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Sarah F. Brosnan

Georgia State University, sbrosnan@gsu.edu

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What Do Capuchin Monkeys Tell Us about Cooperation? *

Sarah F. Brosnan

Abstract

Nature may be red in tooth and claw, but working together with one's group mates can be an efficient way to increase fitness. Cooperation is common, for example, among capuchin monkeys. These monkeys are not only willing to help others obtain resources, but are more likely to share with individuals who help them. Cooperation can be risky, however, and not surprisingly capuchins are much less likely to cooperate when a partner is able to monopolize the reward. However, they also pay attention to the partner's behavior; monkeys who share with their partners promote successful cooperation, and thus actually receive more benefits over the long term than those who always claim the best rewards for themselves. The ability to recognize inequity may be a mechanism by which the monkeys determine which partners are the best collaborators. The study of capuchin monkeys can tell us quite a lot about how, when, and with whom to cooperate, perhaps providing insight in to the design and implementation of our own human cooperative institutions.

Human beings are not the only animals that act as if they are mindful of the behaviors and needs of others. Although often the focus is on those behaviors which supposedly set humans apart from the rest of the animals, many organisms, including both human and nonhuman primates, act in ways that seem to serve "the greater good." From sounding the alarm when a predator is sighted to sharing food with another who has none, many socially oriented animals – humans included – contribute to others' welfare. While the mechanisms leading to these behaviors undoubtedly differ across species, the outcome remains the same; one individual is benefitted by the actions of another. By studying the nature of such cooperative and prosocial behaviors in primates, researchers can provide an enhanced understanding of their evolutionary function. This chapter considers the many ways that contributing to collective outcomes can enhance the fitness of the individual, but also how difficult cooperation can be to maintain.

The Evolution of Cooperation

Cooperation has been an evolutionary conundrum for almost as long as the theory of natural selection has existed (Dugatkin, 1997). After all, the main tenet of natural selection is that a trait is passed on if it provides a specific fitness benefit to an individual, meaning that this individual leaves more or healthier offspring than everyone else. If this is how genes are selected, it seems challenging to explain how traits that provide benefits to others – such as cooperation – could exist.

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One answer is what is now called group selection. This is the idea that traits may be selected because they provide a benefit to the group in which an organism lives, which benefits the individual even if there is an individual fitness cost to the act. Group selection enjoyed an early flurry of support, which was followed by some less-than-rigorous theorizing (Wynne-Edwards, 1962), and then the inevitable challenges (Williams, 1966). More recently, group selection, or more broadly, multi-level selection, has been resurrected as potentially viable (e.g. Sober & Wilson, 1998), particularly with regard to gene-culture co-evolution in humans (Richerson & Boyd, 2005). However, group selection is limited to a rather specific set of circumstances, leaving open the question of how cooperation evolves in other situations.

Cooperation certainly does exist (Brosnan & Bshary, in press). Organisms from single-cell beings (Strassmann, 2000) to our closest relatives, the apes (Melis, Hare, & Tomasello, 2006b), cooperate, and some of the most impressive examples of cooperation on earth come from the so-called superorganisms, or insect societies (Holldobler & Wilson, 2008). This latter form of cooperation is so extreme that the majority of individuals never even breed, but instead support a queen or queens who do the breeding for the entire colony. So how does individual selection lead to such extensive forms of cooperation?

1.1 The mechanisms of cooperation

There are generally considered to be three mechanisms for cooperation (Dugatkin, 1997). First is by-product mutualism, in which individuals work together to achieve a common goal (Brown, 1983). Mutualism is not difficult to explain from an evolution standpoint. There is no incentive to cheat, as individuals benefit jointly and immediately. Mutualism requires no cognitive mechanisms such as memory for previous encounters, individual recognition, or an ability to delay gratification. Individuals don't even need to understand that they are cooperating; cooperation can be functional rather than intentional (Brosnan, Salwiczek, & Bshary, in press).

The second form of cooperation is cooperation among kin (Hamilton, 1964). Although ideas related to kin selection existed previously, Hamilton was the first to outline the theory of how individuals benefit from helping kin. A critical recognition was that fitness could be divided into direct fitness – your personal fitness – and indirect fitness – fitness you get through the success of other kin not in your direct lineage (together these are called inclusive fitness). Thus, since you share 50% of your genes with your offspring and only 25% of your genes with your nieces and nephews, you should require a greater benefit or lower costs to help the latter.

