

# 'Animal Behavioural Economics': Lessons Learnt From Primate Research

Manuel Wörsdörfer<sup>1</sup>, Goethe University, Frankfurt, Germany  
[woersdoerfer@wiwi.uni-frankfurt.de](mailto:woersdoerfer@wiwi.uni-frankfurt.de)

---

## Abstract

The paper gives an overview of primate research and the economic-ethical 'lessons'<sup>2</sup> we can derive from it. In particular, it examines the complex, multi-faceted and partially conflicting nature of (non-) human primates. Our closest living relatives, the chimpanzees and bonobos, apparently walk on two legs: a selfish and a groupish leg. Given evolutionary continuity and gradualism between monkeys, apes and humans, human primates seem to be bipolar apes as well. They, too, tend to display a dual structure: there seems to be a pro-social and a self-interested side to our species and a bipolar tension seems to exist between competition and cooperation respectively between self-interest and the common good. We are apparently at the same time *Homines oeconomici* and *Homines culturali*. Our inner ape tries to combine self-interested and common good motives. Based on de Waal's *Russian doll model*, the essay investigates the evolutionary origins of morality and 'eusociality'. With the help of selected case studies stemming from behavioural sciences/economics, the paper illustrates examples of empathy, altruism, reciprocal fairness, pro-social and other-regarding preferences, inequity aversion and altruistic punishment in (non-)human primates. Beside this selfless and groupish side, the paper also reflects on the self-interest and egoistic nature of (non-)human primates and the behavioural and cognitive differences between monkeys, apes and humans.

**Keywords:** primate research, mirror neurons, empathy, theory of mind, token economy, multi-level natural selection/group selection, dual motive theory, triune brain

---

## 1. Introduction

Nowadays, two ideas of man apparently face each other in economics and economic ethics: the *Homo oeconomicus* idea of man present in most standard economic textbooks and the *Homo culturalis* (or *Homo moralis*, *reciprocans-cooperativus*) idea of man within some strands of economic ethics as well as behavioural economics, neuroeconomics, economic psychology and happiness economics.

The *Homo oeconomicus* model is based on the self-interest axiom and the complete rationality assumption. Following the self-interest calculus or economic principle, people aim at personal utility maximisation. Given their individual preferences, rational actors choose those alternatives that are 'purposive-rational' (*zweckrational*), that is, they chose those options which maximise personal utility (those decisions are made under certain restrictions

---

<sup>1</sup> Address for correspondence: Manuel Wörsdörfer, Postdoctoral Research Fellow, Cluster of Excellence 'The Formation of Normative Orders', Goethe University Frankfurt, Grueneburgplatz 1, 60323 Frankfurt, Germany; Phone: +49 (0)69-798-34782; Fax: +49 (0)69-798-35015.

<sup>2</sup> The term 'lesson' refers to the insights we can gain about economic ethics from primate research. It thus refers (mainly) to the empirical-descriptive level; yet it does not (necessarily) imply normative ('ought') conclusions derived from animal research.

such as time constraints or goods scarcities). Individual decision-making is thus based on a rational cost-benefit analysis. The model assumes stable, constant and consistent preferences. The *Homo oeconomicus* idea of man functions as a heuristic or abstract ideal type. It is closely linked to Samuelson's *revealed preference theory* (i.e., preferences of consumers are revealed by their actual decision-making and purchasing habits (Samuelson 1938; 1948)) and (rational choice-like) *methodological individualism* (i.e., social phenomena and outcomes are best explained by viewing them as a result of the (disinterested and unemotional) choices and actions of (rational) individual agents) (Kirchgässner, 1991).

In recent years, the *Homo oeconomicus* model has come under fire from different quarters: economic ethics, behavioural economics, neuroeconomics, economic psychology and happiness economics, to name a few. The main points of criticism refer to the following keywords: *bounded rationality* and *satisficing* (instead of maximising or optimising) man (Simon, 1957; 1959; 1990; 1991); *brain bugs* (Buonomano, 2011) and cognitive biases such as framing effect, endowment effect, status quo bias, loss aversion and overconfidence (Kahneman, 2011; Thaler and Sunstein, 2008[2009]); the importance of automatic processes ('the automatic brain') and moral intuition (Haidt, 2001; Damasio, 1994[2006]) as well as the interplay of cognition/reason and emotion; the special role of empathy and in particular *mirror neurons*; *animal spirits* (Keynes, 1936[1973]) and herd behaviour; and last but not least, the existence of other-regarding preferences and pro-social behaviour such as reciprocal altruism, altruistic punishment, inequity aversion and fairness norms (see the indicated works of Fehr et al.). These points of criticism – among others – have led to the development of a more realistic and down-to-earth idea of man – at least within heterodox economics – the so called *Homo culturalis* idea of man (Davis, 2003; Akerlof and Kranton, 2010).

A similar debate mirroring the one within economics and economic ethics – the *Homo oeconomicus* versus the *Homo culturalis* debate – takes place within primate research. Apparently, our closest living relatives, the chimpanzees and bonobos, walk on two legs: a selfish leg and a pro-social leg. Given evolutionary continuity and gradualism between monkeys, apes and humans, human primates seem to be bipolar apes as well. They, too, display a dual structure: there is a social and a selfish side to our species and a bipolar tension apparently exists between competition and cooperation: We are at the same time *Homines oeconomici* and *Homines culturali* (depending on the particular context of interaction). Our inner ape apparently aims at combining self-interested and common-good motives, pointing to the complex and multi-faceted nature of apes and humans. This heterogeneous motivation structure resembles Adam Smith's work which combines self-interest (not necessarily egoistic) motives with considerations of empathy/sympathy and the ideal of an impartial spectator.

The following paper gives an overview of primate research and the economic-ethical insights we can gain from it. In particular, it examines the complex, multi-faceted and partially conflicting nature of (non-)human primates. Based on de Waal's *Russian doll model* the essay investigates the evolutionary origins of morality and 'eusociality'.<sup>3</sup> With the help of selected case studies, the paper illustrates examples of empathy/sympathy, altruism, reciprocal fairness, other-regarding preferences and pro-social behaviour, inequity aversion as well as altruistic punishment in non-human primates. Beside these selfless and groupish sides of (non-)humans, the paper also reflects on the selfish (and sometimes egoistic) nature of (non-)human primates and the behavioural and cognitive differences between monkeys, apes and humans.

---

<sup>3</sup> The term 'eusociality' stems from the Greek word 'eu' (=good) and the Latin word 'socialis' (of companionship/of allies) and refers to the pro-social behaviour of animals (Batra, 1968; Wilson, 1971).

The paper combines behavioural science, experimental economics and cognitive neuroscience. The advantage of primate research is that non-invasive techniques which are commonly used in humans such as brain scans or brain imaging technology (e.g., EEG, PET, fMRI and TMS) can be combined with invasive techniques used in non-human primates. Together, these two methodologies allow for the study of brain processes in a better and more comprehensive way. Moreover, neuroscience and primate research are combined with the theoretical framework of behavioural economics and experimental (evolutionary) game theory. This cross-disciplinary approach aims at enriching economics and economic ethics by integrating the knowledge gained in primate research and cognitive neuroscience into (behavioural) economics and economic ethics.

The remainder of the paper is structured as follows: the second section gives an overview of recent neuroscientific and primate research on empathy, theory of mind and mirror neurons. The third section deals with the evolutionary origins of morality and eusociality as well as de Waal's thesis of gradualism and continuity. The fourth section introduces the 'token experiments' conducted by de Waal, Tomasello and others. In the fifth section, the essay analyses the dual nature of (non-)human primates (i.e., 'animal *oeconomicus*' versus 'animal *culturalis*'). Here the debates between the de Waal and the Tomasello research groups are (re) examined. In the sixth section, the theory of reciprocal altruism is critically analysed from a primate research perspective. The paper ends with some concluding remarks (i.e., 'lessons' learnt from primate research).

## **2. 'Mirror Neurons', Empathy and 'Theory of Mind'**

### **2.1 Mirror Neurons**

*Mirror neurons* were first discovered in the 1990s by Rizzolatti, Di Pellegrino, Fadiga, Fogassi and Gallese at Parma University. The Italian neuroscientists found out that mirror neurons fire not only when an animal or a human being actively performs an act, but also when they observe the same action performed by another animal or human being. In particular, they detected that a specific set of neurons of macaque monkeys is active both when the monkey makes active movements itself (*action execution*) and when it observes or 'mirrors' specific purposeful and intended actions performed by the experimenter (*action observation and simulation*); hence the name mirror neurons (Gallese et al., 1996). In order to be triggered by visual stimuli, mirror neurons require an observation of a 'meaningful, goal-related hand-object interaction' (Gallese, 2001, p. 35).

Furthermore, Rizzolatti, Gallese et al. found that mirror neurons as a particular class of visuomotor neurons are mainly located in an area of the ventral premotor cortex called F5 (inferior frontal gyrus), an area directly related to goal-directed hand and mouth movements. Other cortical areas with mirror-like properties include the posterior parietal cortex, namely area 7b or PF of Von Economo.<sup>4</sup> This area forms the rostral part of the inferior parietal lobule which receives input from the superior temporal sulcus and sends output to the ventral premotor cortex including area F5.

Mirror neurons have been directly observed in (non-)human primates and other species. So far, *direct* evidence about the existence of mirror neurons in humans is lacking (due to the fact that invasive techniques as in non-human primates are less often used). *Indirect* evidence, however, suggests the presence of a human 'mirror matching system'

---

<sup>4</sup> For more information on Von Economo neurons/VEN-cells or spindle neurons see Economo and Koskinas 1925; Fajardo et al., 2008; Butti et al. 2009; Hakeem et al., 2009; de Waal, 2009, p. 138ff.

similar to that in apes (Keysers, 2011, chapter 3). Evidence comes from brain imaging studies as well as neuro-physiological experiments (Gallese et al., 1996, p. 606ff.; Gallese, 2001, p. 37; Rizzolatti and Craighero, 2004, p. 174ff.; Iacoboni, 2009; Iacoboni and Mazziotta, 2007). It is widely believed that the mirror neuron system in humans is much more pronounced compared to the one in non-human primates. Furthermore, humans have much stronger connections to emotion-related areas of the brain (Haidt, 2012, p. 272ff.). This might be one of the reasons why humans are more likely to mirror and empathise with others and are more willing to collaborate – compared with monkeys and apes.

The functional role of mirror neurons is also disputed (Singer, 2009, p. 256ff.): mirror neurons seem to mediate *imitation learning*: imitation and learning processes are based on action observation, simulation and execution similar to that of the mirror neuron system. Furthermore, the activity of the mirror neuron system seems to correlate with *action understanding* ('understanding of motor events' (Gallese et al., 1996, p. 606) and *gestural communication* (e.g., understanding of facial expressions). Since speech mostly evolved from gestural communication, the mirror neuron system might also be responsible for *language evolution*. Interestingly, Broca's area, the hypothesised language region of the brain, is closely related to mirror neuron brain areas. A mirror neuron theory of language and speech evolution has been proposed by Rizzolatti and Craighero (2004, p. 18ff.) among others (Keysers, 2011, chapter 5).

