GENETIC and CULTURAL CHANGE in HUMAN SOCIAL BEHAVIOUR

a multifaceted exploration

Pieter van den Berg
Genetic and Cultural Change in Human Social Behaviour
A Multifaceted Exploration

Pieter van den Berg
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General introduction

Pieter van den Berg
The way humans behave is by no means constant over the generations. Traditions, technologies, social norms, and politics are always changing. For example, comparing humans living today to those living only 15,000 years ago (not more than a flash in evolutionary time) reveals striking differences. Even though our ancestors living at that time were anatomically modern humans (Bradshaw, 1997), they had not yet invented farming, did not live in cities (let alone nations or empires), did not work metal, and did not write down language. But even when we consider our ancestors living 100 years ago, around the time when my grandparents were born, we see they lived in very different circumstances than we do. They lived in a world with a much smaller human population, of which only a small fraction lived in cities (compared to more than half of the worldwide human population today), and where people almost exclusively communicated face to face, or perhaps through books, with telephones still rare and the internet completely unimaginable.

Changes that occur in human populations over the generations originate from changes in our nature, cultural changes, or an interaction between both. Changes in human nature occur through genetic evolution; innovations originate by mutation of genetic material, and can spread through a population by the transmission of genetic material from parent to offspring in biological reproduction. Like genetic change, cultural change also starts with an innovation typically originating in a single individual, for example through trial-and-error learning or creative problem-solving. And like genetic innovations, cultural innovations can be transmitted to other individuals, and thereby spread through a population. However, the transmission of cultural innovations occurs via forms of social learning, rather than through biological reproduction. The realization that genetic and cultural change are both processes of innovation within individuals and subsequently spread through populations by transmission processes, has given rise to the field of cultural evolution (Cavalli-Sforza & Feldman, 1981; Boyd & Richerson, 1985; Henrich & McElreath, 2003; Mesoudi, 2011a). In this field, scientists attempt to understand cultural change using tools borrowed from evolutionary biology, such as population genetics and methods for phylogenetic analysis. As detailed further below, this framework has led to significant advances in our understanding of cultural change, and has helped pinpoint the origins of a range of cultural variants, such as major language families and modes of political organization.

In addition to the generation of variation and the faithful transmission of variants between individuals (inheritance), there is third ingredient necessary for adaptive evolution: selection (Lewontin 1970). In genetic evolution, selection occurs because organisms compete for limited resources; not all individuals can survive and reproduce (Darwin (1859) called this ‘struggle for existence’). If some variants are associated with better survival and/or reproduction than others, we speak of selection for those variants. In cultural evolution, variants can be regarded as competing for the limited resource of human minds. Indeed, Darwin himself already alluded to this in his book *The Descent of Man* (1871):
“A struggle for life is constantly going on amongst the words and grammatical forms in each language. The better, the shorter, the easier forms are constantly gaining the upper hand.”

In the case of cultural evolution, we can speak of selection if some variants are more likely to be transmitted than others (not necessarily because of enhanced biological survival or reproduction of their carriers). Whatever the mode of selection, it affects the frequencies of different variants in the population, thus shaping the evolution of traits.

This may seem relatively straightforward, but the situation becomes considerably more complicated when considering social traits. Social traits do not only affect the fitness of the individuals that carry them, but also the fitness of other individuals in the population. This can lead to complicated evolutionary dynamics, including chaos (Nowak & May, 1992). Social traits are prominent in virtually all species, but one could argue that they are of particular importance in humans. Humans have many different types of social interactions, often on enormous scales, and with perfect strangers. Some have argued that it is our social nature that led to the evolution of our extreme intelligence, allowing us to employ ever more sophisticated social strategies to advance our interests, and defuse the strategies of others (Byrne & Whiten, 1988; Whiten & Byrne, 1997; Dunbar, 2003). In addition, our unrivalled capability for social learning is what put us on the fast track of cultural evolution.

I am an evolutionary biologist, which means that I am primarily trained to understand processes on the population level. However, my interests have always been broader than that. The study of human social behaviour takes place on a crossroads where many disciplines meet, sometimes competing for answers, sometimes complementary in their approaches, and more often than not proceeding on separate paths. Economists, social psychologists, sociologists, and anthropologists all study human social behaviour, all using their own tools and frameworks, and sometimes meeting to learn from each other. This thesis is to be regarded as an exploration of the study of change in human social behaviour, flirting with some of the above mentioned disciplines, but always with an evolutionary perspective in mind. I do not mean to provide an in-depth analysis of a strictly defined subject or a systematic inventory of methods. The studies presented in this thesis may not appear very closely connected at first sight, but they are all steps towards coming to a more integrated perspective on the evolution of human social behaviour. I have been learning by doing. Although not all studies in this thesis may be equally readable to scholars from the humanities or the social sciences, I hope many of them are relatively easy to read (especially Chapter 2 is explicitly aimed at an interdisciplinary audience). For this Introduction and the Afterthoughts at the end of this thesis, I have tried to take special care that they are understandable to a broad audience.

There is a recurring theme in this thesis: individual differences. This is no coincidence; it is social evolution that can particularly drive the emergence of individual differences, and, in return, the presence of individual differences can have dramatic consequences for the outcome of social evo-
lution. Moreover, the study of individual differences fits with the interdisciplinary character of this thesis; psychologists have a long history of describing individual variation, but this subject has recently also started to attract much attention among biologists. As usual, scientists from those different disciplines ask different questions, even though they are interested in the same subject material. These issues are discussed in particular in Chapter 2 of this thesis, but recur throughout.

**GENETIC VS CULTURAL CHANGE**

Despite the fact that he knew nothing about genes and how they are inherited, Darwin’s theory of evolution is still very much intact today (Darwin, 1859). This shows that the concept of evolution by natural selection does not depend on the details of the underlying processes. About halfway between the publication of *The Origin of Species* and today, the theory of evolution and knowledge about inheritance of genetically determined traits were combined into the Modern Synthesis (Huxley, 1942). This transformed the highly conceptual theory of evolution into a rigorous formal theory, more precise (but also more specific) than Darwin’s original idea. Together with the discovery of the molecular basis of genes and how they are expressed, the Modern Synthesis has added fundamental ingredients to our understanding of the process of genetic evolution.

There is a clear distinction (Johannsen, 1911) between the genetic information carried by individuals (the genotype) and that what selection acts on (the phenotype), and there is a particulate unit of inheritance (the gene). Also, for most eukaryote species such as ourselves, genetic inheritance follows well-understood and strict rules. The strict rules of Mendelian inheritance dictate that alleles competing for the same locus have equal chances of being transmitted to the next generation. The genotype, in close interaction with the environment, determines the phenotype. The central dogma of molecular biology states that this is a one-way street of causation: there is no direct transfer of information from the phenotype back to the genotype (Crick, 1970). Today, we know that the boundaries are not always that clear – acquired information can be transferred to future generations through epigenetic inheritance (Jablonka & Raz, 2009). Having said that, the vast majority of modern evolutionary models implicitly incorporate the central dogma of molecular biology as a basic assumption.

There is a long history of drawing parallels between genetic evolution and cultural change (Richerson & Christiansen, 2013). However, cultural evolution as a field of research only really started getting off the ground in the last quarter of the 20th century, marked by the publication of two ground-breaking books on the subject (Cavalli-Sforza & Feldman, 1981; Boyd & Richerson, 1985). Drawing on formal methods from evolutionary biology with roots in the Modern Synthesis, these authors introduced a formal framework to studying the change in population frequencies of cultural variants over time. The field of cultural evolution has since then been developing in various directions, including experimental studies to investigate how variants are transmitted.
(e.g. Mesoudi & O’Brien, 2008; Derex et al., 2013), modelling studies to investigate the dynamics and outcomes of cultural evolution (e.g. Kendal et al., 2009; Aoki et al., 2012), and sophisticated data-analyses to reconstruct histories of cultural change (e.g. Currie et al., 2010; O’Brien et al., 2014).

Culture has the three ingredients that are necessary for a process of adaptive evolution: variation, selection and inheritance (Lewontin, 1970). At the same time, there are some fundamental differences with genetic evolution. For example, the insights of the Modern Synthesis listed above are not easily applicable to the process of cultural change. The concept of the ‘genotype’ does not readily translate to a similar concept in cultural evolution. Even though cultural variants ultimately have some kind of neurological basis, there is no faithful transmission of physical information from one individual to another. Rather, cultural transmission occurs at the phenotypic level, when an individual imitates the expression of a cultural variant in another individual. The expression of a variant is what is copied – the underlying physical basis may be completely different in individuals that the variant was transmitted between. To date, the potential consequences of this difference have not fully been explored.

Perhaps the most important difference with genetic evolution is that the transmission rules of cultural evolution are much less clear-cut than the Mendelian laws of genetic inheritance. Genes are only transmitted vertically (from parents to offspring), and fair meiosis ensures that their probability of transmission is independent of their content. In contrast, culture can be transmitted both up and down the generations, as well as horizontally. Additionally, the fact that individuals often actively choose which cultural variants they will adopt leads to a content-dependence of cultural transmission. For example, it has been shown that social information spreads more readily than non-social information does (Mesoudi et al., 2006). Although this content-dependence of cultural transmission may play an important role in cultural evolution, efforts have mostly been devoted to charting from whom and under what circumstances people acquire cultural variants.

Identifying the rules of cultural transmission, and understanding their consequences for the dynamics and outcomes of cultural evolution has been a primary area of focus among scholars of cultural evolution. There is quite some evidence that people are more likely to learn from some individuals than from others (for a review, see Rendell et al., 2011). Examples include higher tendencies to learn from individuals that are related, prestigious, knowledgeable, or of the same age or sex. Two modes of cultural transmission that have received much attention are ‘success-based learning’, where individuals preferentially imitate cultural variants that are associated with high pay-offs, and ‘frequency-based learning’, where the imitation tendency changes with the frequency of a cultural variant in the population. The best-known example of frequency-based learning is conformist transmission, where individual have a strong tendency to imitate variants that are common. Both these types of social learning have repeatedly been shown to be used by humans (Efferson et al., 2008; Morgan & Laland, 2012; Traulsen et al., 2010), and theoretical models have suggested that their use can lead to interesting evolutionary outcomes (Henrich &
Boyd, 1998; Henrich & Boyd, 2001; Molleman et al., 2013a). Success-based and frequency-based learning, and their ramifications for cultural evolution, both prominently feature in Chapters 5 and 6 of this thesis.

Social learning is often studied from a functional perspective in the field of cultural evolution. The ways people learn from each other are commonly conceptualized as strategies, which reveals a strong connection to decision theory and economics. Much theoretical work has been dedicated to identifying the forms of social learning that are optimal under given circumstances (Henrich & Boyd, 1998; Laland, 2004; Kendal et al., 2009), reflecting the functional focus of the mother disciplines of evolutionary biology and economics. This is perhaps best illustrated by the ‘social learning tournament’, in which social learning strategies submitted by academics from all over the world competed with each other in a variable environment (Rendell et al., 2010). Although this functional perspective is certainly instructive, it may have overshadowed an appreciation of the mechanisms of social learning in this field (but see Heyes & Pearce, 2015). There is currently a growing call in evolutionary biology to more closely incorporate a mechanistic perspective in evolutionary models. Interestingly, there is a similar movement among scholars of decision making to move from thinking in terms of utility and optimization towards a perspective more grounded in cognitive process (even likened to a paradigm shift by some authors; Oppenheimer & Kelso, 2015). I will save a deeper discussion of these similarities and their consequences for the field of cultural evolution for the Afterthoughts (Chapter 8) of this thesis.

The conceptualization of cultural change as an evolutionary process has geared a number of significant breakthroughs in the understanding of how, when and where cultural variants have evolved. For example, a study borrowing phylogenetic methods from evolutionary biology made a powerful contribution towards understanding the origin of the Indo-European languages (Gray & Atkinson, 2003). In linguistics, there has been a long-standing controversy over the timing and location of the initial divergence of the Indo-European languages, which was hard to resolve because methods commonly used in linguistics are inadequate for providing reliable estimates of divergence dates. Using phylogenetic methods, Gray and Atkinson were able arrive at a date estimate (between 5,800 BCE and 7,800 BCE), providing support for the hypothesis placing the origin in Anatolia (with the spread of agriculture). Another example is a study in which a model of cultural evolution was used to explain the loss of skills and technologies in Tasmania (Henrich, 2004). This model shows that a relatively sudden reduction in population size (due to rising ocean levels) may have caused a cultural evolutionary process in which relatively complex skills deteriorate. There are a number of other cultural phenomena that have been studied with the use of cultural evolution methods, such as grammar (Dunn et al., 2005), political organization (Currie et al., 2010), post-marital residence rules (Jordan et al., 2009), and religion (Botero et al., 2014).

It is important to note that genetic and cultural change in human populations are not separate processes, but are closely interwoven (Jablonska & Lamb, 2005). A textbook example of gene-culture coevolution is how the cultural evolution of pastoralism led to the genetic evolution
of lactase persistence (Beja-Pereira et al., 2003). When humans started herding livestock, being able to digest milk after childhood suddenly conferred a selective advantage. As a result of this, lactase persistence evolved at least twice independently in human populations (Tishkoff et al., 2007). Other examples abound; there are clear signs that various genetic factors contribute to our language abilities, and it is likely that their evolution closely interacts with the cultural evolution of languages themselves (Levinson & Dediu, 2013). Others have conjectured that the cultural innovation of using fire to cook has changed our innate social psychology through changing meat sharing from a dispersed to a centralized event (Jordan et al., 2013). An overall picture of human evolution is not complete without considering the evolution of genes and culture in concert. Having said that, many pieces of the puzzle do come from studying each of the processes in isolation. Although it is an intriguing and important topic, studying both evolutionary processes in concert is beyond the scope of this thesis.

THE INTRICACIES OF SOCIAL EVOLUTION

Extremely elaborate culture is perhaps the most prominent characteristic of human societies, but the scale and intricacy of human social interactions in those societies is certainly also high on that list. In a sense, both can be regarded as two sides of the same coin. We commonly use the term ‘to ape’ or expressions such as ‘monkey see, monkey do’ in reference to imitation, but we often forget that humans are the real champions of aping. Look at a toddler and you will realise that she spends an enormous amount of time imitating others, and not just things that are useful to learn, but almost anything. In fact, experiments have shown that human children will imitate completely irrelevant acts in a sequence of acts to retrieve a reward, whereas chimpanzees tend to copy only the relevant acts (Horner & Whiten, 2005). But even when we are not imitating, we are very interested in what others are doing. It has been argued that our tendency to gossip has an adaptive function in establishing reputations, and thereby maintaining cooperation (Nowak & Sigmund, 1998; Fu et al., 2008). Others have argued that our extreme intelligence is a result of selection for outsmarting each other in social interactions (Byrne & Whiten, 1988; Whiten & Byrne, 1997; Dunbar, 2003). We are not only champions of social learning, but also of elaborate strategies in social interactions.

Human social behaviour is interesting and relevant; the number of scientific disciplines that occupy themselves with its study testify to that. For biologists, social behaviour also holds a special place, for at least two reasons. First, sociality is at the basis of much of the complexity we observe in the biological world. Multicellular organisms are collectives of cells that are so tightly cooperating that they can be regarded as an individual. Some have argued that the tight cooperation of social insects in their colonies can be regarded as an even higher level of individuality (Wilson & Sober, 1989; Gardner & Grafen, 2009). Second, although relevant to almost every
corner of the biological world, social evolution is considerably more intricate than the evolution of non-social traits. This is because an individual’s fitness consequences from a social interaction are partly determined by the behaviour of their interaction partners. In other words, the fitness associated with a social trait is not constant, but depends on the composition of the population (this is referred to as ‘frequency-dependent selection’). Evolutionary game theory is a much-used tool that has been developed to deal with this frequency-dependent nature of social evolution (see Chapter 2). More complications in social evolution arise when individuals in a population do not interact at random. If individuals that are similar to each other are more likely to interact (for example, because they are relatives), the genes underlying social behaviour indirectly affect copies of themselves. William D. Hamilton (1964) introduced the inclusive fitness framework, which allows for the inclusion of such ‘indirect fitness effects’ in models of social evolution. Interaction structure can arise because kin tend to interact, because interactions happen within groups, or can be characterized by an ‘interaction network’, but also because individuals may choose their interaction partners.

The intricacy of social evolution has various consequences. In some types of social interactions, such as the heavily-studied Prisoner’s Dilemma game, the evolution of strategies can be highly dynamic, with strategies continuously sharply increasing and decreasing in frequency, never settling in equilibrium (Nowak & May, 1992; this thesis, Chapter 4). For other types of social interactions, evolution can lead to the stable coexistence of multiple types (this thesis, Chapters 2 and 4). Social evolution can also lead to ‘arms races’. As mentioned above, it has been argued that the highly developed cognitive capacities of humans are a result of such an arms race; to be able to outsmart others in social interactions, there is a continuous selection pressure for increasing intelligence. A domain within social evolution in which arms races are particularly common is sexual selection; they can lead to the evolution of highly exaggerated ornaments, such as the male peacock’s tail. If females prefer a certain characteristic in males, there is a continuous selection pressure on males to be more attractive to females than the other males in the population (Fisher, 1915; Zahavi, 1975; Kuijper et al., 2012; this thesis, Chapter 3).

The extreme sociality of humans combined with the intricate nature of social evolution makes the study of change in social behaviour in human populations both important and intriguing. The process of cultural evolution adds another dimension to the study of change in human social behaviour. Culture and sociality are bound by more than a coincidental relevance in our own species. First, as already mentioned above, the cultural transmission of social information occurs more readily than that of non-social information (Mesoudi et al., 2006). Second, there is significant variation between cultures in their social organization and behaviour. For example, there are substantial differences between cultures in the degree to which social norms are expressed and enforced (Gelfand et al., 2011). Experimental studies have revealed that people from different cultures behave quite differently in simple cooperation set-ups such as the Ultimatum Game (Henrich et al., 2001) and the Public Goods Game (Gächter & Herrmann, 2009). These studies illustrate
that social behaviour is often culturally determined, and therefore a product of cultural evolution. Third, many authors have suggested that cultural and genetic evolution of social behaviour may lead to different outcomes. An example is the debate around ‘cultural group selection’; a discussion whether a strong tendency for conformism can lead to the evolution of group-beneficial traits, through a reduction of within-group variation relative to between-group variation (Henrich & Boyd, 1998; Boyd et al., 2003; Molleman et al., 2013b). Chapter 5 of this thesis investigates what kind of social learning strategies people use in a number of different types of social interactions; Chapter 6 investigates how these learning strategies change social behaviour over time. Chapter 7 is also concerned with how information about others’ social behaviour affects future decisions in a social context.

EVOLUTION AND INDIVIDUAL DIFFERENCES

Throughout this thesis, individual differences are a recurrent theme. Chapter 2 is an extensive discussion about the evolution of individual differences and the impact of individual differences on evolution, so I will not go into this too deeply here. Still, I will briefly introduce why individual differences are interesting and relevant for this thesis.

Variation is the substrate of evolution. This makes it all the more interesting that the generation and maintenance of variation in populations has received relatively little attention in biology – at least, until recently. Around the beginning of this century, the interest for individual differences in biology suddenly soared. Now we know that individual differences can be found all across the biological world, also in the simplest organisms (such as bacteria), and that these differences are not just random noise. Individual variation is often patterned, with the differences between individuals consistent over their lifetimes, and differences in separate kinds of behaviours often occurring together in specific ways (Gosling, 2001; Sih et al., 2004). For example, in sticklebacks, individuals that are more aggressive towards their conspecifics, also tend to explore their environments more (Bell & Sih, 2007). Perhaps not surprisingly, these ‘syndromes’ of individual variation have been called ‘animal personalities’ by biologists (Figueroedo et al., 1995; Carere & Eens, 2005; Wolf et al., 2007). Of course, psychologists are very familiar with the study of personality and individual differences, with whole university curricula and entire scientific journals dedicated to their study. They generally have a very different perspective from biologists; this leaves plenty of scope for interdisciplinary work on individual differences.

The presence of consistent individual differences is not that easy to explain from an evolutionary perspective. Why would evolution lead to rigid behavioural syndromes, rather than to flexible behavioural programs that respond optimally to each new situation? Why does evolution lead to variation, and not to a single optimum? Over the years, a number of potential answers to these questions have been formulated, both by evolutionary biologists and evolutionary psychologists.
(Buss, 2009; Wolf & Weissing, 2010). These answers often involve arguments of social evolution. At the same time, it is clear that the presence of individual differences can dramatically affect the outcome of social evolution (Wolf & Weissing, 2012). The causes and consequences of individual differences using arguments from social evolution (more specifically, evolutionary game theory) are discussed in Chapter 2. Chapter 3 discusses a model that shows how the presence of individual differences can lead to unexpected outcomes (in sexual selection), whereas Chapter 4 discusses a theoretical model that shows how social evolution can lead to individual differences. Chapters 5, 6 and 7 encompass the entire triangle of cooperation, culture and individual differences that this thesis is centred around. They discuss individual differences in the social information people attend to (Chapter 5), and how that changes their social behaviour (Chapter 6). Chapter 7 gives another angle to how individuals respond differently to social information.

**THIS THESIS**

This thesis is not an in-depth investigation, but rather an exploration using various methods. Chapters 2, 3, and 4 consider genetic evolution, and are modelling studies (or, in case of Chapter 2, a review of modelling studies). Chapters 5, 6, and 7 are experimental studies, and mostly revolve around cultural evolution.

In **Chapter 2**, I discuss how evolutionary game theory, a method used specifically for studying social evolution, can be applied to study the evolution of individual differences. Specifically aiming at an audience of psychologists with little background in evolutionary thinking, I first take the time to introduce evolutionary game theory. Next, I discuss a number of studies that develop evolutionary game theory models. Some of those models serve to support potential explanations of the evolution of individual differences, others highlight how the presence of individual differences can influence the dynamics and outcomes of social evolution.

In **Chapter 3**, I discuss a simulation model of the evolution of parent-offspring conflict over mate choice. Although the evolutionary interests of parents and offspring overlap, they do not entirely coincide. Similarly, the evolutionary interests of two mates that produce offspring together are partially overlapping, but also partially conflicting. In this chapter, I show that a conflict between parents and offspring over the distribution of resources can result in a conflict over mate choice. The model discussed in this chapter illustrates that what may sound as a relatively simple situation, concerning only three types of players and their interests (females, their fathers, and their mates), can actually lead to intricate evolutionary dynamics. This complexity arises even though I make the simplest possible assumptions about the mechanisms underlying behaviour, and completely disregard the effects of culture. A discussion in the scientific literature resulting from this study illustrates how easy it is to misunderstand what is exactly happening in the model, even though the underlying assumptions are clear (see **Intermezzo 1**). Despite this fact, I think it
is still possible (and important) to explain the results of this study to a general audience. I have attempted to do this in an op/ed piece for The New York Times about this study (see Intermezzo II).

In Chapter 4, I also discuss a simulation model, but the focus is quite different in this case. Rather than providing a potential explanation for a specific phenomenon of interest observed in the real world (like Chapter 3), this chapter makes a general point by providing a proof of principle that mechanisms can strongly affect the outcome of social evolution. To do this, I discuss a simulation model of the evolution of social behaviour using the highly stylized Iterated Prisoner’s Dilemma game and Iterated Snowdrift game. Both are abstract representations of cooperation interactions, not meant to represent real-life situations, but simplified to their essentials to make their study less complex. The results of the model show that both the outcome and the dynamics of social behaviour in both types of interactions heavily depends on the underlying assumptions about how the genotype eventually causes the behaviour.

In Chapters 5 and 6, I discuss two experimental studies that both revolve around social learning, the mode of transmission in cultural evolution. In Chapter 5, I show that people attend to different types of information about others when they are interacting with them in a social context. Some individuals choose to view information about the earlier behaviour of their fellow group members, whereas others also want to know the payoffs that their fellow group members attained with their behaviour (the ‘frequency-based learning’ and ‘success-based learning’ encountered earlier in this introduction). Chapter 5 also incorporates a small simulation model that shows that the presence of these individual differences in social learning strategies may affect the outcome of cultural evolution. Chapter 6, I replicate the results of Chapter 5 with an entirely independent experiment, and shows that those results are robust (both experiments differ in some of the details of their implementation) and hold over a longer time period. More importantly, the experiment described in Chapter 6 shows empirically that those different social learning strategies lead to different outcomes of social interactions. Particularly, groups consisting of frequency-based learners achieve higher cooperation levels in a social dilemma than groups of success-based learners.

If there is variation in human social behaviour, then one would expect that humans make use of this when taking their decisions. I investigate this with an experimental study in Chapter 7. Here, I study the effect that information about others has on the subsequent behaviour in a social dilemma. However, the set-up is quite different. In this experiment, subjects do not choose the information they view. Rather, all subjects are faced with the same hypothetical situations, in which their fellow group members contributed various amounts to a common project that benefits the entire group. It was already known that people tend respond in different ways to the average contributions of their fellow group members, but I show that they also differ in their response to the heterogeneity in contributions. Some tend to contribute more when the contributions of their fellow group members are more variable, whereas others tend to contribute less in this case. Importantly, I also show that the former types also tend to contribute more when the contributions of their fellow group members are not known to them. This exemplifies that different
types of behaviour in the same domain are often related, and that studying very specific types of behaviour in isolation is often ill-advised. In the Afterthoughts at the end of this thesis (Chapter 8), I discuss this issue in more depth.

