'You scratch my back and I scratch yours' versus 'love thy neighbour'

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CHAPTER 1

Introduction

Imagine that a close friend comes to you and confides that he is in financial trouble because of some misfortune beyond his control; for example, his wallet had been stolen. What would you do should he ask you to lend him some money? If you had sufficient funds in your bank account, you would probably grant his request. How would you react, however, if he should come to you a few days later and asks you to drive him to the police station to report the theft? And what would you do if he should ask you for an additional loan three weeks thereafter, as it was still impossible to access his bank account? You would probably be torn between two considerations or perspectives. On the one hand, your friend’s requests for favors might cause you to become irritated and indignant, since he has not repaid his debts. On the other hand, you care for your friend and want to help him. I refer to the first perspective as “scorekeeping,” as it considers primarily the balance between benefits provided and benefits received. I refer to the second perspective as “bonding,” as it focuses on the needs of the other person. In this case, should the scorekeeping perspective prevail, you would probably refuse to grant your friend’s latest request. In contrast, should the bonding perspective prevail, you will probably help him again.

This dissertation focuses on these two perspectives. I will use evolutionary psychological arguments to provide a theoretical background for the scorekeeping
and bonding perspectives, and derive hypotheses about their occurrence. Evolutionary psychology considers these perspectives to be rules or heuristics that have evolved to cope with recurrent situations that our ancestors encountered. Such rules or heuristics are called *proximate mechanisms*, as they describe how people behave in particular domains of social life. However, when applying an evolutionary framework, proximate mechanisms cannot be studied in isolation from the question of *why* they evolved among our ancestors. In other words, what were the benefits of these proximate mechanisms to the survival and reproduction of individuals (i.e., an individual’s fitness)? The answer to this question provides the *ultimate cause* of these mechanisms. According to evolutionary psychology, the fitness benefit, or ultimate cause of helping or doing favors for another unrelated individual boils down to *reciprocal altruism*: helping another individual can be beneficial if that individual reciprocates in the future.

Most evolutionary psychologists consider scorekeeping to be the primary mechanism of reciprocal altruism. The reason is that individuals who accept help but never return anything are better off in terms of fitness than are individuals who provide unconditional help. Therefore, a mechanism has evolved that leads us to keep track of benefits provided and benefits received and to avoid help individuals who do not repay their debts.

Recently, however, several scholars have come to realize that scorekeeping mechanisms cannot explain all instances of reciprocal altruism and that another mechanism, such as bonding, might be at work. Moreover, taking the conditions of our evolutionary past into account, scorekeeping mechanisms may have even been detrimental to fitness. Yet, the concept of a bonding mechanism has not received much attention in evolutionary psychology.

The primary goal of this dissertation is therefore to demonstrate that the scorekeeping mechanism is not so ubiquitous as is generally believed and to show that there is considerable evidence for the operation of an additional mechanism. At some points I will go a step further, arguing that bonding is the primary mechanism of reciprocal altruism, whereas scorekeeping is a relatively recent cultural adaptation. Since emotions are considered to play an important role in the evolutionary psychological concept of proximate mechanisms, a third goal is to examine the effect of emotions on typical bonding and scorekeeping behavior. Data and findings from various sources will be used to address these issues. Chapter 2 is a critical review of anthropological studies on food sharing among hunter-gatherers. Chapter 3 deals with simulation data, and Chapters 4 and 5 present the results of scenario experiments.
The section to follow begins with a brief discussion of evolutionary psychology. It elaborates on the importance of the ancestral environment, the focus on proximate mechanisms, and the role of emotions in evolutionary psychology. The subsequent section introduces the concept of reciprocal altruism as an ultimate explanation for helping behavior and presents the scorekeeping and bonding mechanisms as alternative proximate mechanisms of reciprocal altruism. Section 4 discusses the merits of an evolutionary perspective for sociology, as well as some well-known criticisms of evolutionary approaches to human social behavior. The final section provides an overview of the dissertation.

2 Evolutionary psychology

Evolutionary psychology applies the theory of evolution to the domain of human behavior. Thus, it assumes 1) that behavior, or behavioral design, has a genetic basis, and 2) that during the course of evolution those behavioral designs have been selected that promoted the propagation of the genes responsible for those behavioral designs (Dawkins 1989). Moreover, evolutionary psychology makes two additional claims. First, our present behavioral designs are the result of selection pressures in ancestral environments. Second, adaptations take the form of domain-specific psychological mechanisms. The two sections to follow elaborate these assumptions. Because emotions play an important role in the concept of psychological mechanisms, the third section discusses the role of emotions.

2.1 Assumption 1: Humans are adapted to ancestral conditions

2.1.1 The environment of evolutionary adaptedness

Evolutionary psychologists argue that it takes many generations for new traits to evolve and become part of a species’ repertoire. Therefore, explanations of current behavior should consider ancestral conditions (e.g., Buss and Kendrick 1998; Crawford 1998; Durrant and Ellis 2003; Rossano 2003; Symons 1992; Tooby and Cosmides 1990b). Understanding any adaptation, regardless of whether it is a morphological or a behavioral design feature, requires consideration of the ancestral environment.
environment in which the trait evolved, the *Environment of Evolutionary Adaptedness* (EEA) (Bowlby 1969). The EEA of a species does not refer to a specific place or time, as different traits or design features originated in different places and at different times. For example, the EEA of the design feature walking (on land) lies about 400 million years in the past, whereas the EEA of bipedality lies only about 5 million years ago. Tooby and Cosmides (1990b, p. 386) define the EEA for a species as “a statistical composite of the adaptation relevant properties of the ancestral environment encountered by the members of ancestral populations, weighted by their frequencies and fitness-consequences.” For most purposes, however, the EEA for a species can be taken to refer to the most recent segment of a species’ evolution, in which it took its present form and diverged from related species. For the human species, this is the Pleistocene era, the period between approximately 1.5 million and 10,000 years ago (Tooby and Cosmides 1990b). With some minor exceptions (e.g., intolerance for milk among some non-white populations [see McCracken 1971]), the post-Pleistocene period was too short to have resulted in any complex changes in behavioral or morphological design (Symons 1992, p. 138; Tooby and Cosmides 1989, p.34).

It should be emphasized that this does not mean that all of our characteristics were formed during the Pleistocene period. Many design and behavioral features originated much earlier and are shared with other species. Examples include our basic body plan, visual system, sexual reproduction patterns (including displays of coyness), and tendency to care for our offspring. Neither does it mean that the Pleistocene period was a featureless monolith in which life was simple and constant (e.g., see Turke [1990] for this criticism). As is evident from the wide geographical range in which human remains have been found and the occurrence of several strong climatic changes, humans did encounter various habitats and changes in environmental conditions during this period. What was constant, however, was their nomadic existence. Our ancestors lived as hunter-gatherers until the emergence of agriculture 10,000 years ago. Evolutionary psychology assumes that those living conditions have shaped our present behavioral design features.

### 2.1.2 Pleistocene selection pressures

Given that humans are adapted to Pleistocene conditions, it is important to know which selection pressures our ancestors encountered in this environment. This section provides a sketch of the Pleistocene selection pressures and how our ancestors changed from arboreal apes to highly social primates. This sketch is
unavoidably speculative. Although climatological, ecological, paleo-
anthropological, and archaeological data support this portrayal, it remains
impossible to go back in time and determine whether it actually happened this way.

Climatic changes at the end of the Miocene era reduced the range of
tropical rain forests and increased the prevalence of savanna-like environments,
which had become abundant as early as five million years ago. Compared to forest
environments, resources in such environments are more spatially patchy, seasonally
variable, and overall less abundant (Boehm 1999; Boyd and Silk 1997; Foley 1987;
1996; Folch and Camarasa 2000; Tooby and DeVore 1987). The open environment
also made our ancestors more vulnerable to predators. Our ancestors, who had
previously lived as tree-dwelling apes, were forced to adapt to the new
environment. Phylogenetic comparisons of extant primates suggest that the social
organization of our hominoid ancestors consisted of small groups ranging through
the forest. Groups were centered on a number of kin-related males, whereas
females dispersed to other groups at maturity (Di Fiore and Rendall 1994; Foley

What types of changes in social organization occurred when the habitat of
these apes changed from rain forest to savanna? The literature on this subject
provides several interconnected arguments. First, the patchy distribution of food
resources (an important part of which consisted of large animals) and the presence
of predators formed a selection pressure for increasing group size to extend
beyond the boundaries of kinship (Boyd and Silk 1997; Hyland 1993; Tooby and
DeVore 1979). Moreover, because individuals had to travel large distances to
acquire food, groups tended to separate into smaller groups during the day,
returning to the campsite to spend the night together (Barrett et al. 2002; Isaac

Social organization in the form of fission-fusion groups required individuals to
maintain a full range of ties in the absence of spatial proximity, which was possible
only in the presence of strong bonds (Foley 1996; Rodseth et al. 1991). The need
to maintain a growing number of complex relationships subsequently selected for
an increase in brain size (Dunbar 1993; Humphrey 1976). The increased
dependence on meat may have played an important role in the expansion of the
brain, because meat provides the body with more proteins and energy than do
plant foods, and takes less energy to digest (Foley 1996; Tooby and DeVore 1979).
In its turn, the increase in brain size selected for even higher levels of sociality
because it led to earlier birth and a longer period of infant altriciality.
Consequently, interdependence increased between group members, with females
becoming particularly more dependent on males (Deacon 1997; Foley 1996).
Finally, food sharing was very adaptive within these interdependent groups living in harsh conditions, as it reduced the risk of starvation (Boyd and Silk 1997; Campbell 1979; Kurland and Beckerman 1985; Winterhalder 1986). Furthermore, the nature of the food sources, particularly meat, made the costs of sharing relatively low: captured animals usually provided more meat than one person could consume. The practical infeasibility of storage made sharing a sensible alternative (Boyd and Silk 1997; de Waal 1996; Tooby and DeVore 1979).