Finally and most importantly for the purpose of this paper, mirror neurons are regarded as the neural basis of *empathy* and *theory of mind* (hereafter, ToM) (Premack and Woodruff, 1978): Mirror neuron systems are believed to play a general role in understanding other people's actions, goals and emotions. They are supposed to be the basis of human self-awareness (i.e., introspection and personal identity formation) as well as other-awareness (i.e., self-other distinction and inter-subjectivity). As such, they allow sharing and understanding others' feelings and emotions (i.e., empathising with other persons' behaviour). They enable us to read other people's minds and mental states, beliefs, desires, intentions and feelings. In summary, mirror neurons play a crucial role in emotional and social cognition. It has been proposed that a deficient and dysfunctional mirror neuron system underlies cognitive disorders such as autism (Santos et al., 2006; Keysers, 2011, chapter 9). Damage to this part of the brain can have serious consequences. A malfunctioning mirror neuron system ('broken mirrors'), potentially leads to disabilities in social skills, e.g., a loss of empathy and cognitive perspective-taking (de Waal, 2009, p. 138ff.). A lack of empathy and ToM in most autistic children might explain their failure in interpersonal communication and social interactions as well as their apparent egocentric bias, their propensity to understand other individual's states in terms of their own (the same holds true for non-human primates and explains the differences between humans, apes and monkeys) (Singer, 2009, p. 255). Studies of patients with specific psycho-pathologies also show deficits in emotional and social cognition. Empirical research further suggests that individual as well as gender differences in the human mirror system – and the level of oxytocin (Kosfeld et al., 2005; Haidt, 2012, p. 270ff.) – exist. That might be one of the reasons why people are not equally empathetic and why women are more empathetic than men.

## **2.2 Empathy and 'Theory of Mind'**

The English word empathy stems from the Greek *empathēia* as well as the German word *Einfühlung* ('feeling into'), first introduced by Lipps (1903; 1913). Originally it denotes the relationship between a painting and an observer, who imaginatively projects herself into the contemplated artwork. Later on, Lipps transferred the concept of empathy to intersubjectivity

and the inner imitation of the perceived behaviour of others. Common experiences of actions and the observation of other's behaviours lead to a state where a person is perceived 'as another being like oneself through an appreciation of *similarity*' (Gallese, 2001, p. 43). Mirror neurons, being part of our social mind, allow for cognitive and emotional perspective-taking (i.e., to put oneself into the shoes of others; adopt the other's perspective). They offer a direct access to the other self and create a link between different individuals (de Waal, 2009, p. 65ff.).

While empathy refers to *emotional* perspective-taking and sharing other's feelings, the concept of ToM, first introduced by Premack and Woodruff in 1978, refers to *cognitive* perspective-taking, mind-reading or mentalising (Singer, 2009, p. 253) as well as the capacity to represent other's intentions, beliefs, desires and thoughts. Empathy and ToM are two distinct abilities and rely on distinct neuronal circuitries. Brain areas typically involved in ToM are the medial prefrontal cortex, temporal poles, superior temporal sulcus and temporo-parietal junction. Brain networks typically involved in empathy are the anterior cingulate cortex, anterior insula and secondary somato-sensory cortex (Singer, 2009, p. 253).

Empathy and ToM abilities – i.e., social reasoning or socio-cognitive skills to represent the mental or psychological states of others – are interdependently linked with each other; they are both required in order to fully understand other people: what is needed is first the ability to understand other people's motor intentions and action goals. Second, we need to understand their emotions and feelings (i.e., empathy or emotional perspective-taking). Third, ToM is required to understand their thoughts and beliefs (i.e., mind-reading and cognitive perspective-taking).

ToM or mentalising includes the person's ability to cognitively understand the mental states of others, including their affective states, without becoming emotionally affected. Empathy, on the other hand, refers to the capacity to share other people's emotions and feelings.

### **2.3 Empathy versus Sympathy**

Empathy, though, is not identical with compassion or sympathy: when we *empathise* with others, a pro-social motivation to enhance the psychological well-being of the other person does not necessarily exist. However, when we *sympathise* with others, a pro-social motivation is necessarily attached to our behaviour (Singer, 2009, p. 254). Sympathy, therefore, differs from empathy in that it is proactive: sympathy reflects an actual concern for the other, an attempt to understand what happened as well as the desire to improve the other's situation (de Waal, 2009, p. 88ff.). Thus sympathy exceeds empathy. Nevertheless, empathy has an important motivational and societal role to fulfil. It is closely related to morality, (reciprocal) altruism, a sense of fairness and justice, as well as other-regarding preferences and cooperative behaviour. Empathy enables people to share others' emotions and feelings, which can help in motivating pro-social behaviour. As such, it is mainly involved in rendering people less selfish. It is a first and essential step in a chain that starts with affect or emotion sharing, an understanding of another person's feelings, which then motivates other-related or pro-social concern and finally direct engagement in helping others. Interestingly enough, Adam Smith, the father of modern economics, seems to have been aware of the distinction between empathy and sympathy; his major concern was sympathy, not empathy (Smith, 1976b).

## **2.4 Empirical Evidence from Primate Research I: Empathy**

What is essential for the argument of this paper is the question of whether the capacity to empathise or mentalise (ToM) is uniquely human. Do non-human primates also have a capacity for emotional and cognitive perspective-taking?

Empathy (and to a much lesser degree sympathy) are common in both humans and other animals. Of all the great apes (i.e., chimpanzees, bonobos, gorillas and orang-utans), bonobos seem to have the highest level of empathy – and even some sense of sympathy (de Waal, 2009; 2012). Empathetic tendencies in apes (which might translate into altruistic behaviour) include emotional contagion, state-matching and sympathetic concern for others, e.g., being affected by the loss of close companions (mourning), consolation (Romero et al., 2010; de Waal, 2000), wound cleaning, grooming/social scratch (Maestripiere, 2012, p. 209ff.) and other forms of comforting body contact.

Empathetic compassion is of particular importance when it comes to bridging the gap between egoism and altruism. It promotes other-regarding and pro-social preferences, motivates altruistic behaviour and helps in overcoming purely selfish concerns. Empathy can be described as a natural instinct, meaning that (most) primates are born with it. The *feeling or social brain* (MacLean, 1990) starts with birth and parental care (i.e., close bonds and social ties between offspring, parents and family). Evolutionary attachment then paves the way for family life, friendship, other-caring and pro-social behaviour. Natural selection has designed primates' brains in such a way that they are in tune with their fellow beings: they feel distress at their distress and pleasure at their pleasure; many animals react to the pain of others. Especially monkeys (and apes) are extremely sensitive to one another's body language; e.g., rhesus monkeys refused to pull a chain which delivered food to themselves if it shocked their companion (de Waal, 2009). Shared laughter and yawn contagion are primary examples of primates' sensitivity to others. Most of the mood transfer happens via body language in general and facial expressions in particular. According to de Waal (2009), the face is the 'emotion highway': it offers the fastest connection to other individuals. It is known that chimpanzees pay particular attention to the orientation of the face. With impoverished facial expressions and body language comes impoverished empathetic understanding. Emotional or mood contagion implies matching of another's emotional state, body mapping or imitation ('to ape'). Embodied cognition and being in sync has a bonding effect. Emotional linkage between individuals has the same natural-biological basis in humans and other animals.

Unfortunately, up to today we know very little about animal empathy due to the fact that empathy research is mainly human-centred. Empathy is most often presented as a process requiring role-taking and higher cognition, sometimes even language; as such, it is allegedly limited to human primates. Primate research, however, has shown that animal empathy exists. Moreover, it has shown the automaticity of empathy and the subconscious nature of the empathetic process which requires identification, self-other distinction (i.e., erasing the line between self and other) and cognitive perspective-taking.

## **2.5 Empirical Evidence from Primate Research II: Theory of Mind**

Empirical results suggest that monkeys do not have (the same) ToM capacities as apes, not to speak of humans (Santos et al., 2006; Rosati et al., 2010). However, ToM abilities seem to exist in a *limited form* in apes and other species like elephants, dolphins and whales – therefore, they are not uniquely human, although humans' ToM abilities exceed those of other land mammals and cetaceans by far (Call and Tomasello, 2008; de Waal, 2008; 2009; Rosati

et al., 2010; Troxler, 2011). Examples of attribution and understanding of goals, intentions, perception and knowledge include aiding behaviour or *targeted and insightful helping*: apes seem to have an inkling of what others feel, need and want. They seem to be able to cognitively change places in sympathy with the sufferer; they show commitment to others and an emotional and cognitive sensitivity to other's situation; and they are also able to understand which kind of help and assistance might be effective.<sup>5</sup>

Furthermore, chimps and other apes seem to be sensitive towards unequal outcomes, pointing in the direction of *inequity aversion* (Sanfey and Dorris, 2009, p. 75; Brosnan and de Waal, 2014). They routinely cooperate in defending their territory (territorial or boundary patrol), form coalitions (coalitionary support), hunt in groups (Wolkenten et al. 2007), share food, engage in reciprocal exchanges (Silk, 2007, p. 1348; Rosati et al., 2010) and punish defectors and non-cooperators (i.e., primate policing, (altruistic) punishment, retaliation and conflict mediation). All these forms of cooperation suggest not only targeted helping, but also a certain form of *mental book- or scorekeeping* (Horner et al., 2011, p. 13849; Cheney, 2011, p. 10905) requiring recognition of other's needs and goals as well as shared intentionality and planning (de Waal, 2009; Cheney, 2011, p. 10905). According to Silk:

'... primates are able to recognise individuals; identify kin; compete the value of resources and services; keep track of past interactions with group members; make transitive inferences; discriminate between cooperators and defectors; and assess the qualities of prospective rivals, mates, and allies. Primates also know something about the nature of relationships between other group members' (Silk, 2007, p. 1348).

Furthermore, monkeys and apes have considerable knowledge about social information. They seem to monitor relationships and are well informed about rank relationships. Moreover, conflict resolution and settlement is a regular, conspicuous part of primate social life: post-conflict behaviour often involves appeasement, consolation, rapprochement and reassurance gestures aiming at relationship repair and restoration. According to de Waal (2000), even forgiveness seems to be involved. Third-party conflict mediation is common as part of the high ranking individuals' policing and pacification function: alpha males commonly intervene in others' conflicts to protect social and cooperative bonds.

