosociality<sup>28</sup>). In these, an individual detects differences between the self and others and diminishes the differences by behaving prosocially. Such empathetic phenomena have been observed in humans and in very few, if any, other animals.

***Combination model's evolutionary perspective***

In this model, I assume independent emergences of the three factors, but not any developmentally or phylogenetically linear progressive change in empathy. The Russian Doll Model assumes a linear development where a new ability is added to the old one. More specifically, matching with others is the first, then prosociality, and finally understanding of others. In contrast, in my combination model, I do not make any assumption about the emergence order of the three. Support for this model would consist of evidence that some species exhibit one factor (e.g., prosociality) but not another (e.g., understanding of others) and other species demonstrate the reverse. Here, I would like to give some examples. As described above, capuchin monkeys demonstrate prosociality in the prosocial choice test,<sup>43,44,45</sup> but do not have sophisticated abilities to understand of others.<sup>46,47</sup> In contrast, chimpanzees are talented in their understanding of others, such as in perspective-taking,<sup>14,21,22</sup> but their prosociality is limited by a lack of proactivity.<sup>13,14,21,27</sup> Comparative studies with 15 primate species showed that only species with extensive alloparental care have proactive prosocial tendencies,<sup>52</sup> although these species do not demonstrate such abilities

of understanding of others as seen in chimpanzees. Such comparative studies have suggested convergent evolution of proactive prosociality in different taxa with alloparental care irrespective of their abilities of understanding of others.<sup>52,53,54</sup> Some developmental studies with human children also support this idea of independent emergence from ontogenetic perspectives. They have shown that several prosocial behaviors, which might be based on different components, develop independently in infants.<sup>55,56</sup> The simple linear model seems to fail to explain these facts.

The proposed model represents some “advanced” or human-like empathetic phenomena, such as sympathy or consolation, as a combination of the factors. Which empathic phenomenon animals demonstrate depends on the on/off status of each factor. Animal species showing phenomena in the category of the combination of plural factors should be inevitably talented, possessing every individual factor involved in it, and the review of empirical evidence for phenomena within each category in nonhuman animals seems to support the idea that the number of species that demonstrate “advanced” empathetic phenomena (i.e., combination of plural factors) decreases as the number of combined factors increases. For example, animals that demonstrate cognitive contagion (a phenomenon of category (e)) inevitably show evidence for both (a) matching with others and (b) understanding of others, at least at their fundamental level. Similarly, category (g) can be found in animals that show all elements to some extent, that is, (a), (b), (c), (d), (e), and (f). Chimpanzees are the only non-human candidate at this moment that might demonstrate some phenomena in category (g) and also all the other categories.

Unfortunately, there is currently insufficient empirical evidence for my combination model and the idea of independent emergence of the three factors. However, this is not because evidence cannot be found, but largely because of a lack of studies that have worked within this framework. Future accumulation of evidence will enable us to engage in phylogenetic analysis, probably via Bayesian statistics. With but limited evidence, we must wait for further studies to test the model. Therefore, at this moment the model is a theoretical basis for stimulating future studies and discussion.

### **Empathy studies’ future direction**

In this paper, I have categorized empathy-related phenomena with reference to three factors and their combinations. Then, I briefly reviewed the evidence for each of them in nonhuman animals. With this broad perspective, studying nonhuman animals is essential for investigating empathy’s origin. Previous efforts have succeeded in revealing each factor’s basis in nonhuman animals. Then, the next step might employ two tactics: one is examination of each category’s details to seek similarities and differences across species, and the other is investigation of links between factors to understand how the empathetic systems work in each species. Although this paper focuses predominantly on primate species, it would be fruitful to broaden the target species to non-primates to reach comprehensive understanding of the evolution (especially convergent evolution) of empathy.

Each factor includes some different subcomponents. For example, a wide range of animals might display emotional contagion as evidence for matching with others, but the types of emotions (e.g., fear, sadness, happiness) transferred between individuals might differ across species. In nonhuman animals, to my knowledge, contagion of positive emotions has been much less reported (observed mostly in only a few primates and dogs as facial or postural mimicry between interacting playmates<sup>57,58,59,60</sup>) than contagion of negative emotions, which can be found in a variety of contexts across species.<sup>7,8</sup> Humans' sensitivity and resonance to positive emotions in others, even in strangers—such as contagion of laughter—might support the abilities probably unique to humans of proactive helping and large-scale cooperation. If a contagion system of positive emotions exists, helping behavior in itself provides psychological reward for the helper since the receiver's happiness can be shared with the helper. In contrast to humans, chimpanzees, which demonstrate less proactive helping, might have a weaker contagion system of positive emotions although they seem to be skilled at making the self-other distinction observed in perspective-taking. Then how about bonobos, who have considerable similarities to humans and differences from chimpanzees?<sup>61</sup> Bonobos demonstrate high inter-individual tolerance and cooperative performance;<sup>34</sup> they share daily fruit items with others, and this might enhance their social bond (see Figure 3).<sup>62</sup> This might suggest that bonobos show stronger development of the matching with others factor. If true, it can be predicted that bonobos show human-like emotional contagion that might be missing in chimpanzees. There may also be layered linear relationships between some sub-components in each factor. For example, "understanding of others" involves expectation of others' behavior, perspective taking, and theory of mind, which might develop linearly. A future challenge is to merge the combination model and the linearly layered model for cognition of each factor.