Research that takes place on the border between different fields is certainly not always truly interdisciplinary. I do not mean to give the impression that all the chapters in this thesis integrate methods or insights from different fields (the extent to which some chapters do is up to the reader to decide). However, writing this thesis, reading work from different fields, and going to conferences where people from many disciplines meet, has given me some insights in how similar issues play in different disciplines. At the time of this writing, there is an intense discussion about the foundations of evolutionary theory. It revolves around the question whether our abstractions of the evolutionary process, characterized by a strong emphasis on selection, have made us blind to the details of how traits are proximately caused, and new variation in them is created. In the study of decision making (traditionally dominated by economics), there is a similar discussion about classical arguments of utility maximization and the accompanying neglect of the psychological details of how decisions are made. I will save a contemplation of how these different disciplines struggle with the same kinds of imbalances, and what I think is the way forward in with respect to this, for the Afterthoughts (Chapter 8) of this thesis.
Evolutionary game theory and personality

Pieter van den Berg
Franz J. Weissing
ABSTRACT

In this chapter, we discuss the links between evolutionary game theory and personality research. Evolutionary game theory is a set of research methods used to investigate the evolution of social behavior, whereas personality research is mainly focused on comprehensively describing individual differences and their correlates. Until recently, these research domains developed independently, and scholars from one domain only scarcely referred to insights obtained in the other domain. This is changing, however, due to two developments. First, models of evolutionary game theory reveal that personality differences may have an adaptive explanation. These models generate new insights into the origins of personality, and some of these models produce novel and testable hypotheses. Second, it is becoming clear that individual differences matter for the course and outcome of evolution. Accordingly, insights from evolutionary game theory (and experiments based on these insights) can be misleading if personality differences are neglected. Here we review these recent developments, emphasizing both the evolutionary causes and the evolutionary consequences of personality differences. Overall, we argue that the behavioral sciences would profit from a closer integration of mechanistic and functional perspectives.
Personality psychology and evolutionary game theory may not seem to be closely connected. Evolutionary game theory is a set of tools for helping us understand the evolution of social behavior; personality psychologists are mostly interested in comprehensively describing consistent individual differences between people (and in predicting the ramifications of these differences for various life outcomes). Traditionally, evolutionary game theory has been used by biologists in their pursuit of understanding the evolutionary origins of animal behavior, but has received much less attention from psychologists trying to understand human behavior. Conversely, the study of personality and individual differences has been a prime interest of psychologists, but has largely been neglected by biologists.

In recent years, however, this has changed and the study of individual differences has become a hot topic in various sub-disciplines within biology. In particular, behavioral studies across the animal kingdom have revealed that the individuals in virtually all species differ systematically and consistently in their behavior (Gosling, 2001; Sih et al., 2004a; 2004b; Réale et al., 2007). This has produced a literature in which these differences are not only described, but also interpreted from an evolutionary perspective. A number of hypotheses about the evolutionary emergence of individual variation have been advanced. Recent years have also seen increased attention to evolutionary explanations of personality differences in psychology, but these literatures have remained segregated (although some cross-references have certainly been made (e.g., Nettle & Penke, 2006). In comparison to psychologists, biologists base their arguments more strongly on formal theory, and in particular on evolutionary game theory, when suggesting explanations for individual differences.

In this chapter, we show that evolutionary game theory is a suitable tool to study the adaptive significance of individual differences. To do this, we first give a brief overview of evolutionary game theory and the study of individual differences in both humans and animals. Next, we discuss a number of evolutionary arguments that provide an adaptive explanation for the existence of individual differences and the structure of personalities. Most of these explanations are based on models from evolutionary game theory. Then we discuss the evolutionary implications of personality differences for the course and outcome of evolution. By means of examples we demonstrate that evolutionary predictions (including those of evolutionary game theory) can be far off target when individual differences are neglected.

**Evolvutionary Game Theory**

For many decades, economists have used game theory as their main tool for modeling and analyzing strategic interactions. Economic game theory (Rasmusen, 2007) is generally normative; it is aimed at identifying optimal decisions, assuming that all involved parties act according to their
own interests and in line with *Homo economicus* (i.e., fully rational and with unlimited computational ability). The central concept is that of Nash equilibrium: a combination of strategies where none of the players can obtain a better payoff by changing their behavior (Nash, 1951).

Maynard Smith and Price (1973) realized that the insights from game theory could be applied to studying interactions between animals in evolutionary biology. For this, the concept of Nash equilibrium had to be adjusted. To apply it to animals, the definition of equilibrium could no longer be based on assumptions of rationality, but rather on fitness considerations. To achieve this, they introduced the concept of evolutionarily stable strategy (ESS). If all individuals in a population adopt an ESS, natural selection does not favor the invasion of any mutant strategy that is initially rare.

Evolutionary game theory is based on the insight that selection in a social context is ‘frequency dependent’ (Heino *et al.*, 1998): the Darwinian fitness of a strategy does not only depend on an individual’s own behavior, but also on the behavior of others in the population. This has important implications. For example, Maynard Smith and Price presented an evolutionary game theoretical model of animal conflict nowadays called the Hawk-Dove game (Maynard Smith, 1982; see Figure 2.1 for the payoff structure of this game). Pairs of individuals compete for a resource, and each individual has to decide whether to do this in a relatively peaceful ritualized manner (‘Dove’) or to employ dangerous weapons (‘Hawk’). When a Dove meets a Hawk, it is overpowered by the Hawk and gives away the resource without fight. The mean fitness of a population is maximized in the absence of Hawks, since Hawk-Hawk interactions may lead to injury and, hence, a reduction in fitness. Yet, a population of Doves is not evolutionarily stable, since in a population of Doves a single Hawk has a higher fitness than the Dove individuals. As long as Hawks are rare, they will typically meet Doves and therefore easily get access to the resource. Hence, the Hawk strategy will have a selective advantage and will spread when rare. When the Hawk strategy becomes more frequent, however, the risk of injury by getting involved in a Hawk-Hawk interaction increases. If the fitness costs of such injuries are high, the Dove strategy will have a selective advantage in a population of Hawks and, hence, will also spread when rare. Consequently, neither a pure Dove population nor a pure Hawk population is evolutionarily stable. The only evolutionarily stable population is a mixture of Hawks and Doves, or a population in which each individual plays Hawk and Dove with some intermediate probability. This simple example illustrates two points. First, when fitness is frequency dependent, evolution will typically not lead to a state where the mean fitness of the population is maximized; in the majority of all social interactions, such fitness maxima are not evolutionarily stable. Second, frequency dependent selection will often lead to a polymorphic population where different individuals employ different strategies. Since the 1980s, the Hawk-Dove game has been studied widely – sometimes ‘disguised’ as other games that have the same

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1 Notice that Hawk and Dove indicate strategies and not different species of animals; evolutionary game theory is typically concerned with interactions within one species.
Figure 2.1 Payoff structures of three prominent two-player games. Payoffs to the row player are shown; arrows indicate the best choice for the row player for both possible actions of the column player. (a) The Hawk-Dove game: two individuals are competing for a resource of value $b$. Hawks pursue the resource aggressively, while Doves try to resolve the conflict peacefully, and retreat from the conflict when competing with a Hawk. $c$ denotes the cost of getting injured in a Hawk-Hawk fight. In this game, it is usually assumed that $c > b$, in which case it is most favorable to play Dove when the opponent plays Hawk, and vice versa. Hence, neither a population of Hawks nor a population of Doves is evolutionarily stable. The evolutionarily stable strategy (ESS) for this game corresponds to a mixed strategy where individuals play Hawk with a probability $p_H = b/c$.

(b) The Snowdrift game: two individuals decide whether to perform a cooperative act that benefits both players (with benefit $b$, regardless of whether one or both individuals perform it), but comes at a cost of $c$. If both players cooperate, they share the cost. In this game, it is usually assumed that $b > c$. The ESS corresponds to a mixed strategy where individuals cooperate with probability $p_C = (2b - 2c)/(2b - c)$. (c) The Prisoner’s Dilemma game: two individuals decide whether to perform a cooperative act that provides a benefit $b$ to the other player, and comes at a cost $c$ to the cooperator. As in the Snowdrift game, it is usually assumed that $b > c$. Defect is always the best option, regardless of the behaviour of the other player. Therefore, the ESS is to cooperate with probability $p_C = 0$. 
basic payoff-structure, such as the Snowdrift game (which is framed as a context of cooperation rather than conflict; see Figure 2.1).

Evolutionary game theory has been used to study many types of interactions (Broom & Rychtář, 2013; Maynard Smith, 1982), but the game that has received by far the most scientific attention is the Prisoner’s Dilemma (Axelrod & Hamilton, 1981). This game exemplifies why cooperation may be difficult to achieve, even if mutual cooperation is more beneficial for all parties than mutual restraint from cooperation. In the Prisoner’s Dilemma, two players simultaneously decide on whether to ‘cooperate’ or to ‘defect’. If a player cooperates, the other player receives a benefit \( b \), while the cooperator has to pay a cost \( c \) (where \( b > c \)). A defector does not create benefits and does not have to pay a cost (see Figure 2.1). Since \( b > c \) the payoff in case of mutual cooperation \( (b – c) \) is larger for both players than the payoff in case of mutual defection (zero). Yet, defection is a dominant strategy: whatever the other player is doing, defection yields a higher payoff than cooperation (see Figure 2.1). This outcome reflects the ‘Tragedy of the Commons’ (Harding, 1968): at evolutionary equilibrium everybody will defect, while mutual cooperation would be a more favorable outcome.

Matters change if the same two players interact with each other repeatedly (the Iterated Prisoner’s Dilemma game [IPD]). Now more sophisticated strategies can emerge that make the behavior of an individual dependent on the history of the game and, in particular, on the cooperativeness of the other player. Human players often employ a simple strategy called Tit-For-Tat (TFT; Axelrod & Hamilton, 1981). TFT always cooperates unless the other player has defected in the previous round; in that case a TFT-player defects in the next round. Hence a population of TFT-players will always cooperate, but since this cooperation is conditional on the behavior of the other player, a TFT-player can less easily be exploited by a free-riding defector. Notice that superior features of a conditional strategy like TFT may not be immediately apparent to an outside observer, since a population of TFT-players behaves in exactly the same way as a population of indiscriminate cooperators. This is another general insight from game theory: crucial aspects of a successful strategy may be hidden below the surface.

While TFT plays a prominent role in treatments of the IPD, this strategy is vulnerable, since the slightest mistake made by one of two interacting TFT-players results in a sequence of alternations between cooperation and defection. Other strategies, notably ‘Generous Tit-For-Tat’, which only retaliate against defection with a certain probability, and ‘Pavlov’, which starts with cooperation and switches behavior when the other player defected in the previous round (the name ‘Pavlov’ refers to the fact that the strategy continues behavior that is ‘rewarded’ with good payoffs, but switches behavior after bad payoffs) have been found to be relatively robust outcomes of evolutionary simulations (Nowak & Sigmund, 1992; 1993). However, even in this simple kind of interaction, the evolutionary dynamics can be complex. This reflects the fact that the IPD and virtually all games with a rich strategic structure have a multitude of Nash equilibrium strategies. In fact, for any outcome between 0 (mutual defection) and \( b-c \) (mutual cooperation) a Nash
equilibrium can be found that realizes it. This ‘Folk Theorem’ of game theory (Gintis, 2009) is still underappreciated in the behavioral sciences, although it has important implications. First, it is not self-evident that the iteration of a cooperation game leads to mutual cooperation; there are many alternative equilibrium outcomes. Second, the fact that many game models have a huge number of potential Nash equilibria makes the choice of equilibrium (i.e., equilibrium selection; Samuelson, 1997) a much harder task than the identification of Nash equilibrium strategies. Even rational players who are able to compute all possible equilibrium strategies have to find ways to coordinate their behavior and to settle on one of these strategies. Personality may be important for resolving the coordination problems that are associated with the complexities of social interactions (discussed below).

There are numerous examples of evolutionary game theoretical analyses that have led to insights that can be overlooked when developing arguments without a basis in formal techniques (McNamara & Weissing, 2010). A striking example is bi-parental care, in which a male and a female have to decide whether they should care for their common offspring, or invest their reproductive effort elsewhere. An evolutionary game theoretical model by McNamara and Houston (2002) found that the outcome of the interaction depends on the order of decision-making of the players. Figure 2.2 shows the payoffs to the male and the female for a generalized version of this model,

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**Figure 2.2.** Payoffs to the female (a) and the male (b) in a parental care game (inspired by a game considered by McNamara and Houston, 2002). In this model, \( B \) represents the benefit of biparental care, \( b \) represents the benefit of uniparental care, \( c \) represents the cost of providing care, and \( a \) represents the fitness accrued through additional mating (we assume that such extra-pair mating opportunities are only available to males). In the model, \( B > b > c \) and \( B < 2b \) (uniparental care provides more benefit per invested effort than biparental care). In the example (digits shown in red), we assume that \( B = 6, b = 4, c = 1, \) and \( a = 2 \).
contingent on the decisions of each parent to either care for the young or desert the nest. If both parents make their choice simultaneously, the female should always care, because this is the best response, both if the male cares and if he deserts. Consequently, given the fact that the female cares, the male will desert. However, if the female decides first, the situation changes, because the male now knows the decision of the female. The male does best to respond to the female’s desertion by caring, and to her caring by desertion. Because of this, the female chooses between a situation in which she cares and the male deserts, and a situation in which the male cares and she deserts. Because the latter situation is the best outcome for her, the female will desert, and the male will respond by caring. Although the male has more information than the female in the latter situation, this works to his disadvantage. This shows that having more information can have negative consequences.

Although evolutionary game theory has generated valuable insights over the years, there are also limitations of the approach. Game theoretical analyses focus on fitness considerations, without regard for the mechanisms that underlie traits. This has been referred to as the ‘phenotypic gambit’: sacrificing realism of mechanisms for tractability of the evolutionary process. It fits in the tradition in biology to separate questions of proximate causation (how is a trait caused by immediate factors? what are the underlying mechanisms?) from ultimate causation (why did a trait emerge in evolution? why does it provide a fitness advantage?; Mayr, 1961; Tinbergen, 1963). However, the relative neglect of mechanisms in evolutionary studies is receiving increasing criticism (Bateson & Laland, 2013; Fawcett et al., 2012; Laland et al., 2011; McNamara, 2012). Mechanisms are of particular importance when considering the evolution of social traits, because they influence the probabilities with which strategies arise through mutation (van den Berg & Weissing, 2015a). This is important, because in social contexts the success of a mutant strategy often strongly depends on the probability that it encounters itself in a resident population.

Another aspect of evolutionary game theory that has come under recent criticism is its focus on finding stable strategies for isolated contexts. Animals are faced with a complex and dynamic world, and it is unlikely that natural selection has equipped them with a perfect behavioral answer to every possible situation that they encounter (Fawcett et al., 2012; 2014). Indeed, animals often value immediate gains over long-term gains in a suboptimal way (Henly et al., 2008), make different decisions when there are ‘decoy’ options available (Bateson & Healy, 2005), and value food options differently depending on whether they were hungry when they previously encountered them (Marsh et al., 2004). Human behavior is also known to be subject to numerous psychological biases, causing them to deviate from rational behavior (Kahneman, 2011; Tversky & Kahneman, 1974). It seems likely that natural selection has equipped organisms with simple heuristics that perform relatively well when faced with a range of contexts (Gigerenzer et al., 1999).

Individual differences are often overlooked in evolutionary game theoretical analyses. Evolutionary game theoretical models consider the fate of mutants in monomorphic resident populations. However, behavioral variation can have a profound effect on the outcome of evolution,
for instance in the case of cooperative behavior (McNamara & Leimar, 2010). If variation in a social trait is present in a population, it can be advantageous to be choosy about with whom to interact. If this social sensitivity indeed evolves, it may in turn affect the evolution of the social trait (Wolf et al., 2011). For this reason and others mentioned below, it is important to consider individual variation when constructing evolutionary game theoretical models (McNamara, 2013; McNamara & Weissing, 2010).

HUMAN AND ANIMAL PERSONALITY

The study of individual differences has been one of the main areas of study in psychology for decades. The field of personality psychology has a long and diverse history, its prominence reflected by the large number of scientific journals, books, and conferences dedicated to it today. The study of personality addresses individual differences in characteristics that are relatively stable over time, but how those characteristics should be defined and measured has remained a matter of controversy (Engler, 2009). Personality research is characterized by a large variation in objectives. Much research is focused on comprehensively describing the individual variation in a population, but much research is also dedicated to correlating outcomes (in education, work, or personal life) with personality factors. Over time, a number of influential systems for describing personality variation have been devised, of which the Five Factor Model (Digman 1990; McCrae & John, 1992; Tupes & Christal, 1961) is the most used and confirmed. Personality is most often measured using self-report data, although ratings by others and behavioral observations are also used.

In biology, research concerning individual differences is a more recent phenomenon. Individual differences between animals of the same species have long been ignored or treated as irrelevant behavioral noise. The idea that evolution does not lead to variation, but rather depletes variation and leads to a single optimal type, is likely to have contributed to this attitude. However, in the last few decades, evidence has accumulated that patterned variation in animal behavior (dubbed ‘coping style’, ‘behavioral syndrome’, or ‘animal personality’) occurs across a wide range of taxa (Gosling, 2001; Groothuis & Carere, 2005; Koolhaas et al., 1999; Réale et al., 2007; Sih et al., 2004a; Wolf & Weissing, 2012). Animal personality has been defined as behavioral variation that is consistent through time as well as across different contexts. It is defined in terms of measurable behavioral tendencies; the fact that self-report data are impossible with animals has helped avoid some of the controversy about the concepts of personality in psychology. Perhaps more importantly, animal personality research distinguishes itself from personality psychology by acceptance of the overarching framework of evolutionary theory. Questions are often inspired from an evolutionary perspective, and the relevance of different characteristics is determined accordingly.

In recent years, there has been some cross-pollination between the fields of personality psychology and animal personality research, particularly in the development of theory to explain
the evolution of individual variation (Buss, 2009; Figueredo et al., 2005; Gosling, 2001; Michalski & Shackelford, 2010; Nettle, 2006; Penke et al., 2007). Recently, Nettle and Penke (2011) have argued that personality psychologists can benefit much from behavioral ecology, especially in adopting an evolutionary perspective. They also argue that adopting the concept of the reaction norm from biology (a rule that defines the response of an organism to environmental conditions) can help solve the long-standing debate in psychology about whether personality or situational parameters are more important in shaping human behavior. Conversely, biologists can learn from the hundred years of experience that psychologists have with devising comprehensive descriptions of behavioral variation. Some have argued that personality differences are especially prevalent in highly social species (Figueredo, Cox, & Rhine, 1995; Figueredo et al., 2005; Penke et al., 2007). Since the evolution of social behavior is governed by frequency-dependent selection, evolutionary game theory is a pre-eminent tool to formally study the evolutionary emergence of personality differences. Moreover, the use of formal techniques such as evolutionary game theory is important for further developing verbal arguments, so that they mature into theories that generate testable predictions.

**EVOLUTIONARY CAUSES OF PERSONALITY DIFFERENCES**

Consistent individual differences are challenging to explain from an evolutionary point of view. First, there is the question of variation: why are there individual differences between members of the same species, where one would expect evolution to deplete variation, leading to a single optimal type? Second, there is the question of consistency: why do individuals behave in the same way across different contexts and over their lifetime, instead of being flexible and optimally adapting their behavior to each specific circumstance? Adaptive explanations for individual differences have started to emerge in both evolutionary psychology and evolutionary biology over the last two decades. In recent years, both fields have started recognizing the same evolutionary mechanisms that can lead to consistent variation. In biology more than in psychology, evolutionary explanations have often been backed by formal theory – often evolutionary game theoretical models.

Buss (1984) remarked that evolutionary biology and personality psychology are connected in an interesting way: personality psychology studies variation, which is the substrate that evolution acts on. Tooby and Cosmides (1990) argued that personality differences are unlikely to have resulted from natural selection, and consider personality variation to be random noise. However, since then, adaptive explanations for personality differences have started emerging in the literature. Notable examples from psychology include the theories of sociosexuality (Gangestad & Simpson, 1990) and sociopathy (Mealey, 1995). The biological literature of the 1990s also saw an increased interest in adaptive explanations for variation in reproductive strategies (see Gross,
1997, for a review), often accompanied by evolutionary game theoretical models, and other studies invoking adaptive arguments for individual differences (e.g., Morris, 1998). More recently, Nettle (2006) took the first steps towards more explicitly connecting the fields of evolutionary biology and personality psychology by offering a number of potentially adaptive explanations for the variation in human personality using the Five Factor Model.

Recent reviews from evolutionary psychology (Buss, 2009) and evolutionary biology (Wolf & Weissing, 2010) reveal that a similar range of adaptive explanations for individual variation is currently being considered in both fields. Three types of adaptive explanations prominently figure in both reviews: 1) state-dependent behavior that is contingent on non-evolved differences, 2) environmental heterogeneity in fitness optima through space and/or time, and 3) negative frequency-dependent selection. These are not all the explanations that are considered in either paper. Buss also includes costly signaling, but this can be considered as a subset of state-dependent behavior, and some non-adaptive explanations such as mutation load. Wolf and Weissing, in turn, also discuss the emergence of individual variation as a result of non-equilibrium dynamics. However, below, we will elaborate on these three adaptive explanations, and give examples of evolutionary game theoretical models that support each of them.

**State-dependent behavior**

The idea that individual variation may arise from underlying differences in state is not new. In fact, it is central to the handicap theory of sexual selection (Zahavi, 1975). In handicap models, it is assumed that there is some kind of variation in quality between males; either heritable (‘good genes’) or non-heritable (e.g., the amount of resources a male has available to invest in offspring). In these models, evolution leads to the development of a costly indicator trait that signals quality in males, and a costly preference for the degree of exaggeration of that indicator trait in females. Thus, the measurable individual variation in the indicator trait is contingent on the underlying variation in male quality.

A more recent example is the idea that individual differences in social dominance may result from minute differences in fighting ability, or even from chance asymmetries regarding who happens to win most fights early in life. Van Doorn et al. (2003) considered the iterated version of the Hawk-Dove game (see Figure 2.1): the same two individuals repeatedly had to fight over resources and in each round could choose between playing Hawk or Dove. In the majority of their simulations, a strategy emerged that resembles the so-called ‘winner-loser effect’ that has been described in many animal populations (Chase et al., 1994). According to this winner-loser strategy (WL), individuals play Hawk with a certain probability in their first rounds, until they are involved in a Hawk-Hawk interaction. From this round onwards, the winner of this interaction plays Hawk in all remaining rounds, while the loser sticks to playing Dove. If both players of an iterated Hawk-Dove interaction adopt the strategy WL, the outcome is a stable dominance convention: the individual that happens to win the first fight keeps obtaining the resource in subsequent
interactions, while the other individual keeps losing the contest. This happens despite of the fact that there are no initial differences in strength or fighting ability. The evolved strategy WL is a strategic convention that leads to consistent individual differences in social dominance on the basis of a single event, the random assignment of a winner or loser position in one escalated fight.

Environmental heterogeneity

If there is variation in fitness optima through space and/or time, this may lead to variation in behavior. However, exactly how phenotypic variation is expected to emerge depends on the details of the situation (Wolf & Weissing, 2010). If individuals have reliable knowledge of their environment and the costs of adapting behavior to environmental conditions are low, phenotypic plasticity is likely to evolve. In this case, the resulting individual variation is a consequence of a form of state-dependent behavior, where ‘states’ correspond to environmental conditions. If information on the environment is noisy or the costs of plasticity are high, polymorphism will typically arise, where different types of individuals coexist that are adapted to some but not all environmental conditions. This polymorphism may either reflect genetic diversity (different genotypes specifying phenotypes adapted to different conditions) or a bet-hedging strategy (where a single genotype produces phenotypically variable offspring).

Olofsson et al. (2009) present an evolutionary model to explain the evolution of bet-hedging strategies. In their model, a population of individuals is living in a temporally variable environment. The variation between years is implemented as a variable minimal weight for the viability of offspring; any offspring below that threshold does not survive. In addition, only a limited number of offspring can survive in each year. In the model, each individual can produce the same total weight of offspring, but has three genes to determine how many offspring to produce. One gene determines the average weight of one offspring, one determines the variability in weight among offspring in a given year, and one determines the variability in weight between years. The outcome of evolution in the model is that individuals produce variable offspring both within and across the generations. The result is a population in which there are individual differences in size, that are not conditional responses to the current environment, but that are also not based on a genetic polymorphism.

Frequency-dependent selection

Frequency-dependent selection is arguably the only ultimate explanation of the sustained persistence of heritable variation. Competing strategies will easily coexist (resulting in individual variation) if each strategy has a fitness advantage when occurring in a low frequency. Such a rareness advantage arises, for example, in case of frequency-dependent selection where the fitness of each strategy decreases with the frequency of this strategy in the population (‘negative’ frequency-dependent selection). Both Gangestad and Simpson’s (1990) theory of sociosexuality and Mealey’s (1995) theory of sociopathy are based on arguments of negative frequency-
Evolutionary game theory is a particularly useful tool for studying the implications of negative frequency-dependent selection.

An example of a game theoretical model that explains the evolution of individual differences by negative frequency-dependent selection is the model of Johnstone and Manica (2011) for the emergence of leaders and followers (but see Weissing, 2011). With their model, they consider a population in which individuals are grouped at random and have to play an n-person version of the game 'battle of the sexes.' The original context of this game is a situation where a couple has to decide how to spend their evening. The man would like to go to the prize fight, the woman would prefer to go to the ballet, but above all they want to spend their evening together. In the model, there is a group of individuals that each have their own preference, but also obtain benefits when they coordinate on the same option with many fellow group members. Each individual has a genetically determined value of leadership: if it is high, the individual tends to choose their own preferred option; if it is low, the individual copies the most recent choice of a randomly selected group member. In this case, leadership is subject to negative frequency dependent selection; the fewer leaders there are, the more it pays to be a leader. The outcome of their model is individual variation because of a genetic polymorphism in leadership; some individuals are leaders, some are followers. Indeed, for some parameter combinations, as many as five different types can arise.