Emotional as well as cognitive perspective-taking is thus not limited to human adults: a basic or limited version of primate empathy and ToM apparently exists. Nevertheless, the human species seems to be special in the degree to which it puts itself into another's shoes. Humans grasp how others feel and what they might need more fully than any other animal species (due to their higher number of mirror neurons and the more pronounced empathy and ToM capacities). Yet the human species is not the first and only one to help others insightfully (de Waal, 2009, p. 107). For example, apes recognise the needs of others and understand when one of their conspecifics is hungry or in need. They show a considerable interest in another's welfare, which has been shown by de Waal's et al. *token experiments* testing for ape altruism (de Waal, 2009, p. 112ff.; see also section 4 of this paper). Furthermore, apes spontaneously help others in need. One chimpanzee, for instance, removed the peg that held the chain, thus allowing its companion to reach out for food. This is a clear example of pro-social choice as well as targeted helping.

Yet pro-social behaviour is not limited to primates. Other species also show this kind of behaviour which was thought of being uniquely human. Elephants are perhaps among the

---

<sup>5</sup> Cf. for an opposing view: Tomasello, 2009.

most empathetic and cognitively advanced animals: they perform concerted actions to support a calf in need or a wounded conspecific and provide care to companions in the form of water and food (Plotnik et al., 2011, p. 5116; Hakeem et al., 2009, p. 248; de Waal, 2009, p. 119ff). Furthermore, both dolphins and whales show deliberative, cooperative-altruistic assistance behaviour: they live in complex social structures, establish long-term bonds, form higher order alliances and cooperative networks, use tools and come to the defence of victims (Butti et al., 2009, p. 244). Some evidence even suggests help which crosses the species barrier (de Waal 2009).

Advanced empathy and ToM are unimaginable without a sense of self or self-awareness. Caring for others behaviour starts with the self. *Mirror Self-Recognition (MSR) experiments* test for self-identity and whether animals recognise their own reflection, their mirror image; if they do so, this would imply a concept of self. The most famous example is the *rouge or mark test*. Rouge makeup is used and a dot is put on the animal's forehead in order to test for MSR. Species that recognise themselves in a mirror are very likely marked by emotional (empathy) and cognitive perspective-taking (ToM). Species that do not recognise themselves in the mirror very likely lack these capacities. Mirror tests show that monkeys which lack MSR do not pass the test, while all anthropoid apes (i.e., chimpanzees, bonobos, gorillas and orang-utans) as well as elephants and dolphins do (de Waal et al., 2005; de Waal, 2005; 2009, p. 147). They thus have a similar (yet not an identical) capacity for MSR as humans.

### **3. The Evolutionary Origins of Morality**

#### **3.1 The 'Russian Doll'-Model**

As we have seen, empathy and ToM work similarly in some animal species as they do in humans – albeit to a differing degree. Humans have more of everything: more empathy, (much) more sympathy, a much more pronounced ToM, more mirror neurons and VEN cells, a (much) higher level of shared 'we' intentionality (Tomasello, 2009). The emotional and intellectual capacities of humans exceed the ones of other animal species. Humans form a small, cognitive or brainy elite which operates on a higher mental level than all other animal species. Yet there are no sharp dividing lines and there is no fundamental cognitive gap between humans and apes. It is not conceivable that empathy, cognitive perspective-taking and self-awareness evolved in a single jump in one species without any intermediate steps in other animal species. Instead, continuity between past and present, child and adult, animals and humans exists. This is the fundamental message of the hypothesis of biological gradualism. Biological and socio-cultural co-evolution – i.e., *gene-culture co-evolution* (Tomasello, 2009; Haidt, 2012; Wilson, 2012) – has not replaced simpler forms of empathy, perspective-taking and self-other awareness with more advanced ones. The latter are mere elaborations on the former and remain dependent on them. There is no such thing as a big bang revolution; rather evolutionary continuity exists (de Waal, 2009, p. 139; 2010).

According to de Waal's *Russian Doll model*, empathy is as multi-layered as a Russian doll, consisting of several inner and outer layers. The doll's inner core consists of the *Perception-Action Mechanism (PAM)* underlying emotional contagion and state-matching (1). The outer layers include cognitive empathy, sympathetic concern and consolation (2) as well as perspective-taking or targeted helping (3) (de Waal, 2012, p. 876). The metaphor of the Russian doll or *Matryoshka* states that the old remains present in the new and that advanced forms of empathy built on the elementary ones (de Waal, 2008, p. 56ff.). Not all species possess all layers; only a few possess the outer layers two and three. These layers are much



more pronounced in humans, apes and cetaceans: cognitive perspective taking and targeted helping are characteristic of hominids – especially humans are masters in these abilities. However, even the most sophisticated and advanced layers of the doll remain firmly tied to its primal inner core.

This indicates that evolution does not occur in revolutionary jumps – it rarely throws out anything: structures are transformed and co-opted for other functions, or tweaked in another direction (de Waal, 2009, p. 208ff.). New features are gradual, step-by-step modifications of old ones. Empathy and the social nature of our species are an innate part of our evolution. It is part of our biological heritage as ancient as the mammalian line. Thus humans should not be placed outside of nature. Instead of emphasising the uniqueness and distinctiveness of humans (i.e. placing the human species on a pedestal), we should focus more on evolutionary continuity and empathy's (and the like) evolutionary antiquity (Brosnan, 2009, p. 291).

Closely related to the 'Russian doll'-model is de Waal's 'theory of moral development'. This theory bears remarkable resemblances to Kohlberg's developmental model (Kohlberg, 1981; 1985; Kohlberg et al., 1983). According to de Waal (2008, p. 184ff.), three stages of moral development have to be distinguished. The first one and a half stages already exist in non-human primates; the second and third stages cannot exist without the previous ones. The world of human moral thinking therefore is a continuum building on primate social life. The first stage is the level of *moral sentiments*, consisting of empathy, reciprocity, conflict resolution and a deeply ingrained sense of fairness, which is characteristic of all primate species. The second stage is called *social pressure*: To realise cooperative behaviour within primate societies as well as social harmony, social norms are required. Norm-compliance needs to be monitored, e.g., by policing alpha males. Those that do not obey the rules, such as free-riders, defectors or non-cooperators, need to be sanctioned. Trust, reputation-building as well as community spirit and social or group cohesion are essential for each society. This second level is also present in some non-human primate societies, but to a far lesser extent and in a less systematic way. The third and most advanced level of moral development is the stage of *deliberation* and *reasoning*. This stage requires self-reflection and abstraction skills as well as full cognitive perspective-taking and ToM. Here the parallels between human and non-human primates end.

In sum, several parallels exist between human and non-human primates: Our closest living relatives share basic levels of emotional (empathy) and cognitive perspective-taking (ToM), other-regarding preferences and pro-social behaviour, reciprocal altruism and a limited sense of fairness, solidarity and community concern with us. Human and non-human primates are both tribal animals and group-seekers; they both have social instincts. As such, we share nepotistic or kin biases, that is, in-group favouritism and cooperation and out-group hostility and xenophobia. Furthermore, we know that most forms of morality start with emotions such as empathy, sympathy, emotional contagion and intuitions. Since emotions are part of our biological heritage, our morality is also part of it. Continuity exists between past and present, old and new (i.e., continual evolutionary line of ancestors). The fundamental difference between human and non-human primates is that humans have a much more pronounced mirror neuron system including distinct empathy and ToM capacities, a unique language system as well as the ability to make deliberate use of reasoning (including cognitive perspective-taking, self-awareness, self-other distinction and the Kantian notions of autonomy, self-legislation and personal freedom). Yet human uniqueness should not be super-elevated. A huge gap or a discontinuity between animals and humans, nature and culture, humans and their animal past does not exist; this kind of dualism (i.e., humans as the crown of creation versus nasty, brutish and primitive animals) stemming back from

Christianity has to be overcome. Primate research has shown the gradual evolution of morality. Humans as *zoon politikons* (Aristotle, 2013) are the descendants of (eu)social animals. Morality is not a cultural innovation that was invented by humans. Instead, moral behaviour is a result of our 'compassionate instincts' (Keltner, 2010) and 'moral sentiments' (Smith, 1976b) we share with other mammals. These instincts are deeply ingrained in our biological heritage. Moral behaviour is therefore not uniquely human; it was not purposefully or consciously developed. It is rather a by-product of biological and cultural co-evolution (i.e., natural evolution of morality) – evolution favours those animals that solidarily help each other, form trusting alliances and establish and maintain coalitionary support. Social connectedness increases evolutionary fitness and reproduction benefits. Thus cooperative and pro-social group animals out-perform less cooperative ones. Bonding ties as well as the ability to function in a group and build a social support network are crucial survival skills; they are essential for survival as well as reproduction.

Human empathy therefore has a long evolutionary history. The origins of altruism and fairness date back to our closest living relatives – monkeys and apes. Empathy and pro-social behaviour comes naturally to us (i.e., natural sympathetic emotions and empathetic concerns); from their first birthday onwards, human children behave already cooperatively (Tomasello, 2009). As such, human morality (i.e., social instincts and a moral sense) is derived from animal sociality; it has deep roots in the helping behaviour of great apes among others. We descend from a long line of group-living primates with a high degree of interdependence and a need for security that shapes social life. Humans are group animals with obligatory parental care and a herd instinct.

### **3.2 Multi-level Natural Selection**

To sum up: humans walk on two legs and face a bipolar tension. On the one side, they are 'natural beings', *Naturwesen* as Kant (1788 [2010]) would say, relying on intuitions, emotions and sentiments. Unconsciousness, automatic processes and passions play a huge role in decision-making. Freud (1923[1989]) speaks in this regard of the 'id', the source of our instinctual and bodily needs, wants, desires, drives and impulses. At the same time, however, humans are also 'rational beings', *Vernunftwesen* (Kant, 1788[2010]), relying on deliberate reasoning and cognitive perspective-taking. Freud (1923[1989]) speaks of the 'super-ego', the source of consciousness and critical and moral reasoning. Moreover, an ongoing conflict between competition and cooperation and between 'selfishness' and 'groupishness' exists within each human being – a conflict between self-interested utility maximisation, egoism and a me-first attitude (Rand, 1961[1964]) on the one hand, and companionship, collegiality, mutual aid, cooperation, community concerns, social bonding, group-oriented behaviour, civic-mindedness and social responsibility on the other hand (Plato, 2011; Damasio, 1994[2006]; Haidt, 2001; Kahneman, 2001; Thaler and Sunstein, 2008[2009]). Pro-social motives in group-living animals (i.e., striving for a well-functioning whole) clash with self-interested motives which set limits to solidarity and collaboration.