Hamilton outlined this in an elegant equation known as Hamilton's rule: $rB > C$. Here r represents the degree of relatedness between you and the potential recipient, B represents the benefit to them (in terms of how many more offspring they successfully rear due specifically to your help), and C represents the potential cost to you, in terms of your offspring's fitness. Note that this is an average cost, which incorporates the degree of risk and the potential extent of the cost (e.g. death). Essentially, you should help your kin if the benefit to them, discounted by their degree of relatedness to you, is greater than the cost to you. Of course, organisms do not need to understand this relationship. Rather, individuals who acted in a way consistent with this rule had higher fitness, which led to them passing on more of their genes, presumably including the gene to help kin in this fashion. Thus ultimately the organisms' behavior reflects this relationship. In fact, helping behavior may have evolved from the behavior present in kin relationships, and some relationships, such as friendships, may provide a safe haven for cooperative and helping relationships between non-kin to develop (Wasilewski, 2003; Ackerman, Kenrick & Schaller, 2007)

The third mechanism for cooperation is reciprocal altruism (Trivers, 1971). Trivers recognized that if a short-term cost, obtained while helping another, is offset by a future benefit, then from a purely self-interested standpoint, the (long-term) benefits of helping outweigh the (short-term) costs. In other words, if I help you out today (at a cost to me and a benefit to you), and this leads you to help me out next week, then we are both better off than we were before. Reciprocal altruism is in practice quite challenging as it may require a number of fairly stringent conditions to be met (Stevens & Hauser 2004; although these conditions may be present in primates; see Dufour et al 2008), however some forms of reciprocity may be simpler. One proposal recommends that reciprocity be divided into three components, symmetry-based, attitudinal, and calculated (Brosnan & de Waal, 2002; de Waal & Luttrell, 1988). Symmetry based reciprocity is a function of the symmetries in the relationships between individuals, while attitudinal is reciprocity affected by one's feelings towards another individual. Neither of these require individuals to remember favors given and received. Only the latter, calculated reciprocity, does so.

These forms of reciprocity are all essentially dyadic and specific to the partnership. However, reciprocity may also involve other configurations. For instance, reciprocity may exist in larger groups (Connor, in press), and individuals may be able to use information from others' interactions to inform their own cooperative behavior (Brosnan, Earley, & Dugatkin, 2003; Earley, in press), leading to the formation of reputations and image scoring (Wenekind & Milinski, 2000; Bshary & Gruter, 2006). Finally, generalized reciprocity may lead to reciprocal interactions on a non-contingent basis (Rutte & Taborsky 2007).

Although there are good examples of reciprocity in the animal kingdom, contingent reciprocity is harder to find. Chimpanzees are often studied in this regard, as their intelligence and phylogenetic closeness to humans seem to make them likely candidates (although see Brosnan, Salwiczek & Bshary, in press, for the point that cooperation need not require cognition). In experiments, chimpanzees often fail to show contingent reciprocity (Brosnan, et al., 2009; Melis, Hare, & Tomasello, 2008), even though they are known to reciprocate in other situations (e.g. de Waal, 1989). There may be several reasons for this. First, most experiments do not allow individuals to choose their own partners, and partner identity is likely critical in reciprocity (de Waal, 1989 did allow for partner choice, potentially explaining the different results). Second, experiments occur over minutes, or at the most hours, while most reciprocity seen in the wild occurs over much longer time frames (days to weeks; Gomes & Boesch, 2009; Gomes, Mundry, & Boesch, 2008). Of course, cooperation is not the only context in which individuals behave in ways that benefit others, as is discussed below.