2.2 Assumption 2: Humans are equipped with domain-specific psychological mechanisms

The previous section argued that humans are adapted to the conditions of the Pleistocene environment. The evolutionary psychological view interprets adaptations as domain-specific mechanisms (Symons 1992; Tooby and Cosmides 1990b). Domain-specific mechanisms are activated by cues that consistently accompanied fitness-relevant situations in the EEA. Through a series of internal monitoring and communication systems, the appropriate perceptual, physiological, and behavioral responses are selected and activated. For example, the cue “large fanged animal approaching” triggers a whole array of physiological changes that prepare the individual to flee, or, if flight is not possible, to fight the animal. The internal cue “low blood sugar” urges the individual to find food and eat. Emotions play an important role in the link between cues and responses: the experience of fear compels an individual to flee; the experience of hunger compels an individual to find food and eat (see Section 2.3). In summary, evolutionary psychologists conceive of the mind (both the human and non-human mind) as a collection of domain-specific mechanisms, each evolved to cope with a specific fitness-relevant situation in the EEA. This is the meaning of the often used metaphor of the mind as a Swiss army-knife.

The focus on domain-specificity stands in contrast to an alternative view, which conceives of humans as fitness maximizers. According to this view (known variously as Darwinian anthropology, Darwinian social science, and sociobiology), an organism’s behavior is not steered by domain-specific mechanisms, but by a general rule to do whatever promotes the individual’s fitness. Rather than using knowledge about the ancestral environment to formulate domain-specific psychological mechanisms and make predictions about present behavior and
preferences, Darwinian anthropologists focus on the adaptive consequences of specific behaviors in the present environment.\footnote{The concept of individuals as fitness maximizers is adopted from the behavioral ecology tradition in biology, which rarely addresses the difference between the ancestral and the current environment. One possible explanation for this difference in focus is that the concept of the EEA is more relevant to human adaptations, as cultural and technological changes have outpaced organic evolution more in humans than in any other species (e.g., Tooby and Cosmides 1989, p. 35; Symons 1990). Others have argued, however, that behavioral ecologists would also benefit from focusing more on ancestral conditions, as there are also mismatches between the contemporary environments and the EEAs of non-human animals (e.g., Crawford 1993; Daly and Wilson 1999).}

Most evolutionary psychologists consider the claim that organisms are fitness maximizers to be fundamentally wrong or, at the very least, highly susceptible to misinterpretation (Symons 1992; Tooby and Cosmides 1990b). If organisms are fitness maximizers, or if they behave as if they are maximizing fitness, then organisms must somehow be able to respond adaptively to any given situation. In other words, the claim implies that organisms are able to adapt instantaneously to novel conditions. This is in contradiction to the basic principles of evolution, namely, that natural selection acts on variation in a population, resulting in well-adapted traits over the course of generations (e.g., Cosmides and Tooby 1995; Dewsbury 1992, p. 98; Symons 1992; Tooby and Cosmides 1990b). For example, the presence of large predatory fish forms a selection pressure for small fish to become larger. This does not mean that little Nemo actually grows bigger. It means that if little Nemo is slightly larger than his friends are, he has a higher chance of surviving and propagating his genes than do smaller fish. Given that size is linked to genes, the following generation will contain a larger proportion of slightly bigger fish. As long as the selection pressure of large predatory fish is present, and as long as there are no conflicting selection pressures, new generations of fish will have a larger average size than the previous ones. In retrospect, this process can be summarized as small fish maximizing their fitness by becoming larger. They are not actually maximizing fitness, however; they are only expressing the body plan that was selected in previous generations. The same argument holds for human behavior: \textit{humans are adaptation-executioners, not fitness-strivers} (Tooby and Cosmides 1990b, p. 420; see also Barkow 1990, p. 344).

The assumption that individuals are fitness maximizers is also present in such phrases as, “animals have an ability to learn how to maximize fitness,” “their flexibility allows them to learn the best response,” “humans have a capacity for culture,” and “human consciousness enables us to maximize fitness” (Cosmides and Tooby 1995). All of these statements are black-box explanations, as they do not explicate \textit{how} organisms maximize fitness. Upon explication of the mechanism,
these explanations become problematic. The following paragraphs discuss two additional explications of such mechanisms: learning and consciousness.

The view that animals are like blank slates, acquiring information about how to maximize fitness through a process of trial-and-error learning is problematic because such a process would be extremely inefficient (Cosmides and Tooby 1995). For example, what should you do when you are confronted for the first time in your life with a large fanged animal approaching? Talk to it? Stand on your head? It seems highly unlikely that, from an almost endless number of responses, you would randomly pick one that would promote your survival and allow you to bring your newly learned response into practice in a subsequent encounter. A less ridiculous account may point to the ability to imitate or learn adaptive behavior from parents or co-specifics. However, imitation or learning only leads to adaptive behavior if the teachers have already solved the adaptive problem. This does not mean that evolutionary psychology denies the power of learning. It only denies that our learning is domain-general – that our minds are completely blank and absorb any information that is presented to them. Section 4.2.1 discusses the evolutionary psychological view of learning in more detail.

Human consciousness is a second mechanism that has been proposed as a general fitness maximizing system. According to this argument, human consciousness enables us to plan, to formulate goals, and to oversee the consequences of various courses of action (scenario-building), thereby helping us to adapt quickly to novel conditions (e.g., Alexander 1990; Turke 1990). Again, evolutionary psychologists do not deny that consciousness and its associated qualities are important adaptations. However, the ability to plan, to formulate goals, and to build scenarios does not imply the pursuit of fitness maximization. According to evolutionary psychologists, we do not pursue the general goal of fitness maximization, but rather a large number of intermediate goals that have evolved in the process of natural selection, including the desire for sex, the need to belong, and the tendency to care for our offspring (Symons 1992).

2.3 The importance of emotions

The previous section elaborated on the arguments that evolutionary psychologists provide for the concept of domain-specific psychological mechanisms. This section focuses on describing these mechanisms. As mentioned above, emotions play an important role in these mechanisms.

The function of emotions has received considerable attention within the field of social psychology. According to Plutchik (1962, p. 151), an emotion is “a
patterned bodily reaction of either destruction, reproduction, incorporation, orientation, protection, reintegration, rejection or exploration or some combination of these, which is brought about by a stimulus. Emotions are typically transient, adaptive, biological reactions which are usually (but not necessarily) triggered by external stimuli.” Lazarus (1991, p. 38) defines an emotion as a complex disturbance that includes three main components: subjective affect, physiological changes related to species-specific forms of mobilization for adapted action, and action impulses having both instrumental and expressive qualities. According to Frijda (1986, p. 371-372), emotions are changes in action readiness in response to events that are relevant to the individual's concerns. These concerns are, to some extent, a reflection of his or her biological interests. Finally, Cosmides and Tooby (2000, p. 93) define an emotion as a super-ordinate program whose function is to direct the activities and interactions of the subprograms governing perception, attention, inference, learning, memory, goal choice, motivational priorities, categorization and conceptual frameworks, physiological reactions, behavioral decision rules, and many other processes (see also Nesse 1990; Parker 1998; Scherer 1996).

All these definitions agree on at least three points. First, emotions have a bodily component. Second, they form the link between cues and responses. Third, emotions are the result of selection processes; they have evolved to cope with specific fitness-relevant situations. Note that a definition including these elements points does not exclude non-human animals from having emotions. Plutchik (2003, p. 225-226) thus states, “[a]ll organisms have sensors that detect special chemicals as well as gradients of intensity. All organisms have start and stop mechanisms that determine the beginning and end of actions. […] Given the fact that emotions are forms of adaptation made to environmental events, is there any reason to limit the application of the term to humans?” (see also Cosmides and Tooby 2000).