*Multi-level natural selection* (MLNS) helps in explaining this conflicted dual nature of motivations (Wilson, 2012; Haidt, 2012, p. 217ff.): MLNS theory refers to the interaction of individual selection and group selection. *Individual-level selection* comprises in-group competition and self-interested motivations; the main aim of the individual is intra-group survival and reproduction (i.e., passing on of genes to the next generation). *Group-level selection*, on the contrary, refers to between-group competition, in-group altruism, social cohesion and cooperation. Group-level traits include cooperativeness, empathy and networking. Natural selection thus works at multiple levels simultaneously – at the individual

and the group level. Selection pressures within groups as well as between groups (i.e., competition between groups vs. competition among individuals within groups). What is important is that group selection pulls for cooperation and helps to transcend self-interestedness; it aims to suppress or regulate self-interestedness and allows for cooperative societies (i.e., self-domestication of self-interest). Group selection favours group-mindedness, i.e., the ability to learn and conform to social norms, obedience to social institutions and sharing of collective and group-related emotions and concerns. It tends to suppress anti-social behaviour such as free-riding, defection and opportunism and spurs individuals to act in ways that benefit the group as a whole. It also allows for a transition from selfish individuals to groupish team-players (Haidt, 2012, p. 217ff.). Group selection – and not kin selection and inclusive fitness (see Dawkins' hypothesis of the 'selfish gene' (Dawkins 1976[2009]) –, is therefore responsible for advanced pro-social behaviour. It is one of the main driving forces of evolution and at the same time the evolutionary origin of eusociality.

It is remarkable that cohesive and cooperative groups mainly consisting of (reciprocal) altruists usually win the competition with other groups; they out-perform those groups that mainly consist of selfish individuals. Selfish individuals and free riders, however, can beat altruistic ones. Thus an incentive to cheat and defect exists in this prisoner's dilemma-like situation. Wilson (2012) characterises this situation as a moral 'dilemma of good and evil': While group selection fosters altruism, cooperation, groupishness and virtue (the good in society), individual selection fosters selfishness and competition for survival and reproduction (the evil in society).

### **3.3 Dual Motive Theory and the Model of the Triune Brain**

This constant tug and pull between cooperation and competition, ego and sympathy, self-interest and other-interest can also be explained by *dual motive theory* (Cory, 1999; 2006a; 2006b) and the model of the *triune brain* (MacLean, 1990). According to Cory and MacLean, the human brain consists of an evolutionary developed tri-partite structure: a reptilian complex, a paleo-mammalian complex and a neo-mammalian complex. The *reptilian complex* is mainly responsible for physiological operations, reproduction and self-preservation. Here self-interest motives dominate. The *paleo-mammalian complex* is responsible for maternal care, nursing, infant attachment, family life, social bonding, emotional and pro-social behaviour. Finally, the *neo-mammalian complex* or neo-cortex is in charge of problem-solving, learning, memory and communication of thoughts and feelings which allow for behavioural adaptations to complex environments. The paleo- and neo-mammalian complexes are mainly dominated by empathy and other-interest motivations. Thus the model of the triune brain, which is based on dual motive theory, exceeds standard economics with its single motive theory. While the *Homo oeconomicus* idea of man is solely based on self-interest and/or egoism, dual motive and triune brain theories assume a multi-dimensionality and heterogeneity of anthropological motivations. Two dominant motivations – egoistic self-interest and empathetic other-interest – exist side by side. To put it differently: two fundamental behavioural programmes – the self-preservational or ego programme and the affectional or other-interested programme – are running at the same time (i.e., *conflict systems neuro-behavioural model*). The aim is now to balance these two antagonistic programmes and to solve the constant conflict between empathy/other-interest and ego/self-interest (Tomer, 2012).

In sum, human beings display a dual nature; they can be characterised as *Homo duplex*. Human nature is selfish, but it also has a groupish overlay. In other words: human cooperativeness is laid on top of the self-interested foundation. A mixture of selfishness and

selflessness exists. It depends to a large degree on the socio-economic and cultural environment (i.e., situation-specific variability/situational adaptations) which 'card' is played – the selfish/competitive one or the groupish/cooperative one. In different socio-economic contexts different moral games are played and different moral rules and principles are applied (i.e., practice of moral differentiation along changing contexts): For instance, in situations where individuals are being watched or where they are not anonymous, the level of cooperation and altruism is considerably higher compared to situations characterised by a large degree of invisibility and anonymity. In the latter, individuals cheat and free ride more often and the competitive and self-interest cards are played considerably more often (the same holds true for situations which resemble competitive market situations (Falk and Szech, 2013)). This has been shown by comparing experiments played in the 'dark' with those played in the 'spotlight' and by investigating the effects of eyespots on computers or walls on honesty, generosity and cooperation. The reason for the differing behaviour in the different contexts is the importance of reputation for cooperation (and as a consequence the possibility of punishing free-riders and defectors). The higher the level of transparency and information about the other players and the easier it is to identify cooperators and cheaters, the more are people willing to obey to the social norms (Maestripiere, 2012, p. 109ff.; Haidt, 2012, p. 97). The next sections elaborate on this and analyse the dual nature of (non)human primates with the help of experimental economics, game theory and primate research.

#### **4. The 'Token Economy'**

Among the most famous experiments by de Waal and others are the *token economy experiments* or *pro-social choice tests*. Monkeys and apes are introduced to the use of 'money'. The study participants (monkeys and apes) get rewarded with poker chips or 'monkey money' in order to test their bartering and monetary skills. Furthermore, the experiments allow for testing monkey and ape altruism. The chips can be used in a 'chimpomat', a vending machine which delivers food upon token insertion. Tokens are, therefore, used in exchange for goodies. Two kinds of tokens are available: a selfish token which yields a small piece of apple for returning the token just for the 'deliverer' of the token, while the other partner gets nothing, and a pro-social token which rewards both monkeys or apes equally.

Monkeys and apes interestingly show a clear preference for pro-social tokens: they clearly prefer sharing over solitary consumption, which in turn might be interpreted as a caring for others or altruistic behaviour (de Waal, 2009, p. 112ff. and p. 193ff.). Pro-social behaviour seems to be a key characteristic of our closest relatives. De Waal's et al. experiments thus suggest a long evolutionary history of pro-social or fairness 'norms'.

Nevertheless, selfish or egoistic behaviour is always around the corner; e.g., capuchin monkeys are in a much more egoistic mood with other conspecifics that they have never met before. Pairing a capuchin monkey with a stranger will reduce pro-social behaviour and increase selfish behaviour. To put it differently: the stronger the personal tie of a monkey with its partner, the more it would pick the pro-social rather than the selfish token. A strong in-group bias thus seems to exist.

Reduced pro-social behaviour is also observable when monkeys do not see each other (here they share considerably less). A further way to reduce pro-social acts is when the monkey's partner gets a superior reward. Here the monkey becomes reluctant to pick the pro-social option, pointing in the direction of a self-centred inequity aversion or an egocentric sense of fairness. In sum, monkeys are perfectly willing to share and behave pro-socially

given that their partner is visible and gets equal rewards. As soon as the partner is better off or invisible, competition kicks in and interferes with generosity (de Waal, 2009, p. 194ff.).

Similar experiments combining economic game theory and primate research were conducted with apes, in particular with chimpanzees, and human children at the age of 3-5 (Tomasello, 2009). Both were tested in a modified version of the ultimatum game (UG) (Güth et al., 1982):

'One individual choose between two tokens that, with their partner's cooperation, could be exchanged for rewards. One token offered equal rewards to both players, whereas the other token favoured the chooser. Both apes and children responded like humans typically do. If their partner's cooperation was required, they split the rewards equally. However, with passive partners – a situation akin to the so-called dictator game – they preferred the selfish option. Thus, humans and chimpanzees show similar preferences regarding reward division, suggesting a long evolutionary history to the human sense of fairness' (Proctor et al., 2013, p. 1).

In other versions of the modified UG, participants face a choice of two tokens: one represents an equal reward distribution, while the other represents an unequal distribution favouring solely the proposer. The tokens work again like money, which means that they can be exchanged for food. As a result, chimps, just like human children, chose the equitable token much more often; they made equitable offers respectively choose a more equitable split of rewards in the UG. Consequently, children and chimps are similarly sensitive to the contingencies of the UG. Further parallels between chimps and human children exist with regard to the dictator game (DG):

'In a simple choice task resembling the DG, with either a passive partner (chimpanzees) or while alone (children), both species preferentially chose a "selfish" offer that brought the majority of rewards to themselves. In the UG condition, in contrast, respondents could affect the outcome (by accepting or rejecting the offer), and both species shifted their choices to a more equitable distribution. This shift is similar to the way adult humans change their offers between DGs and UGs. Most adult humans are more selfish in DGs than in UGs' (Proctor et al., 2013, p. 3).

## **5. 'Animal *oeconomicus*' versus 'Animal *moralis*'**

In primate research there is an intense debate going on about the nature and motivation of non-human primates. Just like humans, our closest living relatives – chimpanzees and bonobos – seem to be bipolar apes. Like humans they have a pro-social as well as a selfish side (i.e., dual motivational structure). They walk on two legs – a selfish one and a pro-social one (de Waal, 2009, p. 159). Furthermore, there is this bipolar tension between the 'animal *oeconomicus*' and the 'animal *moralis*', between self-interest and the common good as well as between competition and cooperation. Part of the 'nasty' (i.e., anti-social, egoistic) side of the primate species is the violent nature, the inborn aggressiveness as well as the Machiavellian-like power struggles. There is definitely no shortage of aggression and violent conflicts in primate societies (de Waal, 2009, p. 44ff.). On the contrary, there is plenty of on-upmanship, egoism, competition, jealousy and nastiness among primates. Power struggles

and hierarchy fights are a central part of every primate society, so that conflict is always around the corner. No primate can afford to treat everyone nicely all the time, since every individual faces harsh environmental conditions as well as competition and rivalry over food (Tomasello, 2009, p. 83), mates and territory. At the same time, primate societies in the wild are characterised by a substantial level of cooperation, close social relationships as well as far reaching social embeddedness and social cohesion. Primates are – up to a certain degree – cooperative and empathetic animals that need to work hard to keep selfish and aggressive urges under control. Although they are highly competitive animals they have the ability to engage in give-and-take; they are masters in connecting and establishing social ties, which in turn help constraining the selfish and competitive side. The right (Smithian) balance between self-interest and sympathetic concern for the welfare of others has to be found: unconditional trust, cooperation and empathy are naïve and detrimental, whereas unconstrained greed and egoism only lead to the sort of (self-destructive) dog-eat-dog world or Hobbes' (1651[2012]) *bellum omnium contra omnes*.

The debate about the nature of (human and) non-human primates is mainly shaped by two research groups, the one led by Tomasello at the Max Planck Institute for Evolutionary Anthropology in Leipzig, the other one led by de Waal at the Living Links Centre at the Yerkes National Primate Research Center in Atlanta. The primate research debate revolves around the following questions: are our closest living relatives rational utility maximisers? Are they sensitive to fairness and (in-)equity? How do they solve collective action problems and prisoners' dilemma-like situations? Does third-party punishment of free-riders and defectors occur in non-human primates?

