1 Introduction

This dissertation centered on two proximate mechanisms of reciprocal altruism. The scorekeeping mechanism was described as primarily directed at maintaining a balanced relationship, that is: avoiding both underbenefiting and overbenefiting with regard to one’s interaction partner. The bonding mechanism, in contrast, was described as primarily focused on helping one’s friends if they are in need. Evolutionary psychologists generally consider scorekeeping as the mechanism of reciprocal altruism. The previous chapters examined whether bonding forms an alternative to the conventional scorekeeping mechanism, whether bonding is more biologically prepared than scorekeeping, and what is the role of emotions in scorekeeping and bonding behavior. In the concluding chapter I evaluate the answers to these questions, provided in the different chapters. Each of the following sections is devoted to one chapter. After a summary of the study, I conclude with assessing the degree to which the results support the idea that the bonding mechanism forms an alternative to the scorekeeping mechanism, or whether it provides support to the bonding mechanism being more prepared than the scorekeeping mechanism. Each section ends with suggestions for future research and a glance at recent developments. The final section of this chapter contains a general conclusion.
2 Evidence for bonding and scorekeeping behavior from anthropological studies on food sharing

2.1 Summary of study

When evolutionary psychologists argue for the importance of scorekeeping or cheater detection mechanisms, they often refer to food sharing practices in hunter-gatherer societies. Since hunter-gatherers live in conditions that are most similar to those of our ancestors, evidence for scorekeeping in those people would form a strong indication for the conventional idea that our ancestors have evolved a scorekeeping mechanism to cope with the risk of being cheated. In Chapter 2, I took a closer look at anthropological studies on food sharing to determine whether they supported a scorekeeping mechanism or whether the observed sharing practices could also be explained by a bonding mechanism.

Both more descriptive cultural anthropological studies and more quantitative evolutionary anthropological studies were scrutinized. Since neither of those traditions explicitly dealt with the question whether food sharing practices are the result of a bonding mechanism or a scorekeeping mechanism, hypotheses were derived that could be tested with the available data or were actually tested. The cultural anthropological studies were generally supportive to the hypotheses based on the bonding mechanism. Sharing patterns are egalitarian in small groups, and individuals who are in need of food receive food from their group members or friends. There was no strong support for the hypothesis that in larger groups, individuals restrict their sharing to a limited number of friends.

Hypotheses about scorekeeping reciprocity were mainly taken up by the evolutionary anthropological tradition. There was no evidence that individuals avoid to give to free-riders, avoid to be considered a free-rider, or exchange food for other commodities (e.g., sex). In contrast to this, several studies reported support to the most important hypothesis following from the scorekeeping mechanism, i.e., that giving is contingent upon receiving.

In the final section, however, I argued that these results do not provide convincing evidence to the scorekeeping mechanism for two reasons. First, most of these studies use relative measures of sharing. Since these measures control for a person’s or household’s total amount of food resources, they are confounded with the ability to give, and, as a consequence, with need. Second, to assess the relation between the total amount of food a person has received from another person, and the total amount he has provided to this person, all of these studies use correlational measures, or at best, regression analyses in which a limited number of variables are controlled for. However, a positive correlation between food received
and food provided does not necessarily imply that sharing behavior is governed by a concern with maintaining a balanced relationship. It can also be the result of individuals preferentially sharing food with a small group of friends in a non-contingent way. To determine whether people engage in contingent sharing, sequential data of food sharing practices are needed.

2.2 Main conclusions

Based on this review, the frequent references to anthropological studies on hunter-gatherer food sharing as illustrations of scorekeeping behavior can be questioned. The data are either supportive or empirically equivalent to the idea of a bonding mechanism. Therefore, based on the anthropological data, the bonding mechanism can indeed be considered an important alternative to the conventional scorekeeping mechanism.

2.3 Suggestions for future research and recent developments

The importance of using time-dependent measures to assess contingent sharing has also been acknowledged by anthropologists, but is difficult to implement because it requires a sufficiently large sample size and time duration (Gurven, in preparation). In a recent study, Gurven used a crude time-dependent estimate by splitting his sample into two time periods (of approximately one month each), and regressing the amount of food B received from A in the second time period on the amount of food A received from B in the first time period (Gurven, in preparation). Although contingency estimates of some of the resources types remained highly significant, they were much smaller than the conventional contingency estimates in which the total amount of food B received from A was regressed on the total amount of food A received from B. Therefore, it is doubtful whether contingency estimates would remain significant if less crude measures were used. Nevertheless, more studies using time-dependent measures are needed to settle the issue of whether sharing is contingent.
3  