Many scholars have described the relevant cues and adaptive consequences of specific emotions. For example, love is triggered by the long-standing and stable presence of another person (particularly a mate), urging us to stay with this person even in the presence of attractive alternatives (Frank 1988; Nesse 1990). Guilt is triggered by the ill treatment of another person by the subject, and functions to urge reparation of the relationship (Eisenberg 2000; Fessler and Haley 2003; Lewis 1993; Parker 1998). Shame is a stronger form of guilt and leads individuals to avoid those whom they have harmed (Eisenberg 2000; Lewis 1993). Finally, anger is triggered by harm done by another person, and leads to behavior aimed at punishing the offending person (Nesse 1990; Trivers 1971).
But do we really need emotions? Couldn’t we survive with specific programs linking each cue to the adaptive response without the intervention of an emotion? In other words: It’s fine that my body tells me to withdraw my foot if I step on a thorn, but why does it have to hurt so much? Why don’t we simply have a program that leads us to withdraw our foot if it makes contact with an object that damages the upper skin layer? These questions actually touch on two different issues, and answering them requires that we distinguish between emotions and feelings. An emotion is the internal program that links cues with responses. A feeling is the subjective experience that accompanies an emotion (Cosmides and Tooby 2000; Damasio 1994, 2000).

The answer to the question, “Do we need emotions?” is therefore an unequivocal “yes.” We need emotions for the same reason that we need domain-specific mechanisms. Without them, there would be no mechanism for linking fitness-relevant cues to responses. We would somehow need to know, or learn through trial and error, the responses that would be most suitable in each situation. Damasio (1994) made a similar argument, asserting that it is simply impossible to select the appropriate response from all possible responses. Emotions function to highlight the one that has proved to be the best response in the past.\(^3\) A number of case studies of people with neurological impairments provide evidence that the absence of emotions is associated with an inability to make decisions (Damasio 1994).

The question, “Why do we suffer if we step on a thorn?” boils down to the question, “Why do we have feelings?” Its answer is less straightforward. Given that feelings are not prerequisites for emotions, they may seem unnecessary and even burdensome in some cases. According to Damasio (2000, p. 284-285), however, this is incorrect. Feelings are incentives to heed the consequences of an emotion – in the case of pain, to tend the wound and protect it while it is healing. In his view, the emergence of consciousness served to extend the reach of an emotion even further. Knowing that we have feelings associated with an emotion forms a much stronger incentive than would the feeling of an emotion alone. This allows us to plan specific and non-stereotyped responses that can either

\(^3\) The phrase “in the past” is left ambiguous on purpose. In his book, *Descartes’ error*, Damasio argued that at least our secondary or social emotions are the result of learning processes in the past (Damasio 1994, p. 174), suggesting some form of the trial-and-error learning that I just criticized. In his later work, *The feeling of what happens* he corrected this confusing claim by emphasizing that secondary emotions are not solely the result of education within a culture. They are biologically preset, either partly or mostly. Because many emotions appear only later in human development (e.g., guilt or shame), however, environmental factors appear to play an important role (Damasio 2000, note 13 of chapter 2). Anticipating the argument on the interactions between nature and learning (see Section 4.2.1), we might say that humans are biologically prepared to learn to feel guilt and shame.
complement the emotion or guarantee that the immediate gains brought by the emotions are maintained over time.

3 Reciprocal altruism

The subject of altruism has been of major importance in sociobiology and evolutionary psychology. The founding father of sociobiology, Edward O. Wilson, described it as the central theoretical problem of sociobiology: “How can altruism, which by definition reduces personal fitness, possibly evolve by natural selection?” (Wilson 1975, p. 3). Part of the answer to this question lies in the theory of kin selection (Hamilton 1964), in which the adaptiveness of altruistic behavior is presented as a linear function of the genetic relatedness to the beneficiary. To explain altruism between unrelated individuals, Robert Trivers (1971) introduced the term reciprocal altruism. Trivers argued that providing a benefit to a non-related individual is beneficial to an actor’s fitness if the costs of this action are lower than the benefits received in return over the long term. Individuals who are willing to provide benefits to non-related others are better off in the long term than are individuals who reap benefits from altruistic others without bothering to reciprocate, provided that altruists respond to cheaters by curtailing all future possible altruistic gestures to such individuals (Trivers 1971, p. 36).

When Trivers formulated his theory, evolutionary psychology did not yet exist. Although he presented a psychological system underlying reciprocity, and although he noted that a hominid species in the Pleistocene period would have met the preconditions for the evolution of reciprocal altruism (for example, life in small, mutually dependent social groups), his focus was on the benefits and (especially) the potential costs of reciprocal altruism in the present environment. Also most later scholars deduced the specific mechanism or strategy of reciprocal altruism by using a game theoretical argument, rather than by analyzing specific adaptive problems in the ancestral environment. The next section provides a discussion of this conventional mechanism of reciprocal altruism, including a review of the empirical support. Section 3.2 discusses a number of criticisms of the scorekeeping account. Section 3.3 introduces an alternative mechanism that incorporates ancestral selection pressures. The discussion concludes with Section 3.4, which addresses the question of how these two mechanisms are related.
3.1 The scorekeeping mechanism

The basic argument underlying the scorekeeping mechanism is that a group of mutually sharing individuals is vulnerable to free-riders. In a group of generous individuals, a free-rider, who gladly accepts the benefits of his generous group members without returning anything, is better off in terms of time and resources. Consequently, she has higher reproductive fitness. The only way to avoid exploitation by free-riders is to use a conditionally cooperative strategy: to make cooperative behavior contingent on the behavior of the other. Thus, if someone shares food with me, I will then share with that person as well. If the other does not return a benefit when I have shared with her, she is apparently a free-rider and should be excluded from sharing (Cosmides and Tooby 1992; Reeve 1998; Trivers 1971).

According to the scorekeeping account, one’s behavioral response in such a situation is based on (unconscious) calculations regarding the amount of benefits one has provided to another individual and the amount of benefits received from this person. In the case of an unfavorable imbalance, (i.e., if the benefits one has provided exceed the benefits one has received) any further benefits are suspended until the other has restored balance.

Individuals also attempt to restore balance in the opposite situation. A favorable imbalance, therefore, compels an individual to restore balance by providing benefits to the other person (Boehm 1999, p. 183-184; Bugental 2000, p. 199-200; Krebs 1998, p. 347). The reason being that if a person acts only on unfavorable imbalances, while ignoring (or even pursuing) favorable imbalances, his interaction partners will conclude that the person is a free-rider and refuse to provide any more benefits.

Although the scorekeeping mechanism presumes some cognitive abilities, it does not necessarily rely on purely calculative processes. Unfavorable imbalances may elicit emotions of indignation or even anger. These emotions, in turn, trigger behavioral responses aimed at restoring balance (Nesse 1991; Parker 1998). On the other hand, favorable imbalances may lead to compensating behavior through emotions of gratitude and obligation or, in the case of longer standing debts, shame, guilt, and humiliation (Nesse 1991; Parker 1998; Pinker 1998; Trivers 1971).

The scorekeeping mechanism is strongly rooted in game theory. When Trivers introduced the concept of reciprocal altruism, he referred to the analogy with the Prisoner’s Dilemma, as introduced by Luce and Raiffa (1957), and Rapoport and Chammah (1965) (for an elaboration of the Prisoner’s Dilemma, see Chapter 2, note 2; and Chapter 3). Trivers’ concept of reciprocal altruism was
identical to the optimal strategy in an iterated Prisoner’s Dilemma (Trivers 1971, p. 38). More recently, evolutionary game theorists confirmed the success of a reciprocal altruistic strategy. In a study by Axelrod (1984), simulated actors with different strategies competed in iterated Prisoner’s Dilemmas. The most successful strategy was a strategy called “Tit-for-Tat,” which cooperated on the first move and thereafter imitated the move of its interaction partner. Thus, it rewarded cooperative behavior with cooperation and punished defecting behavior with defection. This strategy came to be known as the embodiment of Trivers’ reciprocal altruism.

Following Axelrod’s tournaments, many mathematical and simulation studies have been conducted with other payoff matrices, additional parameters, large groups instead of dyads, different strategies, et cetera (e.g., Boyd and Richerson 1988; 1989; Hayashi 1993; Kollock 1993; Nowak and Sigmund 1993; Roberts and Sherrat 1998; for a critical review, see Gotts et al. 2003). In general, these studies agree that, by the nature of the game, cooperative actors are able to withstand non-cooperative actors only if they make their behavior conditional on the behavior of their interaction partners (i.e., by adopting some form of Tit-for-Tat strategy or by keeping track of each other’s contributions) (Brown 1983; Dugatkin 1997).