According to a study conducted by the Tomasello group in 2007, chimpanzees are rational utility maximisers and more or less insensitive to fairness. Contrary to humans, chimpanzees show only a very limited version of other-regarding preferences or inequity aversion, that is, aversion towards inequitable outcomes. Instead, they behave more like *Homines oeconomici* and act in accordance with the self-interest economic model. In their study, Tomasello and colleagues tested chimpanzees in a *mini-ultimatum game*, a game in '... which proposers are given a choice between making one of two pre-set offers [typically a fair (50/50) versus an unfair split (80/20)] which the responder can then accept or reject' (Jensen et al., 2007a, p. 107). In an UG with humans, proposers typically make offers of 40-50% and responders typically reject offers under 20%. Testing the mini-UG on other primate species revealed that chimpanzee responders tended to accept any non-zero offer; chimps only rejected offers of zero. Even worse, chimpanzees offered the most selfish offer (the smallest amount possible). This is exactly what the self-interest principle or the *Homo oeconomicus* model would predict. The authors conclude that since chimps show only limited concern for others – i.e., other-regarding preferences – or a very basic concern for fairness and reciprocity, they differ fundamentally from humans. A full sense of fairness and justice (including a willingness to cooperate and to punish non-cooperators) seems to be uniquely human.

In a further study, the Tomasello group tested chimpanzees and bonobos to discover whether they are sensitive to food theft and punish thieves in response. In the *ultimatum theft game*, a bonobo or chimpanzee proposer consistently steals food from responders. Although one would expect signs of arousal as well as attempts to punish thieves, responders still accepted all positive offers (i.e., no rejection of non-zero offers) without punishing thieves or showing signs of anger (Jensen et al., 2007b; Skoyles, 2011). This indifference towards outcomes confirms previous findings of the Tomasello research group. Moreover, it extends the results of their previous studies to socially more tolerant bonobos, the other 'Pan species' beside chimpanzees: even bonobos did not punish unfair outcomes or actions or display

sensitivity to fairness and equity. The rejection rates of bonobos and chimpanzees were similar. The authors conclude with regard to the evolutionary origins of fairness norms:

‘... bonobos, like chimpanzees, are self-regarding in an ultimatum game that uses unfair actions to produce unfair outcomes. Both apes act like rational maximisers, with no concern for fairness or the effect of their choices on the outcomes affecting others. This finding is very different from what is found in humans, including children. While humans are strongly affected by concerns for fair allocations and fair intent, chimpanzees and bonobos do not appear to be. Concern for fairness and other-regarding preferences may thus be a derived trait in humans.’

In summary, only ‘[h]umans but not chimpanzees [and bonobos] punish unfair offers in ultimatum games, suggesting that fairness concerns evolved sometime after the split between the lineages that gave rise to *Homo* and *Pan*’ (Kaiser et al., 2012, p. 944 and p. 942).

Riedl, Jensen, Call and Tomasello (2012) further investigate whether chimpanzees engage in *third-party punishment* of free riders and defectors. Social punishment is essential in order to maintain and stabilise cooperation by deterring non-cooperation, opportunism, free-riding and cheating. In the case of third-party punishment, individuals impose sanctions on a perceived transgressor or social norm violator for uncooperative acts even when the punishers themselves are not directly affected and when it is costly to do so. Riedl et al. (2012) conducted one of the first third-party punishment studies with non-human animals in order to determine whether human third-party punishment and norm enforcement have their evolutionary origins in other great apes. Chimpanzees were confronted with third-party theft in the form of stolen food. The experimenters expected that if chimpanzees were sensitive to third-party violations, they would react most strongly to third-party theft in which one chimpanzee – the thief – stole food from another individual – the victim. Furthermore, they investigated whether dominant individuals like alpha males are more likely than subordinates to use coercive and punitive strategies and whether kin-based nepotism leads to more retaliation. The key findings are that chimps punish those who take food away from them directly, but they do not punish third parties, that is, individuals who steal food from others, for their violations of cooperative behaviour. In addition, dominant chimpanzees are more likely than subordinates to retaliate when they are stolen from. Yet dominants rarely intervene by punishing third parties. Even kin-based relatedness with the victim does not induce third-party punishment. In general, chimpanzees do punish others, but they do not do so when they are not personally affected. In contrast to humans, an apparent tolerance of free-loaders exists: chimpanzees engage in second-party punishment (where a punisher gains for directly securing a resource) but not in third-party punishment (which reveals a sensitivity of the punisher to social norms applicable to all). According to Riedl and colleagues, chimpanzees do not cooperate in the same manner or to the same degree as humans, although they have a primitive(!) sense of fairness and sociality. From the perspective of the Riedl et al. study it is at least questionable whether they are averse to inequity.

The last study worth mentioning deals with chimpanzees solving *collective action problems*. Schneider, Melis and Tomasello (2012) found that pushers tended to be individuals higher in rank, while free-riders tended to be subordinate individuals. Dominant or higher-ranked individuals who pushed had the security of knowing that they would be rewarded for their effort. They were always assured a share of the reward, which lessened the risk of

action. It is therefore in their own interest to provide public goods even when case-by-case free-riding occurs. For subordinates, however, the situation looks different: they usually pay a very high price for pushing as they are typically unable to gain much access to the reward and thus they tend not to act or volunteer. In sum, chimpanzees are able to overcome volunteer's dilemma scenarios, but they have a limited set of mechanisms available to do so.

The Tomasello research group studies show that apes (mainly) act in a self-interested manner. In contrast to the human tendency to split rewards more or less equally, non-human primates offered the smallest amount possible and respondents accepted virtually all offers. Here apes appear as rational utility maximisers. The studies also showed that chimps and other great apes are more competitive (especially over food and other resources) and less socially tolerant; they only have a limited sense of fairness, pointing towards a gap between humans and great apes. Apparently, apes are much more self-focused or self-centred, which explains their egoistic behaviour; a shared intentionality and a 'we'-mode seem to be much less developed (Tomasello, 2009). Nevertheless, a basic form of cooperation and collaboration and a limited sense of fairness – although a self-focused one – cannot be denied.

The Tomasello research group studies, however, differ sharply from the UG and DG studies conducted by the de Waal research group. In a recent token economy study, Proctor, Williamson, de Waal and Brosnan (2013) found that non-human primates such as chimps and capuchin monkeys resemble humans in their decisions about cooperation and aversion to inequitable reward distribution (Wolkenten et al., 2007); e.g., chimps make equitable and fair offers in UG (Milinski, 2013). Moreover, chimps protest against inequity in experimental settings, indicating that they are up to a certain degree sensitive towards unequal outcomes and that (basic) social norms among chimps exist.

In a further *Pro-social Choice Test* (PCT) by Suchak and de Waal (2012), capuchin monkeys were spontaneously pro-social, selecting pro-social tokens which rewarded both individuals much more often than the selfish ones that rewarded the chooser only. Interestingly, they assisted or benefited their partners regardless of whether they were paired with an in-group or an out-group conspecific (de Waal et al., 2008, p. 13685). Not only did capuchin monkeys show pro-social tendencies and social reciprocity, they were also quite sensitive to inequity as well as to payoff distribution: They behaved pro-socially unless their partner received a higher-quality reward, e.g., grapes instead of apples. The results of this study have been replicated with PCT as well as in *giving assistance tests* with chimpanzees and bonobos (Horner et al., 2011). In the latter, individuals can choose between providing instrumental help to other individuals pursuing a recognizable goal (e.g., out-of-reach object) or doing nothing. The controlled experiments by Horner et al. show that chimpanzees as well as the chimpanzees' congener, the bonobo, were proactively pro-social: They showed helping behaviour, sensitivity to the needs of others as well as pro-social preferences (i.e., they picked the pro-social token considerably more often). One reason for this might be that all participants in this study were female. Interestingly, high-ranking individuals tended to behave more pro-socially than subordinates. Furthermore, there was no correlation between pro-social choice on the one hand, and kinship, affiliation and rank on the other hand: Chimps behaved equally pro-socially towards all partners regardless of whether they were kin or unrelated group-mates (Barnes et al., 2008).

These results are compatible with chimpanzee behaviour in the field. Here chimps routinely cooperate in defending territories; they form coalitions, hunt together in groups, share food, engage in reciprocal exchanges and targeted helping, mutually groom and console each other. A high rate of pro-social behaviour, successful cooperation and sharing of rewards exists in the wild chimpanzee's natural social life. The reason for this is that



chimps that do not share food with others are more likely to encounter threats and temper tantrums; e.g., chimps may refuse to share with others who did not previously groom them.

As the debate between Tomasello's and de Waal's research groups has shown, the empirical results are not consistent. Some research suggests that apes are somewhat indifferent to the welfare of other group members, highly competitive and less socially tolerant, while other research suggests that apes are motivated to provide benefits to others and respond positively to the needs of others. Although the empirical results are reliable and robust, we receive seemingly incompatible conclusions about social preferences in apes, pointing once again to the complex, multi-faceted and dual nature of (non-)human primates: They are walking on two legs – a selfish and a pro-social one. Equally important is the fact that apes – just like humans – behave differently in different contexts (cooperative vs. competitive environments) (Maestripiere, 2012, p. 109ff.): Some primate species' lives are filled with frequent aggression and violence, while others are filled with peaceful communitarianism, cooperation and egalitarianism, pointing to the interplay of evolution and ecology. Social structures and ecological settings matter! In cooperation with genes and the biological heritage, the environment and social milieu influences behaviour (i.e., behavioural and brain plasticity due to epigenetical factors). Of particular importance is the sex ratio, the question whether females or males are predominant. In harsh and competitive environmental conditions – when survival is at stake – primates tend to behave counter-empathetic with competitors. Under these conditions rivals are treated with hostility and primates show the opposite of empathy. In a cooperative setting, however, non-human as well as human primates are much more empathetic with their respective partners (Sapolsky, 2010; Silk, 2009). The studies also point at evolutionary continuity (i.e., the evolutionary origins of human cooperation date back to our closest living relatives) and our primate legacy, that is, gradual differences as well as parallels in the behaviour of apes and humans can be detected (see the next section).

## **6. Human vs. Non-Human Primate Societies**

Altruistic behaviour is widespread in nature (Maestripiere, 2012, p. 171ff.), but typically limited to kin and reciprocating partners. It is a form of sacrificing behaviour that is costly to the actor and beneficial to the recipient in that it increases the recipient's fitness. In primate societies, the most common forms of altruistic behaviour are social grooming, coalitionary support, alarm-calling, parental care and food-sharing. Primate research now gives information on the evolutionary foundation and deployment of morality in general and reciprocal altruism in particular.