1.2 Prosocial behavior in non-cooperative contexts

Some behavior which benefits others also occurs outside of the context of cooperation (although such behaviors may later lead to cooperative interactions). Such prosocial behavior cannot easily be explained by the above three mechanisms. These behaviors include such acts as tipping in a restaurant to which you will never return, giving blood, and even voting, for which it is unlikely that any one person's vote will be the deciding factor. These behaviors are common in humans (Eisenberg & Mussen, 1989) but also occur in other species (*marmosets*: Burkart, Fehr, Efferson, & van Schaik, 2007; *capuchins*: Lakshminarayanan & Santos, 2008; de Waal, et al, 2008, Takimoto et al, 2010; *chimpanzees*: Warneken, Hare, Melis, Hanus, & Tomasello, 2007; Warneken & Tomasello, 2006; although see Cronin, Schroeder, Rothwell, Silk, & Snowdon, 2009; Silk, et al., 2005; Vonk et al, 2008; Jensen et al, 2006).

Despite the lack of immediate benefits, there are several potential functions to prosocial behavior. For instance, prosocial behavior may serve as a commitment device which demonstrates to others the actor's dedication to equity, and thus their general merit as a social partner (Frank, 1988). Humans' behavior supports this in some experimental settings, as people will make decisions which lower their

absolute and relative outcomes, presumably to send a signal to their partner (Yamagishi, et al., 2009). Related to this, prosocial behaviors may also improve one's own reputation, providing benefits in the future (Milinski, Semmann, & Krambeck, 2002; Wenekind, 2000). Additionally, helping others may avoid punishment or harassment which ensues if help is not given (Blurton-Jones, 1987). For instance, chimpanzees and other primate species harass food possessors, which makes the possessor more likely to share (Gilby, 2006; Stevens, 2004).

One mechanism which increases the chances of such prosocial behavior may be the 'warm glow' people get from helping others (Andreoni, 1989; Batson, 1991), a mechanism which may be shared with other species (de Waal et al 2008). This mechanism may encourage us to perform behaviors which benefits us in the long run despite the immediate costs (Brosnan, Salwiczek, & Bshary, in press).

Capuchin monkeys are an interesting species to study with respect to prosocial and cooperative behaviors. First of all, they demonstrate both of these types of behaviors in the lab (see below for details). Moreover, many studies have been done investigating both types of behavior, and attempting to understand the tradeoffs the monkeys face as they make determinations whether or not to cooperate or share. Below I discuss what capuchin monkeys can tell us about the evolution of cooperation and prosocial behavior.

2. Cooperation lessons from capuchins

Capuchin monkeys are a gregarious monkey species indigenous to South and Central America. The brown capuchin monkey (*Cebus apella*), discussed here, is particularly well suited for studies of cooperation. They have the largest brain-to-body ratio of any monkey species, on par with that of apes (Rilling & Insel, 1999), and show an array of advanced cognitive behaviors (for a review, see Fragaszy, Visalberghi, & Fedigan, 2004). Thus, if cognition is required for some types of cooperation, they are likely to have the necessary prerequisites. Moreover, their social behavior predisposes them to cooperate. They are highly tolerant, and even subordinates can maintain access to resources which are in their possession (de Waal & Brosnan, 2006). Capuchins also collaborate, for instance on hunts (Rose, 1997) and group defense (Boinski, 1988), and share food (de Waal, 1997; Perry & Rose, 1994), an unusual trait among adult primates (Feistner & McGrew, 1989).

Below I discuss a series of studies which were done in the lab, using non-kin pairs drawn from the same social group. All lived in large social groups (15-20 individuals) and so spent their days interacting with the monkeys with whom they are tested. Most were done using a 'barpull' tray, which is a counterweighted tray which can be pulled in by the monkeys to obtain rewards. Adjustments can be made to the weight of the tray (to require monkeys to pull together) and rewards (offering them in different locations, quantities, or types) to examine how different features and contexts affect cooperation. This flexibility allowed the barpull apparatus to be used to examine both mutualism and reciprocity.

2.1 Cooperation requires coordination

Capuchin monkeys easily coordinate their behavior to jointly pull in the tray to each receive an identical reward (e.g. a mutualism task: Mendres & de Waal, 2000). Moreover, the capuchins were actively synchronizing their behavior. First, the capuchins glanced at their partner more often in the coordination task than in a control in which they could pull in the tray without their partner's help. Second, when an opaque panel blocked the capuchins' visual access to each other, cooperation almost disappeared, indicating visual coordination was required for success. Finally, there was a condition in

which the partner could come and go freely, but the subject could not. The subject pulled more frequently when the partner was present than absent, indicating that they understood that a partner's presence was necessary for success.