Studies from several fields show that people actually behave according to such a scorekeeping mechanism. Exchange experiments have shown that subjects do indeed match the benefits they provide to the benefits provided by their interaction partners (Chertkoff and Esser 1976; Galluci and Perugini 2000; Komorita and Esser 1975; Pruitt 1968; Rapoport and Chammah 1964). Support for the avoidance of advantageous imbalances, or overbenefiting, is provided by studies in the field of equity theory (Griffith et al. 1989; Walster et al. 1973; Walster et al. 1978). Many studies have shown that people avoid asking others for help if they are unable to repay them (Castro 1974; Greenberg and Shapiro 1971; Morris and Rosen 1973), are more motivated to offer help to a person if this person has helped before (Greenberg and Bar-Tal 1976; Gross and Latané 1974; Shumaker and Jackson 1979), and experience negative emotions after overbenefiting (Bar-Tal and Greenberg 1974; Buunk et al. 1993; Castro 1974; Gross and Latané 1974; Shumaker and Jackson 1979).

The only study that makes an explicit attempt to demonstrate that humans have a domain-specific psychological mechanism for scorekeeping is Cosmides and Tooby’s cheater detection study (Cosmides 1989; Cosmides and Tooby 1992). Cosmides and Tooby argued that, if humans have evolved a domain-specific psychological mechanism to cope with the presence of cheaters, they should be
extremely sensitive to situations in which there is a possibility of being cheated. Following experiments by Peter Wason (1966), they presented subjects with a conditional “if … then” rule concerning either a descriptive rule (e.g., “If one goes to Boston, then one takes the subway”), or a rule involving a social contract (e.g., “If you take the benefit, then you pay the cost”). They then asked which of four cards should be turned over to determine if the rule was violated. For example, the correct logical solution for the “If one goes to Boston, then one takes the subway” rule is to turn over the “goes to Boston” (P) and “take the train” (not Q) cards (see Figure 1.1).

The results of their experiments showed that persons are much better at detecting violations of rules that have the form of a social contract than they were at detecting violations of descriptive rules. Cosmides and Tooby (1992) interpreted this as support for the hypothesis that humans have a domain-specific mechanism for detecting cheaters (see also Gigerenzer and Hug 1992).

Figure 1.1: Example of the Wason selection task

Indicate only those card(s) that you definitely need to turn over to see if the following rule is violated: “If one goes to Boston, then one takes the subway”.

The idea that reciprocal altruism takes the form of scorekeeping has also pervaded into other disciplines. Since the sharing of food is often mentioned as the prototypical instance of scorekeeping behavior, anthropologists have used field data to test this idea (see for a review Gurven 2004). Primatologists have also been interested in demonstrating scorekeeping behavior in their research subjects (for a review, see Brosnan and de Waal 2002). Given that human and non-human primates are closely related, evidence of scorekeeping among non-human primates would imply that the evolutionary origins of this behavior are very old. Section 3.2.2 discusses the problem of assessing contingency that is present in many of these anthropological and primatological studies. Chapter 2 elaborates further on anthropological studies concerning scorekeeping reciprocity and the validity of their conclusions.
3.2 Criticisms of the scorekeeping account

The idea that reciprocal altruism is governed by a scorekeeping mechanism has been influential in evolutionary psychology. Analyses of cooperation between unrelated individuals usually consider the interaction partners to be scorekeepers or cheater detectors. A number of criticisms can be made on this account, however. The following sections argue that not all relations are governed by scorekeeping considerations, that the empirical evidence for the scorekeeping mechanism is not as strong as has been suggested, and that the scorekeeping explanation ignores ancestral selection pressures.

3.2.1 Friends do not keep scores

Recently, several authors have begun to question the ubiquity of scorekeeping. An important example of a relationship involving the mutual provision of benefits concerns the relationship between friends. However, a defining feature of friendships is that they are not characterized by scorekeeping. According to Tooby and Cosmides (1996), scorekeeping behavior is restricted to the exchange domain, which is characterized by explicit contingent exchange and turn-taking reciprocation. Altruistic adaptations in the friendship domain do not map unto the structure of tit for tat or any other standard model of reciprocal altruism. Instead, friendships are characterized by a spontaneous pleasure in helping the other, without looking for a contingent return (Tooby and Cosmides 1996, p. 131, 139). Silk (2003, p. 37) makes a similar point, stating, “Tit-for-Tat reciprocity is antithetical to the formation and maintenance of close friendship.”

These remarks are consistent with the prevalent social science definition of friendship, which emphasizes non-instrumentality and concern for the other. For example, Hays (1988, p. 393) puts forth the following argument: “[t]he primary goal of the interdependence between friends is social-emotional rather than instrumental, meaning that friends derive satisfaction from their interactions themselves (e.g., in the form of companionship, stimulation, belongingness, emotional support), rather than engaging in interactions primarily to achieve an ulterior motive.” Similarly, Allan (1979, p. 43) observes that “individuals can be useful because they are friends, but not friends because they are useful.” A study by Hays (1985) suggests that friends even value the costs that are associated with this relationship. Friendship intensity appeared to be more highly correlated with benefits-plus-costs-scores than with benefits-minus-costs-scores. In addition, a
strong concern for maintaining a balanced relationship may be considered a betrayal of the friendship (Shackelford and Buss 1996)

The distinction between an exchange domain and a friendship domain, as present in the reasoning by Tooby and Cosmides (1996) and Silk (2003), is similar to a common distinction in the social science literature. Clark and Mills (1979; see also Clark and Grote 2003) distinguish between exchange relationships and communal relationships. Communal relationships, which typically involve relationships with family members, romantic partners, and friends, are characterized by mutual concern for the welfare of the other person and a positive attitude toward helping the other in times of need. Exchange relationships, on the other hand, which typically exist between acquaintances, strangers, and business partners, are characterized by the obligation to reciprocate a benefit received with a comparable return benefit (for similar distinctions, see Bugenthal 2000; Deutsch 1975; Ekeh 1974; Fiske 1992; Lindenberg 2000; Sahlins 1972; Weiss 1998). Support for this distinction comes from studies in the fields of equity theory and distributive justice theory, which show that friends are less interested in maintaining balanced relationships than are strangers or individuals who are more distant (Clark 1984; Greenberg 1983; Lerner 1974; Morgan and Sawyer 1979; Roberto and Scott 1986a). Further, they are more concerned with responding to each other's needs (Clark et al. 1989; Lamm and Schwinger 1980, 1983).

In contrast to these studies, another tradition explicitly extends the assumptions of equity theory to the realm of close relationships. Based on the notion that inequitable relationships lead to distress (Walster et al. 1973), this tradition predicts that individuals who perceive their relationship as equitable are more satisfied with the relationship and experience less loneliness than do individuals who feel overbenefited or underbenefited (for a review, see Buunk and Schaufeli 1999). Many studies have found support for this hypothesis, in both intimate relationships (Hatfield et al. 1985; Sprecher 1992; van Yperen and Buunk 1990) and friendships (Buunk and Prins 1999; Roberto and Scott 1986b; Rook 1987a). Although these studies apparently contradict the claim that people involved in close relationships do not keep scores, it is important to note that such studies mainly consider socio-emotional benefits, as opposed to such instrumental benefits as physical effort or material resources. For example, Walster, Walster, and Traupmann (1978; see also Hatfield et al. 1979) introduced a “global measure” which simply asks subjects to indicate what kind of “deal” they are getting in their relationship, considering their inputs and outputs and their partner’s inputs and outputs. When answering this question, individuals tend to focus on socio-emotional contributions, including companionship, liking and loving, acceptance,
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commitment, and attentiveness (Smith and Schroeder 1984; van Yperen and Buunk 1990). These benefits are quite different from the instrumental benefits that are typically associated with scorekeeping and cheater detection. Whereas instrumental benefits concern instances of somatic effort, which have (or had) a direct effect on an individual’s fitness, socio-emotional benefits coincide with the proximate goals or emotions that individuals pursue. As a consequence, such benefits are highly confounded with the notion of a bonding mechanism, as described in Section 3.3.

In summary, there are strong indications that scorekeeping does not occur in all relationships that involve the exchange of benefits. Reciprocal altruistic interactions between friends are apparently governed by a psychological mechanism other than scorekeeping: a bonding mechanism (see Section 3.3).

3.2.2 Absence of strong support for scorekeeping

Although considerable evidence exists to support the presence of a scorekeeping mechanism (see Section 3.1), a closer look at some of those studies casts doubts on their conclusions. The following sections discuss the validity of the anthropological and primatological studies on reciprocal altruism and scrutinize the cheater detection study of Cosmides and Tooby.

Problems with assessing contingency

The scorekeeping mechanism concerns the contingent exchange of benefits. Many studies that report evidence of scorekeeping behavior, however, do not actually assess contingency. The majority of anthropological and primatological studies are restricted to analyses of correlations between benefits provided and benefits received. This is problematic, as a positive correlation between benefits provided and benefits received does not necessarily indicate contingency. It could also be the result of a mutual preference for providing benefits to close associates, or friends. To disentangle these explanations, de Waal and Luttrell (1988) made a distinction between calculated and symmetry-based reciprocity, which is very similar to the distinction between scorekeeping and bonding mechanisms. Calculated reciprocity is regulated by feedback; the continuation of helpful behavior is contingent upon the partner’s reciprocation. In contrast, symmetry-based reciprocity involves exchanges between closely bonded individuals who help each other without stipulating equivalent returns (p. 103).