Overall, constraints play an important role in the evolution of consistent individual differences. If the optimal strategy cannot be attained, because of imperfect information, cognitive limitations, costs of plasticity, or for whatever other reason, frequency-dependent selection will often lead to the emergence of consistent individual variation. For a simple way of illustrating this, again consider the hawk-dove game. If individuals can have mixed strategies (their strategy can be to play Hawk with a certain probability), evolution leads to the emergence of a single type (Wolf et al., 2011). However, the strategy space is constrained so that only pure strategies are allowed (individuals can only always play Hawk or always play Dove), evolution leads to a population that consists of some individuals that always play Hawk, and some that always play Dove. Because of a constraint on the flexibility of behavior, both variation and consistency in behavior emerge.

Most animals are faced with numerous different contexts throughout their lives, and they usually lack detailed information about the specific context that they are in. It is not difficult to see that informational and cognitive constraints render it close to impossible for animals to have a perfect behavioral response for each possible context that they may face. Instead, they often resort to imperfect behavioral responses: general purpose mechanisms or ‘rules of thumb’. These imperfect mechanisms leave room to be exploited by other imperfect mechanisms, and individual variation can emerge as a result (Botero et al., 2010). A recent empirical example of variation in general purpose mechanisms in human behavior is individual variation in social learning strategies (Molleman et al., 2014). Molleman et al. (2014) show experimentally that humans are different in the extent to which they are interested in social information. Moreover, there is variation in the type of information individuals are interested in; some try to identify the type of behavior that is
associated with the highest payoffs, whereas others are only interested in finding out what the majority is doing. Interestingly, these differences were consistent across a number of different contexts that the subjects were confronted with. This indicates that there may be limitations to flexibly adapting social learning strategies to each different context, potentially explaining the observed variation.

**Evolutionary consequences of personality differences**

Even though there has recently been interest in evolutionary explanations for personality differences, questions concerning the evolutionary consequences of individual variation have received less attention. However, as summarized in two recent reviews (Sih et al., 2012, Wolf & Weissing, 2012), there are many potential ecological and evolutionary consequences of the presence of behavioral variation in a population. Consequences of individual differences can impact three qualitatively different domains. First, it can affect ecological parameters, such as population density, the spatial distribution of different behavioral types over different habitats, and disease transmission dynamics. Second, it can affect qualitative aspects of the evolutionary process, such as evolvability, constraints on evolution, and the likelihood of evolution to lead to speciation. Third, the presence of consistent individual variation can alter selective forces acting within populations. This latter consequence of consistent individual variation is especially suited for analysis with formal techniques from evolutionary game theory. Below, we elaborate on the consequences of both consistency and individual variation for the outcome of evolution, giving examples of evolutionary game theoretical models in both cases.

**Implications of individual variation**

To illustrate the evolutionary consequences of individual differences, we can again refer back to handicap models of sexual selection (Zahavi, 1975). In those models, males signal their mate value (whether heritable or not) with a costly indicator trait. In response, a costly female preference for the extent of expression of this trait can emerge. Under the right circumstances, the benefits of such a preference (leading to mating with higher-quality males) will outweigh the cost of being choosy. However, a costly female preference can only be maintained if there is something to choose – there must be variation between males for the preference to have a selective advantage. Without individual variation in male quality, female preference for the indicator trait will be lost from the population. As a result, male investment in the indicator trait also loses its selective advantage, and will also be lost. In summary, without individual differences in male quality, there can be no evolution of exaggerated indicator traits and female preferences for those traits.

Noe and Hammerstein (1994; 1995) recognized the importance of the evolution of choosiness in ‘biological markets’, where one class of individual has something to offer for another class of individuals. They consider the case of mating, but also of cooperation and mutualism between
different species. However, although variation is a prerequisite for any market to function, they do not explicitly consider the importance of variation in their models.

Recently, McNamara et al. (2008) developed an evolutionary game model that explicitly considers the importance of individual variation for the evolution of choosiness in the context of cooperation. In the model, they consider a population in which pairs of individuals engage in a variant of the Iterated Prisoner’s Dilemma. Each individual carries two genetically determined traits: degree of cooperativeness and degree of choosiness. At the beginning of each interaction, both individuals simultaneously invest an amount of effort, which is determined by their degree of cooperativeness. Both individuals incur a cost for the amount of effort that they invest, but gain a benefit from the amount of effort invested by the other player. The degree of choosiness next determines the minimal cooperative effort that is accepted from the other player. If the choosiness of both players is satisfied, the two players interact again – unless one of them does not survive to the next round, which happens with a small fixed probability. If the choosiness of at least one of the players is not satisfied, both players find a new interaction partner, at a small cost. The outcome of the model is that the evolution of choosiness and cooperation strongly depend on the mutation rate, which determines the amount of individual variation in the population. If the mutation rate is high enough, there are sufficient individual differences in cooperativeness, which provides a selective advantage for being choosy. Consequently, as a result of the evolution of increased choosiness, it pays to cooperate more, and high levels of cooperativeness evolve. In contrast, if the mutation rate is too low, choosiness does not pay, and levels of cooperation remain low as a consequence. In summary, this model shows that the amount of individual variation that is present in a population can profoundly affect the evolution of cooperation and choosiness.

Implications of behavioral consistency

As noted, many types of interactions have a huge number of Nash equilibria. Even if there are several Nash equilibria that are favorable for all individuals involved, the participants of an interaction first have to zoom in on one particular equilibrium. In the absence of efficient and reliable communication, this may be a difficult task, corresponding to a ‘coordination game’. (A classic example of a coordination game with different equilibria is whether to drive on the left side or the right side of the road; see McNamara & Weissing, 2010). Behavioral consistency can be helpful in solving problems of coordination. By being consistent, individuals can inform others about how they are likely to behave in the future. Others can use this information to choose their own behavior in such a way that successful coordination is the result.

By means of an evolutionary game model, Wolf et al. (2010) show how consistency and responsiveness to consistency may arise in evolution, and how a small amount of consistency may lead to the emergence of even more consistent strategies. They model a population in which individuals are engaged in pairwise Hawk-Dove game interactions. Each individual has a genetically determined trait that dictates with what probability they play Hawk. As described
before, the evolutionary outcome in the simplest version of this model is a population in which each individual plays Hawk with some intermediate probability (the exact value depends on the specifics of the payoff parameters; see Figure 2.1). In an expanded version of the model, each individual also carries a gene that allows for social responsiveness. Responsive individuals watch their future interaction partners in one interaction with a third individual and subsequently make their behavior contingent on the choice of strategy in this interaction: if the future interaction partner played Hawk, the responsive individual plays Dove, and vice versa. Surprisingly low levels of individual variation in the probability to play Hawk already provide social responsiveness with a selective advantage. The ensuing presence of responsive individuals in the population selects for consistency, since the best reply to the strategy employed by responsive individuals is to stick to one's previous behavior. In turn, responsive individuals profit from the consistency of their interaction partners. Accordingly, there is a positive feedback loop: the more consistent individuals there are, the more it pays to be socially responsive, which can in turn lead to even greater consistency. In the end, a population may result that differs substantially from the original population (e.g., in the frequency of Hawk-Hawk interactions).

CONCLUSIONS AND FUTURE DIRECTIONS

We have given a number of examples where evolutionary game theory has been used as a formal tool to support arguments for the adaptive significance of consistent individual differences. Both when studying the evolutionary causes and the consequences of consistent individual variation, evolutionary game models can be used to sharpen intuition, make arguments more precise, and help formulate predictions and new questions. Personality psychologists can benefit from the use of evolutionary game models in advancing our understanding of individual differences in human populations. Especially in humans, where the study of individual variation has a long and rich tradition, there is a huge amount of empirical substrate for formulating evolutionary hypotheses that could benefit from formal approaches.

We have argued that a better understanding of evolutionary constraints is crucial for getting a better grasp on the evolution of individual variation. Mechanistic constraints are often (perhaps even always) at the basis of the evolution of heritable individual differences. However, developing such a theory of constraints is a rather unfamiliar practice to evolutionary biologists. Traditionally, evolutionary biologists have separated proximate (how does it work?) and ultimate (why does it exist?) questions, and evolutionary models have reflected this separation in their neglect of mechanistic constraints. However, there is now a growing appreciation that asking evolutionary questions without regard for proximate mechanisms can be misleading. We contend that the study of the evolution of individual differences would be an ideal test-case for the development of a more mature theory of the relation between ultimate explanations and proximate mechanisms.
The evolution of parent-offspring conflict over mate choice

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ABSTRACT

In human societies, parents often have a strong influence on the mate choice of their offspring. Moreover, empirical studies show that conflict over mate choice between parents and offspring is widespread across human cultures. Here we provide the first theoretical investigation into this conflict, showing that it may result from an underlying evolutionary conflict over parental resource distribution. We present a series of evolutionary simulations in which we gradually expand a standard model of sexual selection by the stepwise addition of elements of parental involvement. In our model, females obtain resources enhancing their fecundity from both their chosen mate and their parents. Potential mates differ in their ability to provide resources and may signal this ability. Both females and their parents can develop a preference for the signal, with both preferences influencing the realized mate choice of the female. Parents may differentially allocate resources among their daughters depending on the resource-provisioning abilities of their sons-in-law. When fecundity returns on investment are diminishing, we find that parents invest most in daughters whose mates provide few resources. Subsequently, the daughters evolve to exploit this allocation rule through their mate choice, which is not in the parents’ best interests. This results in a conflict over mate choice between parents and their offspring, manifested as an on-going divergence of offspring and parental preferences. We predict that the conflict should be most pronounced when fathers, as opposed to mothers, control resource allocation.
INTRODUCTION

Existing models of sexual selection focus on the coevolution of an exaggerated trait in one sex and a preference for that trait in the other sex (Andersson, 1994; Kokko et al., 2006; Kuijper et al., 2012). These models assume that mate choice is influenced only by the choosing individuals and their prospective partners. Although this approach may be instructive for most organisms, it disregards the involvement of parents in their offspring's mating decisions – a salient feature of mate choice in humans (Apostolou, 2007a).

Parental influence on mate choice is commonly observed across human cultures (Minturn et al., 1969; Apostolou, 2007a). The degree of parental influence varies strongly between cultures (Apostolou, 2010a; 2010b), from limited influence in much of Western Europe to almost complete influence in some Hindu and Islamic societies, and, in general, in collectivistic societies (Buunk et al., 2010). For instance, near the end of the 20th century, about half of the marriages of Indian immigrants in the United States were arranged by the married couple’s parents (Menon, 1989). Among present-day hunter-gatherer societies, there is some degree of parental influence on mate choice in 96% of 190 investigated societies (Apostolou, 2007a). Overall, evidence suggests that parental involvement in offspring mating decisions is the norm, rather than the exception, across cultures and throughout history (Buunk et al., 2010; Apostolou, 2010a; 2010b; 2012). This suggests that parental influence on mate choice probably played an important role in the human ancestral environment, and may therefore have been an important force in the course of human evolution.

Parental influence on mate choice would be of little consequence if parental and offspring preferences were in complete agreement. However, recent research has revealed considerable conflict between parents and offspring over the latter’s choice of a partner. Specifically, parents show a stronger preference than their offspring for attributes such as social class, family background, ethnic background and educational level, whereas offspring show a stronger preference than their parents for qualities such as physical attractiveness, smell, sense of humor and creativity (Buunk et al., 2008; Apostolou, 2008a; 2008b; 2011; Dubbs & Buunk, 2010; Perilloux et al., 2011). These results hold across a number of different sample groups, including Dutch and American students, as well as Kurdish people and young Argentinean people (Buunk & Castro Solano, 2010), and are found both when parents and offspring are questioned (Dubbs & Buunk, 2010). Evidence suggests that it is more often fathers than mothers that exercise influence over mate choice, and that daughters are more strongly influenced than sons (Apostolou, 2007a; 2010a; 2012).

In his famous paper on parent-offspring conflict, Trivers (1974) already alluded to the possibility of a parent-offspring conflict over mate choice. Although the evolutionary interests of parents and offspring overlap to a great extent, they do not coincide. Several authors (Apostolou, 2007a; 2008a; 2008b; 2011; 2012; Buunk et al., 2008; Perilloux et al., 2011) have suggested that parent–offspring conflict over mate choice is a consequence of differences in genetic relatedness to the grandoffspring. Because of the diluting effect of meiosis, a human being (like any other diploid,
sexually reproducing organism) is twice as closely related to its child (relatedness coefficient \( r = 0.5 \)) as to its grandchild (\( r = 0.25 \)). This difference in genetic relatedness, it has been argued, implies that traits indicating genetic quality should be more highly valued in a spouse than in a son- or daughter-in-law (Apostolou, 2007a; 2008a; 2008b; 2011; 2012).

Although this verbal argument is intuitively appealing, we doubt whether the difference in genetic relatedness is sufficient to explain parent–offspring conflict over mate choice. The relatedness difference means that non-heritable quality is also more important in a spouse than in a son- or daughter-in-law, so on this basis alone there is no reason why parents and offspring would differ in their preferences. The situation might change, however, if offspring compete for access to parental resources. Parents are equally related to all their offspring, but offspring are more related to themselves than to their siblings. As Trivers (1974) recognized, this leads to a fundamental evolutionary conflict, in which offspring are expected to prioritize their own reproductive success over that of their siblings. Offspring should try to secure more parental resources for themselves than for their siblings, whereas parents should favor a more equal distribution.

We hypothesize that the parent-offspring conflict over mate choice is rooted in this parent-offspring conflict over resource distribution. In humans, parents continue to invest resources in their descendent kin long after they have stopped reproducing (Hawkes et al., 1998; Sear et al., 2000; Lahdenperä et al., 2004), often beyond the point at which their offspring are sexually mature (Coall & Hertwig, 2010). Thus the intergenerational conflict over resources may impact on various aspects of adult behavior, including mate choice.

We explain the basic logic of this idea by considering a simple scenario, in which a female can receive resources both from her parents and from her chosen mate, and the total amount of resources she receives determines her fecundity. For clarity, we refer hereafter to the female who is choosing a mate as the focal female. The focal female may also be referred to as a daughter, and she and her siblings may be referred to as offspring. The parents of the focal female will be referred to as the parents, and her offspring will be referred to as the grandoffspring.

We assume that males vary in their provisioning ability, in terms of the amount of resources they provide to their mate. If parents have more than one mated daughter, these daughters may differ in the amount of resources they receive from their mates. In that case, depending on the specific relationship between resources and fecundity, it may pay parents to distribute their resources unequally between their daughters (Whyte, 1978). This, in turn, provides an incentive for the daughters to adjust their mate preferences in an attempt to exploit the investment patterns of their parents. The daughters’ mate choice may then be suboptimal from the parents’ point of view – creating an evolutionary conflict between parents and offspring over mate choice.

To investigate this formally, we built an individual-based model of sexual selection that incorporates the possibility for parents to influence the mate choice of their offspring. To the best of our knowledge, this is the first theoretical study to consider the direct involvement of parents in the mate-choice process (but see Welbergen & Quader (2006) for a model of mate choice influ-
enced by the chooser’s offspring). To explore how this might influence the coevolution of male traits and female preferences, we built up our model in four steps, gradually adding different components of parental involvement. We took as our starting point the ‘good parent’ model of sexual selection (Iwasa & Pomiankowski, 1999), which is closely related to the more familiar ‘good genes’ models of sexual selection (Zahavi, 1975; Grafen, 1990a; Grafen, 1990b; Iwasa et al., 1991).

In good-parent models of sexual selection, males vary in the direct fitness benefits they provide to their mates. Males signal the amount of resources they can provide (their provisioning ability) using a costly, condition-dependent indicator trait. Females express varying degrees of (costly) preference for this trait; those with stronger preferences tend to mate with males showing greater trait expression. In this first step of our model, the focal female’s parents have no influence on her mate choice.

In the second step, we incorporate a parental preference for the potential mate of the focal female (i.e. for their son-in-law). Parents are still assumed not to invest any resources, however, so the parental preference for the potential mate of the focal female should coincide with the focal female’s own preference. That is, we expect no conflict between parents and daughters over mate choice.

In the third step, we allow parents to invest resources in their daughters, but impose a fixed pattern of resource allocation. We investigate three allocation patterns: (a) parents invest equally in all daughters (equal allocation); (b) parents invest more in daughters that receive fewer resources from their mate (compensatory allocation); and (c) parents invest more in daughters that receive more resources from their mate (augmenting allocation). Under equal allocation (a), similar to the situation with no parental investment, we expect no conflict over mate choice. Under compensatory allocation (b), daughters with a weaker preference than their sisters will tend to choose mates who invest less, and as a result will receive relatively more resources from their parents. Therefore, we expect that female preference will decrease over evolutionary time to ‘exploit’ the investment pattern of their parents. Parents, in turn, should be selected to counteract the reduced preference of their daughters by strengthening their parental preference, resulting in parent-offspring conflict over mate choice. Under augmenting allocation (c), we expect females to exploit parental investment patterns in the opposite direction, by increasing their preference for males who invest heavily. This should be counteracted by a reduction in the parental preference, again leading to parent-offspring conflict over mate choice.

In the fourth and final step, we allow the parental resource-allocation strategy to evolve. We assume that fecundity returns on investment are diminishing (for alternative functions, see Appendix). Under these conditions, parents maximize the total fecundity of their daughters by using a compensatory allocation strategy, giving more resources to daughters with low-investing partners (Fawcett et al., 2010). Therefore, as in the fixed pattern of compensatory allocation imposed in (b) above, we expect daughters to develop weaker preferences for males who invest heavily, resulting in parent-offspring conflict over mate choice.
The logic of our hypothesis would also apply to male mate preferences, where parents allocate resources to their sons and influence his choice of a female partner (i.e. their daughter-in-law), but we do not investigate this scenario here.

THE MODEL

We created a model with discrete and overlapping generations, with two generations present in the population at any one time, hereafter referred to as the ‘parent generation’ and the ‘offspring generation’. Each individual in the offspring generation experiences the following sequence of events: fitness costs of trait or preference expression, mate choice, investment of resources in reproduction and finally reproduction itself. Individuals in the parent generation experience the following sequence of events: exerting influence on their offspring’s mate choice, investment of resources in their offspring’s reproduction, and finally death. The offspring generation then becomes the parent generation and the newly created generation becomes the offspring generation, before the cycle repeats. For simplicity, we assume that only one of the parents influences the mate choice of their offspring and distributes resources among them. This allows us to explore how the pattern of conflict depends on whether the father or the mother is in control.

All individuals carry diploid loci coding for the following traits: preference for the indicator trait in their own mate \( p \) (hereafter referred to as ‘female preference’; expressed only in females in the offspring generation), preference for the indicator trait in their daughter’s mate \( q \) (hereafter referred to as ‘parental preference’; expressed only in the controlling sex in the parent generation), male provisioning ability \( r_m \) (expressed only in males in the offspring generation), male indicator trait \( t \) (expressed only in males in the offspring generation) and resource-allocation strategy among daughters \( \alpha \) (expressed only in the controlling sex in the parent generation). There is independent Mendelian inheritance at all loci and complete additivity within all loci.

Male provisioning ability and indicator trait

A male’s provisioning ability \( r_m \) (which ranges between 0 and 1) directly determines the amount of resources he provides to his mate. Males can signal their provisioning ability with an indicator trait. The expressed value of the indicator trait \( t_e \) is determined by the male’s genetic value \( t \) for signaling intensity, but it also depends on his provisioning ability \( r_m \):

\[
t_e = t \cdot r_m^2
\]  
(3.1)
Fitness costs of male indicator trait and female preference

In line with standard models of sexual selection (Andersson, 1994), we assume that both male indicator traits and female preferences are costly to express. Following Iwasa and colleagues (Iwasa et al., 1991; Iwasa & Pomiankowski, 1999), the survival probability from birth to reproductive age for males \( v_m \) is determined by the expressed value of the indicator trait as follows:

\[
    v_m = \exp(-ct_e^2)
\]  

(3.2)

where \( c \) is a scaling parameter (\( c = 0.1 \) for all data shown). The probability that a female mates \( v_f \) is given by

\[
    v_f = \exp\left[-b(p + q)^2\right]
\]

(3.3)

where \( p \) denotes the female’s own mate preference, \( q \) denotes the parental preference of her father or mother (whichever is the controlling sex), and \( b \) is a scaling parameter (\( b = 0.01 \) for all data shown). In this implementation, the female pays a cost both for her own choosiness and for the choosiness of her parent. This is consistent with the assumption that choosiness, whether exerted by herself or her parent, reduces the probability that a female mates at all. Males that die before reproductive age and females that fail to mate are disregarded in all subsequent stages described below.

Mate choice

The remaining males and females enter the mating pool. At this stage, each mating female samples a random subset of 10 males from the mating pool and chooses one of them as her mate. The probability \( w \) that a given candidate male with expressed indicator trait value \( t_e \) is chosen from this subset depends on the female’s own preference and the parental preference of her parent, according to

\[
    w \propto \exp\left[(p + q)t_e\right]
\]

(3.4)

That is, we assume that the female’s own preference and her parent’s preference carry equal weight (other weightings are possible, but we do not consider them here).

Parental investment

The amount of resources \( r_z \) a parent allocates to a given daughter depends on the number of daughters they have, the provisioning abilities of the mates of those daughters and their resource-allocation strategy. Each parent has the same total amount of resources, \( R_z \), to invest (\( R_z = 1.0 \) for all data shown), which must be divided among their daughters. We consider various possible
resource-allocation strategies that are determined by the parent's allocation trait $\alpha$ (the specific relation between $\alpha$ and resource-allocation strategy is discussed in the Appendix). If $\alpha = 0$, parents use an equal allocation strategy, distributing their resources evenly among their daughters. If $\alpha < 0$, parents use a compensatory allocation strategy, allocating more resources to daughters that have received fewer resources from their mate. If $\alpha > 0$, parents use an augmenting allocation strategy, allocating more resources to daughters that have received more resources from their mate.

**Reproduction**

The fecundity of a female depends on the total amount of resources $r$ available to her. This is given by the sum of the amount of resources received from her mate (determined by his provisioning ability $r_m$) and the amount received from her parent ($r_z$). We assume diminishing fecundity returns on investment:

$$f(r) = \frac{r}{r + 1}$$  \hspace{1cm} (3.5)

(other possible returns-on-investment functions are considered in the Appendix). All pairs reproduce and their reproductive output is proportional to the fecundity of the female. An equal number of male and female offspring are produced. For the baseline case of our model (Step 1 in the results below), each pair produced on average 2.0071 offspring. The maximum number of offspring produced per pair averaged 9.51 per generation and 26.8% of pairs had two or more daughters.

During inheritance, the traits $t$, $p$, $q$, $\alpha$ and $r_m$ each mutate with probability $\mu$, with the magnitude of the mutations drawn from a uniform distribution between 0 and $s$ (in all simulations shown here, $\mu = 0.01$ and $s = 0.05$). Upwards and downwards mutations are equally likely, except in the case of $r_m$, where the direction of the mutation is affected by a mutation bias. In this case, there is a probability of 0.75 that $r_m$ mutates to a lower value and a probability 0.25 that it mutates to a higher value. This assumption is consistent with the idea that most mutations will decrease provisioning ability (as in Iwasa & Pomiankowski, 1999), and ensures the maintenance of population-level variation in male provisioning ability. If the value of $r_m$ after mutation ($r_{m, mut}$) is smaller than zero, it is set to zero. If $r_{m, mut}$ is larger than 1, $r_m$ is replaced by $2 - r_{m, mut}$ (i.e. the mutation is ‘reflected’ back from the upper limit of 1). In this way, we ensure that the maximal provisioning ability is not reached too easily. After reproduction, the parent generation dies and is replaced by the former offspring generation, which is replaced by the newly created grandoffspring.

We ran 40 replicate simulations for each scenario, using a population of $n = 5,000$ individuals and a time span of 500,000 generations. Throughout the paper, we report means and standard errors of the evolvable traits in the last generation across all replicates. We refer to these evolved
values as $p^*$ (female preference), $q^*$ (parental preference), $t^*$ (genetic value of the indicator trait) and $\alpha^*$ (resource-allocation strategy).

RESULTS

We used a step-by-step approach to investigate how parental influence on mate choice and parental investment change the dynamics of sexual selection. In Step 1, we studied the behavior of the model when $q$ and $\alpha$ are set to zero and not allowed to evolve; $R_z$ is also set to zero. In other words, parents do not influence the mate choice of their daughters, nor do they distribute any resources among them. In Step 2, $q$ is allowed to evolve, but $\alpha$ and $R_z$ still remain at zero. Hence, a parental influence on mate choice can evolve in this situation, but there is no parental resource allocation. In Step 3, $q$ is allowed to evolve, $R_z$ is set equal to 1, and $\alpha$ is fixed at one of three values: $\alpha = -2$ (compensatory allocation), $\alpha = 0$ (equal allocation) or $\alpha = 2$ (augmenting allocation). This means that we allow both parental influence on mate choice and parental resource allocation, but the resource-allocation strategy is fixed and not allowed to evolve. Finally, in Step 4, we allow both $q$ and $\alpha$ to evolve, with $R_z$ again equal to 1.

We investigated two versions of the model: one in which fathers control resource allocation and can influence their daughter’s mate choice, and one in which mothers play this role. The only difference between these two versions is whether it is the father’s or the mother’s values of $\alpha$ and $q$ that are expressed; all other details are identical. The results for maternal and paternal involvement are qualitatively the same. Quantitatively, however, the predicted degree of conflict differs, as summarized in Table 3.1. In the results below we focus on the case of paternal involvement, to reflect the observation in human cultures that men typically have more say in arranging the

Table 3.1. Evolved values of $p$, $q$ and $p^* - q^*$ for all four steps of the model. Mean ± SE across 40 replicates of the evolved values at generation 500,000 are shown. The columns on the left show results for when fathers can exert influence on their daughters’ mate choice and allocate resources among them; the columns on the right show results for when mothers play that role. The last column gives the P-value of a 2-tailed paired t-test (D.F. = 39) that tests whether $p^* - q^*$ is significantly different from zero.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Paternal influence</th>
<th>Maternal influence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$p^*$</td>
<td>$q^*$</td>
</tr>
<tr>
<td>Step 1</td>
<td>3.65 ± 0.06</td>
<td>-</td>
</tr>
<tr>
<td>Step 2</td>
<td>2.05 ± 0.17</td>
<td>1.75 ± 0.17</td>
</tr>
<tr>
<td>Step 3, $\alpha = -2$</td>
<td>1.07 ± 0.19</td>
<td>2.76 ± 0.19</td>
</tr>
<tr>
<td>Step 3, $\alpha = 0$</td>
<td>1.62 ± 0.17</td>
<td>2.02 ± 0.19</td>
</tr>
<tr>
<td>Step 3, $\alpha = 2$</td>
<td>2.46 ± 0.21</td>
<td>0.69 ± 0.22</td>
</tr>
<tr>
<td>Step 4</td>
<td>1.16 ± 0.18</td>
<td>3.05 ± 0.20</td>
</tr>
</tbody>
</table>
marriages of their children than women do (Whyte, 1978); corresponding graphs for the maternal involvement case are shown in the Appendix.