In order to successfully cooperate, capuchins seem to require an intuitive task, or one which is both biologically relevant and provides appropriate kinesthetic feedback. In an earlier study, capuchin monkeys were trained to pull two handles simultaneously to activate a food reward. The handles were gradually moved further apart until two monkeys were required to activate the apparatus. The monkeys never learned to do this task (Visalberghi, Quarantotti, & Tranchida, 2000). To understand the difference between these results and those with the barpull apparatus, we ran an analogue of the Visalberghi study using the capuchins which had been successful in the Mendres study (Brosnan & de Waal, 2002). The monkeys were trained to push a lever to activate a juice dispenser, which they quickly learned to do. We then placed the monkeys next to each other, each with a lever and a juice dispenser, and required the monkeys to press their levers together to activate their juice dispensers. None of the monkeys learned this. We then altered the task so that the levers were adjacent and several feet from the adjacent juice dispensers, which encouraged the monkeys to move together and, potentially, pay attention to their partner's relevance (e.g. synchronize their behaviors). At this point, one adult female monkey learned to alter her behavior contingent upon her partners'. This female pressed her lever more often when her partner was also near the levers. Despite her success, no other monkeys learned to activate the juice boxes, even though these monkeys learn socially in other situations (Brosnan & de Waal, 2004).

Based on these studies, we concluded that a critical feature of any cooperative task is that the individuals must be able to understand it. Apparently the monkeys did not understand the contingencies of the electronic lever-pressing tasks, and thus never learned to pattern their behavior based on their partners'. On the other hand, the barpull was intuitive; the tray could only be pulled with the partner and if the partner let go, the tray immediately became too heavy for the remaining individual. Thus there was immediate kinesthetic feedback. Of course, an intuitive task is necessary, but not sufficient; the work of Mendres & de Waal shows that the monkeys must also be able to see each other to coordinate their behavior.

2.2 Cooperation depends on the partner's behavior

Since cooperation necessarily involves two (or more) individuals, there is always a potentially weak link in the interaction. When making a decision to cooperate, individuals have to not only understand the task, but determine whether their partner will be a good partner. Capuchins are sensitive to situations in which a partner might fail to cooperate. In the previous study, the rewards were always dispersed, such that each monkey could control 'their' rewards. When rewards were clustered together in the middle of the tray, such that one individual could monopolize them, cooperation was much less common (de Waal & Davis, 2002). This was true from the first trial, indicating that their reticence to cooperate when rewards were clumped is not based on learning during the course of the experiment.

Capuchins are also sensitive to their partner's actual behavior. If rewards are altered such that only one of the monkeys gets rewarded, the unlucky monkeys cooperated at higher rates when their partner shared the food bonanza. Moreover, the rates of food sharing were lower in a control in which the subject could pull the tray in by themselves (also for a single reward). This indicates that the subjects understood when their partner's help was essential and rewarded their partners for their assistance (de Waal & Berger, 2000).

Finally, capuchins are sensitive to relative payoffs between themselves and others, and are more likely to cooperate with partners who do not dominate rewards. In this mutual barpull, the food rewards were dispersed, but varied between the two monkeys. In some conditions, the monkeys received the same high- or low-value food, while in others, one monkey received a high-value food while the other received a low-value one. Critically, in this test the monkeys were not separated from one another and the experimenter did not determine which monkey received which reward. Instead, the monkeys had to work out for themselves which one got the high-value reward and which one got the low-value reward (Brosnan, Freeman, & de Waal, 2006).

We found that cooperation increased when partners shared access to the higher-value food. When one monkey repeatedly claimed the higher-value food, their partner quit cooperating. Interestingly, this held true across all conditions, not just the inequitable ones. So if a monkey consistently took the high-value reward, their partner quit cooperating with them not only when the rewards were unequal, but also when the rewards were equal and high. Thus, it seems that they were not reacting to the actual distribution of the rewards, but instead to their partner's behavior.

It is also of note that in this study, the monkeys were willing to accept short-term inequity – getting the lower value of the two rewards – as long as the long-term outcomes were approximately equal. This implies that the monkeys were evaluating their interactions based on the long-term relationship rather than each individual interaction. This is important for cooperation in natural situations, as it is rare that individual outcomes are ever completely equitable. In fact, these monkeys normally react negatively to inequitable outcomes as compared to a partner, a topic discussed in depth in the following section.