<<< Figure 3 around here>>>

Investigating links and interactions between the factors is also interesting and important. As mentioned above, a chimpanzee's understanding of a partner's problem-solving situation does not automatically connect to the onset of helping behavior unless the partner explicitly requests it.<sup>13,14,21</sup> Thus, human proactive prosociality developed by acknowledgement of another person's need is particularly notable. Investigation of the automatic link between the two factors, i.e., how understanding of others leads automatically to prosociality, is important for understanding how humans' specific empathetic systems work and how this is related to our highly sophisticated cooperative societies.

When considering the interactions between the three factors, it is important to investigate the link between the factors and their specific brain regions. Previous human neuroimaging studies have revealed that different brain regions are activated for emotional contagion and perspective-taking, and that both regions are activated in some social contexts; this suggests interactions exist between them.<sup>63,64</sup> The combination of factors might need a connecting circuit between some brain regions, and this might require considerable evolutionary development. In this opinion piece, I focused on primate empathy. However, it is important to also study non-primate species, especially from these neuroscience perspectives. Unfortunately, however, empathy-related brain regions in nonhuman animals have been investigated predominantly in relation to emotional contagion,<sup>65</sup> that

is, the factor of matching with others. Further studies on brain regions associated with the other two factors (i.e., understanding of others and prosociality) and the connection and interaction among the three factors would be the next step for deepening our understanding of empathetic systems and their evolutionary roots.

## Conclusion

In this opinion piece, I reorganized empathy-related phenomena by proposing a combination model instead of the linear-development model. The model's components (i.e., matching with others, understanding of others, and prosociality) might be originally independent, but are closely related and interact to generate various empathy-related phenomena. Considerable evidence has accumulated with respect to nonhuman animals for each of the empathy-related phenomena, but more data are nevertheless needed. Along efforts to collect evidence, the next step to investigate the evolution of empathy should employ two tactics: examination of each category's details to reveal similarities and differences across species, and investigation of links between factors to understand how empathetic systems work in each species. Empathy's complexity might be measured as a combination of factors, which can be represented in sympathy and consolation—expressions which are found in a limited number of animals, such as humans and apes. Chimpanzees demonstrate targeted helping (i.e., the combination of understanding of others and prosociality); however, their sophisticated perspective-taking abilities do not automatically provoke their proactive prosociality, whereas humans often simply help others when noticing their troubles. Therefore, the automatic link between understanding of others and prosociality might be a human-specific phenomenon. This might have manifested humans' specific highly cooperative society although we must refrain from drawing this conclusion until we obtain more comparative data from other animals, such as bonobos, our other evolutionarily closest living relatives. To deepen our understanding of the evolution of empathy, studying the neural basis for differences across species would also be important. This three-factor combination model will be powerful and form a theoretical basis for these types of studies from comparative viewpoints, not only with humans, but also with various nonhuman animals.

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## Figure captions

Figure 1. Chimpanzees's flexible targeted helping upon request. The experiments were conducted for two conditions: "can see" conditions (a) and (c), in which a helper chimpanzee could see the partner's tool-use ("stick" or "straw"), and "cannot see" condition (b), in which the partition was opaque so that a helper could not see the partner's situation, although the partner could demonstrate a request through the partition's small opening. The graphs represent helpers' first tool selection from seven objects that was offered to their conspecific partner. This shows that chimpanzees can understand what specific tool the partner needs when they see the partner's situation although this understanding does not provoke their proactive helping. (This figure is republished from Yamamoto et al., 2012 Proceedings of the National Academy of Sciences, USA.<sup>14</sup>)

Figure 2. Three major facets and their combinations for empathy-related phenomena. Any one of the empathy-related phenomena can fall into one of seven categories (a-g). Recent studies have revealed evidence, or at least some elements, for each category in nonhuman animals, but the range of animal species that demonstrate the phenomena depends on the categories. It seems that the combination of two or more factors in this model requires considerable evolutionary development. See the text for details.

Figure 3. Bonobos' fruit sharing. They often share daily fruit items that are much more easily available than meat, and this might strengthen their social bond.<sup>63</sup> The bonobo is one of the most interesting and important species in which to investigate the evolution of empathy from comparative cognitive viewpoints. (Photograph by Shinya Yamamoto at Wamba, the Democratic Republic of the Congo.)

## Related Articles

Article ID	Article title
COGSCI-347	Empathy
COGSCI-228	Animal Cognition
COGSCI-232	Cognitive Primatology

(a)



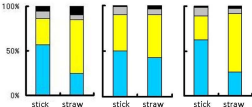
(b)



(c)



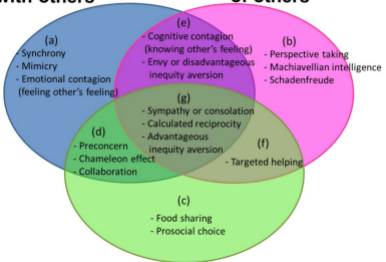
Helper's first offer: stick straw others no offer



Tool which a recipient needed

## Matching with others

## Understanding of others



## Prosociality