**Step 1: No parental involvement**

This first step introduces the classic ‘good parent’ sexual selection model where males indicate their provisioning ability with an indicator trait, and females may evolve a preference for that indicator trait. Figure 3.1a shows the evolution of trait and preference over 500,000 generations. The male indicator trait \( t \) evolves to \( t^* = 4.726 \pm 0.016 \) (mean ± SE) and the female preference evolves to \( p^* = 3.647 \pm 0.060 \). These outcomes are in line with the analytical results of Iwasa and Pomiankowski (1999), where stable exaggeration of indicator trait and preference was also found.

While the simulations in Step 1 were initialized at \( p = t = 0 \), we used \( p = q = 2.0 \) and \( t = 4.5 \) as initial values in all subsequent steps; this value of \( t \) is close to the evolved value \( t^* \) from Step 1, while \( p + q \) is close to the evolved value \( p^* \).

**Step 2: Parental influence on mate choice, but no differential resource allocation**

In this step, parental preference is introduced as an evolving variable \( q \), but parental investment is not yet introduced. Hence, a female’s fecundity is solely dependent on the provisioning ability of her mate. In these simulations, the indicator trait, female preference and parental preference all evolve to stable levels (Figure 3.1b). The female and parental preferences are not significantly different in this situation (see Table 3.1), and their sum is not significantly different from the female preference in Step 1 \( (p^* + q^* = 3.803 \pm 0.076) \); two-sample \( t \) test: \( t_{78} = 1.407, P = 0.163 \). In other words, in the absence of parental investment, we do not predict a conflict over mate choice between parents and their daughters.

**Step 3: Differential parental resource allocation, fixed allocation strategy**

We next investigated the effect of three different fixed parental resource-allocation strategies: (a) equal allocation \( (\alpha = 0) \), (b) compensatory allocation \( (\alpha = –2) \), and (c) augmenting allocation \( (\alpha = 2) \). The summary statistics of these simulations are shown in Table 3.1 and Figure 3.2. When \( \alpha = 0 \), \( p^* \) and \( q^* \) are not significantly different. In other words, when parents use an equal allocation strategy, no conflict over mate choice between parents and daughters is observed; this fits with our expectations. When \( \alpha = –2 \), \( p^* \) is significantly smaller than \( q^* \) (evolutionary trajectories are shown in Figure 3.1c). Hence, when parents use a compensatory allocation strategy, the parental preference evolves to higher levels than the female preference. This is in line with our hypothesis that daughters tend to exploit their parents’ willingness to compensate them for choosing a mate that provides relatively few resources. In Figure 3.1c, it can be seen that female preference and parental preference do not reach a stable level but continue to diverge over evolutionary time, representing increasing degrees of conflict. Finally, when \( \alpha = 2 \), \( p^* \) is significantly greater than \( q^* \). This is also in line with our expectations: females exploit their parents’ augmenting resource-
Figure 3.1. The coevolution of female preference $p$ paternal preference $q$ and male indicator trait $t$ in Steps 1–3 of our model. (a) In Step 1, there is no paternal involvement in mate choice. (b) In Step 2, fathers have an influence on their daughters’ mate choice but do not allocate any resources to them. (c) In Step 3, fathers both have an influence on their daughters’ mate choice and allocate resources among them; specifically, fathers use a compensatory allocation strategy ($\alpha$ was fixed at $-2$), giving more resources to daughters with low-investing partners. The graphs show mean and standard errors across 40 replicates.
allocation strategy by choosing a mate that provides relatively many resources, leading to the evolution of a stronger female preference than parental preference. As in the compensatory case, these preferences continue to diverge over time (results not shown).

Step 4: Differential parental resource allocation, evolvable allocation strategy

The final step allows the parental resource-allocation strategy to evolve. The evolutionary trajectories are shown in Figure 3.3. In this case, $\alpha^*$ is significantly below zero ($\alpha^* = -2.772 \pm 0.157$; one-sample t test: $t_{39} = 17.656$, $P < 0.001$). This is in line with our expectations; if returns on investment are diminishing, parents can maximize the total fecundity of their daughters by using a compensatory allocation strategy. Consequently, the opportunity for daughters to exploit this resource-allocation strategy leads to the evolution of lower levels of female preference, which parents are selected to counteract by increasing their parental preference: thus $p^*$ is significantly smaller than $q^*$ (Figure 3.3; Table 3.1). This represents a conflict over mate choice, with parents having a stronger preference than their daughter for a high-investing son-in-law.

**Figure 3.2.** The evolved difference between female and paternal preferences in Step 3, where fathers distribute resources among their daughters according to a fixed allocation rule. If $\alpha < 0$, fathers allocate more resources to daughters receiving fewer resources from their mate (compensatory allocation); if $\alpha = 0$, fathers distribute resources uniformly across daughters (equal allocation); if $\alpha > 0$, fathers allocate more resources to daughters obtaining more resources from their mate (augmenting allocation). The graph shows the degree of conflict over mate choice, represented as means and standard errors (across 40 replicate simulations) of $p^* - q^*$, the difference between the evolved values of female preference and paternal preference; zero indicates no conflict. Significant differences from zero are indicated with *** ($P < 0.001$), non-significant differences from zero are indicated with NS ($P > 0.05$).
Parent-offspring conflict over mate choice

Chapter 3

Paternal vs. maternal involvement

Table 3.1 compares the results of the model for paternal involvement (shown in the figures) with those obtained for maternal involvement (shown in Figures 3.A4 and 3.A5 in Appendix). The results are qualitatively the same regardless of which parent is in control. Quantitatively, however, the differences between $p^*$ and $q^*$ are more pronounced under paternal involvement than under maternal involvement, indicating a stronger conflict when fathers, rather than mothers, control resource allocation and influence mate choice. This is the case for every step of the model.

**DISCUSSION**

Our results confirm that parent-offspring conflict over resource distribution can generate conflict between the same parties over the offspring's mate choice. Three conditions are sufficient for this conflict to arise: (i) variability between potential mates in their ability to provide resources, which the opposite sex is able to assess (e.g. via an indicator trait); (ii) additional investment by parents in their offspring's reproduction; and (iii) the ability of parents to exert an influence on their offspring's mate choice. Under these conditions, parental resource-allocation strategies evolve to be dependent on the level of resources provided by their offspring’s mates. Subsequently, the offspring evolve to exploit this allocation rule through their mate choice, which is not in the parents’ best interests. This results in a conflict over mate choice between parents and offspring, manifested as an on-going divergence of offspring and parental preferences. The widespread oc-
currence of parent-offspring conflict over mate choice already suggested that it is not contingent on cultural factors alone. The results of this study corroborate the notion that this conflict has an evolutionary basis by providing a possible mechanistic explanation for the observed patterns.

Our evolutionary model suggests that, contrary to some verbal arguments (Apostolou 2007b; 2008a; 2008b; 2011; 2012), the weaker relatedness of grandparents to their grandoffspring than parents to their offspring is not sufficient to generate conflict over mate choice. This can be seen by comparing the results of Step 2 (Figure 3.1b) with the results of Steps 3 (Figure 3.1c) and 4 (Figure 3.3). The relatedness difference is present in all steps of our model, but in Step 2 there is no opportunity for parental investment in the offspring, and here no conflict emerges (Figure 3.1b). Only when parents can allocate resources to their offspring do parental and offspring preferences diverge (Figures 3.1c and 3.3).

The conflict that evolves in our model is a difference in preference strength (i.e. choosiness), not in preference direction. It is important to realize that both a parent and their daughter will benefit if the latter happens to pair with a high-investing male; in this respect, their evolutionary interests are overlapping. But a conflict arises because the costs and benefits of being choosy differentially affect the fitness of parents and daughters. If a parent has two or more daughters, they value them equally in fitness terms, whereas each daughter values her own reproduction more than that of her sisters, and should therefore try to ensure that she is the one who profits most from the particular pattern of parental resource allocation (Fawcett et al., 2010). Under a strategy of augmenting resource allocation, parents give more resources to daughters who end up with higher-investing mates. Selection therefore favors daughters who have a stronger preference than their sisters, because the extra choosiness costs they pay are balanced by the extra input of resources from their parents. Under compensatory allocation, in contrast, selection favors weaker female preferences, because a daughter can be less choosy than her sisters and yet still end up with abundant resources, thanks to her parent’s compensatory input. This is the evolutionary basis of the conflict that emerges in our model.

Our model predicts that parents will have stronger preferences than their daughters for male traits that indicate the ability to provide resources. Empirical evidence on this is mixed. Several previous studies have found that parents and daughters agree on the importance of earning capacity (Apostolou 2008a; Perilloux et al., 2011) and financial prospects (Apostolou, 2011). A study by Buunk et al. (2008) suggested that poor males are less acceptable to parents than to their daughters, whereas Dubbs & Buunk (2010) found no such difference. A consistent finding across all these studies is that parents value the male’s family background more than their daughters (Apostolou 2008a; 2011; Buunk et al., 2008; Dubbs & Buunk, 2010; Perilloux et al., 2011). Perilloux et al. (2011) also found that parents have a stronger preference than their daughters for males who are ‘good housekeepers’. In general, though, we are concerned that the interpretation of these results hinges on what particular qualities the characteristics studied are presumed to indicate. Further research is needed to clarify the nature of parental and offspring preferences.
The qualitative pattern of conflict in our model is the same regardless of whether it is fathers or mothers who influence the mate choice of their daughters and decide how to distribute resources among them. Quantitatively, however, the differences between $p^*$ and $q^*$ are more pronounced under paternal control (the more common pattern of control across human societies; Whyte, 1978) than under maternal control. One explanation for this is that daughters subsequently become mothers, and the female preference genes $p$ are exposed to contrasting selection pressures at these two generational stages (see Bossan et al., 2013). Because mothers and daughters are closely related, females who heavily exploit the resource-allocation pattern of their mothers are likely subsequently to have their own resource-allocation pattern similarly exploited by their own daughters. In contrast, females who exploit the resource-allocation patterns of their fathers do not face such consequences; they are not confronted with the negative effects of exploiting parental resource-allocation patterns when in the role of the parent themselves. This may favor the evolution of more exploitative female strategies when fathers influence mate choice and control resource allocation, thereby generating a stronger parent-offspring conflict over mate choice in this case.

The intensity of the conflict is also likely to depend on the degree of parental influence on their offspring’s mate choice, which varies widely across cultures (Buunk et al., 2010; Apostolou, 2010a; 2010b). In this study, we assumed that parents and offspring have equal influence on the mate choice of the offspring. An obvious next step would be to study how variation in the degree of parental influence affects the evolution of parent-offspring conflict over mate choice. In our model, one could account for unequal influence by attaching different weightings to the preferences $p$ and $q$ in equations (3.3) and (3.4). One could then allow the degree of parental influence to evolve by treating these weightings as two new loci, one for the parents’ attempt to influence the mate choice of their offspring, and one for the offspring’s effort in resisting the interference of their parents in mate choice. Another interesting extension would be to vary the total amount of resources, $R_z$, parents can invest. If the ability of parents to accumulate resources is another evolvable trait, we might expect this to influence the coevolution between parental and offspring mate preferences.

One of the most important assumptions in our model is that parents can condition their resource-allocation strategy on the provisioning ability of their offspring’s mates. If this is not the case (as in Steps 1 and 2), our model does not predict the emergence of parent-offspring conflict over mate choice. Therefore, to check the plausibility of our model as an evolutionary explanation for parent-offspring conflict over mate choice, we need empirical data on whether parents actually bias their allocation patterns in the way predicted by our model. To the best of our knowledge, such data are lacking. Further studies into parental resource-allocation strategies in humans would be an important next step towards understanding parent-offspring conflict over mate choice.
Buunk et al. (2008) suggest that in choosing a mate, women tend to focus on male traits that may be interpreted as indicators of good genes, whereas their parents place more emphasis on male traits that are indicative of provisioning ability or other direct benefits (see also Apostolou 2008a; 2008b). Since our model only considers male traits that indicate provisioning ability, it does not make any predictions on such qualitative differences between the preferences of parents and their offspring. One possible extension of our model would be to include variation in both viability genes and provisioning ability, with different indicator traits for these two types of variation. However, even in a simpler scenario without parental influences on mate choice, such multiple-indicator models can have intricate dynamical behavior (Van Doorn & Weissing, 2004; 2006). We therefore leave the analysis of such models in the context of parent-offspring conflict to future work.

In our model, the parents are not directly affected by the resources provided by their children-in-law. In many societies this may be quite different, since in their old age, parents are often supported by one or more children-in-law. It is therefore conceivable that parents prefer specific male traits because they indicate that a potential son-in-law would be inclined to care for them. Indeed, several studies have shown that there is a positive relationship between survival in old age and support from children and/or grandchildren (Okabayashi et al., 2004; Esbensen et al., 2007). However, a parental preference for sons-in-law that care for their parents-in-law would only be adaptive if it would enhance the parents’ inclusive fitness. This will often not be the case, since the parents are typically beyond reproductive age at the stage when they require care. Still, such a preference could persist as a by-product of a more general will to survive that is adaptive in other phases of life. Extending our model with these elements might lead to the evolution of more extreme parental preferences for the caring ability of their sons-in-law, possibly leading to even stronger parent-offspring conflict over mate choice.

In conclusion, our model provides a first proof of principle that parent-offspring conflict over resources can lead to parent-offspring conflict over mate choice. This provides a novel, evolutionary explanation for the robust finding across many human cultures that parents and their offspring frequently disagree over what constitutes a suitable mate for the latter. We hope that our findings will stimulate further empirical and theoretical research aimed at understanding how offspring preferences, parental preferences and patterns of resource allocation interact dynamically in the course of human evolution.

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Appendix

This appendix consists of three sections. First, we give a detailed explanation of how $\alpha$ determines the parental resource-allocation strategy. Second, we discuss how the model results are affected when the fecundity returns on investment are not diminishing (as assumed in the main text) but constant or increasing. Third, we present graphs for the case where mothers (instead of fathers) influence the mate choice of their daughters and allocate resources among them.

1. DESCRIPTION OF THE PARENTAL RESOURCE-ALLOCATION STRATEGIES

As illustrated in Figure 3.A1, we consider a continuum of possible parental resource-allocation strategies that are characterized by a parameter $\alpha$. If $\alpha = 0$, parents use an equal allocation strategy, distributing their resources equally among their daughters, leading to the following equation for the amount of resources given to the $i$th daughter:

$$ r_{z,i} = \frac{1}{N_D} R_z $$

(3.A1a)

where $R_z$ is the total amount of resources the parent has to invest and $N_D$ equals the number of daughters they have. If $\alpha < 0$, parents use a compensatory allocation strategy, allocating more resources to daughters that have received fewer resources from their mate (see Figure 3.A1a):

$$ r_{z,i} \propto \left( \frac{1 - \frac{r_{m,i}}{\sum_{j=1}^{N_D} r_{m,j}}}{N_D} \right)^{-\alpha} $$

(3.A1b)
Figure 3.A1. The relative investment of resources by the father in a focal female, as a function of the relative amount of resources that the female has already received from her mate. Separate graphs are shown for (a) negative values of $\alpha$ (equation 3.A1b) and (b) positive values of $\alpha$ (equation 3.A1c). In both graphs, the case of $\alpha = 0$ is also shown (equation 3.A1a). Investment patterns for a number of possible values for $\alpha$ are given for illustration purposes. Investment is always relative to investment in sisters of the focal female.
where $r_{m,i}$ is the amount of resources invested in daughter $i$ by her chosen mate and the summation is over all daughters the parent has. If $\alpha > 0$, parents use an augmenting allocation strategy, allocating more resources to daughters that have received more resources from their mate (see Figure 3.A1b):

$$r_{z,i} \propto \left( \frac{r_{m,i}}{\sum_{j=1}^{N_p} r_{m,j}} \right)^{\alpha}$$

(3.A1c)

The values for $r_z$ are scaled so that their total (over all daughters of a parent) is equal to $R_z$, thus yielding the actual amounts of resources the daughters receive from their parent. The total amount of resources available to female $i$ is $r_i = r_{z,i} + r_{m,i}$.

### 2. INCREASING VERSUS DIMINISHING FECUNDITY RETURNS ON INVESTMENT

In Step 4 of our model, we allowed the parental resource-allocation rule $\alpha$ to evolve. The simulations in the main text are based on the assumption that a daughter’s fecundity $f$ is a decelerating function of the total amount of resources $r$ available to her, implying diminishing returns on investment. More specifically, we considered the relationship:

$$f(r) \propto \frac{r}{r+1}$$

(S2a)

As discussed in the main text, this decelerating function promotes the evolution of a compensatory parental resource-allocation strategy (i.e. a negative value of $\alpha$) and, as a consequence, to a conflict situation where the parents have a stronger preference than their daughters (i.e. a negative difference $p - q$).

We also ran corresponding simulations using two other functions for the relationship between resources and female fecundity: an accelerating function, implying increasing returns per unit of investment:

$$f(r) \propto \exp(0.25r)$$

(S2b)

and a linear function, implying constant returns per unit of investment:

$$f(r) \propto r$$

(S2c)
Figure 3.A2. Evolved values of (a) the paternal resource-allocation parameter $\alpha$ and (b) the degree of conflict over mate choice (difference between female and paternal preferences, $p - q$) in Step 4, where fathers distribute resources among their daughters according to an evolving allocation rule. Results are shown for three different assumptions about fecundity returns per unit investment: diminishing, constant, and increasing. The graphs show mean and standard errors across 40 replicate simulations at generation 500,000. Significant differences from zero are indicated by *** ($P < 0.001$).
Figures 3.A2 and 3.A3 (respectively for paternal and maternal involvement; note the different scales on the y-axis in both graphs) summarize the outcome of these simulations. As with the results presented in the main text, the results for maternal and paternal involvement are qualitatively in close agreement with each other. When returns on investment are increasing (i.e. \( f \) is given by 3.A2b), the parental resource-allocation rule evolves to a positive value and female preference \( p^* \) is significantly stronger than parental preference \( q^* \). Again these results are in line with our expectations; if returns on investment are increasing, parents achieve the highest total fecundity of their daughters by using an augmenting allocation strategy. Daughters evolve to exploit this allocation rule by expressing a stronger preference than their parents, resulting in conflict over mate choice.

The simulations for a linear function (equation 3.A2c) had a similar outcome to those with diminishing returns on investment: both \( \alpha \) and \( p - q \) evolved to negative values. This outcome is somewhat unexpected, because now the fecundity returns per unit of investment are constant, implying that any resource-allocation pattern of the parent should have the same effect on the total fecundity of their daughters. However, upon closer inspection, this results appears to be contingent on the assumption that parents have a limited (and, in our case, fixed) amount of resources to invest in their daughters. If any daughter fails to produce daughters of her own, those resources are effectively lost. This means that it is in the interest of parents to maximize the chance that all of their daughters produce at least some granddaughters. This is achieved by the evolution of a negative value of \( \alpha \), which ensures that the minimum fecundity among daughters is maximized.

### 3. Graphs for Maternal Influence on Mate Choice

We considered two versions of the model: one where fathers exert control over their daughters’ mate choice and distribute resources among them, and one where mothers play this role. The only difference between these two versions is in whose values of \( \alpha \) and \( q \), the father’s or the mother’s, are used in equations 3.3, 3.4, and 3.A1a–c; all other details of the model are identical. In the main text we presented the results for paternal involvement. The corresponding graphs for maternal involvement are shown in Figs 3.A4 and 3.A5. The observed parent-offspring conflict is qualitatively the same under both paternal and maternal involvement, but quantitatively stronger in the case of paternal involvement.
Figure 3.A3. Evolved values of (a) the maternal resource-allocation parameter $\alpha$ and (b) the degree of conflict over mate choice (difference between female and maternal preferences, $p - q$) in Step 4, where mothers distribute resources among their daughters according to an evolving allocation rule. Results are shown for three different assumptions about fecundity returns per unit investment: diminishing, constant, and increasing. The graphs show mean and standard errors across 40 replicate simulations at generation 500,000. Significant differences from zero are indicated by * ($P < 0.05$) and *** ($P < 0.001$).
Figure 3.A4. The coevolution of female preference $p$, maternal preference $q$, male indicator trait $t$ and maternal resource-allocation strategy $\alpha$ in Steps 1-4 of the modified version of the model in which mothers can influence the mate choice of their daughters, as well as allocate resources among them. As in Figure 3.1 in the main text, (a), (b) and (c) show results for Steps 1-3 of the model (in step 3, $\alpha$ is fixed at $-2$). Panel (d) shows results for Step 4 of the model, and corresponds to Figure 3.3 in the main text. The graphs show averages and standard errors of the mean across 40 replicates.
Figure 3.A5. The evolved difference between female and maternal preferences in Step 3, where mothers distribute resources among their daughters according to a fixed allocation rule. This figure is the counterpart of Figure 3.2 in the main text, where fathers allocate resources according to a fixed allocation rule. The graph shows the degree of conflict over mate choice, represented as means and standard errors (across 40 replicate simulations) of $p^* - q^*$, for three different fixed values of $\alpha$. Significant differences from zero are indicated with * ($P < 0.05$) and *** ($P < 0.001$), non-significant differences from zero are indicated with NS ($P > 0.05$).
Parent-offspring conflict in mate choice: A comment on van den Berg et al.

Paul E. Smaldino
Lesley Newson

Conflict over resources generates conflict over mate choice: reply to Smaldino and Newson

Pieter van den Berg
Tim W. Fawcett
Abraham P. Buunk
Franz J. Weissing

The publication of the previous Chapter 3 led to some scientific discussion, which was published in a later issue of the same journal as the original article (*Evolution and Human Behavior*). I here reproduce the comment on our original article by Paul E. Smaldino and Lesley Newson, followed by our reply to this comment.

**Parent-offspring conflict in mate choice: A comment on van den Berg *et al.***

Paul E. Smaldino & Lesley Newson

In a recent *Evolution and Human Behavior* paper, van den Berg, Fawcett, Buunk, and Weissing (2013) used a computational model to address the problem of how parent–offspring conflict in human mate choice might have evolved. This paper will be referred to henceforth in this commentary as BFBW.

Parent–offspring conflict in mate choice is a uniquely human concern and has important ramifications for understanding our social evolution, yet its existence has only recently been recognized and it remains poorly understood. The problem of understanding its evolution lends itself to analysis through computational modeling. However, the model presented in BFBW relies on a number of unrealistic assumptions. Our analysis of their model design suggests that the paper’s conclusion – that the evolution of parent–offspring conflict in mate choice is driven by sibling competition for parental resources in childrearing – is not supported. We describe below the assumptions of a model which we are questioning and propose an explanation for how they generated the results reported in the paper.

**Relation between male signaling and mate quality**

In the BFBW model, the cost of exhibiting the costly trait (in terms of survival and mating rates), is *higher* for male individuals of higher mate quality. We question this because, as noted by Iwasa and Pomiankowski (1999), “For increasing handicap trait size to increase with male quality to be an evolutionary outcome..., the marginal cost of producing a larger trait must be smaller for individuals with higher quality.” In other words signaling quality must incur a cost which only quality individuals can afford. The BFBW model ignores this well accepted common sense rule of costly signaling.

**The evolution of male provisioning ability**

A number of traits in the BFBW model are heritable and mutable. Although negative or positive mutation was equally likely for most traits, the male provisioning ability, \( r_m \), was assumed to
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The authors justify this assumption with the claim that it “is consistent with the idea that most mutations will decrease provisioning ability…, and ensures the maintenance of population-level variation in male provisioning ability” (p. 407).

We find this justification questionable because, although it is true that most genetic mutations are harmful, the resulting negative consequences generally manifest before reproductive age; most mutations are harmful because they interfere with proper development (Wimsatt, 1986). The predominance of harmful mutations should not, in general, contribute so substantially to variance among adults of reproductive age. Moreover, this justification relies on another assumption, which the authors do not address: that the influences of social learning and cumulative culture, which should stabilize variation in ability (Henrich, 2004 and Smaldino & Richerson, 2014), can be ignored.

In the BFBW model, the combination of a high mutation rate with a strong tendency for negative mutations quickly pushes a population under neutral selection toward almost insignificant levels of male provisioning ability. To illustrate this, we ran a simulation with a population of \( N = 2500 \) asexually reproducing individuals (corresponding to the initial number of males in BFBW’s model). We initialized each individual in the population with a trait, \( r_m \), randomly drawn from a uniform distribution between 0 and 1, as in BFBW. We then simulated 50,000 generations of evolution – one-tenth of the length of simulations in BFBW – using the same mutation parameters as BFBW. We found that the mean value of this trait quickly sank from 0.5 to nearly zero, kept only slightly positive through mutation (Figure I.1). Moreover, the population variance on this trait went from 0.0812 at the start to 0.000729 by the end, casting doubt on the claim that a high mutation rate maintained variation in the population.

A negative trajectory on a trait through neutral drift can be countered by positive natural selection. However, as discussed above, positive trait values actually decreased male fitness. In short, in the BFBW model, strongly negative selection drove down male provisioning levels so that the average resource contribution to child-rearing from partnered males was negligible. This means that nearly all resource contributions related to child-rearing came from the focal female’s parents. The strong reliance on parental resources for child-rearing that is dictated by the model partly explains BFBW’s results. More insight can be gained by examining how the model dictates that parents will allocate resources to their daughters.