Other studies present partial correlations, or regression coefficients, thereby controlling for such variables as time spent in association (e.g., de Waal
and Luttrell 1988) or residential distance (Gurven 2000b). However, to really distinguish between symmetry-based and calculated reciprocity, one should either study time-sequenced instances of providing benefits, or experimentally create an imbalance between benefits provided and benefits received, and subsequently determine whether the subjects attempt to restore a balance (e.g., de Waal 2000).

As argued in Chapter 2, keeping this restriction in mind, we see that most anthropological studies fail to demonstrate scorekeeping behavior. The primatology literature, in contrast, includes a number of time-sequenced studies (de Waal 1997a, 1997b, 2000), as well as one study involving an experimental manipulation of the balance between benefits provided and benefits received (Hemelrijk 1994).

In the latter study, grooming behavior of long-tail macaques was manipulated by smearing them with a sticky substance, and then provoking aggressive interactions. It was found that, if A had been groomed by B, he was more likely to provide support to B than he was if he had not been groomed. However, since Hemelrijk’s study did not address the question of whether A’s willingness to intervene in a conflict was restricted to B, a good-mood explanation may also account for this result. This explanation argues that the receipt of benefits leads to an indiscriminate increase in beneficial behavior (de Waal 1997a, p. 384).

In a study among chimpanzees, de Waal (1997b) found that subjects who had been groomed in the past hour were more likely to share a bundle of branches and leaves (provided by the experimenter) with their previous groomers. Since subjects restricted their sharing to their previous groomers, the good-mood explanation does not hold. An explanation in terms of symmetry-based reciprocity still cannot be excluded, however. If we assume that subjects have a small number of close associates, this might result in both preferential grooming and preferential sharing with those associates, without sharing being the consequence of being groomed.

Another study by de Waal (2000; see also de Waal 1997a) challenges this alternative explanation. De Waal conducted sharing experiments with pairs of capuchin monkeys, one of whom had access to a bowl of food. Roles were reversed several times, such that each monkey had access to food a number of times while the other had not. Correlations between sharing rates between the different test phases were positive. Because the effect of pre-existing affiliative tendencies between the two individuals was held constant, this study provides some support for the existence of a crude mechanism of calculated reciprocity.

In a related vein, Chapter 4 investigates whether helping behavior among human subjects can best be described as symmetry-based reciprocity (bonding) or
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by calculated reciprocity (scorekeeping). The results of two scenario experiments are reported, in which subjects were asked to imagine a situation in which they are indebted to another person, or in which another person is indebted to them. The situation and the answering categories were constructed in such a way that one's response indicated either a bonding or a scorekeeping response.

Criticism on the cheater detection mechanism

Cosmides and Tooby’s famous study on cheater detection has been severely criticized on logical grounds (Davies et al. 1995; Holcomb 1998; Stenning and van Lambalgen 2004; van Lambalgen 2004). Although these criticisms are important, as they question the presence of a domain-specific psychological mechanism for cheater detection, most evolutionary psychologists seem to be unaware of them.

As discussed in Section 2.1, Cosmides and Tooby (1992) argue that, if individuals have a domain-general mechanism for logical reasoning, they should perform equally well on two conjectures of the same logical form, regardless of content. Because people perform much better on social contract rules (e.g., “If you take the benefit, than you pay the cost”) than they do on descriptive rules (e.g., “If one goes to Boston, than one takes the subway”), Cosmides and Tooby conclude that humans have no domain-general mechanism for logical reasoning. Instead, they have a domain-specific mechanism for detecting violations of social contracts. Although Cosmides and Tooby claim that the descriptive rule has the same logical form as the social contract rule, they differ in some crucial aspects. These differences, and not the fact that our minds are equipped with a cheater detection mechanism, might be responsible for the difference in performance. For example, the two rules differ in that one is descriptive and the other is prescriptive. Whereas a descriptive rule describes a state of the world that is either true or false, a prescriptive rule has no truth value. As a consequence, a descriptive rule needs only one violation to be falsified. For prescriptive rules, the violation of the rule by one card is independent of whether another card violates the rule. This difference might have had the result that subjects in the descriptive rule condition were satisfied after picking one card, while subjects in the social contract rule condition did not stop after detecting one violation, but also considered the remaining cards (Stenning and van Lambalgen 2004; van Lambalgen 2004). In a replication of Cosmides and Tooby’s experiments that eliminated this and other sources of confusion, Stenning and van Lambalgen (2004) found a strong increase in the performance on the descriptive rule.
Even more important, according to Stenning and van Lambalgen (2004; see also van Lambalgen 2004), is that Cosmides and Tooby endorse an incorrect conception of logic. They assume that, if humans have a domain-specific mechanism for logical reasoning, it takes the form of classical propositional logic, including the accompanying semantics and truth tables that define the validity of arguments. Classical propositional logic is only one of many possible logical systems, however. Before applying logic, a person first has to determine the appropriate logical form, which is obviously not trivial in the Wason selection task. Stenning and van Lambalgen (2004, p. 483) therefore conclude that “Wason got his own task wrong in stipulating that there was a particular ‘obviously correct’ answer.” In summary, it is possible to reason logically without using classical propositional logic. This implies that the correct use of classical propositional logic is not a precondition for a domain-general mechanism for logical reasoning.

3.2.3 The scorekeeping mechanism ignores the ancestral environment

As mentioned before, the scorekeeping mechanism is based on the argument that, although each person is better off in situations in which everybody helps each other than they are in situations in which nobody helps anyone, each person benefits even more by reaping the benevolence of others without paying the costs of repaying their help. As a consequence, helpful individuals can only withstand the constant threat of exploitation if they keep account of benefits provided and benefits received with regard to each individual.

This argument, however, is based on an overestimation of both the expected benefits of cheating and the expected benefits of scorekeeping. These estimations are based on a Prisoner’s Dilemma situation – an environment in which unrelated actors are assigned to interaction partners and are forced to make a decision either to cooperate or to defect (or, as in delayed games, they take turns making moves). If we take the living conditions in the ancestral environment into account, it becomes clear that both the expected benefits of cheating and the expected benefits of scorekeeping are lower than is generally suggested (see Section 2.1.2).

Our ancestors lived in small, kin-based groups in harsh conditions. Predators lurked and food was patchily distributed: finding food was difficult, but when it was found, there was usually more than one individual could consume. Under these conditions, the expected benefits of cheating would have been small. First, the costs of sharing food were relatively low (Tooby and Cosmides 1996). Although finding and killing an animal was difficult, each captured animal yielded enough
meat for several individuals. Moreover, the meat could not be stored, so the finder of the food gained nothing by refusing to share. Second, since groups were based on kinship, cheating the members of one’s group would often amount to cheating one’s own kin. Third, considering the harshness of conditions, groups containing a large number of cheaters were at considerable risk of extinction. In general, such group selection arguments are considered invalid, as the individual benefits that a cheater may accrue override the effects of between-group selection. Under some conditions, however, the effects of between-group selection have been shown to be stronger than the effects of within-group selection (Sober and Wilson 1998; Wilson and Sober 1994). If groups are demographically closed or have low phenotypic variation (e.g., because individuals tend to imitate or conform to the behavior of the majority), and if competition between groups is high or groups run a high risk of extinction, groups of generally cooperative individuals surpass groups containing mainly cheaters. It is plausible that these conditions applied to the hominid groups in the ancestral environment (Boehm 1999; Fehr and Fischbacher 2003; Gintis 2000; Gintis et al. 2003; Richerson and Boyd 1998).

Consideration of ancestral conditions also leads to an adjusted notion of the expected benefits of scorekeeping. Scorekeeping is a useful strategy in situations in which interaction partners call upon each other in predictable, systematic ways. The exemplary model of such a situation is the delayed Prisoner’s Dilemma, in which two actors take turns deciding whether to cooperate or defect. In contrast, the Pleistocene savanna was anything but predictable. Due to the patchy distribution of food, the risk of failing to find any food on a number of subsequent days was considerable. An individual who kept track of the benefits that she and her interaction partner provided and who avoided giving benefits if the other still owed her would run the risk of losing a committed interaction partner. This could result either from driving the other to seek interaction partners who were less concerned about balanced exchange or – even worse – by letting the other perish when there was nowhere else to turn. In the words of Tooby and Cosmides, “[T]he ability to attract assistance during such threatening reversals in welfare, where the absence of help might be deadly, may have had far more significant selective consequences than the ability to cultivate social exchange relationships that promote marginal increases in returns during times when one is healthy, safe, and well-fed” (Tooby and Cosmides 1996, p.132).