Morality originally evolved in small face-to-face (primate) communities consisting mainly of close kin (e.g., relatives). It is dependent on biological imperatives such as survival and reproduction. That is why morality is kin-biased (kin selection theory) (Hamilton, 1964; Maynard Smith, 1964; Wilson, 2012) or biased towards reciprocating partners (reciprocal altruism).<sup>6</sup> In primates, in-group favouritism and nepotistic biases exist: Social interactions, e.g., cooperative breeding and coalitionary support, are typically restricted to group members that have strong social bonds. Responses towards strangers and members of neighbouring groups range from passive avoidance to active hostility. So far, there is only little empirical evidence of cooperation among members of neighbouring primate groups in the wild. Thus

---

<sup>6</sup> Trivers, 1971; Bolton and Ockenfels, 2000; Falk and Fischbacher, 2000; Gintis, 2000; Fehr, Fischbacher and Gächter, 2002; Bowles and Gintis, 2004; Fehr and Schmidt, 1999; Fehr and Fischbacher, 2003; Axelrod and Hamilton, 1981; Silk, 2009.

non-human primate societies function considerably more on the basis of kinship, nepotism and direct reciprocity compared to human primate societies (Tomasello, 2009).

Humans, however, rely on cooperation to a far greater extent than most other animals do (i.e., large-scale collaboration within socio-cultural institutions). They are able to orchestrate cooperation in substantially larger groups which is not kin-based or limited to familiar group members such as close kin, mates and reciprocating partners. The pattern of cooperation (i.e., scope and scale) is different in the sense that humans have a general disposition to behave altruistically to others and extend (reciprocally) altruistic behaviour towards strangers (Silk, 2009; Silk and House, 2011). Humans are one of the rare animal species that regularly provide aid to strangers and impose costly punishment on defectors and non-cooperators in anonymous, one-shot interactions. Cooperation in humans is based on a willingness to impose costly punishment on those who shirk social obligations. It is motivated by other-regarding and pro-social preferences based on concern for others, empathy and inequity aversion.

Non-human primate behaviour can now be explained by individuals' attempts to reward those individuals who help them and punish those individuals who hurt them, i.e., rectify wrongs and reward good behaviour. Altruism by one individual, therefore, enhances the likelihood of cooperation by the other (i.e., contingent cooperation or altruism towards direct-reciprocating partners). Human primates – as well as other species such as eusocial insects –, however, often punish individuals that violate social norms or fail to cooperate, even when they are not directly affected or harmed. This form of punishment is called *altruistic or third-party punishment*. Such behaviour is altruistic because the individual who imposes sanctions incurs a cost, while the benefits are widely shared by other group members. Altruistic punishment helps to stabilise social cooperation. It carries short-term costs for an individual since sanctioning is costly, but this 'investment' is more than recouped by the long-term gains of being treated fairly in the near future.

Altruistic punishment which benefits the group has to be distinguished from punitive action which benefits the individual. Individual-level selection favours the latter one (*retaliation*) since it generates direct fitness benefits for the self-interested individual actor. Group selection, however, favours collaboration and altruistic punishment since it generates benefits for the whole group (Wilson, 2012). Retaliation is widespread in non-human primate groups. There is some (limited) empirical evidence and anecdotes for altruistic punishment in non-human primates (Silk, 2009), suggesting that apes punish norm-violators and non-cooperators. In some non-human primate species, policing individuals mediate disputes among other group members. Impartial mediation and conflict resolution ideally brings disputes to a speedy end, thus reducing the costs incurred by the participants and avoiding the possibility of escalating conflicts.

Empirical research on the behaviour of chimps and other great apes in captivity and in the wild has led to the conclusion that a basic sense of justice and fairness exists in their societies, e.g., they assist other individuals who are victims of attempted theft. Both chimps and capuchin monkeys commonly share food among adults as well as unrelated (non-kin) individuals. They not only share food; they also tend to do so reciprocally, which means that they share food more often with those who shared with them (i.e., contingent cooperation). As such, food sharing appears to be a special form of repayment for a service. Capuchins, for example, are more likely to share food with a partner who recently helped them in a cooperative task such as successful hunts (i.e., hunting prey together requires a cooperative effort and a coordination of hunting behaviour). Other sharing services include grooming (Silk 2009) and coalitionary support, e.g., cooperative defence against predators and competitors. Furthermore, they seem to be sensitive to the distribution of rewards in a cooperative task,

which implies sensitivity to payoffs. Monkeys and apes are apparently aware of their partner both as potential cooperators and competitors. They seem to be sensitive to the social context, whether it is a cooperative or competitive environment, and cooperate significantly more frequently with socially tolerant partners. Moreover, it seems as if socio-economic interactions in non-human primate life are based on a primitive form of social capital consisting of trust, personal networks, communication and reciprocal altruism. Here the fulfilment of expectations and obligations according to the motto *quid pro quo* is essential. Monkeys and apes test the strength of their social bonds by playing *trust games* such as hand-sniffing, eyeball poking and fondling of genitalia (de Waal, 2009, p. 164ff.; Maestripiere, 2012, p. 186ff.). They seem to recall previous favours such as grooming and establish a buddy system of mutually positive partnerships. A clear tendency to return favours apparently exists. This kind of exchange must rest on memory of previous events combined with a psychological mechanism similar to gratitude, that is, positive feelings toward an individual whose act of kindness the other individual recalls. Sharing food and other items fosters cooperation in animal communities. Monkeys and apes seem to connect effort with compensation and reward, so that joint effort requires joint rewards. Their relationships seem to rest on direct reciprocity and mutualism. Especially chimps look back, remembering previous events very clearly. De Waal (2009, p. 178ff.) speaks in this regard of 'deliberate and calculated reciprocity'. Chimps and other great apes do not only look back, they also seem to look forward anticipating events; e.g., they treat others nicely so as to curry favours. As such, chimps and other apes may have foresight and planning abilities following the motto 'If I do this for another individual, I may get that in return'. Interestingly, kinship is not necessarily required for chimps to work closely together; cooperation and reciprocal altruism among non-relatives also exists. Moreover, chimps and other great apes show signs of other-regarding feelings as well as inequity aversion. They are apparently sensitive to unequal treatment – at least up to a certain degree – and engage in 'tit for tat' strategies (to discourage exploitation and free riding, defectors and non-cooperators must be punished).

However, according to de Waal (2009, p. 190) and others, monkeys (and to a lesser degree also apes) have an egocentric version of fairness and justice – one which distinguishes them from human primates. They seem to exhibit disapproval or approval of certain kinds of behaviour, and distinguish between acceptable and non-acceptable actions according to the foreseeable outcomes for themselves; e.g., inequity aversion implies a reaction to both over and under-compensation whereas advantageous inequity is typically preferred to disadvantageous inequity. In apes, basic fairness norms seem to exist (although they differ substantially from human fairness norms). They seem to monitor their interactions more closely and keep better track of each individual's contributions to common goals. They also seem to be able to establish prescriptive social rules. Although primates show altruistic (as well as egoistic) behaviour, it is questionable whether they do so intentionally. The question is whether they behave altruistically on a motivational or intentional level. According to de Waal (2008), animals – contrary to humans who are capable of intentional altruism – only show motivational altruism. Lots of animal altruism is merely functional or instrumental, while intentional (pure altruistic) helping behaviour seems to be restricted to the great apes and some other mammals with large brain size (de Waal, 2008, p. 199). In summary, retributive, friendly emotions such as gratitude (based on a psychological and memory-based process) as well as mutual expectations and prescriptive rules seem to exist. The fundamental difference between a human and a non-human sense of fairness is that the non-human sense is more egocentric than the human one (this is especially true for monkeys); thus, a complete sense of fairness seems to be non-existent for non-human animals.

Following Brosnan (2009, p. 291ff.), four steps in the evolution of the inequity response have to be distinguished:

- (1) The ability to notice when rewards differ between individuals. This first step requires advanced cognition to compare one's own rewards with those of another individual as well as social learning.
- (2) React negatively to discrepancies in the rewards between oneself and another individual. This second step requires individuals not only to notice the results or outcomes of another individual, but also to respond negatively to this difference in payoffs. This capability provides a fitness benefit for the individual, if this negative reaction to inequity leads individuals to look out for new partners who might be more equitable (i.e., shopping around for better partners).
- (3) Take deliberate and cognitive action to rectify inequity towards the self. This third step requires a concise understanding of how one's own behaviour will affect the payoff of the partner, as well as an ability to inhibit, hold back and give up the immediate reward.
- (4) Reaction towards overcompensation or advantageous inequity aversion. Individuals are uncomfortable when the partner receives less than they themselves do and consequently strive for material compensation.

All four stages need to be developed in order to consider the reaction a true sense of fairness or justice. So far, only humans possess this kind of sense of fairness and justice. If, for example, a reaction to overcompensation is missing, the response is a one-sided reaction which is self-centred and ego-centric. Both chimps and capuchins respond negatively when receiving less reward than a partner individual. As such, the response in non-human primates differs from the one in humans. The primary difference is the following: While humans treat fairness as a norm (including both over- and under-compensation), non-human primates seem to be more interested in their own outcome and do not react when receiving more than their partner. What is missing is an equivalent reaction to overcompensation (Brosnan, 2009).

In summary, the (gradual) differences between human and non-human primates include the following aspects: apes show considerably more often egoistic and selfish behaviour (they fail to suppress or transcend their natural selfishness); they are less cooperative and less altruistic (Tomasello, 2009, p. 14ff.) (although they have a basic sense of altruism and cooperation); they are highly competitive especially over food and less socially tolerant; they operate only with some basic social norms of fairness and justice; these norms are moreover often self-focused and self-centred; apes also lack a full sense of shared intentionality and a full 'we'-sense: they usually engage in group activity in 'I'-mode, not in 'we'-mode (Tomasello, 2009, p. 63). This fully developed shared intentionality and 'we'-mode is uniquely human. Only humans engage in large-scale and mutually beneficial collaborative activities (apes, on the contrary, participate much less often in activities that yield group-level benefits; and if they do so, their behaviour is more likely to be based on kinship, nepotism and direct reciprocity). The remarkable human capacity for collaboration makes it possible that humans are able to orchestrate cooperation within large-scale and anonymous groups of individuals with partially conflicting interests. Collaboration requires social norms of fairness and justice, that is socially agreed-upon and mutually known expectations bearing social force, monitored and enforced by third parties (Tomasello, 2009, p. 87). In shared cooperative activities, the co-operators must be mutually responsive to each other's intentional states; they need to coordinate roles and develop interpersonal trust and commitments. Collaboration

also requires shared intentionality, that is, joint intentions and joint commitments in cooperative endeavours and cooperative groupthink.