**Parental allocation strategies**

BFBW initially considers two strategies through which parents unequally allocate resources to their daughters, “augmenting” and “compensatory”. No empirical ethnographic literature was cited to illustrate the use of these strategies. In addition, we are surprised that the authors do not consider the fact that the fitness-optimizing strategy for resource allocation to offspring will vary with the total available resources. An augmenting strategy will be more likely to prevail as
resources become scarcer. A compensatory strategy is likely to prevail as resources become more abundant.

More importantly, however, the mathematical specification of the compensatory and augmenting allocation strategies guaranteed the results obtained in the fixed allocation scenario. Consider an example in which a parent has two daughters, such that daughter A’s husband provides her with double the resources provided to daughter B by her husband. Under the compensatory allocation strategy, the parents will allocate four times as many resources to daughter B compared to daughter A. The reverse is true for the augmenting allocation strategy (daughter A will get four times more parental resources than her sister). Thus, parental allocation overcompensates (or over-augments) for disparities in mate-provided resources. In the compensatory allocation condition, selection will favor daughters who choose low quality mates, since this guarantees them more parental resources. Thus, compensatory allocation will select for lower $p$, and augmenting allocation will select for high $p$.

BFBW does not include an explanation for why parental preference for their offspring’s mate quality balances their offspring’s preferences, leading to consistent values of $(p + q)$. A likely explanation is that because almost all reproductive resources come from parents, parents who have more offspring have to divide those resources more widely. This results in fewer resources – and therefore lower fecundity – per daughter. Strong selection is therefore exerted on parents to have fewer viable daughters. The sum $(p + q)$ therefore remains stable across simulations and $q$ increases among parents who use compensatory allocation. The optimal $(p + q)$ balances the need for having enough surviving daughters to continue the gene line but also few enough so that they remain competitive in terms of resource distribution.

Figure I.1. Neutral selection on male provisioning ability, $r_m$, using the mutation parameters in van den Berg et al. (2013). Plot shows the population mean, $N = 2500$. 

![Graph showing neutral selection on male provisioning ability, $r_m$, with mutation parameters from van den Berg et al. (2013). The plot displays the population mean, $N = 2500$.](image)
Evolving parental compensation

We showed above that by overweighing the allocation strategies in the fixed allocation runs, the design of the BFBW model inevitably generated the results of differential preferences in parents and offspring. However, in runs of the model which allowed parental allocation strategies to evolve, a compensatory allocation strategy emerged, apparently supporting the conclusion that evolution favors such a parental strategy and thereby yields differential preferences for mate quality between parents and offspring. This result stems primarily from costly female preferences for “high quality” males (even though males provide few resources). The negative relationship between mating success and strong preferences for “high quality” male mates should initially select for lowered preferences in both offspring and parents, which is what was found (BFBW Figure 3.3). Because preferences for one’s own mate, \( p \), influence one’s mating success more than preferences for the mate of one’s offspring, \( q \), negative selection will be stronger on \( p \). The proliferation of parents who use an augmenting allocation strategy will be correlated with offspring who favor more attractive mates. Likewise, daughter preferences for less attractive mates will be correlated with parents who compensate them for these choices. All things being equal, however, preferences for lower quality males will have a selective advantage over preferences for high quality males, due to the role of these preferences in mating success. Selection will therefore favor compensatory parental allocation strategies. The disparities between offspring and parental mate preferences will subsequently evolve as discussed above.

Discussion

The problematic assumptions of the BFBW model do not necessarily invalidate its conclusions altogether. We would be interested to see the model run with what we consider to be a more realistic mutation on male provisioning and a more appropriate relation between male quality and signal cost. First, male provisioning ability and its associated indicator trait should incur a positive cost on survival. Second, mutation on male provisioning ability should either be neutral, or the authors should more thoroughly justify their decision to bias mutation on this (and only this) trait so strongly. It is hypothetically possible that the qualitative shape of its results could still hold, but we would be interested in the effect size. We predict that it will be small. Additionally, it would be helpful to see a more thorough analysis of the model with plots illustrating the evolutionary trajectory of male provisioning ability in the full model.

Even if the explanation for parent-offspring conflict in mate choice offered in BFBW were (weakly) supported by a computational model, we would remain skeptical of its external validity. It is implausible that competition for parental resources can be strong enough to create an evolved preference in reproductive age females for mates who will be poor providers of resources as a means of extorting more resources from their parents. Understanding parent-offspring conflict in mate choice, its evolution, and its cultural variation is, as the authors recognize, an important
Conflict over mate choice: discussion

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problem for evolutionary science. We suggest two alternative explanations not considered in BFBW.

First, it is well known that human childrearing relies heavily on resources (e.g., food, care, education and, more recently, money) from individuals other than the child’s parents. This includes grandparents but also aunts, uncles, siblings, cousins, friends and, more recently, employees (Hrdy, 2009). The mate of a focal female is often observed to provide not only for his own offspring, but also for the offspring of her siblings and cousins. It is possible that some parent-offspring conflict in mate choice may stem from competition between a focal female’s primary concern for her own offspring and her older family members’ concerns for more equal allocation of resources to the children of her siblings and cousins. We have recently presented a modeling framework that incorporates family structure, mate choice, and cooperative breeding (Smaldino et al., 2013), with which such questions may be investigated. A second possibility, not mutually exclusive with the first, is that the institution of parental influence is a group-beneficial trait (Smaldino, in press). Parents have wisdom and experience and may simply make better choices that benefit both themselves and their offspring. In this case, the bounded rationality of mate-seeking offspring may be compensated by influence from older family members with shared interests.

Conflict over resources generates conflict over mate choice: reply to Smaldino & Newson

Pieter van den Berg, Tim W. Fawcett, Abraham P. Buunk, & Franz J. Weissing

Evolutionary computer simulations are an important part of the theoretical biologist’s toolkit (Peck, 2004; DeAngelis & Mooij, 2005; Kokko, 2007), offering insights into a range of fundamental evolutionary processes, not least sexual selection (e.g. van Doorn & Weissing 2004; 2006; Fawcett et al., 2007, 2011; van Doorn et al., 2009; reviewed in Kuijper et al., 2012). Like all theoretical tools, they must be used with care (Hamblin, 2012). Smaldino & Newson (2014, henceforth S&N) have challenged our recent work on parent–offspring conflict over mate choice (Van den Berg et al., 2013), arguing that our simulations rely on unrealistic assumptions and that our conclusions are not supported. But all four points of criticism they present are misguided. (1) The accusation that the handicap principle cannot work in our model is wrong; Figure 3.1a in Van den Berg et al. (2013) clearly demonstrates that a costly preference for a signal of male quality does evolve. (2) The assertion that mutation bias drove male quality close to zero in our model is wrong; in fact, male quality reached very high, stable levels in our simulations. (3) The assertion that overcompensation was responsible for our results is wrong; parent and offspring preferences also diverge in the
absence of overcompensation. (4) The alternative explanation offered for our results is wrong, because it predicts the opposite pattern to that we actually observed in our simulations. Below we address each of these misunderstandings and consider two alternative hypotheses suggested by S&N.

Relation between male signaling and mate quality
S&N claim that, in our model, males of higher quality pay a higher cost of exhibiting the trait. This is not true. In our model there is no direct relation between male quality (i.e. provisioning ability) and survival cost; instead, a male’s survival depends solely on his expression of the indicator trait (te). But it is true that for the same genetic value of trait expression (t), we assumed that higher-quality males signal at higher intensity and hence pay higher survival costs. Based on this, S&N conclude that we have ignored the “well accepted common sense rule of costly signaling” that “signaling quality must incur a cost which only quality individuals can afford.” However, standard theory on sexual selection shows that costly preferences can evolve if higher-quality males produce stronger signals for the same genetic value of trait expression (Iwasa et al., 1991; Fawcett et al., 2007). This is the form of costly signaling we implemented in our model. That the handicap principle works in this case is evident from the results in Step 1 of our model, which is a standard sexual selection model without parental involvement: Figure 3.1a in Van den Berg et al. (2013) shows stable exaggeration of a costly female preference for a costly indicator of male quality. More importantly, our findings are robust to the specific assumptions of our model; if we assume, as S&N recommend, that low-quality males pay higher costs of trait expression, we still predict the emergence of parent–offspring conflict over mate choice (Figure I.2).

The evolution of male provisioning ability
S&N criticize our assumption of a negative mutation bias on male quality. However, this is a common assumption in models of sexual selection with heritable male quality (Pomiankowski et al., 1991; Iwasa et al., 1991), including the one S&N refer to (Iwasa & Pomiankowski, 1999). It is a standard way of resolving the so-called ‘lek paradox’ (Kotiaho et al., 2008); without such a mechanism, male quality rapidly tends to fixation at the highest possible value, negating the benefits of female choosiness, which disappears as a result.

It is not surprising that male provisioning ability rapidly declines to zero if a negative mutation bias is the only force affecting its evolution (as in S&N’s Figure I.1), but in our model this mutation bias is opposed by two selection pressures. First, males of higher quality have more resources to invest in their offspring, and therefore on average obtain higher reproductive success. Second, evolved female preferences for males with a larger indicator trait also favor higher-quality males. As a result, male parenting ability is maintained at high levels in our simulations (averages ± s.e.m. over the last generation of all replicates: 0.940 ± 0.001 [step 1]; 0.937 ± 0.001 [step 2]; 0.899 ± 0.001 [step 3]; 0.895 ± 0.001 [step 4]) —far from a “negligible” contribution to child-rearing. This
**Figure I.2.** Parent–offspring conflict over mate choice still emerges when high-quality males pay reduced signaling costs. In this modified version of our model, male survival probability \( v_m \) is dependent on the genetic value for signaling intensity \( t_q \) rather than the expressed trait value \( t_e \), according to \( v_m = \exp(-ct^2) \). To achieve the same level of trait expression \( t_q \), lower-quality males require a higher value of \( t \) (as in our original model) and therefore incur higher survival costs. Means and standard errors over 50 replicate simulations are shown.

**Figure I.3.** Parent–offspring conflict over mate choice still emerges when male quality is not heritable (and therefore not subject to a negative mutation bias). In this modified version of our model, male quality is randomly drawn from a uniform distribution between 0 and 1 at birth. Means and standard errors over 50 replicate simulations are shown.
incorrect assertion appears to be at the root of most of the issues raised by S&N. Nonetheless, to address concerns about our assumptions, we have investigated a modified version of our model without biased mutations (Figure I.3); here, too, we predict the emergence of parent–offspring conflict over mate choice.

**Parental allocation strategies**

S&N suggest that parent–offspring conflict emerges in our model because the parents’ compensatory resource-allocation strategy “overcompensates (or overaugments) for disparities in mate-provided resources.” This is not the case; in Figure 3.3 in Van den Berg et al. (2013), where allocation strategies are free to evolve, the onset of parent–offspring conflict already occurs before parents overcompensate (i.e., while the evolved value of alpha is still smaller than −1). This is confirmed by one of the modified versions of our model presented here (Figure I.2), in which undercompensation evolves but the conflict over mate choice is still strong.

S&N speculate why evolution drives the sum of female and parental preferences \( p + q \) to “consistent values.” Their explanation rests on the presumption that in our model it is in the parents’ interest to avoid having daughters with very low fecundity. This is not true: parents maximize their fitness by maximizing the total fecundity of all of their daughters, regardless of how that fecundity is distributed over individual daughters. In our model, there is a persistent selection pressure on daughters to be less choosy than their sisters, resulting in a weakening of the female preference. Parents, in contrast, use their influence on mate choice to ensure that the realized preference \( p + q \) has the same value as it would have had in the absence of parental involvement, because this represents the optimal compromise for them between the costs and benefits of choosiness.

**Evolving parental compensation**

S&N suggest that our main result (Figure 3.3 in Van den Berg et al., 2013) is caused by an entirely different mechanism than the one we put forward. However, their argument is based on misconceptions about the workings of our model, in particular the incorrect assertion that “the average resource contribution to childrearing from partnered males was negligible” (see section 2).

Our explanation for the evolution of compensatory parental resource allocation strategies is straightforward: if there are diminishing returns on investment, it pays more to invest in daughters that have fewer resources from their partner. If, instead, returns on investment are accelerating, parents evolve an augmenting resource-allocation strategy (see Figure 3.A2 in Van den Berg et al., 2013). This latter pattern would not evolve if the alternative explanation proposed by S&N were correct.

**Comparison with other hypotheses**

S&N find it implausible that sibling competition for parental resources would be strong enough to weaken the female preference for high-investing mates. Yet there is overwhelming evidence in a range of other contexts that sibling competition is a potent evolutionary force with some striking
Conflict over mate choice: discussion

intermezzo I

consequences, including chick begging, siblicide, and genomic imprinting (Kilner & Hinde, 2012; Roulin & Dreiss, 2012). We maintain that our model provides a potentially valid hypothesis that deserves further attention.

S&N mention two alternative hypotheses for the evolution of parent-offspring conflict over mate choice. The first hypothesis, already alluded to by Trivers (1974), rests on the observation that a female’s mate often provides resources not only to their own children, but also to those of her sisters and cousins. Such behavior seems more beneficial to the female’s parents than to the female herself, so potentially it could lead to parent–offspring conflict over mate choice. This is an interesting hypothesis, but it leads to a new problem: why would males divert resources from their own children to less related family members? S&N’s second hypothesis is that parents are more experienced, and therefore better able to choose a mate for their offspring. This may be true, but it does not explain the conflict; why would offspring disagree if their parents know best?

Our model (Van den Berg et al., 2013) explains, from an evolutionary point of view, why parents and offspring should not necessarily agree over the latter’s choice of a mate. We did not claim that it is the only possible explanation for this conflict, nor even the best one, and we welcome alternative hypotheses as well as constructive criticism of our model. To discriminate between competing hypotheses, it is essential to examine the logic closely and derive clear, testable predictions. Evolutionary computer simulations have a vital role to play in this regard.
Evolution and bad boyfriends

Pieter van den Berg
Tim W. Fawcett

After publication of Chapter 3, we were invited by The New York Times to write an article in their newspaper for the section ‘Gray Matter’. This challenged us to explain the outcomes of a relatively complicated modelling study to the general public. I have chosen to reproduce this article here.

Evolution and bad boyfriends

Pieter van den Berg & Tim W. Fawcett

Throughout history and in societies all over the world, parents have tried to influence the love lives of their children — with mixed success. Parents and children frequently don’t see eye to eye on what makes a suitable partner, as studies across cultures have confirmed.

Whenever a pattern of human behavior is widespread, there is reason to suspect that it might have something to do with our evolutionary history. (Think of the fear of snakes, or the incest taboo.) You think your daughter’s boyfriend isn’t good enough? It may be evolution’s fault.

But how could evolution have led to such an awkward situation as parent-child conflict over mates? In a recent paper in the journal Evolution and Human Behavior, we and two colleagues, the biologist Franjo Weissing and the social psychologist Bram Buunk, showed how it could work.

When thinking about mate choice, the natural starting point is the theory of sexual selection. This theory, which focuses not on the struggle for existence but on the competition to attract sexual partners, has been hugely successful in explaining the diverse courtship behaviors and mating patterns in the animal kingdom, from the peacock’s flamboyant tail to the chirping calls of male crickets.

Modern mathematical versions of this theory show how female mating preferences and male characteristics will evolve together. But when you try to apply the theory to humans, you hit a snag. In humans, there is an extra preference involved — that of the parents.

At first sight, it might seem surprising that parents and their children should evolve to have any conflict at all. After all, they share many of the same genes, and both have an evolutionary interest in having those genes persist through the generations. Shouldn’t the preferences of parents and their children be perfectly aligned?

Well, no — not completely. Parents each pass on half of their genes to each of their children, so from a genetic point of view, all children are equally valuable to them. It is in parents’ evolutionary interests to distribute their resources — money, support, etc. — in such a way that leads to as many surviving grandchildren as possible, regardless of which of their children provide them.

Children, by contrast, have a stronger genetic interest in their own reproduction than in that of their siblings, so each child should try to secure more than his or her fair share of parental resources. It is this conflict over parental resources that can lead to a conflict over mate choice.
In our study, we built a computer model to simulate the evolutionary process. We generated a large virtual population of males and females, the males all differing genetically in their ability to invest resources in raising children. The females had a genetically determined preference for this male quality, which meant that females with a strong preference were more likely to end up with a male who invested more.

The males and females that paired up in our model then mated and produced offspring, who inherited (with a small chance of mutation) the investing qualities and mating preferences of their parents. We ran our model over thousands of generations, observing which genetic traits thrived and which didn’t.

Evolutionary biologists had built this kind of model before to understand mating preferences in other animals, but we added some new ingredients. First, we allowed a female’s parents to interfere with her choice of a male. Second, we allowed parents to distribute their resources among their children.

We found that over time, parents in our model evolved to invest more resources in daughters who chose mates with few resources. This unequal investment was in the parents’ best interests, because a daughter with an unsupportive partner would profit more from extra help than her more fortunate sisters (the principle of diminishing returns on investment). By helping their needier daughters, parents maximized their total number of surviving grandchildren.

But this unequal investment created an incentive for daughters to “exploit” their parents’ generosity by choosing a partner who was less supportive. A daughter who was less picky than her sisters would accept a less helpful partner, but since her parents picked up the slack she ended up with a similar amount of support, while sparing herself the costs of holding out for the perfect man.

As a result, the choosiness of females gradually declined over evolutionary time. To counterbalance this, the parental preference for caring sons-in-law increased. Hence the conflict.

We’re not suggesting that the person you choose as a partner comes down entirely to your genes. Cultural factors, personal development and chance events presumably have a far greater influence. But given the prevalence of mate-choice conflict, it seems likely that evolution has played an important role.
The importance of mechanisms for the evolution of cooperation

Pieter van den Berg
Franz J. Weissing

Studies aimed at explaining the evolution of phenotypic traits have often solely focused on fitness considerations, ignoring underlying mechanisms. In recent years, there has been an increasing call for integrating mechanistic perspectives in evolutionary considerations, but it is not clear whether and how mechanisms affect the course and outcome of evolution. To study this, we compare four mechanistic implementations of two well-studied models for the evolution of cooperation, the Iterated Prisoner’s Dilemma (IPD) game and the Iterated Snowdrift (ISD) game. Behavioural strategies are either implemented by a 1:1 genotype-phenotype mapping or by a simple neural network. Moreover, we consider two different scenarios for the effect of mutations. The same set of strategies is feasible in all four implementations, but the probability that a given strategy arises due to mutation is largely dependent on the behavioural and genetic architecture. Our individual-based simulations show that this has major implications for the evolutionary outcome. In the ISD, different evolutionarily stable strategies are predominant in the four implementations, while in the IPD each implementation creates a characteristic dynamical pattern. As a consequence, the evolved average level of cooperation is also strongly dependent on the underlying mechanism. We argue that our findings are of general relevance for the evolution of social behaviour, pleading for the integration of a mechanistic perspective in models of social evolution.
INTRODUCTION

There is a long tradition in biology of separating proximate and ultimate perspectives when explaining phenotypic variation (Mayr, 1961; Tinbergen, 1963). The proximate perspective is concerned with the mechanisms that directly cause the phenotype (such as neurological and physiological processes), whereas the ultimate perspective is concerned with the emergence of the phenotype through (adaptive) evolution. In concordance with this traditional separation, knowledge about the specific mechanisms underlying phenotypes has long been regarded as inconsequential to the question of how phenotypes are shaped by evolution. Accordingly, evolutionary biologists have a strong focus on the fitness consequences of phenotypic traits, thereby largely disregarding the underlying mechanisms. Conceptualisation of evolution is often based on the implicit assumptions that genes interact in a simple way and that there is a one-to-one relationship between genotypes and phenotypes. These assumptions are convenient, since they allow a view of selection as a process directly acting on the genes in the “gene pool” of a population. Although this view has already been criticized as “beanbag genetics” more than fifty years ago (Mayr, 1959), theoretical approaches to explaining the evolution of phenotypes with an explicit focus on mechanisms are not very prominent even today.

Verbal discussions of the importance of underlying mechanisms for the dynamics and outcomes of evolutionary processes started to emerge in the literature in the 1980s (Maynard Smith et al., 1985). In particular, the influential book of John Maynard Smith and Eörs Szathmáry on the “Major Transitions in Evolution” (Maynard Smith & Szathmáry, 1995) clearly showed how crucial genetic and phenotypic architecture are for the course of evolution. This view is now firmly established in the field of evo-devo (Arthur, 2002; Müller, 2007), where the interplay between (developmental) mechanisms and evolution is at centre stage. Similarly, studies on gene-regulatory networks (Lozada-Chavez et al., 2006; Aldana et al., 2007; Cilibarti et al., 2007) have revealed that network topology strongly affects both the robustness and evolvability of living systems, while recent ‘integrative’ models (Pfennig & Ehrenreich, 2014; Schneider et al., 2014; Botero et al., 2015) reveal that the mechanisms underlying phenotypic responses can be important for a full understanding of eco-evolutionary processes.

In line with these general developments, there are now strong pleas (McNamara & Houston, 2009; Fawcett et al., 2013; 2014) to apply “mechanistic thinking” in evolutionary studies of animal and human behaviour as well. Yet, with some notable exceptions (Enquist & Arak, 1994; McNamara et al., 1999; Taylor & Day, 2004; Gross et al., 2008; Akcay et al., 2009; McNally et al., 2012), models for the evolution of behaviour still tend to make the “least constraining” assumptions on the genetic basis and the physiological and psychological processes underlying behaviour. When the direction and intensity of selection do not change in time and when there is a single optimal behaviour, this may not be problematic. In such a case, one would expect evolution to proceed towards the single optimum, regardless of underlying mechanisms. However, whenever there
are multiple equilibria, the situation is no longer so straightforward. And even in relatively simple social contexts, the existence of multiple equilibria is the rule rather than the exception (Van Damme, 1991; Nowak & Sigmund, 1993a; Van Doorn et al., 2003). In other words, the question is not that much “Which strategy is favoured by natural selection” but rather “Which equilibrium will be achieved in the course of evolution” (Harsanyi & Selten, 1988; Samuelson, 1998; Gintis, 2000). It is conceivable that, in such a context, the mechanisms underlying behaviour may be of evolutionary importance, because mechanisms can affect the probabilities with which phenotypes arise and, hence, the likelihood of alternative evolutionary trajectories.

Here we study the evolution of behavioural strategies in two types of social interaction without clearly delineated optimal behaviour. Our question is whether, and to what extent, the mechanistic implementation of the available strategies affects the course and outcome of evolution. We consider two prototype models for the evolution of cooperation: the Iterated Prisoner’s Dilemma game (IPD) and the Iterated Snowdrift game (ISD), which have been the subject of hundreds of earlier studies (IPD [Axelrod & Hamilton, 1981; Boyd & Lorberbaum, 1987; Binmore & Samuelson, 1992; Nowak & Sigmund, 1993b; Nowak & Sigmund, 1998; Doebeli & Hauert, 2005; McNamara et al., 2008], ISD [Maynard Smith & Price, 1973; Sugden, 1986; Santos & Pacheco, 2005; Doebeli & Hauert, 2005; McNamara et al., 2008]). In both games, the players have to decide (repeatedly) on whether to cooperate or to defect. For both players, mutual cooperation is more profitable than mutual defection. However, mutual cooperation is not easy to achieve, since defection yields a higher payoff than cooperation if the other player cooperates. The games differ in their assumption on whether defect (IPD) or cooperate (ISD) yields a higher payoff against a defector. Following the traditions of evolutionary game theory (Maynard Smith, 1982; Weibull, 1995; Hofbauer & Sigmund, 1998; Dugatkin, 1998; Gintis, 2000; Hofbauer & Sigmund, 2003; Nowak et al., 2004; Imhof et al., 2005; Nowak, 2006), but see Weissing (1996)), studies of the evolution of strategies in these games have overwhelmingly assumed a one-to-one relationship between genotypes and strategies. Here we contrast such a one-to-one implementation with a different implementation where selection does not directly act on strategies, but on the architecture (a simple neural network) underlying these strategies. In addition, we consider two genetic mechanisms that determine the probabilities with which the mutation of each strategy yields any other strategy. We will show that the evolutionary dynamics is strongly affected by both the genetic and the behavioural architecture and discuss how the different outcomes can be explained on the basis of the mutational distributions arising from the interplay between genetics and behavioural mechanisms.
THE MODEL

Games and strategies
Throughout, we will consider a Prisoners’ Dilemma game and a Snowdrift game with the following payoff matrices:

\[
\text{PD: } \begin{pmatrix} 3 & 0 \\ 5 & 1 \end{pmatrix}; \quad \text{SD: } \begin{pmatrix} 3 & 1 \\ 5 & 0 \end{pmatrix}.
\]

The top and bottom rows give the payoffs of cooperation and defection, respectively, both for when the opponent cooperates (first column) and defects (second column). In the PD, defection always yields a higher payoff than cooperation, regardless of the action of the opponent. In the one-shot version of this game, mutual defection is therefore the only evolutionarily stable strategy (ESS). In the SD, the highest payoff is always attained by choosing the opposite action than the opponent. In this case, the one-shot game has an ESS that is characterized by a mixture of cooperation and defection.

We consider iterated versions of both games, for which the determination of all ESSs is much less straightforward than for their one-shot counterparts (see Appendix for a game-theoretical analysis). In our simulations, agents repeatedly interact for an indefinite period of rounds; after each round, the game is terminated with probability \(1-m\). The full strategy space of the iterated game is infinite-dimensional (Boyd & Lorberbaum, 1987). Here we confine the strategy space by only allowing individuals to condition their behaviour on the outcome of the previous interaction round. Since there are four possible interaction outcomes (mutual cooperation, mutual defection, and both combinations of cooperation and defection), and a strategy always prescribes one of two possible actions for each outcome (cooperation or defection), there are in total \(2^4 = 16\) possible strategies (see Table 4.1 for a complete list). We assume that individuals are not perfect; they make both perception errors (with probability \(\epsilon_p\), they misinterpret the behaviour of their opponent as the opposite behaviour) and implementation errors (with probability \(\epsilon_i\), they perform the opposite behaviour than dictated by their strategy).