Successfulness of bonding and scorekeeping strategies in a simulation study

3.1  

Summary

The central claim of Chapter 3 was that the popularity of the idea that reciprocal altruism is governed by a scorekeeping or cheater detection mechanism is the result of the use of the Prisoner’s Dilemma game as the conventional way to study the evolution of reciprocal altruism. In the iterated Prisoner’s Dilemma game, actors are externally assigned to each other and forced to make a move, that is: either cooperate or defect. Furthermore, the iterated game consists of a series of one-shot games, in each of which both actors make a move. Chapter 3 introduced an alternative model to study the evolution of reciprocal altruism: the Social Evolution Model (SEM). In contrast to the Prisoner’s Dilemma game, the SEM allows actors to select their interaction partners themselves. This implies that actors are not only endowed with a strategy explicating the conditions under which to cooperate (or help), but also with a strategy explicating which other actor to select as an interaction partner. A second essential difference with the Prisoner’s Dilemma is that nature is added as a player. In each round every actor has a certain probability to be hit by nature and get in distress, and consequently needs to find a helping partner. Given that evolutionary psychologists argue that our behavioral mechanisms have originated in the ancestral environment, which was characterized by highly unpredictable success rates of acquiring food, both of these characteristics make the SEM a better model to investigate the evolution of reciprocal altruism than the Prisoner’s Dilemma game.

Through a series of simulations we investigated the relative success of two cooperative strategies, modeled in accordance to the bonding mechanisms and the scorekeeping mechanism, in invading and subsisting in a population of non-cooperative actors. The scorekeeping strategy (called Keeping Books Balanced) always acted in such a way as to minimize the difference between the number of times that help had been provided from an actor and the number of times that help had been received to this actor. Thus, when asked for help, Keeping Books Balanced actors only helped if the requester was not indebted to them, and preferred to help actors to whom they were indebted themselves. When in need of help, they preferred to be helped by actors who were indebted to them. In contrast, the bonding strategy (called Commitment) always returned to those actors who had proved to be helpful in previous interactions. Thus, both when asked for help and when in need for help, Commitment actors preferred to help or to receive help from those actors who had helped them most often.
In separate simulations, both strategies were confronted with actors following a non-cooperative strategy. Those non-cooperative actors asked for help when in need, but never to the same actor for a second time, and when asked for help they always refused. Simulations were run with different population sizes and various initial proportions of cooperative actors. Additional model parameters were the probability of getting in distress (harshness of conditions), and the costs of helping (operationalized as an increase in the probability of getting in distress in the next round). After 30 rounds the proportion of surviving cooperative actors was recorded as the ratio of the total number of survivors. If this proportion was larger than the initial proportion of cooperative actors, this was interpreted as an increase in cooperators in the next generation. If such an increase occurred at all initial proportions of cooperative actors, this was taken as an invasion by cooperative actors over the course of generations.

The results showed that in general, Commitment actors and Keeping Books Balanced actors were equally successful in resisting an invasion of non-cooperative actors. However, Commitment actors were more successful in invading a population of non-cooperative actors if conditions were harsh or if population sizes were medium-sized or large. In those conditions, the minimum number of actors that could achieve an invasion in a population of non-cooperative actors was lower for Commitment than for Keeping Books Balanced.

3.2 Main conclusions

The results of the simulations indicate that over the course of generations, a reciprocal altruistic strategy that is not primarily focused on avoiding to be exploited does not do worse than a strict scorekeeping strategy. Moreover, in those conditions that are most similar to those of the Pleistocene savanna (i.e., in conditions with the highest probability of getting in distress), the bonding strategy is even more successful than the scorekeeping strategy in invading a population of non-cooperative actors. Therefore, based on this simulation study the bonding mechanism can indeed be considered an important alternative mechanism of reciprocal altruism. Moreover, the results may be interpreted as suggesting that rather than to a scorekeeping mechanism, ancestral conditions gave rise to a bonding mechanism.
3.3 Suggestions for future research and recent developments

Although the simulation study focused on the relative success of two specific cooperative strategies, simulation researchers might raise the criticism that the inclusion of more different strategies - both cooperative and defecting - would have resulted in more robust conclusions. Furthermore, it is also unclear whether the same results would have been found if the model had incorporated noise, that is, the possibility of misperceiving another actor’s behavior. Currently, new simulations are prepared with various cooperative strategies and various cheater strategies, including a strategy that does not keep scores in the sense of primarily acting on the difference between the number of times help has been provided and the number of times help has been received, but that does take note if the other actor has refused to grant a previous request for help (Back 2004). The results of these simulations may be highly relevant to understanding the difference between scorekeeping in the sense of retaliating another person’s indebtedness, and a more literal translation of the Tit for Tat strategy - retaliating a previous refusal to a request for help (see Section 5.3.2).