2.3 Inequity is detrimental to cooperation

Capuchin monkeys dislike inequity. They reject outcomes which are not equitable, even if their reaction does not change their partners' outcomes (Brosnan & de Waal, 2003). This is not a result of individual contrast, as the monkeys respond less strongly if they are offered a high-value reward but then receive a lower-value one after completing a task (Fletcher, 2008; van Wolkenten, Brosnan, & de Waal, 2007). Moreover, the monkeys seem to be much more focused on outcomes than on effort; they react quite negatively to receiving a less good reward, but do not react negatively to having to work less hard for an outcome (Fontenot, Watson, Roberts, & Miller, 2007; van Wolkenten, et al., 2007). There has been much written on the topic, so I refer the reader to several reviews for the details (Brosnan, 2006, 2008) and will refer to only those aspects that are of importance for cooperation.

One hypothesis is that inequity is a mechanism which underpins cooperation (Brosnan, 2006; Fehr & Schmidt, 1999). Individuals who respond negatively to inequity may have better outcomes because they cease interacting with those individuals who do not give them a fair deal. If they then seek a new partner, this will result in a change for the better. There is evidence for this in capuchin monkeys. First, capuchins seem to respond to inequity primarily in the context of a task, and not when rewards are simply handed out for 'free' (Dindo & de Waal, 2006; Dubreuil, Gentile, & Visalberghi, 2006; Roma, Silberberg, Ruggiero, & Suomi, 2006). In other words, if one monkey has to complete a task to receive a particularly preferred reward (a grape), and another has to complete the same task but receives only a less-preferred reward (a cucumber), the monkey which received the cucumber will refuse to either complete the task or accept the cucumber. On the other hand, if one monkey is simply handed the grape and the other is handed the cucumber, the monkey which receives the cucumber will accept the reward (Dindo & de Waal, 2006). This behavior is also seen in tamarins and chimpanzees (Brosnan, Talbot, Ahlgren, Lambeth, & Schapiro, 2010; Neiworth, Johnson, Whillock, Greenberg, & Brown, 2009). As might be expected, dominant subjects tend to be more likely to refuse lower value rewards than subordinates, presumably because they are less accustomed to this situation (Brosnan et al, 2010).

Several explanations exist for this behavior (Brosnan et al, 2010). First, it is possibly a quirk of captivity. Monkeys receive foods on a regular basis from humans (their daily meals, for instance), and dominant individuals routinely claim more than subordinates. Thus, they may be used to unequal outcomes in this context (or consider them equitable). A second possibility is that the act of working together triggers a negative response if rewards are unequal (van Wolkenten, Brosnan & de Waal 2007). If inequity is a mechanism underpinning cooperation, it may be that any effort triggers an expectation of more equal outcomes. In the wild, refusal to participate may lead them to find a new, potentially more equitably behaving, partner. In fact, in cooperative situations, monkeys prefer to help partners who share outcomes (de Waal & Berger, 2000) and do so more equitably (Brosnan, et al., 2006). Given a choice, chimpanzees actively choose more tolerant partners for cooperative tasks (Melis, Hare, & Tomasello, 2006a).

Another way to test this hypothesis is to examine these behaviors phylogenetically. Species which differ on one trait, such as cooperation, may also differ on a second trait, such as responding negatively to inequity. Although this is correlational data, and can tell only if the traits are linked, this is a powerful mechanism for determining if behaviors likely evolved in concert. Thus far, all species which have been shown to respond negatively to inequity are also cooperative (chimpanzees, capuchin monkeys, tamarins, dogs), so it is difficult to tell if this behavior is due to some common characteristic among these species, such as sociality or cooperation (e.g. evolutionary convergence) or if the negative response to inequity is widespread in primates and mammals (e.g. homology). We currently have studies underway with other species of primates which differ in their cooperative tendencies to determine which of these possibilities is more likely.