Behavioural and genetic architecture
Figure 4.1 shows a schematic representation of the behavioural and genetic architectures considered in this study. We consider a “1:1” behavioural architecture and an artificial neural network (ANN) architecture, which can both realize the 16 possible strategies presented in Table 4.1. The 1:1 architecture is the simplest possible architecture, in which behaviour for each of the four possible outcomes of the previous round is under the direct control of a single gene locus. Each of these four loci can only have two values: 1 (for cooperation) or 0 (for defection). In addition, a separate locus determines an individual’s behaviour in the first round; this locus can take on any value of the unit interval, which correspond to the probability of cooperation in the first round.
In the neural network architecture (Enquist & Ghirlanda, 2005; see Figure 4.1 for a graphical representation; see Appendix for a more detailed explanation), behaviour is determined through a very simple underlying structure that translates an input (the behaviours of ‘self’ and ‘partner’ in the previous interaction round) into an output (cooperation or defection). There are two input nodes, one of which receives the previous own behaviour (0 for defection, 1 for cooperation), and the other receives the previous behaviour of the opponent. The input from both these nodes is fed into two ‘hidden layer’ nodes, multiplied by the weights of the connections between the nodes. Each hidden layer node has a threshold; if the summed input into a hidden layer node exceeds its threshold, its output equals 1, otherwise the output is 0. Both hidden layer nodes are

<table>
<thead>
<tr>
<th>behaviour</th>
<th>percentage of genotype space</th>
<th>strategy name</th>
<th>strategy description</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 0 0 0</td>
<td>6.25</td>
<td>ALLD</td>
<td>always defects</td>
</tr>
<tr>
<td>0 0 0 1</td>
<td>6.25</td>
<td>desperate</td>
<td>only cooperates after mutual defection</td>
</tr>
<tr>
<td>0 0 1 0</td>
<td>6.25</td>
<td>Acon-D</td>
<td>anti-conventional, shifts after playing opposite of opponent, otherwise defects</td>
</tr>
<tr>
<td>0 0 1 1</td>
<td>6.25</td>
<td>inconsistent</td>
<td>plays opposite of previous move</td>
</tr>
<tr>
<td>0 1 0 0</td>
<td>6.25</td>
<td>con-D</td>
<td>conventional, stays after playing the opposite of opponent, otherwise defects</td>
</tr>
<tr>
<td>0 1 0 1</td>
<td>6.25</td>
<td>ATFT</td>
<td>anti-tit for tat, plays opposite of opponent’s previous move</td>
</tr>
<tr>
<td>0 1 1 0</td>
<td>6.25</td>
<td>APavlov</td>
<td>win, shift; lose, stay</td>
</tr>
<tr>
<td>0 1 1 1</td>
<td>6.25</td>
<td>hopeless</td>
<td>only defects after mutual cooperation</td>
</tr>
<tr>
<td>1 0 0 0</td>
<td>6.25</td>
<td>grim</td>
<td>only cooperates after mutual cooperation</td>
</tr>
<tr>
<td>1 0 0 1</td>
<td>6.25</td>
<td>Pavlov</td>
<td>win, stay; lose, shift</td>
</tr>
<tr>
<td>1 0 1 0</td>
<td>6.25</td>
<td>TFT</td>
<td>tit for tat, copies opponent’s last move</td>
</tr>
<tr>
<td>1 0 1 1</td>
<td>6.25</td>
<td>MNG</td>
<td>Mr Nice Guy, only defects after ‘being cheated’ (playing C while other plays D)</td>
</tr>
<tr>
<td>1 1 0 0</td>
<td>6.25</td>
<td>consistent</td>
<td>repeats its own previous move</td>
</tr>
<tr>
<td>1 1 0 1</td>
<td>6.25</td>
<td>con-C</td>
<td>conventional, stays after playing the opposite of opponent, otherwise cooperates</td>
</tr>
<tr>
<td>1 1 1 0</td>
<td>6.25</td>
<td>willing</td>
<td>only defects after mutual defection</td>
</tr>
<tr>
<td>1 1 1 1</td>
<td>6.25</td>
<td>ALLC</td>
<td>always cooperates</td>
</tr>
</tbody>
</table>

In the neural network architecture (Enquist & Ghirlanda, 2005; see Figure 4.1 for a graphical representation; see Appendix for a more detailed explanation), behaviour is determined through a very simple underlying structure that translates an input (the behaviours of ‘self’ and ‘partner’ in the previous interaction round) into an output (cooperation or defection). There are two input nodes, one of which receives the previous own behaviour (0 for defection, 1 for cooperation), and the other receives the previous behaviour of the opponent. The input from both these nodes is fed into two ‘hidden layer’ nodes, multiplied by the weights of the connections between the nodes. Each hidden layer node has a threshold; if the summed input into a hidden layer node exceeds its threshold, its output equals 1, otherwise the output is 0. Both hidden layer nodes are
The top row shows illustrations of the two behavioural architectures. In the 1:1 architecture, individuals have four gene loci that each determine the behaviour (cooperate or defect) in a given round for one of the four possible outcomes of the previous round. These four loci are represented by boxes (in the example shown, black boxes represent cooperation and white boxes represent defection). In the neural network architecture, individuals have nine loci, determining the (continuous) values of six connection weights (purple) and three thresholds (orange). The network processes the input (the behaviour of ‘self’ or ‘partner’ in the previous round) into an output (cooperate or defect). In the bottom row, the two mutation regimes are illustrated for both behavioural architectures, representing the four implementations considered in this study. Under per-locus mutation, each locus mutates independently (illustrated by single loci turning yellow after the arrow). In case of whole genome mutation, all loci mutate in the event of a mutation (illustrated by all loci turning yellow after the arrow).

Connected to the output node, which also has a threshold. If the total output from the hidden nodes (multiplied with the relevant connection weights) exceeds this threshold, the individual cooperates. If not, the individual defects. This way, six connection weights and three thresholds determine the strategy implemented by the network. Accordingly, the ANN is encoded by nine gene loci (that can take on any real value): one for each connection weight and one for each threshold. In addition, a tenth locus determines an individual’s behaviour in the first round (as in the 1:1 implementation).

Even under the highly simplifying assumptions on the strategy set and their underlying architectures, there are many ways to implement inheritance. For example, ploidy level and linkage patterns are of considerable importance for the genetic transmission of information on strategies in sexually reproducing organisms. To keep matters as simple as possible, we here only consider...
asexual populations of haploid individuals. In order to study the effect of genetic factors, we restrict attention to two different mutation regimes. In both regimes, the gene locus determining the behaviour in the first round mutates independently (with probability $\mu_F$), the mutational step size being drawn from a normal distribution with mean 0 and standard deviation $\sigma_F$. Under ‘per-locus mutation’, each of the other loci (4 loci in case of the 1:1 architecture and 9 in case of the ANN architecture) has a probability $\mu_L$ of giving rise to a mutation, independently of what is happening at the other loci. Under ‘entire genome mutation’, a mutation event (occurring with probability $\mu_G$) affects all these loci, that is, all these loci mutate at the same time. Under both mutation regimes, mutation is implemented as drawing a random number to replace the current value of the locus (in the 1:1 architecture, this is done by drawing 0 or 1 with equal probability; in the neural network architecture, by drawing a number from a normal distribution with mean 0 and standard deviation $\sigma_N$).

**Simulation setup and parameters**

We simulated a population of 1,000 asexual haploid individuals, with discrete and non-overlapping generations. At the start of each generation, pairs of two individuals are formed at random. These pairs interact repeatedly, where a new round always starts with probability $m = 0.99$ (leading to an average interaction length of 100 rounds). In any given generation, all pairs play the same number of rounds. After the last round of each repeated interaction, individuals reproduce. The probability of reproducing is directly proportional to the payoff individuals accumulate over the entire repeated interaction. Population size was kept constant. After reproduction, a new cycle starts.

At the beginning of each simulation, the loci $\sigma_F$ all individuals were initialized at random: initial values for the locus that determines the behaviour in the first round were drawn from a normal distribution with mean 0.5 and standard deviation 0.1; the four binary loci in the 1:1 architecture were assigned a 0 or a 1 with equal probability; and the nine loci encoding the connection weights and thresholds in the neural network architecture were assigned values that were drawn from a normal distribution with mean 0 and standard deviation $\sigma_N$. Each simulation was run for 100,000 generations. We ran 100 replicate simulations for all four combinations of the two behavioural architectures (1:1 and neural network) and the two mutation regimes (per-locus mutation and entire genome mutation). Resulting cooperation levels and strategy frequencies were calculated by averaging over all interactions in the last generation of each simulation, and then averaging those averages over all replicates.

In all simulations reported here the perception error $\epsilon_P$ and the implementation error $\epsilon_I$ were both set to 0.01; mutation probabilities ($\mu_L$, $\mu_G$, and $\mu_F$) were all set to 0.001, and mutational step sizes for all continuous loci ($\sigma_N$ and $\sigma_F$) were set to 0.1. In the Appendix, we consider different values of these parameters in order to check for the robustness of our results.
RESULTS

Effect of architecture on the average cooperation level

We studied the evolution of cooperation in two games (the ISD and the IPD), with four different implementations (see Figure 4.1) of behavioural strategies, reflecting two scenarios concerning the underlying behavioural architecture (1:1 versus neural network), and two scenarios concerning the mutation regime (per-locus versus entire-genome). Figure 4.2 shows that in both games the evolved cooperation level is strongly affected by both the genetic and the behavioural architecture. In fact, in both games average cooperation levels were 0.4 or lower for one implementation and 0.8 or higher for another implementation. Cooperation levels were higher for the 1:1 architecture when compared to the neural network architecture in all scenarios, but the effect of the mutation regime was different between the two games. In the IPD, per-locus mutation was associated with higher levels of cooperation than whole genome mutation, whereas the opposite was true in the ISD. To understand the causes underlying these large differences, we next zoom in on the data.

**Figure 4.2.** Cooperation levels in the Iterated Prisoners’ Dilemma game (top) and the Iterated Snowdrift game (bottom) for all four mechanistic implementations of the 16 strategies. The bars show average cooperation levels over all interactions in the last generation, across all replicates. Error bars show standard error of the mean.
in on the evolutionary dynamics of the 16 strategies that were considered in this study (see Table 4.1 for a complete list and an explanation of strategy names).

**Evolutionary dynamics in the Iterated Snowdrift game**

A game-theoretical analysis of the 16 strategies in the ISD reveals that there are three evolutionarily stable strategies (see Appendix for details). ESS 1 consists of 83.3% con-D (conventional defector, a strategy that sticks with its previous behaviour if it played the opposite as its opponent in the previous round, and defects otherwise), together with 16.7% ALLD. ESS 2 consists of the pure strategy Pavlov. ESS 3 involves three pure strategies: 96.8% MNG (Mr. Nice Guy, which always cooperates, except if it cooperated while the interaction partner defected in the previous round), 2.2% inconsistent (which always plays the opposite to its previous move) and 1.0% ACon-D (unconventional defector, a strategy that changes behaviour if it played the opposite as its opponent in the previous round, and defects otherwise).

In our simulations, we recover the three ESSs above. Typically, a simulation stays at one of the ESSs for extensive periods of time, followed by a rapid shift to another ESS. In most simulations across all scenarios, ESS 1 evolved first. In some of the simulations, ESS 1 was invaded by Pavlov, leading to the establishment of ESS 2. In a subset of those cases, ESS 2 was ultimately invaded by MNG, establishing ESS 3. ESS 3 was almost never invaded, but in very rare cases could be followed by a new establishment of ESS 1. The probability of transition between two ESSs and, accordingly, the probability to find the population in any of the three ESSs strongly depends on the behavioural architecture and mutation regime (Figure 4.3): In case of the 1:1 architecture, ESS 3 is the dominant state in case of per-locus mutation, while the simulations switch between ESS 2 (attained 81% of the time) and 3 (19%) in case of whole-genome mutation. In case of a neural network architecture, the simulations either end up in ESS 1 (55%) or 3 (45%) in case of per-locus mutation and in ESS 1 (38%) and 2 (62%) in case of whole-genome mutation. In other words, the four implementations differ in their likelihood of attaining each of the ESSs, and this difference is reflected in the average cooperation levels observed in Figure 4.2 (since each ESS induces a different cooperation level; see Table 4.A1 in the Appendix).

Why do the behavioural and the genetic architecture have such a strong effect on the evolutionary outcome? This can be illustrated by considering the transition from ESS 1 to ESS 2. In ESS 1, Pavlov has a slight selective disadvantage when rare, but as soon as it occurs in higher frequencies it achieves a higher payoff than the strategies in ESS 1 (because the payoff of Pavlov against itself is high). Therefore, if Pavlov increases enough against the selection gradient due to mutation and genetic drift, it can invade, and ESS 2 becomes established. Clearly, the probability that Pavlov results from mutation of the strategies in equilibrium 1 is a crucial factor in this regard. As shown in Table 4.1 (and explained in Appendix), Pavlov occupies a much larger part of the genotype space (6.25%) in the 1:1 architecture than in the neural network architecture (0.08%). As a result,
Pavlov almost never invades ESS 1 in the neural network architecture, whereas this does often happen in the 1:1 architecture.

**Evolutionary dynamics in the Iterated Prisoners’ Dilemma game**

A game theoretical analysis of the 16 strategies in the IPD reveals two ESSs, both containing only a single strategy: **ALLD** and **grim** (see Appendix for details).

In our simulations, there indeed were extended periods of time in which either **ALLD** or **grim** are dominant in the population. However, in most cases, the evolution of strategies was very dynamic and often irregular. This is in line with earlier studies that also conclude that the evolutionary dynamics in an IPD is often chaotic and off-equilibrium (Rasmusen, 1989; Nowak & Sigmund, 1993a; Gosak et al., 2008). Like in the ISD, both the behavioural and the genetic architecture had a strong
effect on the evolutionary dynamics (see Figure 4.4). In the case of 1:1 mapping with per-locus mutation, steady cycles of grim, TFT, MNG and Pavlov were observed for all replicate simulations (this is consistent with earlier findings by Nowak & Sigmund [1993]). For whole-genome mutation, the patterns look less consistent (yet highly dynamic), including longer spells of ALLD domination (this explains the relatively low cooperation levels in this scenario). In the neural network architecture, per-locus mutation led to very dynamic yet fairly consistent patterns, mostly involving TFT and MNG, and infrequent ALLD domination spells. Entire-genome mutation typically led to long ALLD domination spells interspersed by short periods with both cyclical dynamics involving various strategies including TFT, ALLC, ALLD, grim, and MNG and non-cyclical coexistence of TFT and inconsistent.

The effect of underlying mechanisms on the evolutionary dynamics can be explained by the fact that different mechanisms induce differences in the “mutational distance” between strategies, that is, the likelihood that a mutation in a strategy gives rise to a given alternative strategy. As an example, consider the extended periods of dominance of grim that were frequently observed. Those periods are typically ended by the invasion of TFT. TFT obtains a slightly worse payoff against grim than grim obtains against itself. However, TFT does obtain better payoffs when it happens to be paired with itself. In other words: if TFT can increase enough against the selection

\[ \text{Figure 4.4. Time series of typical simulation runs in the Iterated Prisoners’ Dilemma game, for all four mechanistic implementations. In each case, a time period of 2,500 generations is shown. The coloured lines represent the frequencies of the 16 different strategies.} \]
Importance of mechanisms for social evolution

Chapter 4

gradient because of genetic drift and mutation, it gains a selective advantage and can invade. The probability that this occurs depends on the implementation: In the 1:1 architecture with per-locus mutation, a mutation of *grim* produces *TFT* with probability $\frac{1}{4}$. In the case of whole genome mutation, this probability is only $\frac{1}{16}$ – this makes it considerably less likely that *TFT* obtains appreciable frequencies, and explains the extended spells of *grim* domination (Figure 4.4) and the lower degree of cooperation (Figure 4.2) in this case.

**DISCUSSION**

Our study demonstrates that behavioural architecture and mutation regime are of considerable importance for the dynamics and outcome of social evolution. In the IPD, we observed three types of dynamic behaviour (predictable cycles; fast and chaotic dynamics; spells of *ALLD* or *grim* domination) whose occurrence crucially depended on both behavioural architecture and mutation structure. Likewise, the prevalence of and the transitions between the three ESSs in the ISD were strongly determined by both architecture and mutation structure. In both games, the differences in evolutionary dynamics resulted in substantial differences in the average level of cooperation. These conclusions are not specific to the parameters considered in our simulations; they also hold for different payoff configurations of both games, and for a lower degree of stochasticity in the simulations (see Appendix).

The effect of mechanisms on the evolutionary dynamics was not caused by ‘hard’ constraints (the inability of mechanisms to produce all phenotypes), since all 16 strategies of the game were feasible in all four implementations. Yet, the mechanisms induced some ‘soft’ constraints on evolution, by strongly affecting the probabilities with which strategies arise by mutation (see Figure 4.5 for a schematic overview of mutation probabilities for each scenario considered in this study). Even in case of small mutation rates, the mutational distribution has a strong effect on the type of variation that can be expected to be present in a given situation. Some strategies only gain a selective advantage once they have increased beyond a certain frequency, and mutation probabilities determine the probability that this will happen. In the 1:1 architecture considered in this study, each strategy has an equal probability to result from a randomly generated genotype, whereas in the neural network architecture, some strategies (notably *ALLD* and *ALLC*) are much more likely to arise due to mutation than others (see Table 4.1). In the case of entire-genome mutation, the strategy of a mutant individual is independent of the strategy of its parent, and mutation probabilities therefore only depend on the behavioural architecture. In the case of per-locus mutation, the parental strategy partly determines the strategy of their mutant offspring.

We are not the first to point out that the genotype-phenotype mapping and the induced mutation structure are important for the course of evolution. In fact, the formal frameworks for modelling evolutionary dynamics can, to a certain extent, take these complexities into account. For
example, the ‘canonical equation’ of adaptive dynamics theory includes a mutational covariance matrix (Dieckmann & Law, 1996; Metz & De Kovel, 2013), which characterizes the likelihood that a combination of phenotypic traits (like a conditional strategy) arises and potentially invades the current resident strategy. Likewise, the multivariate selection equation of quantitative genetics (Lande, 1979; Lande & Arnold, 1983) can be written in a form that it includes a matrix characterizing the covariance in phenotypic traits between parents and offspring (Rice, 2004). Sean Rice has worked out formally how these covariances arise and determine the course of evolution when phenotypic traits are the outcome of (developmental) mechanisms (Rice, 2002; 2004). We are not aware of attempts to actually derive the covariance matrices of adaptive dynamics of quantitative genetics theory on the basis of a concrete mechanistic model. Instead, theoretical studies...

**Figure 4.5.** Mutational distance between the most relevant strategies in the Prisoners’ Dilemma game (top) and the Iterated Snowdrift game (bottom), for both behavioural architectures and the case of per-locus mutation. An arrow pointing from one strategy to another indicates that a mutation of the former strategy has probability of larger than 0.001 to yield the latter strategy. A probability of > 0.05 is indicated by a solid arrow (the thickness of the arrow is proportional to the probability). In the 1:1 model, each strategy can mutate to four other strategies with equal probability, so the arrows in the mutation maps for the 1:1 model all represent a probability of 0.25. To calculate these probabilities, we first generated a large number of random genotypes (in the same way as generating a genotype through ‘entire-genome mutation’), and determined their corresponding strategy. Then, for each strategy, we mutated all corresponding genotypes many times, and again determined the resulting strategies.
tend to make simplifying assumptions, such as replacing the covariance matrix by the identity matrix (e.g. Van Doorn et al., 2003). Already in the case of frequency independent selection and in the absence of stochasticity, assumptions like these are not unimportant, since the covariance structure largely determines which peak of a multi-peaked fitness landscape will be reached.

There are two main reasons why we think that phenotypic covariances and, hence, the mechanisms underlying the development of phenotypes, are of particular importance for social evolution. First, selection will virtually always be frequency-dependent in this case. As a consequence, the success of each strategy will strongly depend on the context, and, in particular, on the presence of selectively favoured competitors. Accordingly, a given architecture will contribute to the stability of a given equilibrium if it makes the production of selectively favoured alternatives less likely, and it will have a destabilizing effect if the opposite is the case. Second, in case of social interactions there are typically many alternative Nash equilibria and ESSs. This is already illustrated in the IPD and the ISD with highly restricted memory considered here. Relaxing the restrictions on the strategy set would lead to a rapid increase in the number of equilibria. In fact, the Folk Theorem of game theory (Van Damme, 1991; Brembs, 1996) implies quite generally that in repeated games the set of Nash equilibrium strategies is so large that virtually any ‘reasonable’ outcome (in case of our IPD: any outcome between 0 and 5; in case of our ISD: any outcome between 1 and 5) can be achieved as the average outcome of an equilibrium. But also non-repeated games typically have several (and often a large number of) Nash equilibria and ESSs (Selten, 1983). In all these cases, it is to be expected that the evolutionary dynamics will be affected in a similar way by mechanisms as in the present study.

We have here focussed on situations where the evolutionary game dynamics (Hofbauer & Sigmund, 2003) are relatively simple. For the payoff structure considered, the IPD and the ISG have a small number of ESSs, and these are the only attractors of the replicator equation (see Appendix). Accordingly, mechanisms will mainly affect the transition between ESSs, as described above. It is conceivable that mechanisms have an even stronger effect in the presence of limit cycles or other non-equilibrium attractors. Such attractors regularly occur in evolutionary games (such as variants of the Rock-Scissors-Paper game; see Weissing, 1991), and it has been shown that seemingly small differences in the genetic implementation of strategies can have major effects on the evolutionary outcome (Weissing & Van Boven, 2001). In the Appendix, we show that non-equilibrium attractors can also occur in the IPD (for slightly different payoff parameters), but a thorough investigation of the interplay of genetic or behavioural architecture and non-equilibrium dynamics is beyond the scope of this study.

Our results should be mainly viewed as proof of principle that mechanisms matter for the course and outcome of social evolution. It would be premature to conclude that one of the four implementations considered in our study is more ‘realistic’ than the others. On purpose, we kept our assumptions on architecture as simple as possible, since this allowed us to develop a sound intuitive understanding of our results (see Figure 4.5). Because of this understanding, we are
confident that our findings are of general relevance. The development of truly ‘realistic’ models remains a major challenge, since the actual genetic, physiological, neurological, and psychological mechanisms behind social behaviour are still largely terra incognita for virtually all organisms and virtually all interaction types. For this reason, it would be premature to abandon the standard 1:1 genotype-phenotype mapping assumption in favour of (for example) a neural network implementation. However, whatever the implementation chosen, researchers should be aware that it may have considerable implications for the course and outcome of evolution.

The evolution of social behaviour is often an intricate process, with many feedbacks at work, and many possible outcomes. We have shown that underlying mechanisms are of decisive importance in determining which outcome eventually emerges in evolution. Therefore, it is of importance that we focus more on mechanisms when trying to explain the evolution of social behaviour. Both empirical work focused on understanding mechanisms and theoretical work investigating their importance for the dynamics and course of evolution have a vital role to play in this regard.
Appendix

This appendix consists of three sections. First, we illustrate with an example how the neural network implements a strategy. Second, we present an ESS analysis of both games that we consider (the IPD and the ISD). Third, we present a sensitivity analysis showing that the main conclusions of our study hold for a number of alternative parameter settings.

1. IMPLEMENTATION OF STRATEGIES BY A NEURAL NETWORK

All sixteen strategies listed in Table 4.1 can be realized by our neural network architecture. To give some more insight in how a neural network configuration implements a strategy, Figure 4.A1 gives an example of one of the many possible networks implementing Pavlov. Pavlov cooperates after mutual cooperation or mutual defection, and defects otherwise. The implementation of Pavlov in the neural network architecture depends on a relatively precise relationship between the weights and thresholds of the network. For example, the sum of \( w_5 \) and \( w_6 \) must exceed \( t_3 \), but neither of the two should exceed \( t_5 \) alone. Also, \( w_1 \) and \( w_3 \) must together exceed \( t_1 \), and only one of those two weights must exceed \( t_1 \) alone, while the other must not. The same necessary relationships hold for weights \( w_2 \) and \( w_4 \) and threshold \( t_2 \). In addition, both \( t_1 \) and \( t_2 \) must be negative. The relatively restrictive conditions needed for a network to correspond to Pavlov give an intuitive understanding of why only a small percentage of the genotype space is associated with this strategy (see Table 4.1).