In addition, the SEM has been extended to investigate the effects of generalized exchange, that is, of actors being able to select their helping partners based on information from third parties. Currently, simulations are being run with actors who provide information about their past interaction history if they are being asked for help while being unable to grant the request themselves (de Vos and Elsas, in preparation).

4 Evidence for bonding and scorekeeping behavior from dilemma situations

4.1 Summary of study

Chapter 4 followed up with the common distinction in the social science literature between communal and exchange relationships. We re-interpreted these two relationships types in terms of the bonding and the scorekeeping mechanism. Whereas the bonding mechanism is triggered by the cue “friend in need”, the scorekeeping mechanism is activated by an imbalance in the amount of benefits provided and received. The main question of Chapter 4 was what happens when individuals are confronted with cues from both mechanisms, thus posing a dilemma between bonding and scorekeeping. Under what conditions will they
respond by providing help to a needy person, and under what conditions will they try to maintain a balanced relationship?

These questions were addressed through two scenario experiments, in which subjects had to indicate their responses to a number of dilemma situations. One scenario posed a dilemma between helping a needy person and reciprocating a creditor (Reciprocate vs help dilemma), a second scenario concerned a dilemma between helping and refusing a person who was in one’s debt (Debtor in need dilemma), and a third one posed a dilemma between helping and refusing a person who himself had refused to help at a previous encounter (Refuser in need dilemma). Both the context of the helping situation (lending money versus providing assistance in the case of illness) and the relationship with the requester (good friend versus acquaintance) were varied between subjects.

In addition, the second study also included an attempt to assess whether one of the two mechanisms had a higher priority, or was more biologically prepared, than the other one. This was done by presenting subjects with an implicit prime in the form of a language correction task, concerning stories about either a typical bonding, a typical scorekeeping, or a neutral situation.

In line with expectations subjects were more likely to perform bonding behavior towards friends than towards acquaintances. Furthermore, in the illness context the degree of bonding responses was much higher than it was in the money context. The effects of the implicit prime were inconsistent and difficult to interpret.

4.2 Main conclusions

The scenario experiments show that different conditions elicit different responses on a dilemma between helping a needy one and avoiding an imbalanced relationship. Although there is no support that the bonding mechanism is more prepared than the scorekeeping mechanism, the results show that individuals do not keep scores of benefits provided and benefits received in all conditions. Moreover, the specific conditions that foster bonding behavior, i.e., the other being a friend and the other being ill and in need of assistance, are most similar to the living conditions and the adaptive problems of our ancestors. Therefore, Chapter 4 does demonstrate the importance of considering bonding as an alternative to the conventional scorekeeping mechanism.
4.3 Suggestions for future research and recent developments

4.3.1 Studying biological preparedness by implicit primes

Although the implicit prime manipulation failed in this study, it would be premature to discard it as a possible method of testing hypotheses about differences in biological preparedness. If highly prepared responses are more easily triggered by an implicit prime than less prepared responses, it might be a valuable method to test whether certain behavioral patterns are the result of evolved psychological mechanisms or whether they are primarily “cultural” patterns. However, before engaging in tests concerning complex mechanisms like scorekeeping and bonding, the implicit prime method should be calibrated using more straightforward mechanisms whose evolutionary status is no longer under debate. For example, one might follow up on Seligman's (1971) suggestions concerning differences in preparedness to learn specific kinds of fear responses. Starting with the assumption that fear responses to rats, spiders, or snakes are more prepared than fear responses to household objects or, let's say, lambs, one would expect that an implicit prime concerning a snake would evoke stronger fear responses on a mood scale, compared to an implicit prime concerning a lamb or a wooden block. When such preliminary studies show that responses whose biological preparedness is not under debate anymore, such as fear responses to snakes, are indeed triggered more easily by implicit primes than non-prepared responses, one can use this method to determine preparedness differences between psychological mechanisms.

In addition, both content and form of the implicit primes should be the subject of preliminary studies. Before presenting specific cues (e.g., stories, pictures, words) as implicit primes, their validity as scorekeeping or bonding cues should be ascertained.