2.4 Be nice when you can, but never if it costs you too much

In all of the previous work discussed, the capuchins' behavior could easily be explained by mutualism, which provides an immediate benefit to the self, or reciprocity, which provides a benefit in the future. However, sometimes animals do things which help their partners for no obvious benefit. There has been a recent interest in prosocial behavior, or the willingness to benefit another at either no or a very small cost to the self. Initial studies in nonhumans (Jensen, Hare, Call, & Tomasello, 2006; Silk, et al., 2005; Vonk, et al., 2008) found that chimpanzees did not bring food to conspecifics, even when it did not cost them anything. In these studies, the chimpanzees were given a choice between an option which brought food only to themselves or an option which brought food to both themselves and a partner. The subject received the same food no matter which choice they made, so there was no cost to behaving prosocially. To control for the possibility that they preferred the option with more food items, the subjects' behaviors were compared when paired with another chimp versus when alone. In none of these studies did chimpanzees choose to bring food to their partners more often when their partner was present than when they were next to an empty cage.

A series of similar studies have been run with capuchin monkeys with very different results. The capuchins behaved prosocially, choosing outcomes which benefit their partners over those which did not (de Waal, Leimgruber, & Greenberg, 2008; Lakshminarayanan & Santos, 2008; Takimoto 2009). Additional research indicates that there are many factors which affect prosocial behavior. Chimpanzees, despite failing to bring food to their partners, do help them in non-food related tasks (Warneken & Tomasello, 2006; Warnken et al, 2007). Moreover, callitrichids vary, with some species behaving prosocially (Burkart et al, 2007) and some not (Cronin et al, 2009). The fact that some cooperative breeders are prosocial, including humans, has led to the hypothesis that cooperative breeding creates the interdependence which selects for prosocial behavior (Burkhart et al, 2007). However, additional data is required before firm conclusions can be drawn.

Note that capuchins monkeys' behavior seems on the surface contradictory. These monkeys make choices which are prosocial, choosing to bring food to their partners when it doesn't cost them anything to do so, yet they also dislike inequity, refusing to participate when outcomes are unequal or when their partners do not share better rewards. Thus, what happens when capuchins must decide whether or not to be prosocial when doing so will also create inequity?

To test this we recently ran a study in which monkeys had to decide whether to bring a set reward to themselves and their partner (Brosnan, et al., in press). Rewards varied such that they were either equal, somewhat unequal (no vs less-preferred reward or less-preferred vs more-preferred reward), or very unequal (no vs more-preferred reward). Capuchins were prosocial – that is, they chose to pull in the rewards more often when a partner was present than absent – when reward were equal or moderately unequal. However, when rewards were very unequal, the subjects were no longer prosocial. This cannot be explained by the presence or absence of a reward for the subject, since the subject received no reward in one of the low-inequity conditions. Thus, it appears that capuchins are willing to be prosocial even when it results in inequity, as long as the inequity is not too great.

3. Conclusions

What can capuchins tell us about the evolution of cooperation? Based on these experiments, quite a lot. To be successful in cooperation, individuals must be able to understand how to cooperate. Although this seems straightforward, it is clear that if the opportunity for cooperation is not intuitive and clear to the interactors, cooperation will fail. Thus providing opportunities to cooperate may not be sufficient if individuals' don't recognize them as such. Second, cooperation will often fail if one individual can monopolize the rewards. In humans, this means that the institutional structure should encourage fair distribution. If this is not possible, then the behavior of the partner is paramount. Cooperation can occur even when one individual gets all of the rewards as long as that individual shares those rewards.

As important as what cooperation requires is what cooperation does not require. Cooperation does not require that each individual get exactly the same payoff on each interaction. Cooperation can survive short-term inequity as long as outcomes are equitable over the long term. Moreover, capuchins behave prosocially towards their partners, even when outcomes are somewhat inequitable. This is of critical importance since outcomes are rarely, if ever, exactly the same in cooperative interactions.

Probably the most critical lesson is that joint efforts seem to require joint payoffs (van Wolkenten, et al., 2007). In other words, individuals seem to expect that their payoffs will be commensurate with the level of effort which they put in. If one individual does not get rewarded appropriately, the interaction falls apart. While this lesson seems rather intuitive, it is important in every enterprise from interpersonal interactions to global politics. As with the monkeys, human cooperation cannot succeed in situations in which inequity prevails. On the other hand, we have a long evolutionary history of cooperative behavior and with a little care, cooperation can be achieved in even the most unlikely of situations.

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