When considering the network in Figure 4.A1, it also becomes easier to understand why the strategies ALLD and ALLC are so likely to result from a random configuration of the network. If the value of \( t_3 \) in this network is changed from 4 to 6, then this threshold can never be exceeded, meaning this network will always defect. More generally, all networks for which \( t_3 > w_5 + w_6 \) and \( t_3 > 0 \) implement ALLD, regardless of the values of the other weights and thresholds. Similarly, all networks for which \( t_3 < w_5 + w_6 \) and \( t_3 < 0 \) implement ALLC. However, this only one of many ways that the network in Figure 4.A1 could mutate towards a network implementing ALLD. For example, since both \( t_1 \) and \( t_2 \) must be exceeded for this network to cooperate, any mutation that increases the value of either of these two thresholds so that it cannot be exceeded by the preceding weights would result in an ALLD network.
Figure 4.A1. A neural network corresponding to the Pavlov strategy. The network on top shows the values of all the weights ($w_1$ – $w_6$) and thresholds ($t_1$ – $t_3$); green lines depict positive values, red lines depict negative values, and their thickness indicate their absolute values. The input nodes receive the previous own decision (top) and the previous decision of the interaction partner (bottom); 1 for cooperation and 0 for defection. The four networks on the bottom show in detail how the output of the network is generated for each of the four possible outcomes of the previous round. The values of the input nodes are multiplied with weights $w_1$ to $w_4$; the resulting values are summed and fed into the hidden layer. If the summed values exceed the respective threshold values of the hidden layer, their output is 1; otherwise, it is 0. Those values are then multiplied with weights $w_5$ and $w_6$, and the sum of the resulting values is fed into the output node. If this value exceeds the threshold of the output node, the network cooperates; otherwise, it defects.
2. ESS ANALYSIS OF THE IPD AND THE ISD

Repeated games like the Iterated Prisoners’ Dilemma game (IPD) or the Iterated Snowdrift Game (ISD) have a huge strategy set, and even for games as simple as these a full game theoretical analysis has not yet been achieved. Such an analysis is a formidable task, since the number of Nash equilibria is huge (Van Doorn et al., 2003). In fact, the ‘Folk Theorem’ of game theory implies that any reasonable outcome can be realized by a Nash equilibrium of the iterated game (for details see Van Damme, 1991). On the other hand, no pure strategy is evolutionarily stable in the IPD or the ISD (e.g. Boyd & Lorberbaum, 1987).

Here, we consider simpler versions of the IPD and the ISD where the strategy set is restricted to 16 pure strategies with limited memory (only the moves in the previous round are memorized). These versions of the IPD and the ISD have been the subject of many studies, but to our best knowledge a full characterization of all Nash equilibria or all evolutionarily stable strategies (ESS) has never been given. This is understandable, since even under the restriction to 16 pure strategies the game theoretical analysis remains a challenge. Here we show how to classify all ESSs with support 1, 2 and 3 of the two repeated games for the payoff configuration considered in the main text. A Mathematica file with all calculations is available upon request. An overview of all ESSs with support 1, 2 and 3 is shown in Table 4.A1. By means of numerical iterations based on the replicator equation, we demonstrate that most likely there are no other ESSs with a larger support.

Construction of the 16x16 payoff matrix

As a first step, we determine the payoff matrix of the game by calculating the expected payoffs for any pair of pure strategies. Any such pair of strategies induces a sequence of transitions between the four different ‘cooperation states’ of a game round (mutual cooperation, mutual defection, mutual cooperation and the other player defected, mutual cooperation and the other player cooperated, mutual defection and the other player cooperated).

Table 4.A1. The evolutionarily stable strategies (ESS) identified by the game theoretical analysis of the IPD and the ISD. In case of the ISD, the three ESSs are numbered in line with the three equilibrium outcomes of the simulations described in the main text. The last column gives the average cooperation level in each equilibrium.

<table>
<thead>
<tr>
<th>Game</th>
<th>ESS</th>
<th>Strategies</th>
<th>Fraction</th>
<th>Cooperation</th>
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<tbody>
<tr>
<td>IPD</td>
<td>1</td>
<td>ALLD</td>
<td>1.000</td>
<td>0.010</td>
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<tr>
<td></td>
<td>2</td>
<td>grim</td>
<td>1.000</td>
<td>0.013</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>Pavlov</td>
<td>0.968</td>
<td>0.698</td>
</tr>
<tr>
<td></td>
<td></td>
<td>inconsistent</td>
<td>0.022</td>
<td>0.698</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Acon-D</td>
<td>0.010</td>
<td></td>
</tr>
<tr>
<td>ISD</td>
<td>1</td>
<td>con-D</td>
<td>0.833</td>
<td>0.180</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ALLD</td>
<td>0.167</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Pavlov</td>
<td>1.000</td>
<td>0.943</td>
</tr>
<tr>
<td></td>
<td></td>
<td>MNG</td>
<td>0.968</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>inconsistent</td>
<td>0.022</td>
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<td>Acon-D</td>
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cooperation-defection, defection-cooperation). In the absence of errors, this sequence would be deterministic and mainly dependent on the combination of moves in the first round. The inclusion of perception and implementation errors, however, turns the transition between states into a stochastic process with a well-defined 4x4-matrix of transition probabilities between cooperation states. The right eigenvector corresponding to the dominant eigenvalue of this matrix (which is typically the only positive eigenvalue of the matrix) is proportional to the stationary distribution over states generated by the interaction of the two pure strategies. The four elements of the (normalized) eigenvector correspond to the fraction of time spent in each of the four cooperation states in an infinitely repeated interaction. Weighing the four elements of the payoff matrix of the one-shot game by these elements and summing up the results therefore yields the expected per-round payoff for each of the two strategies. Notice that this pair of payoffs does not depend on the initial pair of moves (these are irrelevant from a long-term perspective), but reflects the perception and implementation errors made by the players (both were kept at 0.01, as in the simulations). All subsequent ESS calculations are based on the 16x16 payoff matrix that results by applying the above recipe to all pairs of pure strategies.

**Determination of all pure-strategy ESSs**

It is straightforward to characterize all pure-strategy Nash equilibria: A pure strategy i is a Nash equilibrium if no alternative pure strategy j attains a higher payoff against i than i attains against itself. If i is a 'strong' Nash equilibrium (any alternative pure strategy j attains a lower payoff against i than i attains against itself), then i is an ESS (Maynard Smith, 1982; Selten, 1983; Hofbauer & Sigmund, 1988; Van Damme, 1991; Weissing, 1991). It turned out that the IPD has two pure-strategy Nash equilibria (grim and ALLD), which both are strong Nash equilibria and therefore an ESS. The ISD has a single pure-strategy Nash equilibrium (Pavlov), which again is a strong Nash equilibrium and an ESS.

**Determination of all ESSs with two coexisting pure strategies**

To calculate all ESSs with support two, we first determined all those pairs of pure strategies i and j that can mutually invade each other: j has a higher payoff against i than i has against itself; and i has a higher payoff against j than j has against itself. This condition of mutual invadability is equivalent to the existence of a mixed-strategy ESS of the restricted game with only these two pure strategies (Hofbauer & Sigmund, 1988; Weissing, 1991). This ESS can easily be calculated on the basis of the condition that the fitness of both pure strategies needs to be identical at the ESS (Maynard Smith, 1982). The ESS thus found is an ESS of the full game (with all 16 strategies) if all other strategies have a lower payoff at this two-strategy equilibrium than the two equilibrium strategies (Weissing & Van Boven, 2001). It turned out that the IPD has no ESS with support two, while the ISD has one such ESS: 83.3% con-D and 16.7% ALLD.
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Determination of all ESSs with three coexisting pure strategies

The calculation of all ESSs with support three is more tedious. For each triplet \(i, j,\) and \(k\) of pure strategies we first checked whether the three strategies can coexist at equilibrium. This was done by checking whether the system of linear equations specifying fitness equality of the three strategies in the restricted three-strategy game has a positive solution. This solution specifies a candidate-ESS. In a second step, the ‘internal’ stability of this candidate-ESS (i.e., its evolutionary stability in the restricted three-strategy game) was checked, making use of a criterion for evolutionary stability in 3x3 games (Hofbauer & Sigmund, 1988; Weissing, 1991). In a third step, the ‘external’ stability of the candidate-ESS was determined by checking whether all other 13 pure strategies of the full 16-strategy game have a lower payoff at the candidate-ESS than the three strategies being part of the candidate-ESS (Weissing & Van Boven, 2001). It turned out that the IPD has no ESS with support three, while the ISD has one such ESS: 96.8% MNG, 2.2% inconsistent, and 1.0% Acon-D.

Numerical iterations based on the replicator equation

To check whether the equilibria identified in the game theoretical analysis are actually attainable and dynamically stable, and whether any other attractors are present in the system, we performed extensive numerical iterations using the replicator equation (Hofbauer & Sigmund, 1988; Weissing, 1991). To do this, we used the same 16x16 payoff matrices calculated for the game theoretical analysis of both games (described above). Starting from around \(6 \times 10^7\) different initial population constitutions, we iterated the replicator equation until an attractor was reached. For each iteration, the minimum frequency of each strategy was set to 0.001 so that invasion of any strategy was always in principle possible. The outcome of these iterations was congruent with the game theoretical analysis; all iterations (for both of the games) ended up in one of the ESSs in Table 4.A1, and each of the ESSs was commonly attained (depending on the initial conditions). The oscillating behaviour commonly observed in the individual-based simulations of the IPD was never observed in the (deterministic) numerical iterations. This suggests that those observations correspond to transient (‘away from equilibrium’) behaviour driven by the stochastic component of the individual-based simulations.

3. SENSITIVITY ANALYSIS

In the main text, we have shown that the mechanisms underlying the strategies of an evolutionary game can be of substantial importance for the evolutionary dynamics and the evolutionary outcome. For ease of representation, all simulations were conducted for one set of parameters. In this section, we show that our main conclusion also holds for a number of altered parameter
settings. Specifically, we consider versions of our model with a reduced mutation rate and with an altered payoff configuration in both games.

**Reduced mutation rate**

The simulations of the IPD discussed in the main text commonly exhibited highly dynamical behaviour, even though no non-equilibrium attractors were identified in the game theoretical analysis or numerical iterations of the replicator equation (see Appendix section 2). It is likely that this discrepancy is caused by the stochastic component of the simulations. The degree of stochasticity can be reduced by increasing the population size or by decreasing the mutation rate. Here, we investigate how our evolutionary simulations are affected by a reduction of the

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**Figure 4.A2.** Typical simulation runs for the IPD, for different behavioural architectures, mutation regimes, and mutation rates. For each parameter combination, excerpts of five replicate simulation runs are shown. Each excerpt comprises a time period of 2,000 generations. The excerpts were chosen from 100 replicate simulation runs (comprising 100,000 generations each) to give an impression of the 'typical' dynamics observed for each parameter combination. Graphs of all 100 replicate simulation runs for each parameter combination are available upon request.
mutation rate from $10^{-3}$ to $10^{-4}$. In addition, we also give an idea of how replicate simulation runs can differ from each other.

Figure 4.A2 shows typical simulation runs of the IPD for each of the scenarios (behavioural architecture and mutation regime), for both mutation rates. The game theoretical analysis identified two pure-strategy ESSs for this game: ALLD and grim (see Table 4.A1). Most simulation runs consist of periods of stasis (with one or two strategies in an equilibrium-like situation), followed by periods of strong fluctuations. As a rule, the periods of stasis are longer in case of a lower mutation rate, but even in that case, highly dynamical periods are common. During the periods of stasis, one of the two ESSs (ALLD or grim) is typically the predominant strategy. However, many simulation runs included prolonged periods of stasis dominated by the non-ESS strategies Pavlov or MNG, or con-D or static periods where TFT and inconsistent coexisted in almost equal frequencies. Interestingly, these deviations from the game theoretical ESS predictions were mainly observed in simulations with a low mutation rate.

Besides these effects of a lowered mutation rate on the simulation dynamics, Figure 4.A2 clearly shows that lowering the mutation rate does not change our main conclusion that underlying

![Figure 4.A3. Evolutionary outcome of the simulations of the ISD for the different mechanistic implementations and mutation rates. The left bars of each pair show high mutation rates ($H, \mu = 0.001$), bars on the right show low mutation rates ($L, \mu = 0.0001$). Bars indicate the fraction of 100 replicate simulations ending up in each of the three ESSs of the ISD (Table 4.A1) after 100,000 generations.](image-url)
mechanisms strongly affect the evolutionary outcome. For example, ALLD domination was more commonly observed in the simulations with the neural network implementation, whereas grim domination was more common for the 1:1 mapping.

The game theoretical analysis of the ISD identified three ESSs (see Table 4.A1). Irrespective of the mutation rate, most simulations quickly converged to one of these ESSs; transitions between ESSs occurred, but only on rare occasions. When transitions occurred, ESS 1 was generally attained first, eventually succeeded by ESS 2, and finally followed by ESS 3 in some simulations. As expected, such transitions were less frequent in case of a lower mutation rate.

Figure 4.A3 shows how frequently each of the three ESSs was attained after 100,000 generations in 100 replicate simulations of the ISD, for each behavioural architecture, mutation regime, and mutation rate. In all cases, ESS 1 was observed more often for low mutation rate than for high mutation rate (except for the 1:1 mapping with entire genome mutation, where this ESS was never the outcome, regardless of the mutation rate). Similarly, ESS 3 was always observed more often for the higher mutation rate (except for the neural network with entire genome mutation, where this equilibrium was never observed). Besides these effects, lowering the mutation rate does not alter our main conclusion: also in the ISD the underlying mechanisms strongly affect the outcome of evolution.

Alternative payoff configurations

A full sensitivity analysis concerning the effect of the payoff parameters of the IPD or the ISD on the evolutionary outcome is beyond the scope of this study. As mentioned above, even an ESS analysis or an analysis of the attractors of the replicator equation as a function of the payoffs is quite a challenge. This is exemplified by the game theoretical analysis in section 2 of this appendix, which shows that the 16x16 payoff matrix of the two games does not have a straightforward relationship with the payoffs of the underlying one-shot game. Instead of conducting a comprehensive analysis of the effect of payoffs, we here just give an illustration, by redoing our analysis for one alternative payoff configuration for each of the games. As will become clear, even this relatively small alteration qualitatively changes the equilibrium structure of both games, but does not affect our main conclusion that underlying mechanisms strongly affect the outcome of social evolution.

In this analysis, we replaced the payoffs for defecting while the interaction partner cooperates from 5 to 4 in both games, yielding the following payoff matrices:

$$PD: \begin{pmatrix} 3 & 0 \\ 4 & 1 \end{pmatrix}; \quad SD: \begin{pmatrix} 3 & 0 \\ 4 & 1 \end{pmatrix}.$$ 

First, we performed a game theoretical ESS analysis on the iterated versions of these games (as described in section 2 of this appendix); all ESSs with support 1, 2 or 3 are shown in Table 4.A2. In case of the IPD, the game theoretical analysis identifies the same pure-strategy ESSs as
in the original game (\textit{ALLD} and \textit{grim}), but also identifies a third (\textit{Pavlov}). As in the original game, there are no ESSs with 2 or 3 coexisting strategies in this game. In the ISD, we also find the same pure-strategy ESS as in the original game (\textit{Pavlov}). In addition, we find another pure-strategy ESS: \textit{con-D}. This ESS is relatively similar to ESS 1 of the original model (that equilibrium also consisted of mostly \textit{con-D}, but also included a relatively low frequency of \textit{ALLD}; see Table 4.A1). These two pure-strategy ESSs are the only ESSs identified by the game theoretical analysis; ESS 3 (or a similar ESS) was not identified in this version of the ISD.

To check whether there are any other attractors in the system, we also did extensive numerical iterations of the replicator equation (see section 2 of this appendix for details). It turned out that all the ESSs described above were commonly attained; and that there is apparently no alternative stable equilibrium. Interestingly, a non-equilibrium attractor appeared in the replicator dynamics of the IPD: about 18% of all iterations converged to the stable limit cycle shown in Figure 4.A4. This cyclical attractor includes most of the 16 pure strategies. The most prominent role is for \textit{TFT}, followed in time by \textit{con-C} (and, in lower frequencies, \textit{willing} and \textit{ALLC}), then by a mix of strategies including \textit{ATFT}, \textit{desperate}, \textit{con-D}, \textit{grim}, \textit{ALLD}, and \textit{Pavlov}, to be followed by \textit{TFT} again. After this second peak of \textit{TFT}, a similar mix of strategies follows as after the first peak, although \textit{ATFT} is absent this time, there is a small peak of \textit{inconsistent}, and there is a longer period of a mix of \textit{ALLD} and \textit{grim} before the cycle starts over again. Except for this last stretch, a small frequency of \textit{MNG} is present throughout. Only a minority of strategies do not play a role in this cyclical attractor: \textit{Acon-D}, \textit{APavlov}, \textit{hopeless}, and \textit{consistent}.

Figure 4.A5 shows typical behaviour of simulations of the IPD for the altered payoff configuration. These simulations were run for all mechanistic implementations, and also for high ($10^{-3}$) and low ($10^{-4}$) mutation rates. It is apparent that in comparison to the original game the periods of stasis are more pronounced, while the periods of fluctuation tend to be much shorter. For example, the 1:1 mapping with per-locus mutation now typically converges to the ESS \textit{Pavlov}, while strong fluctuations were the rule in the original game (Figure 4.A2). The reduced tendency

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<td>ISD</td>
<td>1</td>
<td>\textit{con-D}</td>
<td>1.000</td>
<td>0.206</td>
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<td></td>
<td>2</td>
<td>\textit{Pavlov}</td>
<td>1.000</td>
<td>0.943</td>
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Figure 4.A4. A cyclical attractor in the IPD with alternative payoff matrix. Note that some of the colours associated with the strategies are different than in the other graphs.

Figure 4.A5. Typical simulation runs for the IPD with altered payoff matrix, for different behavioural architectures, mutation regimes, and mutation rates. As in Figure 4.A2, representative excerpts of 100 replicate simulation runs are shown for each parameter combination. Graphs of all 100 replicate simulation runs for each parameter combination are available upon request.
to cycle is somewhat surprising, since the altered IPD has a cyclic attractor (Figure 4.A4) while the original game only had two pure-strategy attractors (Table 4.A1).

As in the original model, behavioural architecture and mutation regime strongly affect the outcome and dynamics of evolution. For instance, in the 1:1 mapping, the Pavlov equilibrium is a much more common outcome than in the neural network implementation. The Pavlov equilibrium was never observed to be invaded by any other strategy in any of the replicate simulations across all implementations. This suggests that given enough time, all simulations should end up in this equilibrium, the waiting time until this happens being determined by the mechanistic implementation. Consistently with this, the Pavlov equilibrium was more frequently observed for higher mutation rates. As for the original payoff configuration, the incidence of highly dynamic periods is lower for reduced mutation rates (especially in the neural network implementation).
Some of the simulation dynamics bear some resemblance to the cyclical attractor that was identified for this payoff configuration (periods with many subsequent peaks of TFT).

Figure 4.A6 shows the equilibria that were attained in the simulations of the ISD with alternative payoff configuration, again for all mechanistic implementations. This altered version of the ISD has two pure-strategy ESSs: con-D and Pavlov (similar to ESSs 1 and 2 in the original game). From the figure, it is obvious that the mechanistic implementation has a strong effect on the simulation outcome; in the 1:1 mapping, ESS 2 was by far the most common outcome, whereas in the neural network, ESS 1 was more common. The mutation regime also affected the outcome, especially in the neural network implementation, where ESS 2 was more common for entire-genome mutation than for per-locus mutation. As in the original game, ESS 2 was observed to succeed ESS 1, but never vice versa. Accordingly, one would expect to find ESS 2 more frequently in case of a higher mutation rate (since a higher mutation rate should lead to a faster transition from ESS 1 to ESS 2). Indeed, ESS 2 was observed less frequently for the lower mutation rate across all implementations. However, this effect is not very pronounced except for the neural network implementation with entire-genome mutation.
Consistent individual differences in human social learning strategies

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ABSTRACT

Social learning has caused humans to build up extensive cultural repertoires, allowing them to adapt to a wide variety of environmental and social conditions. However, it is unclear which social learning strategies people use, especially in social contexts where their payoffs depend on the behaviour of others. Here we show experimentally that individuals differ in their social learning strategies and that they tend to employ the same learning strategy irrespective of the interaction context. Payoff-based learners focus on their peers’ success, while decision-based learners disregard payoffs and exclusively focus on their peers’ past behaviour. These individual differences may be of considerable importance for cultural evolution. By means of a simple model we demonstrate that groups harbouring individuals with different learning strategies may be faster in adopting technological innovations, and can be more efficient through successful role differentiation. Our study highlights the importance of individual variation for human interactions and sheds new light on the dynamics of cultural evolution.
INTRODUCTION

Human success in colonising nearly all terrestrial habitats of our planet was facilitated by our social nature (Boyd et al., 2011a; Whiten & Erdal, 2012). Humans excel in collective action, are able to cooperate in social dilemmas and to employ high degrees of group coordination and cooperation to solve adaptive problems. The transmission of information between individuals through social learning was a key factor for the spread of humans across the whole planet. Such cultural transmission has led to the accumulation of huge amounts of adaptive information in very little time. It has been argued that social learning leads to a parallel inheritance system giving rise to a process that is in many ways analogous to genetic evolution (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Dawkins, 1976; Molleman et al., 2013a). The dynamics and outcome of this process of cultural evolution is to a large extent determined by the rules that govern the transmission of cultural information between individuals; i.e. the social learning mechanisms that people use. Several social learning strategies have been described that may each be adaptive under particular circumstances (Galef Jr & Laland, 2005; Laland, 2004; Rendell et al., 2010; Valone, 2007, 1-14; Rendell et al., 2011; Kendal et al., 2009). A social learning strategy can specify under which circumstances to pay attention to social information; which individuals to choose as target for collecting information; which type of information to gather from these individuals; and how to use this information as guidance for future behaviour (Laland, 2004; Hoppitt and Laland, 2013). Prominent examples of social learning strategies are ‘frequency-based learning’ (e.g., to conform to a local majority (Boyd & Richerson, 1985; Rogers, 1988; Richerson & Boyd, 2004; Kendal et al., 2009; Molleman et al., 2013b), ‘payoff-based learning’ (to imitate the behaviour of peers who achieved high payoffs in the recent past (Boyd & Richerson, 1985; Schlag, 1998; Henrich & Gil-White, 2001; Lehmann et al., 2008; Lehmann & Feldman, 2008), or ‘prestige-based learning’ (to imitate or follow the advice of high-status individuals such as leaders or teachers (Henrich & Gil-White, 2001; Lehmann & Feldman, 2008; Lehmann et al., 2008).

Empirical evidence from the field suggests that these learning strategies do indeed affect the spread of behaviour in human groups (Henrich & Henrich, 2010; Henrich & Broesch, 2011). The results of such investigations are corroborated by evidence from controlled laboratory studies, which indicate that people attend to the frequencies of their peers’ behaviour, as well as to the payoffs associated with it (McElreath et al., 2005; Efferson et al., 2007; McElreath et al., 2008; Efferson et al., 2008; Mesoudi, 2008; Traulsen et al., 2010; Mesoudi, 2011b). In addition, there are indications that the extent to which people resort to social information depends on factors like task difficulty, confidence in their own information (Morgan et al., 2012) and environmental variability (Toelch et al., 2009). Experimental results suggest that individuals differ in the extent to which they rely on social information when making decisions under uncertainty (McElreath et al., 2005; Mesoudi, 2011b), and vary in their tendency to conform to behaviour of the majority (Efferson et al., 2008).
As yet, there is no strong evidence that individuals differ with respect to the type of social information that they rely on in making decisions. This is not surprising, since experimental studies of human social information use have predominantly focused on the spread of technological innovations that are mainly relevant in non-social contexts. When attempting to acquire technological know-how, individuals almost exclusively use payoff-based learning (by copying behaviour of successful individuals) when explicitly presented with a choice between multiple social learning strategies (Mesoudi, 2011b). Finding the adequate behaviour in a social setting is quite a different task, which might require different learning strategies. Social ‘know-how’ differs from technological know-how in that the payoffs of the various alternatives do not only depend on the external environment, but also on the behaviour of others in the population. When having to choose among alternatives in a non-social setting, the information obtained from others is mainly useful for obtaining a more accurate estimate of the payoffs of these alternatives in a noisy world. In a social setting, these payoffs reflect the behaviour of others. As a consequence, social learning gets a new dimension, namely acquiring information on the distribution of behavioural tendencies in the population. The importance of such frequency information strongly depends on the type of social interaction. We here study social learning in various social interactions with different signatures. This way we get a more general impression of whether and how social learning differs between technological and social contexts. Moreover, the inclusion of different types of social context allows us to investigate whether individuals are consistent across those contexts.

To obtain a better understanding of human social learning in both social and non-social settings, we designed an experiment. Subjects were distributed in groups of eight individuals, and experienced four interaction contexts in sequence: a best choice situation (where one of the options yielded a higher payoff on average, irrespective of the behaviour of the other members), a social dilemma (where cooperation is costly to the individual but beneficial for the group), a coordination game (where it is favourable to follow the behaviour of the majority) and an evasion game (where it is favourable to deviate from the behaviour of the majority). Payoffs were noisy, so that it required several trials to find the best option. Before making a decision, all subjects were allowed to request up to six pieces of information about the behaviours and payoffs of their peers, at a small cost (see Methods for details). The information available about each peer included the previous decision, the payoff associated with the previous decision, and the total payoff acquired in the current context. We evaluate social learning strategies by tracking the types of information requests that subjects made and by investigating how these requests influenced their behaviour.

We will demonstrate that individuals differ substantially and consistently with respect to their social learning strategies. Some strongly rely on social information in making their decisions, whereas others tend to learn individually. Those individuals making use of social information differ in the type of information they are interested in: some individuals only focus on the decisions of their group members (thereby neglecting payoff-related information), whereas others consistently request information about both decisions and the payoffs that were associated with
them. Since we found these results remarkable, we repeated our primary experiment in a larger follow-up study (see Methods) in order to get an impression of the robustness and replicability of our results. Finally, we built a simple model for decision-making in groups, in order to investigate whether individual differences in social learning strategies will affect the direction and outcome of cultural evolution.

RESULTS

We will first describe the results of our primary experiment and later report on the outcome of the follow-up experiment.