4.3.2 The effect of relationship

Chapter 4 reported only a modest effect of relationship with Alter. However, many studies have found strong evidence for an effect of relationship on helping behavior or preferred distributions of resources. Compared to strangers, friends have been shown to be less concerned with maintaining a balanced relationship, and more concerned with responding to each others’ needs (see Clark and Grote 2003). Recently, even non-human primates have been found to react differently to situational cues closely related to scorekeeping, dependent on the closeness of the relationship with their interaction partner. Brosnan and de Waal (2003; see also
Brosnan et al., in press) conducted experiments among capuchin monkeys and chimpanzees that were based on Ultimatum and Dictator Games used in behavioral economics (e.g., Fehr and Schmidt 2003). Pairs of subjects were taught to exchange tokens for food rewards with a human experimenter. It was found that subjects responded negatively to unequal distributions. Thus, they often refused to exchange, or rejected the reward, when their partner received a better reward, an effect which was amplified if the partner received the better reward without needing to hand over the token. The chimpanzee experiments also considered the effect of relational variables. Dominance rank did not have any effect, but relationship closeness did. Pairs of chimpanzees who had been co-housed in the same group for a long time were less likely to reject unequal distributions than pairs who were co-housed for a shorter time.

The results of these experiments, suggesting that non-human primates do not like underbenefiting compared to a co-specific, seem to contradict the hypothesis that scorekeeping is a recent cultural adaptation to market society. At the same time, however, they also question the ubiquity of the scorekeeping mechanism. Thus, the authors conclude that “tolerance of inequity may increase with social closeness between partners, such as friends and family, in a wide variety of species, a hypothesis that deserves further testing in both humans and non-human primates.” (Brosnan et al., in press, p. 11)

A planned collaborative study with some of the authors elaborates on the effect of relationship on inequity aversion among human subjects. This study will not only re-examine the effect of social closeness, but also focus on the effect of another basic relationship type: one between two individuals of different status. An interesting hypotheses is that high status individuals are more interested in (and more capable) to boast their status by “generously” giving up resources at the benefit of lower status individuals, resulting in a preference for underbenefiting, both to overbenefiting and a balanced relationship. The focus on different types of relationship may increase our knowledge about the conditions favoring different mechanisms of reciprocal altruism.

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1 In defense of this hypothesis, it should be mentioned that the exchanges did not occur “spontaneously” but required explicit training, that the reported results of the capuchin experiment only concerned five female subjects since pretests had shown that males did not react to inequity (Brosnan and de Waal 2003), and that neither of the studies provided support to the other component of scorekeeping behavior, avoidance of overbenefiting.
5 Emotions associated with bonding and scorekeeping behavior

5.1 Summary of study

The scenario experiments discussed in Chapter 4 also contained measures of emotional responses. Chapter 5 focused on the emotion responses obtained in one of those experiments. In contrast to the previous chapters, this study was not so much concerned with the question whether or under what conditions individuals behave according to the bonding or the scorekeeping mechanism. Rather, the two mechanisms were considered as given, and used to derive hypotheses about the relation between emotions and behavioral responses. Based on the scorekeeping mechanism, it was hypothesized that refusing to help a requester who is in one's debt or who has refused to help at a previous encounter is instigated by Retaliatory emotions like indignation and anger. Similarly, reciprocating someone to whom one is indebted was predicted to be the effect of Urge-to-Reciprocate emotions like guilt, obligation, gratitude and fear of retaliation. Based on the bonding mechanism, we predicted that helping a needy person is the result of Bonding emotions like commitment and warmth.

In addition to relations between specific emotions and behavioral responses, we also tested the general evolutionary psychological assumption that emotions form the link between cues and behavior. This was done by examining the degree to which the emotion variables mediated the effect of situational variables (e.g., object of help and relationship with the requester) on behavioral responses. We also predicted that emotions would mediate the effect of personality variables on behavioral responses.

Logistic regression analyses confirmed the relation between Bonding emotions and helping behavior, as well as the relation between Retaliatory emotions and refusing to help a debtor or refuser. There was less support for the effect of Urge-to-Reciprocate emotions. Only subjects who were highly sensitive to injustice showed the expected relation between guilt and reciprocating behavior. Moreover, only in the case of money did obligation lead to reciprocating behavior. Gratitude and fear of retaliation did not have any effect on behavioral response.

The intermediating role of emotions was supported for the dilemma between helping and refusing a debtor or refuser. In contrast, in the dilemma between helping a needy one and reciprocating a creditor, there was no support for a mediating role of emotions between situational and personality characteristics on the one hand, and behavior response on the other hand. Rather, they seem to play a moderating role.
5.2 Main conclusions

Chapter 5 did not involve a confrontation of the scorekeeping and the bonding mechanism, but considered both as given. Therefore, it does not provide a test concerning the biological primacy of either mechanism. However, the results of Chapter 5 do demonstrate that individuals’ responses on requests for help are not only affected by typical scorekeeping emotions like anger and indignation, but also by emotions expressing a bond to the other person and a concern for his well-being. Furthermore, Chapter 5 provided partial support to the evolutionary psychological interpretation of emotions, namely as forming the link between cues from the environment and personality characteristics on the one hand, and behavioral responses on the other hand.