The last argument is investigated in Chapter 3, which reports the results of a series of simulations. In these simulations, a strict scorekeeping strategy is imposed on an environment in which actors experience the need for help in an unsystematic and unpredictable way, and where they must select their helping
partners rather than having them externally assigned. The results of these simulations are compared to those of simulations that feature a strategy that is less concerned with keeping scores and more concerned with sticking to actors who have proved to be most helpful in the past, with regard to both providing and asking for help.

3.3 The bonding mechanism

Whereas the scorekeeping mechanism proceeds from an analysis of costs and benefits associated with different strategies in a game theoretical environment, the bonding account is more closely attuned to the living conditions of our ancestors. For this reason, it is more firmly based on evolutionary psychological arguments than is the scorekeeping account.

The central idea underlying the concept of a bonding mechanism is that the Pleistocene savanna exerted selection pressures for social group living. Food resources were patchily distributed, making an individual's foraging success unpredictable, and isolated individuals were more vulnerable to predator attacks than were those who lived in groups. As a consequence, individuals equipped with mechanisms that supported the maintenance of group membership were therefore more likely to survive and reproduce than were those without such mechanisms (cf. Baumeister and Leary 1995; Caporael et al. 1989; Smith et al. 1999; Smith, Coats, and Murphy 2001). Moreover, the high level of interdependence forced individuals not only to reap the benefits of group membership, but also to care for the survival and well-being of their group members. As argued above, ignoring a group member's need for help could result in the loss of a valuable protective and reciprocity partner (Tooby and Cosmides 1996).

Therefore, the bonding mechanism generated not only feelings of attachment toward one's group members, leading an individual to stay with the group, thereby receiving the benefits of protection and food sharing. It also generated feelings of commitment and care, resulting in the provision of benefits to group members. It is plausible that the bonding mechanism was originally based on pre-existing adaptations for care toward kin and attachment toward caretakers (Bowlby 1969), and evolved to extend such emotions and behaviors toward sexual partners and unrelated but familiar others as well (Panksepp 1998; Zeifman and Hazan 1997).

The central cues for a bonding mechanism include both the needs of the other person and the relationship with the other. When confronted with a group member who was in need of help, individuals would respond with helping
behavior, even if such help would result in an imbalanced relationship. This does not imply, however, that the relationships would not be balanced over the long term. On the contrary, because even the best hunter had a fair chance of failing in capturing game, responding to each other's needs would have produced a situation in which the frequency with which each group member helped others would be approximately equal. The difference with the scorekeeping mechanism is that helping behavior depends on the needs of the other person rather than on the difference between benefits provided and benefits received.

In the ancestral environment, individuals spent most of their lives in the same group. It is plausible therefore, that every group member triggered the emotions of commitment and care, and the appropriate bonding behavior, when in need. In the present environment, group membership is no longer so clear. The most appropriate translation of “an individual’s group” would be the circle of that individual’s closest affiliates (i.e., friends and family). When one of those persons is in need, emotions of commitment and care will be triggered, resulting in a willingness to provide help, regardless of possible imbalances.

3.4 How do the scorekeeping and bonding mechanisms relate to each other?

The presentation of scorekeeping and bonding as two alternative mechanisms of reciprocal altruism raises the question of how the two mechanisms might be related. Are they two mechanisms that co-exist on the same level, both originating in the evolutionary past, or does one predominate in terms of evolutionary origins? The first possibility is implicit in many accounts that interpret behaviors or considerations that are equivalent to scorekeeping and bonding as two algorithms that have evolved to cope with specific problems (e.g., Bugenthal 2000; Ten Houten 1999), or two norms that are associated with different domains of life (e.g., Clark and Mills 1979; Deutsch 1975; Fiske 1992), or two goal-frames that can vary in salience according to the context of the situation (Lindenberg 1990, p. 743; 1993, p. 29; 1999; but see Lindenberg 2001, p. 661, for a priori differences in the salience of frames). Considering the accounts of both mechanisms provided in the previous sections, it is unlikely that scorekeeping and bonding are two complementary mechanisms with equal evolutionary primacy. The bonding mechanism was explicitly introduced as an alternative to the scorekeeping mechanism, which was criticized for ignoring the ancestral environment.

However, if we assume that the ancestral environment gave rise to a psychological mechanism for bonding behavior rather than to a psychological
mechanism for scorekeeping behavior, how are we to explain the numerous instances of scorekeeping that we encounter every day? A speculative answer to this question is that scorekeeping behavior is a cultural adaptation to the demands of market society. The emergence of sedentary societies, about 10,000 years ago, marks the start of the development of market society. Characteristic of this shift from a nomadic existence to a sedentary way of life was that the acquisition of food through hunting and gathering practices was more and more replaced by people producing their food themselves. This went hand in hand with domestication of plants and animals, and as a consequence, with storage of food and property rights of land and livestock. These conditions set the stage for the emergence and expansion of market society (cf. de Vos and Wielers 2003; Diamond 1999).

According to de Vos and Wielers (2003; see also de Vos 2004), while humans are able to act according to economic reason, doing so takes effort, and it is therefore easy to fall back into older modes of behavior (e.g., bonding behavior). A similar argument is provided by Elizabeth Hoyt, a forgotten economist who used insights from psychology, economics, and cultural anthropology to demonstrate that, in spite of influential accounts of humans as economic exchangers by nature (Malinowski 1926; see also Ofek 2001), economic rationality is not basic to human nature, but must largely be learned instead (Hoyt 1926). The first exchanges among humans involved gifts and intimate personal services provided out of good will, and were based on the ability of the giver and the need of the receiver. From this, Hoyt concludes that “[t]he transformation of the standard of valuation from good will to utility was a matter of learning and was brought about through the extension of trading relations” (p. 95).

De Vos and Wielers (2003) provide two arguments in favor of the evolutionary primacy of bonding behavior. First, the resistance to market expansion that existed (and still exists) - including the historical suspicion toward traders and attempts to construct communities shielding against market intrusion - may be interpreted as an indication of the large amount effort it takes to learn behaviors that are novel in an evolutionary sense. Tooby and Cosmides (1996, p. 139) make a similar point, arguing that “[t]he widespread alienation many feel with modern society is the result of an evolved psychological mechanism that experiences this level of explicit contingent exchange in our lives as a message about how deeply (or rather, how shallowly) we are engaged with others.”

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4 Note that this notion of market society is different from the conception that market society is a phenomenon of the last centuries. The emergence of market society should be seen as stretching much further back in time than the Industrial Revolution or the Renaissance, or even antique Greece.
Second, they refer to exchange experiments that demonstrate the tendency of individuals to attach higher priority to bonds with their interaction partners than to monetary benefits. Kollock (1994) found that subjects preferred offers from interaction partners with whom they had interacted for a number of rounds to better offers from new interaction partners, even under conditions in which the risk associated with changing partners was low. Similarly, Lawler and Yoon (1996; 1998; see also Lawler et al. 2000) found support for the hypothesis that frequent exchanges lead to positive emotions, the perception of the relationship as a valuable object on its own, and to behaviors that express commitment (e.g., staying with the interaction partner in spite of better offers, contributing to joint ventures, and giving gifts).

The study reported in Chapter 4 includes an attempt to test the hypothesis that bonding is an evolved psychological mechanism, while scorekeeping is not.

4 Evolutionary psychology and sociology

Few sociologists have incorporated ideas from evolutionary psychology into their theories (e.g., Lord and Sanderson 1999; Sanderson and Ellis 1991). Given that sociology is the study of human society and social phenomena, this seems somewhat surprising. Many critics of sociology have addressed the possible causes of this reluctance, focusing on the historical development of sociology (e.g., Ellis 1996; Lopreato and Crippen 1999, p. 52; Pearson 1996; Sanderson 2001, p. 137; Urdry 1995; Wielers and de Vos 2003), or on ideological issues (e.g., Carey and Lopreato 1994; Degler 1991; Marsland and Leoussi 1996; Sanderson 2001, p. 136).

I will not go into this discussion, but focus instead on the possible relevance of an evolutionary psychological perspective for sociology. I then elaborate on the objective of this study in light of two persistent criticisms of evolutionary approaches to human behavior.

4.1 What is the relevance of evolutionary psychology to sociology?

Many non-sociologists, as well as sociologists who embrace an evolutionary perspective, have tried to persuade sociologists of “the need for Darwin” (for references, see Lopreato and Crippen 1999). For example, Nielsen (1994) identifies three domains in which evolutionary psychology might contribute to sociology: sex and gender, collective action, and human nature. Lopreato and Crippen (1999) make a similar case for the subjects of sex differences, relations between the sexes,
ethnocentrism, and social stratification. Studies by Wielers and de Vos (1999) and by Kanazawa (2001) offer improvements to rational choice theory that focus on the importance of emotions and the explication of the goals humans pursue. Sanderson (2001) presents a “unified theory of human society,” which seeks to show that the basic principles of sociobiology are highly compatible with some traditional models of social theorizing (p. 143). De Vos (2004) argues that sociological concepts of community could profit greatly from grounding in modern insights about human social nature.