To get from ape group activities to human collaboration, three basic sets of processes are required (Tomasello, 2009, p. 54ff.):

1. Socio-cognitive intelligence, skills and motivations for shared intentionality, collaboration, communication and social learning.;
2. Tolerance and trust.
3. Social norms and cultural institutions.

Apes lack the full and comprehensive socio-cognitive capacity for joint attention, mutual common knowledge and a sense of inter-subjectivity and interdependency. Only humans show a distinct commitment to joint goals (i.e., shared intentionality) and act in a distinct 'we'-mode (i.e., human uniqueness and distinctiveness). They are also able to internalize social norms (i.e., social norms of cooperation, norms of conformity and moral norms) – often accompanied by the feelings of shame and guilt; this helps to transcend selfishness and transforms problems of competition into those of collaboration. Last but not least, humans show more concern for others wellbeing than apes do; other-regarding preferences and pro-social behaviour are considerably more pronounced in human than non-human primates.

## **7. 'Lessons' Learnt From Primate Research**

The following ten insights can be gained from primate research:

1. Human and non-human primates display a complex and multi-faceted anthropological nature. A dualism or heterogeneity of motives exists; self-interest and altruistic motives (partially) conflict with each other (i.e., *dual motive theory*).
2. Human and non-human primates stand on two legs (*animal duplex*): a self-interested one and a pro-social one. A bipolar tension exists between the 'animal oeconomicus' and the 'animal culturalis' or 'animal moralis'. This dual nature can be explained with evolutionary models such as triune brain theory.
3. Human and non-human primates are 'equipped' with pro-social/other-regarding preferences, a basic sense of fairness and inequity aversion. Both engage in reciprocal altruism and altruistic punishment – albeit to differing degrees.
4. Empathy, ToM and mirror neurons are present both in human and non-human primates (albeit to differing degrees). They are essential for other-regarding preferences, which translate into pro-social behaviour.
5. The context determines whether the selfish or the pro-social side dominates. In competitive environments, human and non-human primates commonly behave in a more self-interested and even egoistic way, while in a cooperative environment they behave more pro-socially and are common-good oriented.
6. Selfish behaviour is more likely when interacting with strangers and out-group members that are not kin-based or when the level of anonymity is large. Moreover, when the partner is not visible and/or present and when no reputation or social capital effects are involved, individuals behave more in line with the self-interest 'animal oeconomicus' model. Furthermore, human and non-human primates behave similarly in UG and DG. In UG, where reputation is at stake, individuals behave more pro-

socially, while in DG, where the level of anonymity is much higher than in UG, individuals typically behave considerably more selfishly.

7. Institutions matter! The formal and informal institutional framework is decisive in steering individuals' behaviour either in a more competitive or in a more cooperative direction. The behaviour of humans will be either more self-interested or more pro-socially oriented depending on socialisation, education, socio-economic policies as well as the respective (formal-jurisdictional) enforcement, monitoring and sanctioning mechanisms.
8. Different evolutionary forces are at play (i.e., multi-level natural selection): individual selection explains self-interested behaviour aiming at survival and reproduction, while group selection helps to explain the evolution of eusociality (i.e., collaboration and social norms of fairness).
9. The evolutionary origins of human morality can be traced back to animal sociality (and morality). According to the gradualism hypothesis of de Waal, evolutionary continuity between monkeys, apes and humans exists. Human morality is just a further development or advancement of animal morality and sociality. While non-human primates display a more egocentric version of fairness, human morality can under certain preconditions transcend egoism and selfishness. Furthermore, it is able to transcend tribalism, nepotism and in-group biases (human morality is commonly applied towards (reciprocating) in-group partners as well as strangers and out-group members). It thus opens up new possibilities for large-scale collaboration beyond local, regional and national boundaries.
10. Last but not least, although empirical evidence for evolutionary continuity and our primate legacy exists, the differences between human and non-human primates should not be neglected. Uniquely human are (the degree of) shared or 'we'-intentionality. Human primates are considerably more socially tolerant and cooperative; at the same time, they are less egoistic and less competitive.

The aforementioned insights gained from animal research illustrate how ethology and primatology in combination with behavioural economics and neuroscience can enrich economics as well as (economic) ethics. In particular, they might help to lay the foundations of a more realistic idea of man and to transcend the anthropological foundations of *Homo oeconomicus*. But further interdisciplinary research is required to fully grasp the moral foundations of human behaviour.

### **Acknowledgements**

The author would like to thank John F. Tomer and John Latsis for their critical feedback. Their comments helped to improve the paper a lot. The usual caveats apply.

### **References**

- Akerlof, G.A. and Kranton, R.E. (2010) *Identity Economics. How our identities shape our work, wages and well-being*. Princeton: Princeton University Press.
- Aristotle (2013) *Politics*. Chicago: University of Chicago Press.
- Axelrod, R. and Hamilton, W.D. (1981) 'The Evolution of Cooperation'. *Science*, 211; 1390-1396.

- Barnes, J.L., Hill, T., Langer, M., Martinez, M. and Santos, L.R. (2008) 'Helping behaviour and regard for others in capuchin monkeys'. *Biology Letters*, 4; 638-640.
- Batra, S.W.T. (1968) 'Behavior of Some Social and Solitary Halictine Bees Within Their Nests: A Comparative Study'. *Journal of the Kansas Entomological Society*, 41(1); 120–133.
- Bolton, G.E. and Ockenfels, A. (2000) 'ERC: A Theory of Equity, Reciprocity, and Competition'. *American Economic Review*, 90(1); 166-193.
- Bowles, S. and Gintis, H. (2004) 'The Evolution of Strong Reciprocity. Cooperation in Heterogeneous Populations'. *Theoretical Population Biology*, 65; 17-28.
- Brosnan, S.F. (2009) 'Responses to Inequity in Non-human Primates' in: Glimcher, Camerer, Fehr and Poldrack (eds.) *Neuroeconomics. Decision Making and the Brain*. Amsterdam: Elsevier; 285-301.
- Brosnan, S.F. and de Waal, F. (2014) 'Evolution of responses to (un)fairness'. *Science Express*, 18 September 2014; 1-9.
- Buonomano, D. (2011) *Brain Bugs. How the Brain's Flaws Shape Our Life*. New York: Norton.
- Butti, C., Sherwood, C.C., Hakeem, A.Y. and Allman, J.M. (2009) 'Total Number and Volume of Von Economo Neurons in the Cerebral Cortex of Cetaceans'. *Journal of Comparative Neurology*, 515; 243-259.
- Call, J. and Tomasello, M. (2008) 'Does the chimpanzee have a theory of mind? 30 years later'. *Trends in Cognitive Sciences*, 12(5); 187-192.
- Cheney, D. (2011) 'Extent and limits of cooperation in animals'. *Proceedings of the National Academy of Sciences*, 108(2); 10902-10909.
- Cory, G.A. (1999) *The Reciprocal Modular Brain in Economics and Politics. Shaping the Rational and Moral Basis of Organization, Exchange, and Choice*. New York: Kluwer Academic Publishers.
- Cory, G.A. (2006a) 'A behavioural model of the dual motive approach to behavioural economics and social exchange'. *Journal of Socio-Economics*, 35; 592–612.
- Cory, G.A. (2006b) 'Physiology and Behavioral Economics. The New Findings from Evolutionary Neuroscience' in: Altman (ed.): *Handbook of Contemporary Behavioral Economics. Foundations and Developments*. London: Sharpe; 24-49.
- Damasio, A. (1994[2006]) *Descartes' Error. Emotion, Reason and the Human Brain*. London: Vintage.
- Davis, J. B. (2003) *The theory of the individual in economics: Identity and value*. London: Routledge.
- Dawkins, R. (1976[2009]) *The Selfish Gene*. Oxford: Oxford University Press.
- de Waal, F. (2000) 'Primates – A Natural Heritage of Conflict Resolution'. *Science*, 289; 586-590.
- de Waal, F. (2008) *Primaten und Philosophen. Wie die Evolution die Moral hervorbrachte*. München: DTV.
- de Waal, F. (2009) *The Age of Empathy. Nature's Lessons for a kinder Society*. New York: Three Rivers Press.
- de Waal, F. (2010) 'The Evolution of Empathy' in: Keltner, Marsh and Smith (eds.): *The Compassionate Instinct. The Science of Human Goodness*. New York, Norton; 16-25.
- de Waal, F. (2012) 'The Antiquity of Empathy'. *Science*, 336; 874-876.
- de Waal, F., Dindo, M., Freeman, C.A. and Hall, M.J. (2005) 'The monkey in the mirror: Hardly a stranger'. *Proceedings of the National Academy of Sciences*, 102(32); 11140-11147.

- de Waal, F., Leimgruber, K. and Greenberg, A.R. (2008) 'Giving is self-rewarding for monkeys'. *Proceedings of the National Academy of Sciences*, 105(36); 13685-13689.
- Economo, K. and Koskinas, G.N. (1925) *Die Cytoarchitektonik der Hirnrinde des erwachsenen Menschen*. Wien: Springer.
- Fajardo, C., Escobar, M.I., Buritica, E., Arteaga, G., Umbarila, J., Casanova, M.F. and Pimienta, H. (2008): 'Von Economo neurons are present in the dorsolateral (dysgranular) prefrontal cortex of humans'. *Neuroscience Letters*, 435; 215-218.
- Falk, A. and Fischbacher, U. (2000): 'A Theory of Reciprocity'. Zurich, Working Paper Institute for Empirical Research in Economics.
- Falk, A. and Szech, N. (2013) 'Morals and Markets'. *Science*, 340; 707-711.
- Fehr, E. and Fischbacher, U. (2003) 'The Nature of Human Altruism'. *Nature*, 425; 785-791.
- Fehr, E., Fischbacher, U. and Gächter, S. (2002) 'Strong Reciprocity, Human Cooperation and the Enforcement of Social Norms'. *Human Nature*, 1-25.
- Fehr, E. and Schmidt, K.M. (1999) 'A Theory of Fairness, Competition, and Cooperation'. *Quarterly Journal of Economics*, 114(3); 817-868.
- Freud, S. (1923[1989]) *The Ego and the Id*. New York: Norton.
- Gallese, V. (2001) 'The "Shared Manifold" Hypothesis. From Mirror Neurons to Empathy'. *Journal of Consciousness Studies*, 8(7); 33-50.
- Gallese, V., Fadiga, L., Fogassi, L. and Rizzolatti, G. (1996) 'Action recognition in the premotor cortex'. *Brain*, 119; 593-609.
- Gintis, H. (2000) 'Strong Reciprocity and Human Sociality'. *Journal of Theoretical Biology*, 206; 169-179.
- Güth, W., Schmittberger, R. and Schwarze, B. (1982) 'An Experimental Analysis of Ultimatum Bargaining'. *Journal of Economic Behavior and Organization*, 3; 367-388.
- Haidt, J. (2001) 'The Emotional Dog and Its Rational Tail: A Social Intuitionist Approach to Moral Judgment'. *Psychological Review*, 108(4); 814-834.
- Haidt, J. (2012) *The Righteous Mind. Why Good People are divided by Politics and Religion*. New York: Vintage.
- Hakeem, A.Y., Sherwood, C.C., Bonar, C.J., Butti, C., Hof, P.R. and Allman, J.M. (2009) 'Von Economo Neurons in the Elephant Brain'. *Anatomical Record*, 292; 242-248.
- Hamilton, W.D. (1964) 'The Genetical Evolution of Social Behavior'. *Journal of Theoretical Biology*, 7; 1-52.
- Hobbes, T. (1651[2012]) *Leviathan*. Oxford: Clarendon Press.
- Horner, V., Carter, J.D., Suchak, M. and de Waal, F. (2011) 'Spontaneous prosocial choice by chimpanzees'. *Proceedings of the National Academy of Sciences*, 108(33); 13847-13851.
- Iacoboni, M. (2009) 'Imitation, empathy, and mirror neurons'. *Annual Review of Psychology*, 60; 653-670.
- Iacoboni, M. and Mazziotta, J.C. (2007) 'Mirror neuron system: basic findings and clinical applications'. *Annals of Neurology*, 62(3); 213-218.
- Jensen, K., Call, J. and Tomasello, M. (2007a) 'Chimpanzees Are Rational Maximisers in an Ultimatum Game'. *Science*, 318; 107-109.
- Jensen, K., Call, J. and Tomasello, M. (2007b) 'Chimpanzees are vengeful but not spiteful'. *Proceedings of the National Academy of Sciences*, 104(32); 13046-13050.
- Kahneman, D. (2011) *Thinking, fast and slow*. London: Allen Lane.