5.3 Suggestions for future research

5.3.1 Effect of specific emotions

Chapter 5 provided support to the importance of Bonding emotions, like commitment and warmth, for helping behavior, as well as the importance of Retaliatory emotions, like anger and indignation, for avoiding underbenefiting. In contrast, the role of the alleged Urge-to-Reciprocate emotions, like gratitude, obligation and fear of retaliation, is unclear. As was suggested, this might be due to the fact that these emotions concern secondary emotions and are more liable to differences in interpretation. However, it is also possible that these emotions have different functions than the ones hypothesized. For example, rather than functioning as an incentive to directly return a favor, the emotion of gratitude might simply function to strengthen one’s bond with a benefactor. More studies on the functions of specific emotions are needed to solve these issues.

5.3.2 Indebtedness versus refusals

A number of findings of both Chapter 4 and Chapter 5 suggested that we may need to qualify the scorekeeping mechanism. In both chapters, avoiding underbenefiting was operationalized in two ways. In the Debtor in need dilemma it was operationalized as avoiding Alter to be in my debt. In the Refuser in need dilemma, a more literal translation of the Tit for Tat strategy was followed, with avoiding underbenefiting being operationalized as avoiding to provide help to Alter if he refused to help me at a previous encounter.
Although the general pattern in behavioral and emotional responses was more or less similar, subjects reacted much more negatively to a requester who had refused to help them at a previous encounter than they did to a requester who was in their debt. This was especially the case in the illness context, where subjects were less likely to grant a request for help, reported less Bonding emotions and Obligation and more Retaliatory emotions, needed to be relatively prosocial to grant the request, and needed to have a relatively close relationship with the other person to grant the request. These results may be interpreted as pointing to the importance of responding to each other’s needs. Although people do not mind if someone is indebted to them, they do mind if someone refused to help them when they were in need.

Future research should shed more light on the differences between these two types of relationship imbalances. The reported results suggest that people are more likely to forgive debts than to forgive refusals. Moreover, one might speculate that friendship dissolution is not the result of me giving more benefits to my friend than he returns to me, but of my friend letting me down when I need his help.

6 General conclusion

After reviewing the four chapters, can we conclude that the attempt to establish bonding as an alternative to the conventional scorekeeping mechanism of reciprocal altruism has succeeded? I think we can. Food sharing practices by hunter-gatherers, which are often used as an illustration of scorekeeping, were demonstrated either to explicitly support or to be empirically equivalent to a bonding mechanism. Furthermore, compared to a scorekeeping strategy, bonding proved to be an equally or even more successful strategy when confronted with a non-cooperative strategy in a simulated environment characterized by a high probability of getting in distress. Moreover, when confronted with a dilemma between bonding and scorekeeping behavior, many subjects responded in accordance with the bonding mechanism, especially in conditions that were most similar to the ancestral environment. Finally, typical bonding emotions like commitment and warmth were shown to have a significant effect on reciprocal altruistic behavior.

Can we also draw conclusions about the biological primacy of one either mechanisms? In Chapter 1, I speculated that the bonding mechanism might be more biologically prepared than the scorekeeping mechanism. According to this
idea, the bonding mechanism has evolved far back in our evolutionary past, whereas scorekeeping is a relatively recent cultural adaptation. As a consequence, bonding behavior is learnt and triggered very easily, whereas it takes more effort to learn and to perform scorekeeping behavior (cf. de Vos 2004; de Vos and Wielers 2003; Hoyt 1926; Tooby and Cosmides 1996). Did the previous chapters provide any evidence to the evolutionary primacy of one of either mechanisms? The simulation study provided some support to the claim that the bonding mechanism is more likely to have been selected for in the ancestral environment than the scorekeeping mechanism is. The only empirical test of the hypothesis about differences in preparedness concerned a comparison of behavioral responses between subjects who were confronted with implicit primes for either scorekeeping or bonding behavior. This test did not give a definite answer.

In sum, although this dissertation has demonstrated that the scorekeeping mechanism is not so ubiquitous as is generally believed, many questions still have to be answered. More research is needed to determine what are the relevant cues for bonding and scorekeeping, what are the conditions in which the bonding and scorekeeping mechanism are operational, and what emotions are associated with either bonding or scorekeeping behavior. And finally, the issue of whether one of either mechanisms is more biologically prepared than the other, and how to determine differences in biological preparedness in general, needs both theoretical and empirical elaboration.