Either implicitly or explicitly, all of these scholars criticise sociologists for ignoring the biological nature of humans and claim that sociological theories would benefit from paying more attention to the evolved psychological mechanisms with which the human brain is equipped. Pinker (2002) refers to the denial of human biological nature as *blank slateism*. Cosmides and Tooby (1992) consider it the primary characteristic of their conception of the *Standard Social Science Model*. According to this model, humans have been able to transcend their biological tendencies, due to their cognitive capabilities. They have developed a capacity for culture and learning that makes them boundlessly flexible. At birth, the human mind is a “blank slate” that must be filled with knowledge about the world and how to behave. This knowledge is assumed to be acquired from the social and cultural environment.

The blank slate assumption has been influential in the social sciences, particularly in the 1920s to 1960s. Sociology, cultural anthropology, and psychology were all permeated with the idea that humans are products of their (social) environments or their cultures. In sociology, the feminist idea prevailed that typical feminine and masculine behaviors can be explained completely by environmental inputs. According to this idea, baby boys differ from baby girls only in their genitals. This difference leads parents to raise their sons and daughters differently, with the result that men become more aggressive, assertive, and interested in sex, while women become more caring, empathic, and coy in sexual affairs (e.g., Fausto-Sterling 1985). Cultural anthropology was characterized by a strong cultural deterministic tradition. This was most evident in the work of Margaret Mead, whose famous description of Samoan society as a society whose attitudes toward sex were much more relaxed than those of Western society (e.g., girls could engage in exploratory sex before marriage and violent rape was non-existent) was used as the ultimate proof that different cultures are infinitely variable. Finally, the behaviorist tradition in psychology assumed the environment to play an exclusive role in shaping human (and animal) behavior. According to this perspective,
selective reinforcement could be used to form associations between any given stimulus and any behavioral response.

All of the traditions described above have been severely criticized. The notion that sex differences are determined socially has been falsified by a number of “natural experiments” in which biological boys were raised as girls because of disease or accident. The “girls” in all of these cases turned out to be strongly masculine (Colapinto 2000; Reiner et al. 2004). Furthermore, the likelihood that the behaviors of genetically neutral children, who have female body plans, and are therefore usually raised as girls, will be more characteristically feminine or masculine depends on whether they received their single X-chromosome from their mothers or from their fathers (Skuse et al. 1997; for further references, see Campbell 2002). Second, the idea that different cultures are infinitely variable, as implicated by the cultural determinist tradition in anthropology, has been falsified as well. Critics have demonstrated that Mead’s conclusions were strongly biased, and that Samoan culture was sexually no more relaxed than any other society (e.g., Freeman 1998). More generally, there are numerous attributes that are universal: in all cultures humans use spoken language, live in groups, are interested in sex, have coyness displays, care for their children, compete for status, prefer ingroup members to outgroup members, have childhood fear of strangers, gossip, cry, make jokes, insult each other, have myths, dance, make music, have beliefs about death, have a division of labor, et cetera (for a list of human universals, see Brown, 1991). Finally, the environmental determinism that is inherent in the behaviorist tradition implies that there are no restrictions concerning the content or timing of things that are to be learned. Numerous studies have suggested that learning is not global, but biologically constrained (Klein and Mowrer 1989). For example, rats easily learn the connection between drinking a specific substance and (X-ray invoked) nausea, but they have much more trouble learning the connection between drinking a specific substance and flashing lights or noise (Garcia and Koelling 1966; for a review of related experiments, see Logue 1988). Moreover, although human babies are extremely flexible in learning language, this ability to learn disappears once a “critical period” has elapsed (Cummins and Cummins 1999). I return to the issue of the limits of learning in Section 4.2.1.

There is also a fundamental problem with the perception of humans as blank slates. As I argued in the discussion of the darwinian anthropological concept of humans as fitness maximizers, learning adaptive behavior through trial and error is impossible in the presence of an endless number of possible cues and responses. Chomsky (1980) made a similar point in the proposition that humans are endowed with a Universal Grammar. Given that the spoken language children
hear from their parents could be compatible with an infinite number of possible grammars, the only possible explanation for the fact that children succeed in learning the correct grammar is that they have an innate language device. In its most basic form, the argument holds that there can be no learning without an innate circuitry to do the learning (Pinker 2002, p. 35). A “blank slate” will stay forever blank (Cosmides and Tooby 1995, p. 45).

Although the influence of the social and cultural deterministic traditions has faded in psychology and cultural anthropology, it has not happened in sociology (Lord and Sanderson 1999; Lieberman 1989; Sanderson and Ellis 1992). Most sociological textbooks still insist on the separation of culture and biology (e.g., Bruce 1999; Tischler 1993).

4.2 Criticisms of evolutionary approaches to human behavior

This section elaborates on what the objective of this dissertation is, and, more importantly, what it is not. I present this elaboration in light of two persistent criticisms of evolutionary approaches to human social behavior that are shared by many sociologists: the criticism that such studies amount to genetic determinism, and the criticism that they are nothing but “storytelling.”

4.2.1 Genetic determinism

The first criticism concerns the idea that evolutionary approaches to human behavior amount to genetic determinism (e.g., Bleier 1984; Freese 1994; Lewontin 1979; Rose et al. 1984; Rose 1978). In its most extreme form, this criticism holds that evolutionary psychologists (and other proponents of evolutionary approaches to human behavior) claim that we are fully driven by our genes, with environmental factors having no influence at all; people are born with a set of genes that determine their preferences, personalities, and behavioral tendencies. There are genes that make some people helpful and genes that condemn others to lives of criminality.

This dissertation seeks to test evolutionary hypotheses concerning reciprocal altruistic behavior and emotions in humans. Making evolutionary claims about reciprocal altruism implies that there must be a genetic origin of reciprocal altruism. However, I do not claim that reciprocal altruistic behavior is the result of a single gene, nor do I wish to show that reciprocal altruistic behavior is exclusively governed by genetic factors. Both issues are discussed next.
No genes for scorekeeping and bonding behavior

Although a claim that a behavior has evolutionary origins presupposes a genetic basis, I am not investigating whether there exists a “bonding gene” or a “scorekeeping gene.” First of all, it should be emphasized that investigating the link between genes and behavior is the domain of behavioral and developmental genetics. Studies in these fields (e.g., experiments involving artificial selection and studies assessing the degree to which behavioral characteristics are similar among fraternal and identical twins) provide ample evidence that such a link exists (Alcock 2001).

Given the work of behavioral and developmental geneticists, it would be unrealistic to postulate genes for such complex behaviors as bonding or scorekeeping. Genes are segments of DNA coding for specific enzymes. Enzymes produce specific biochemical reactions that might affect the development or operation of hormonal, muscular, or nervous systems. This may result in specific behavioral tendencies in certain environments. When behavioral geneticists announce the discovery of a gene for drinking behavior, smoking, anxiety, or anti-social behavior, it does not mean that they have found some kind of directive, written in the genes, which condemns the bearer to a life of drinking, smoking, anxiety, or anti-sociality. It means, rather, that possession of a particular gene produces different biochemical pathways, which, under certain environmental conditions, translates into behavioral differences, compared to individuals who do not have the gene (Alcock 2001; Bailey 1998; Barash 2001, p. 28).

Moreover, even if it were our goal, it would be impossible to pinpoint the genetic basis of scorekeeping or bonding behavior. This dissertation, as well as the majority of evolutionary psychological research, focuses on behavioral designs that were favored to such a high degree in the ancestral environment that they are now present in all “normal” members of the human species (Alcock 2001, p. 42; Bailey 1998; Cartwright 2001, p. 71; Tooby and Cosmides 1990a). Just as few humans lack the correct genetic make-up for having eyes, there are also few humans who lack the genetic make-up for reciprocal altruistic behavior. In the absence of genetic variation of a trait, it is impossible for behavioral geneticists to pinpoint the relevant genes (Bailey 1998, p. 212).

Beyond nature-nurture

By formulating evolutionary hypotheses about scorekeeping and bonding behavior, I do not claim that these behaviors are due entirely to genetic factors and that environmental, social, and cultural factors play no role. Many scholars have tried to
show that the rigid distinction between “nature” and “nurture” makes no sense (for example, see Ehrlich 2000; Pinker 2002; Ridley 2003). Genes and environment are inextricably intertwined in shaping human behavior. In different environments, a single gene may translate into different behavioral tendencies, or it may not be expressed at all. For example, a gene that produces a quick break-down of a neurotransmitter responsible for feelings of excitement and arousal might result in a criminal career for one person and a career on Wall Street for another.