- Kaiser, I., Jensen, K., Call, J. and Tomasello, M. (2012) 'Theft in an ultimatum game: chimpanzees and bonobos are insensitive to unfairness'. *Biology Letters*, 8; 942-945.
- Kant, I. (1788[2010]) *Critique of Practical Reason*. CreateSpace: North Charleston.
- Keltner, D. (2010) 'The Compassionate Instinct' in: Keltner, Marsh and Smith (eds.): *The Compassionate Instinct. The Science of Human Goodness*. New York: Norton; 8-15.
- Keynes, J.M. (1936[1973]) 'The General Theory of Employment, Interest and Money' in: Moggridge (ed.): *The Collected Writings of John Maynard Keynes, Vol. VII*; London: Macmillan.
- Keysers, C. (2011) *The Empathic Brain. How the Discovery of Mirror Neurons Changes our Understanding of Human Nature*. Social Brain Press.
- Kirchgässner, G. (1991) *Homo oeconomicus: Das ökonomische Modell individuellen Verhaltens und seine Anwendung in den Wirtschafts- und Sozialwissenschaften*. Tübingen: Mohr Siebeck.
- Kohlberg, L. (1981) *Essays on Moral Development Vol. I: The Philosophy of Moral Development*. San Francisco: Harper & Row.
- Kohlberg, L. (1985) *The Philosophy of Moral Development. Moral Stages and the Idea of Justice*. San Francisco, Harper & Row.
- Kohlberg, L., Levine, C. and Hewer, A. (1983) *Moral Stages. A Current Formulation and a Response to Critics*. Basel: Karger.
- Kosfeld, M., Heinrichs, M., Zak, P.J., Fischbacher, U. and Fehr, E. (2005) 'Oxytocin increases trust in humans'. *Nature*, 435; 673-676.
- Lipps, T. (1903) *Grundlegung der Ästhetik*. Hamburg: Voss.
- Lipps, T. (1913) *Zur Einfühlung*. Leipzig: Engelmann.
- MacLean, P.D. (1990) *The Triune Brain in Evolution. Role in Paleocerebral Functions*. New York: Plenum Press.
- Maestripiere, M. (2012) *Games Primates Play. An Undercover Investigation of the Evolution and Economics of Human Relationships*. New York: Basic Books.
- Maynard Smith, J. (1964) 'Group Selection and Kin Selection'. *Nature*, 201; 1145-1147.
- Milinski, M. (2013) 'Chimps play fair in the ultimatum game'. *Proceedings of the National Academy of Sciences*, 110(6); 1978-1979.
- Plato (2011) *Phaedrus*. Cambridge: Cambridge University Press.
- Plotnik, J.M., Lair, R., Suphachoksakun, W. and de Waal, F. (2011) 'Elephants know when they need a helping trunk in a cooperative task'. *Proceedings of the National Academy of Sciences*, 108(12); 5116-5121.
- Premack, D. and Woodruff, G. (1978) 'Does the chimpanzee have a theory of mind?'. *Behavioral and Brain Sciences*, 4; 515-26.
- Proctor, D., Williamson, R.A., de Waal, F. and Brosnan, S.F. (2013) 'Chimpanzees play the ultimatum game'. *Proceedings of the National Academy of Sciences*, January 14, 2013; 1-6.
- Rand, A. (1961[1964]) *The Virtue of Selfishness*. New York: Signet.
- Riedl, K., Jensen, K., Call, J. and Tomasello, M. (2012) 'No Third-Party Punishment in Chimpanzees'. *Proceedings of the National Academy of Sciences*, August 27, 2012; 1-6.
- Rizzolatti, G. and Craighero, L. (2004) 'The Mirror-Neuron System'. *Annual Review of Neuroscience*, 27; 169-192.

- Romero, T., Castellanos, M.A. and de Waal, F. (2010) 'Consolation as possible expression of sympathetic concern among chimpanzees'. *Proceedings of the National Academy of Sciences*, 107(27); 12110-12115.
- Rosati, A.G., Santos, L.R. and Hare, B. (2010) 'Primate Social Cognition: Thirty Years After Premack and Woodruff' in: Platt and Ghazanfar (eds.): *Primate Neuroethology*. Oxford: Oxford University Press; 117-143.
- Samuelson, P.A. (1938) 'A Note on the Pure Theory of Consumers' Behaviour'. *Economica*, 5(17); 61-71.
- Samuelson, P.A. (1948) 'Consumption Theory in Terms of Revealed Preference'. *Economica*, 15; 243-253.
- Sanfey, A. and Dorris, M. (2009) 'Games in Humans and Non-human Primates: Scanners to Single Units' in: Glimcher, Camerer, Fehr and Poldrack (eds.): *Neuroeconomics. Decision Making and the Brain*. Amsterdam: Elsevier; 63-80.
- Santos, L.R., Flombaum, J.I. and Phillips, W. (2006) 'The Evolution of Human Mindreading: How Non-Human Primates Can Inform Social Cognitive Neuroscience' in: Platek, Shackelford and Keenan (eds.): *Evolutionary Cognitive Neuroscience*. Cambridge: MIT Press; 433-456.
- Sapolsky, R.M. (2010) 'Peace among Primates' in: Keltner, Marsh and Smith (eds.): *The Compassionate Instinct. The Science of Human Goodness*. New York: Norton; 26-35.
- Schneider, A.C., Melis, A.P. and Tomasello, M. (2012) 'How Chimpanzees Solve Collective Action Problems'. *Proceedings of the Royal Society Biological Sciences*; 1-9.
- Silk, J.B. (2007) 'Social Components of Fitness in Primate Groups'. *Science*, 317; 1347-1351.
- Silk, J.B. (2009) 'Social Preferences in Primates' in: Glimcher, Camerer, Fehr and Poldrack (eds.): *Neuroeconomics. Decision Making and the Brain*. Amsterdam: Elsevier; 269-284.
- Silk, J.B. and House, B.R. (2011) 'Evolutionary foundations of human prosocial sentiments'. *Proceedings of the National Academy of Sciences*, 108, Suppl. 2; 10910-10917.
- Simon, H.A. (1957) 'A Behavioral Model of Rational Choice' in: *Models of Man, Social and Rational: Mathematical Essays on Rational Human Behavior in a Social Setting*; New York: Wiley.
- Simon, H.A. (1959) 'Theories of Decision-Making in Economic and Behavioral Science'. *American Economic Review*, 49(3); 253-283.
- Simon, H.A. (1990) 'A Mechanism for Social Selection and Successful Altruism'. *Science* 250(4988); 1665-8.
- Simon, H.A. (1991) 'Bounded Rationality and Organizational Learning'. *Organization Science*, 2(1); 125-134.
- Singer, T. (2009) 'Understanding Others: Brain Mechanisms of Theory of Mind and Empathy' in: Glimcher, Camerer, Fehr and Poldrack (eds.): *Neuroeconomics. Decision Making and the Brain*; Amsterdam: Elsevier; 251-268.
- Skoyles, J.R. (2011) 'Chimpanzees make mean-spirited, not prosocial choices'. *Proceedings of the National Academy of Sciences*, 108(42); E835.
- Smith, A. (1976a) *An Inquiry into the Nature and Causes of the Wealth of Nations*. Oxford: Clarendon.
- Smith, A. (1976b) *The Theory of Moral Sentiments*. Oxford: Clarendon.
- Suchak, M. and de Waal, F. (2012) 'Monkeys benefit from reciprocity without the cognitive burden'. *Proceedings of the National Academy of Sciences*, 109(38); 15191-15196.
- Tomasello, M. (2009) *Why we cooperate*. Cambridge: MIT Press.

Thaler, R.H. and Sunstein, C.R. (2008[2009]) *Nudge. Improving Decisions About Health, Wealth, and Happiness*. London: Penguin.

Tomer, J.F. (2012) 'Brain Physiology, Egoistic and Empathic Motivation, and Brain Plasticity: Toward a More Human Economics'. available at:

<http://wejdiscussion.worldeconomicsassociation.org/?post=brain-physiology-egoistic-and-empathic-motivation-and-brain-plasticity-toward-a-more-human-economics>

Trivers, R.L. (1971) 'The Evolution of Reciprocal Altruism'. *Quarterly Review of Biology*, 46(1); 35-57.

Troxler, N. (2011) *Theory of mind in chimpanzees – An overview of the recent debate*. Osnabrück: Institute of Cognitive Science.

Wilson, E.O. (1971) *The insect societies*. Cambridge: Harvard University Press.

Wilson, E.O. (2012) *The Social Conquest of Earth*. New York: Liveright Publishing.

Wolkentin, M., Brosnan, S.F., de Waal, F. (2007) 'Inequity responses of monkeys modified by effort'. *Proceedings of the National Academy of Sciences*, 104(47); 18854-18859.

---

SUGGESTED CITATION:

Wörsdörfer, M. (2015) "'Animal Behavioural Economics": Lessons Learnt From Primate Research'. *Economic Thought*, 4.1, pp. 80-106. <http://www.worldeconomicsassociation.org/files/journals/economicthought/WEA-ET-4-1-Worsdorfer.pdf>