The exact ways in which environment and biology interact to produce behavior is still a matter of discussion (for a review, see Janicki and Krebs 1998). In the meme perspective, culture and biology are completely independent (Dawkins 1989, p. 191). Their tremendous capacity for learning allows humans to imitate all types of behavior, both adaptive and inadaptive. Dawkins (p. 198-199) gives the example of celibacy: the cultural behavior of celibacy is extremely inadaptive, as it constrains individuals from reproduction. This is, however, exactly what makes it a very successful meme: because celibate people do not “waste” their time in efforts to reproduce, they have plenty of opportunities to spread the meme to other individuals. In the end, however, biological evolution always triumphs over memetic evolution; the absolute peak of the success of the celibacy meme would inevitably mark its downfall, because in the absence of newly born humans, the meme would become extinct.

In stark contrast to the meme view is the idea that culture is a tool for maximizing fitness. According to this view, humans have evolved a capacity for culture that enables them to track the environment, making adaptive adjustments to their behavior – both consciously and unconsciously – as conditions change (Alexander 1979; Irons 1979). This view is most prevalent among darwinian anthropologists, who assume that humans behave in such a way as to maximize their current fitness. As mentioned before (see Section 2), this idea contradicts both assumptions of evolutionary psychology (i.e., that humans are equipped with domain-specific psychological mechanisms and that these psychological mechanisms are adapted to ancestral conditions).

At present, most evolutionary psychologists adhere to a more moderate account of the interaction of environmental and biological factors. In this view, the structure of our brains makes it easier to learn some behaviors than it is to learn others. Drawing upon classical conditioning studies, Seligman (1970, 1971; see also Marks 1987) suggested that organisms are more prepared to learn fear responses to classes of objects that may threaten their survival than they are to learn such responses to non-threatening objects. The finding by Garcia and Koelling (1966; see also Garcia et al. 1989) that rats have more trouble learning the connection
between food tastes and flashing lights or noises than they have in learning the connection between food tastes and nausea (see Section 4.1), can thus be interpreted as evidence that rats are innately pre-programmed to form adaptively relevant associations more easily than adaptively irrelevant associations. A similar preparedness to link the eating of a specific food with nausea has been shown in humans (e.g., Logue 1988). Furthermore, Öhman and Dimberg (1978; see also Öhman 1985) have shown that negative facial expressions (pictures of angry faces) are more easily associated with electrical shocks than are positive or neutral facial expressions. In summary, organisms seem to have a biological preparedness to very quickly develop specialized cognitive functions for solving classes of problems that were critical to the survival and reproduction of their ancestors (cf. Ariew 1996; Cosmides and Tooby 1995; Cummins and Cummins 1999, p. B45).

It is important to stress that evolutionary psychologists do not claim that individuals are only able to learn behaviors that are (or were) adaptive, and avoid behaviors that are (or were) inadaptive. On the contrary, humans owe their dominance over the world to their extraordinary capacity to learn. The argument implies only that it takes more time and effort to learn behaviors that were inadaptive, or adaptively insignificant, in the past (de Vos and Wielers 2003, Papineau 2000). Thus, human children can be taught to eat both sweet and bitter foods, even though the perception of bitterness evolved to warn us that some foods were poisonous. Individuals can learn to drive cars and computers, even though cars and computers have not yet existed long enough to play any role in the process of natural selection. And, as speculated in Section 3.4, humans can learn to function in market societies by learning scorekeeping behavior.

However, although human children can be taught to eat (and to like) Brussels sprouts, it takes more trouble than it does to teach them to like apple pie. Similarly, humans can learn to drive cars and use computers, but it takes a considerable amount of practice. And finally, although humans can learn to keep score, it takes little more than a few positive interactions for business partners to be perceived as friends, resulting in bonding behavior.

4.2.2 Storytelling
A second criticism of evolutionary approaches to human behavior is that the focus on explaining behavior in terms of the benefits to individual survival and reproduction leads evolutionary psychologists to invent evolutionary explanations for all behaviors. This is expressed in criticisms concerning ad hoc explanations and just-so stories. In its most extreme form, this critique argues that evolutionary
researchers just pick an empirically founded fact and provide it with an interesting evolutionary explanation – the more ingenious the better (Gould 1978a; Kitcher 1985). A related criticism is that evolutionary researchers use tautological arguments, “explaining” a specific behavior by referring to empirical evidence for the prevalence of this behavior and concluding that people exhibit the behavior because it is (or was) adaptive (e.g., Freese 1994; Lindenberg 1999a, p. 407; Maryanski 1994).

The hypotheses offered in this dissertation are neither unfalsifiable nor tautological. Assuming that proximate mechanisms of reciprocal altruism evolved in the Pleistocene environment, I speculate that, in this environment, a bonding mechanism would have been more conducive to individual fitness than a scorekeeping mechanism would have been. I subsequently predict that many instances of reciprocal altruism can be more accurately described by a bonding mechanism than by the conventional scorekeeping mechanism, and that the bonding mechanism is more biologically prepared than is the scorekeeping mechanism.

Many potential outcomes could falsify these hypotheses. For example, the finding that people do not exhibit bonding behavior in conditions that are most similar to the ancestral environment would falsify the hypothesis that bonding is an evolved psychological mechanism. In addition, the finding that people are much more easily induced to perform scorekeeping behavior than they are to perform bonding behavior would falsify the hypothesis that bonding is the primary mechanism underlying reciprocal altruism. The hypotheses formulated in this dissertation can therefore not be written off as instances of “storytelling.”

The criticism of tautology has also been raised against the theory of evolution in general. It based on a misunderstanding of the phrase “survival of the fittest.” As long as fitness is determined independently from survival, there is no tautology (Gould 1977; 1989, p. 236). When providing an ultimate explanation of a behavioral tendency, it does not suffice to say that organisms behave in such a way because it is (or was) adaptive. Instead, we must explain why it is (or was) adaptive. As are most evolutionary psychological hypotheses (see for references Buss et al. 1998), my predictions concerning the bonding mechanism are based on an analysis of the conditions in the Environment of Evolutionary Adaptedness, which specifies why particular behaviors increased reproduction and survival under these conditions. For this reason, the criticism of tautological reasoning also does not hold.
INTRODUCTION

5 Design of this dissertation

Because each of the chapters in this dissertation was written as a separate article, there is some overlap. All of the chapters focus on the distinction between the conventional scorekeeping mechanism and the relatively new concept of a bonding mechanism. To recapitulate, the primary goal of this dissertation is to investigate whether the scorekeeping mechanism is as ubiquitous as evolutionary psychologists generally assert. At times, I go a step further and address the question of whether the bonding mechanism is more biologically prepared than is the scorekeeping mechanism. Finally, I focus on emotions as intermediators between adaptation-relevant cues and behavioral responses.

Chapter 2 takes a closer look at the mechanisms underlying food sharing among hunter-gatherers, who live in conditions that are most similar to those of our ancestors and who are therefore the most suitable candidates for providing evidence of ancestrally evolved psychological mechanisms. Anthropologists have conducted many studies on food sharing. Chapter 2 scrutinizes those studies for their potential support to either bonding or scorekeeping mechanisms.

Chapter 3 is a simulation study, investigating the relative success of a strategy based on the scorekeeping mechanism (called “Keeping Books Balanced”) and a strategy based on the bonding mechanism (called “Commitment”). The primary aim of this chapter is to show that the conventional scorekeeping strategy owes its popularity to its success in the context of a Prisoner’s Dilemma environment. In the context of an environment that more closely resembles the EEA, (i.e., where actors get in need of help in an unsystematic and unpredictable way), and in which they must select their interaction partners rather than having them assigned externally, a scorekeeping strategy is expected to perform worse than a bonding strategy.

Chapters 4 and 5 address the question of how those psychological mechanisms work. Chapter 4 focuses on the relation between cues and behavioral responses, while Chapter 5 centers on the role of emotions. Both studies are based on scenario data. Subjects were asked to imagine a situation in which they are indebted to another person, or in which another person is indebted to them. The scenarios were constructed in such a way as to pose a dilemma between bonding and scorekeeping. As a result, a subject’s behavioral response was indicative of either scorekeeping or bonding behavior. Chapter 4 is closely related to social psychological studies on communal and exchange relationships, as it focuses on the effects of situational characteristics that are typical for either communal or exchange relationships. This was done by varying the object of help (either
assistance in the case of illness or lending money) and the relationship with the other person (either a good friend or an acquaintance). Finally, by using an implicit prime the chapter also includes an attempt to test the speculation that bonding is an evolved psychological mechanism, while scorekeeping is not.

Chapter 5 focuses on the role of emotions in the bonding and scorekeeping mechanisms. It addresses both the question of which emotions are associated with the bonding mechanism and which emotions with the scorekeeping mechanism and the question of the extent to which emotions play an intermediating role between cues and behavior.

Finally, Chapter 6 summarizes the preceding chapters, draws conclusions concerning the research questions, and considers recent developments and suggestions for future research.