Dynamics of behaviour and social information use

In the course of time, the behaviour in all groups converged to a Nash equilibrium of the game describing the social context (Figure 5.1, top row, broken lines), indicating that subjects adjusted their behaviour according to the underlying payoff structure (see Methods for details). The availability of social information was associated with a faster adoption of the superior option in the best choice context and the dominant strategy in the social dilemma game (Figure 5.A1; see Appendix). Subjects frequently made use of costly social information (Figure 5.1; bottom row; the fraction of decisions preceded by costly requests for information was BC: 0.23, SD: 0.25, CO: 0.21 and EV: 0.31). Information requests decreased over time; presumably because there is less need for subjects to adjust their behaviour once their group has approached equilibrium. Individuals usually requested information about only the previous decision (Figure 5.1, red bars), or the combination of the previous decision and the associated payoff (Figure 5.1, light blue bars) of their peers. In the vast majority of these cases, requested information entirely consisted of either of those two types; the previous decision of six of their peers, or the combination of the previous decision and payoffs of three of their peers (also adding up to the maximally allowed six pieces of information). These types of information requests are consistent with frequency-based learning strategies (such as conformism) and payoff-based learning strategies, respectively. On average, subjects requested social information more often when their own previous decision yielded low payoffs (Figure 5.A2; see Appendix). Also, individuals tended to change their behaviour when information on the behaviour and payoffs of others indicated that alternative behaviour yielded a higher payoff (Figure 5.A3; see Appendix; consistent with payoff-based learning). Reactions to information on the frequencies of peers’ behaviour depended on the interaction context (Figure 5.A4; see Appendix). In the best choice context, the proportion of information requests including requests for payoffs (0.61) was significantly higher than in the social contexts (SD: 0.40, CO: 0.26, EV: 0.33; Tukey contrasts between effect estimates of the factor ‘context’ in a generalised linear model: $n = 9728$ decisions; $P < 0.001$). Subjects requested total payoffs almost exclusively in the
Figure 5.1. Change in behaviour and information requests in the course of time. 

**a.** Change in the relative frequency of cases that option A was chosen for each context (sixteen replicate groups in grey, averages in colour). Over time, replicate groups approach a Nash equilibrium of the games (broken lines, arrows; option B yielded a higher payoff than A in both the best choice and the social dilemma context).

**b.** Counts of combinations of information types requested in corresponding rounds. Before making their decision, subjects could collect six pieces of costly information about their peer group members. For each peer, available information was his decision in the previous round, his payoff in the previous round, and his total payoff obtained in the present context. Requests for payoffs (and associated decisions; light blue bars) prevail in the best choice context and occur regularly in the social contexts; requests only involving recent decisions (red bars) prevail in the social contexts and occur regularly in the best choice context. With the exception of the final round (where subjects often request information on total payoffs) other types of requests are very rare.
Individual differences in social learning

last round (Figure 5.1, dark green, light green, yellow and orange bars); presumably out of curiosity to compare their own performance to that of others.

Individual variation in social learning strategies

Subjects strongly varied in their reliance on social learning. In each context, about 20% of all subjects never requested information (Figure 5.2a). In contrast, some other individuals based most of their decisions on information about their peers.

The subjects also differed strongly in the degree to which they requested information on payoffs (Figure 5.2b). While the overall fraction of information requests that included requests for payoffs was intermediate in each context (see above), the underlying individual behaviour was surprisingly extreme. For each context separately, we found that most subjects can be categorized in two largely distinct groups with consistent behaviour: those who rarely include payoff information in their requests, and those who do this in the majority of cases (Figure 5.2b).

Consistency of social learning strategies

For each of the four contexts, we categorised subjects' reliance on social learning as low or high, when they requested social information in less or more than 25% of the cases, respectively. This cut-off point divided the data in two roughly equal portions for each context (cf. Figure 5.2a). Individuals were significantly more consistent in their reliance on social information (i.e. either categorised as ‘high’ or as ‘low’ in all contexts) than expected based on independence between contexts (Figure 5.3a). Subjects showed a similar consistency with regard to the type of social information they relied on; many of them either strongly relied on payoff-information across all contexts (Figure 5.3b, red bar), or hardly relied on payoff-information at all (Figure 5.3b, blue bar; an individual’s reliance on payoffs was categorised as ‘low’ or ‘high’, depending on whether her information requests included payoffs in less or more than 50% of the cases). The abundance of these consistent individuals was much higher than expected based on independence between contexts (subjects with consistent high and low reliance on payoffs occurring 6.13 and 2.77 times more than expected on the basis of independence, respectively; \( \chi^2 = 9.811, n = 128, \text{d.f.} = 1, P = 0.002 \), and \( \chi^2 = 7.093, n = 128, \text{d.f.} = 1, P = 0.008 \)). Another large fraction of subjects employed a specific flexible social learning strategy, with high reliance on payoffs in the (non-social) best choice context and low reliance on payoffs in the other (social) contexts – this is the social learning behaviour that one might intuitively expect (see introduction). However, these ‘sensible switchers’ are not more abundant than expected based on independence between contexts (\( \chi^2 = 0.319, n = 128, \text{d.f.} = 1, P = 0.572 \)). We did not observe significant differences between types of social learning strategies and performance in the experiment, as reflected in total earnings (Tukey contrasts on a linear model: \( n = 128, P > 0.121 \) for comparisons between the three types of social learners highlighted in Figure 5.3b).
Figure 5.2. Variation among subjects in their reliance on social information and their reliance on payoff information. a, Distribution of individuals’ reliance on social learning in decision making, measured as the fraction of decisions in which subjects chose to collect peer information. b, Distribution of individuals’ reliance on payoffs in social learning, measured as the fraction of requests for peer information that included previous payoffs. All distributions are broad and strongly overdispersed when compared to binomial expectations: individuals strongly vary in their reliance on social learning, but even more strongly so with respect to their reliance on payoff information.
Robustness and replicability

To check for the robustness and replicability of the results obtained, we conducted a follow-up experiment, sharing the same general set-up with the primary experiment, but differed in various aspects (group size was five instead of eight, individuals were allowed to view only four pieces of information per round, the payoff matrices were slightly different, the stochastic component in the payoffs was increased; see Methods for details). In general, our follow-up experiment confirmed all main results of the primary experiment. As in the primary experiment, groups approach the Nash equilibria of the one-shot version of the games in all four contexts (Figure 5.A5; see Appendix). Again, most requests were for either a combination of previous decision and associated payoffs, or for previous decisions only. In all four contexts, subjects tended to request information more often in the follow-up experiment (ANOVAs; BC: $P = 0.035$; SD: $P < 0.001$; CO: $P = 0.071$; EV: $P < 0.001$, $n = 328$ for each test). Since the stochasticity in payoffs was higher in the follow-up experiment, this finding is in line with results reported in the literature (e.g. Morgan et al., 2012; Toelch et al., 2009).

As in the primary experiment, subjects varied strongly in the extent to which they based their decisions on social information (Figure 5.A6; see Appendix). When requesting information, in-
individuals again differed substantially in the type of information they were interested in; some always included payoff information in their requests, whereas others ignored payoff information altogether. These differences among individuals were even more pronounced in the follow-up experiment than in the primary experiment.

As in our primary experiment, we find (Figure 5.A7; see Appendix) that the fraction of individuals that was consistent in their social information use is significantly larger than expected on the basis of independence ($\chi^2 = 29.551, n = 200, \text{d.f.} = 1, P < 0.001$). This is also the case for individuals’ consistency in reliance on payoffs ($\chi^2 = 13.673, n = 200, \text{d.f.} = 1, P < 0.001$). In other words, as in our primary experiment, many individuals were consistent in either strongly or weakly relying on social information, and many individuals were consistent in the type of social information they requested.

**Implications of individual variation for cultural evolution**

Our experimental results indicate that there are strong and consistent individual differences in social learning strategies. But does this individual variation matter? To address this question, we developed a simple model of cultural evolution in which individuals interact in small groups and are allowed to update their behaviour by either payoff-based learning or frequency-based learning. We imposed two conditions: a homogeneous population, in which all individuals updated their strategy by payoff-based learning or frequency-based learning with a 50-50 probability, and a heterogeneous population, in which half of the individuals in a group always updated based on payoffs, and the other half always updated based on frequencies. In our simulations, we documented the fixation probability of behaviour A or B after the introduction of a single B mutant in a population of A players. Figure 5.4 shows the outcome of simulations after an average of 20 updates per individual (in correspondence to the number of rounds in the experiments).

In three out of four contexts, the existence of individual variation in social learning strategies considerably affects the outcome of cultural evolution. In the coordination game, payoff-based and frequency-based learning both disfavour the spread of rare behaviours, so B will be rapidly lost both in homogeneous and heterogeneous populations. In the best choice context, a newly introduced superior technology (B) is more likely to reach fixation in heterogeneous populations; payoff-based learners readily adopt B, and the increase in frequency of B reduces the risk that the superior technology disappears due to frequency-based learning or stochastic processes (e.g. copying errors). The same logic applies to the social dilemma: a newly introduced ‘cheater’ mutant will obtain higher payoffs, and payoff-based learners in a heterogeneous population will readily switch to defection; once cooperators are no longer in the majority, conformists start defecting, and cooperation is lost. In the evasion game, variation in social learning strategies enhances the stability of the coexistence of A and B. When assuming the same noise on payoffs as in the primary experiment, the mean time until fixation of either behaviour is increased by 50% in groups that are heterogeneous with respect to social learning strategies, compared to homogenous groups.
When payoffs are less noisy the strength of this effect increases, further stabilising the coexistence of different behaviours. Interestingly, in heterogeneous populations, social learning strategies become correlated with behaviour in this game (playing A or B; see Figure 5.A8, and Appendix section 2 for model details and additional model analyses). The emerging role differentiation can thus increase average payoffs in a group.

Cross-cultural experiments have established that human social behaviour strongly varies between cultures (Henrich et al., 2001; Herrmann et al., 2008). This suggests that the behaviour of typical ('WEIRD'; Henrich et al., 2010) participants in decision making experiments is likely to underestimate the variation present in the human population. Our experiment shows that even within such a relatively homogeneous sample of subjects there is strong and consistent variation in the way people behave. The pronounced individual differences in social learning strategies we report emphasize that the average behaviour in a group or population is far from representative for the behaviour of its constituent individuals. Furthermore, our simulation model suggests that individual variation can affect the dynamics and outcome of social interactions. Although individual differences have been at the heart of personality research in psychology (e.g., John et al., 2010), they are often disregarded in many other areas of the social sciences. Our results strongly suggest that individual differences need to be taken seriously, both in theoretical models and in

**Figure 5.4. Effect of diversity in social learning strategies on the outcome of cultural evolution.** For each of the four contexts, we simulated groups of eight individuals that were allowed to update their behaviour using payoff-based or conformist learning (tendencies to copy either successful or popular behaviour, respectively). Pairs of bars present the state of the groups after 160 iterations (corresponding to the 20 rounds of our experiments) when initialised with one B player in a group of A players (10^5 replicates each). The top row of bars shows the outcome in homogeneous groups, where each individual uses either form of learning with equal probability. The bottom row of bars shows the outcome in case of heterogeneous groups, where four individuals always use payoff-based learning, while the four others always use conformist learning. Individual variation can cause groups to adopt superior technologies (option B) more readily in a best choice context, but cooperation (option A) tends to be less stable in a social dilemma. Moreover, in heterogeneous groups, A and B coexist more stably in an evasion game.

**DISCUSSION**

Cross-cultural experiments have established that human social behaviour strongly varies between cultures (Henrich et al., 2001; Herrmann et al., 2008). This suggests that the behaviour of typical ('WEIRD'; Henrich et al., 2010) participants in decision making experiments is likely to underestimate the variation present in the human population. Our experiment shows that even within such a relatively homogeneous sample of subjects there is strong and consistent variation in the way people behave. The pronounced individual differences in social learning strategies we report emphasize that the average behaviour in a group or population is far from representative for the behaviour of its constituent individuals. Furthermore, our simulation model suggests that individual variation can affect the dynamics and outcome of social interactions. Although individual differences have been at the heart of personality research in psychology (e.g., John et al., 2010), they are often disregarded in many other areas of the social sciences. Our results strongly suggest that individual differences need to be taken seriously, both in theoretical models and in
the analysis of empirical data. More specifically, we advocate that models of cultural evolution take individual differences in social learning strategies into account.

In the best choice context, the availability of social information was associated with an increase in the adoption of the optimal behaviour. This is in line with earlier findings in the experimental and theoretical literature that social learning can increase an individual’s performance in non-social contexts (Boyd & Richerson, 1985; Rendell et al., 2010; Efferson et al., 2008). The way in which social information was used in this context, substantially differed between individuals, which is in agreement with earlier experimental evidence (McElreath et al., 2005; Efferson et al., 2008). Our experimental results indicate that individual variation in social learning strategies is even more pronounced in social contexts, where payoffs depend on the behaviour of others.

Of course, the results of highly stylized experimental study like ours should not be over-interpreted. Decision-making experiments in a lab setting allow for a high degree of control, but inevitably abstract from potentially important aspects of reality. Even though our experimental design imposed relatively few restrictions on how individuals could track their social environment, our study does not account for a variety of factors that play a role in real-life cultural transmission. For instance, it was impossible for subjects to bias their attention towards older, more experienced, or more dominant peers (Henrich & Broesch, 2011; Dugatkin & Godin, 1993; Duffy et al., 2009), and active teaching (Hoppitt et al., 2008) was excluded by design. Also, subjects were unable to control the accessibility of information about their own behaviour and payoffs (Mesoudi, 2008). Moreover, subjects in our experiment were informed about the general structure of the interaction contexts in which they were interacting. In reality, this structure is typically unclear and people have to base their decisions on their best guess of how their behaviours and the behaviour of others affect their payoffs. More specific to our design including different contexts, subjects in a session always encountered the simplest (non-social) best choice situation first and subsequently interacted in the other (social) contexts in random order. Some of these concerns can be addressed by additional experiments. Still, whereas laboratory experiments can unravel interesting features of human behaviour, they only present a first step: these aspects should subsequently be scrutinized under more realistic conditions.

Assuming that the individual variation found in our study is ‘real’, why should individuals differ in their learning strategies, and why should they be consistent in their use of social information across different contexts? Possible explanations can be found in the literature on ‘animal personalities’. In recent years, evidence has accumulated that consistent individual differences in behaviour (‘behavioural syndromes’ or ‘personalities’) are not only prevalent in humans, but also exist throughout the animal kingdom (Sih et al., 2004; Gosling, 2001). In the past, it has often been assumed that selection on behaviour should result in a single, optimally adapted phenotype. By studying animal personalities it has become apparent that a variety of mechanisms (reviewed in Wolf & Weissing, 2010) can lead to the evolutionary emergence of consistent individual variation in behaviour. More specific models based on this theoretical framework predict the coexistence of
alternative life history strategies (Wolf et al., 2007; Réale et al., 2010a); the coexistence of individuals differing strongly in responsiveness and social sensitivity (Wolf et al., 2008; Wolf et al., 2011); and the coexistence of different communication strategies (Botero et al., 2010). These results may serve as a useful starting point for understanding the consistent individual differences in social learning strategies observed in this study. Cognitive constraints and incomplete information on the learning context will often prevent the evolution of learning strategies that are optimal in every possible circumstance. Instead, evolution may result in the coexistence of locally suboptimal but cognitively ‘cheap’ strategies using rules-of-thumb (cf. Gigerenzer et al., 1999) such as payoff-based learning or frequency-based learning. Other mechanisms facilitating the coexistence of behavioural strategies may apply to social learning as well. For example, the benefits of information are often negatively frequency-dependent: the value of information decreases when more individuals also have this information. This immediately explains why individuals relying heavily on information coexist with others that are seemingly not interested in gathering information at all (Wolf et al., 2008). Last, but not least, the coexistence of learning strategies could be explained by ‘synergy’ between different forms of learning. As suggested by our simulation model, group heterogeneity with respect to learning strategies may under some circumstances lead to more efficient outcomes. Such synergetic effects might again induce negative frequency-dependent selection and result in the coexistence of alternative learning strategies.

Even if different learning strategies do coexist, one might expect that individuals are flexible and employ different strategies in different contexts. Again, the literature on animal personalities has revealed various mechanisms explaining a more rigid behaviour, corresponding to the consistent use of the same type of behaviour in different contexts. Behavioural consistency can be favoured when strategic conventions are establishing (McNamara & Weissing, 2010) or when behaviour serves as a signal to others. For example, already a small fraction of ‘socially responsive’ individuals in a population may exert a strong selection pressure in favour of consistency (Wolf et al., 2011). Consistency can also be supported by all kinds of positive feedbacks: individuals can increase their performance with the consistent use of a certain social learning strategy, due to an increased efficiency in the collection, interpretation and application of the kind of information as they get more experienced in using this strategy.

Rather than explaining individual variation from an evolutionary perspective, scholars of human personality have focused on characterising the structure of individual differences. This has resulted in a number of models that aim to describe human personality along a few dimensions (the ‘Five Factor Model’; Digman, 1990) being best-known example). It is not unlikely that that the observed variation in social learning strategies is associated with these dimensions or factors, and this possibility presents an interesting objective for further research. For instance, one might predict that reliance on social information is associated with openness, or with an orientation towards collectivism (as opposed to individualism; Oyserman et al., 2002); in fact, this latter association has just recently been observed by Toelch and colleagues (2014). Similarly, one might
expect that individuals that focus on payoff-information are inclined to behave more competitively (rather than cooperatively) in social interactions.

To our knowledge, there is no empirical evidence showing how social learning strategies themselves transmit between individuals. As a result, a discussion about the origin of the individual differences we report is highly speculative. In humans as well as in other animals, personality traits often have a high heritability (Bouchard Jr & Loehlin, 2001; Van Oers & Sinn, 2013). If social learning strategies are related to personalities, they might be heritable too. However, this does not mean that the environment does not affect the expression of social learning strategies. Orientations towards individualism/collectivism can shift within one generation (Hamamura, 2012), and the same could happen for social learning strategies. Such flexibility is possible even in case of a strong genetic basis, provided that the expressed learning strategy reflects a heritable norm of reaction (where the genotype determines how a trait is expressed in response to the environment (Dingemanse et al., 2010; Wolf and Weissing, 2010). An interesting alternative possibility is that social learning strategies themselves are acquired through social learning (Heyes, 2012). The behaviour of children is often strongly influenced by those that raise them, and social learning strategies may be one of their social tendencies that are shaped in this process.

Another interesting future direction would be to address whether the presence of individual differences in social learning strategies affect the dynamics of behaviour (as predicted by our simulation model). One could experimentally test this by creating groups of individuals assorted according to their social learning strategies, and comparing these homogeneous groups to un assorted (heterogeneous) groups. Another interesting question that could be tested in such a setup is whether the behavioural dynamics are different between groups that are homogeneous for different social learning strategies (such as payoff-based learning and frequency-based learning). For example, one might expect that a group of payoff-based learners may more readily adopt new superior technologies, whereas groups of frequency-based learners may be faster in reaching equilibrium in a coordination context.

**METHODS**

In eight independent sessions of our first experiment (the ‘primary experiment’), we confronted sixteen subjects \((n = 128)\) with four settings (‘contexts’). In each context, the subjects had to make choices between two options \(A\) or \(B\), but the contexts differed in the way payoffs depended on the subject’s own decision and the decisions of others. We based our design on the experimental paradigm of McElreath et al. (2005), and we extended this setup to include interactions in the three strategically different classes of games with pure strategies (Mollemann et al., 2013b), each of which has been extensively researched in the literature on the evolution of cooperation (Gintis, 2000). Each subject sequentially encountered a best choice (BC) situation where one options
(B) yields on average a higher payoff; a social dilemma (SD) where one option (A) increases the payoffs of all group members but in each situation yields a lower payoff than the other option (B) for each individual employing it; a coordination game (CO), where the payoff of each option (A or B) increases with the number of subjects employing this option; and an evasion game (EV), where the payoff of either option (A or B) decreases with the number of subject choosing this option. The best choice context corresponds to a non-social (technological) decision situation, while the other three contexts represent different types of social settings.

Decision making was formulated as planting crops on the land of an imaginary farm. In each of the twenty rounds of each interaction context, subjects could decide which of two crops they would plant on their farm (we used actual crop names, but for simplicity we will refer to the options as A and B). Payoffs were noisy, so that it would require several trials to find out which option was better (see below for details). In each round, subjects had to decide simultaneously and anonymously for one of the two options. Before making their decisions, subjects could pay a small cost to collect information about their peers. The information available about each peer included the previous decision, previous payoff, and the total payoff acquired in the current context. If a subject chose to collect information, she could freely request up to six pieces of information. For example, a subject might request all three types of information of two (out of seven) of her peers, or she might request only the previous decision of six of her peers. At the end of each round, subjects were informed about the payoff of their decision in that round. As a benchmark, we ran four control sessions with sixteen subjects each (n = 64), in which subjects could not collect social information from their peers before making their decision. Otherwise, the setup of these sessions was identical to the setup of our primary experiment. In Figure 5.A1 (see Appendix), we report on the findings of the control sessions.

To check for the replicability and robustness of the results obtained, we also conducted a second experiment (the ‘follow-up experiment’), consisting of ten sessions with 20 subjects each (n = 200). The basic setup of this follow-up experiment was the same as the primary experiment reported in the main text: we confronted participants with four interaction contexts in sequence, each consisting of a block of 20 rounds. In each round subjects made a decision between two options, and before making their decision, subjects could collect social information about their peers. However, there were a few differences with the primary experiment. First, subjects interacted in groups of five instead of eight; second, because the group size was not the same, the payoff matrices were changed (see below); third, the stochastic component of the payoffs was larger (also, see below); fourth, the maximum number of pieces of information subjects could collect in a round was limited to four, instead of six; finally, subjects could no longer request information about the total payoffs of their group members, but only about their previous decisions and previous payoffs.
Subjects, earnings and experimental details

In total, we ran 22 independent experimental sessions with \( n = 396 \) subjects. Subjects were recruited using the database of the Sociological Laboratory of the University of Groningen. Participation was by informed consent, and the experimental setup was approved by the Sociological Laboratory. Subjects (132 male, 264 female; aged 18 to 31, mean age 22) were mostly undergraduate students from the social sciences, economics and biology. Experimental sessions lasted around 90 minutes, in which subjects earned €29.60 on average according to their performance, excluding a show-up fee of €5.

Instructions were handed out in the reception room of the laboratory and read out loud by one of the experimenters. Each participant received a randomly chosen number corresponding to a desk in the laboratory. Before the experiment itself started, subjects played a test trial of five rounds, making them familiar with the decision making environment. After that, four blocks of 20 rounds were started, each presenting a different context of social interaction. At the beginning of each block of rounds, specific instructions for the upcoming interaction context were given on the computer screen, and participants had to fill out a brief quiz to check their understanding (see Supplementary Material of the original article for instructions on paper, and on-screen instructions, including screenshots). Subjects were randomly grouped, labelled with a number 1-8, and each received 3,000 points to play with (1,000 points = 1 euro). During the block of rounds subjects could make substantial profits, but subjects could also lose their initial endowment in case of negative outcomes. After a block of twenty rounds ended, new groups were formed, and subjects were informed about the payoff structure of the new context (again followed by a short quiz). Sessions finished with a questionnaire including items about personal demographic background. Participants were paid individually in the reception room. The experiment was conducted using Z-Tree (Fischbacher, 2007); code is available upon request.

Subjects were always confronted with the ‘best choice’ context first. Starting with this most simple interaction context facilitated the subjects’ understanding of the context they were in and how their decisions affected their payoffs. The three other interaction contexts – in which payoffs depended on the decisions of others – were played in randomized order. These other contexts correspond to the three different classes of games: a social dilemma, a coordination game and an evasion game.

Interaction contexts

Each of the interaction contexts was characterized by a payoff matrix \((a, b; c, d)\). This means that the deterministic component of the payoff of a subject choosing \(A\) and \(B\) was given by \(pa + (1 – p)b\) and \(pc + (1 – p)d\), respectively, where \(p\) denotes the relative frequency with which \(A\) is chosen in the group. The payoff matrices were chosen such that at \(p = 0.5\), the payoff difference between \(A\) and \(B\) was equal in each of the interaction contexts.
Payoff matrices: primary experiment

In the best choice context (BC), a subjects’ payoff did not depend on the decisions of the other subjects in their \( \binom{50}{50} \) group \( (a = b \text{ and } c = d) \); the payoff matrix was given by \( \begin{pmatrix} 50 & 50 \\ 50 & 50 \end{pmatrix} \). Irrespective of the behaviour of the other players, option B yielded higher payoffs on average. In game theoretical terms, B dominates A and therefore \( p^* = 0 \) is the Nash equilibrium of the one-shot version of the ‘game’.

In the social dilemma (SD), cooperation (A) is dominated by defection (B): \( a < c \text{ and } b < d \); the payoff matrix was given by \( \begin{pmatrix} 100 & -250 \\ -250 & 100 \end{pmatrix} \). Therefore, like in the best choice context, \( p^* = 0 \) was the Nash equilibrium of the one-shot version of the game. However, all subjects obtained a higher payoff when they all cooperated \( (p = 1) \), compared to this equilibrium \( (a > d) \). This shows that in this context, collective interests and individual interests are opposed to each other, like in the famous (two-player) Prisoner’s Dilemma game.

In the coordination game (CO), the payoff of choosing one of the two options increased with the number of others also choosing it \((a > c \text{ and } b < d)\). The payoff matrix was given by \( \begin{pmatrix} 175 & -75 \\ -75 & 175 \end{pmatrix} \). In this case, both \( p^* = 0 \) and \( p^* = 1 \) are Nash equilibria. However, the Nash equilibrium at \( p^* = 0 \) is Pareto superior; the payoff to all players was higher compared to the equilibrium at \( p^* = 1 \). There was a (dynamically unstable) equilibrium located at \( p^* = (d - b)/(a - b - c + d) \). In this equilibrium (in our case, when two subjects chose A and six subjects chose B), the expected payoffs of choosing A and choosing B were equal, but any deviation from this equilibrium leads towards either of the Nash equilibria. Typical examples of coordination games are the Stag-Hunt game and the Battle of the Sexes (Luce & Raiffa, 1957).

In the evasion game (EV), the payoff of choosing one of the two options decreased with the number of others also choosing it \((a < c \text{ and } b > d)\). The payoff matrix was given by \( \begin{pmatrix} 150 & 200 \\ 200 & 150 \end{pmatrix} \). In this case, there was a Nash equilibrium given by equation \( p^* = (d - b)/(a - b - c + d) \), where, in our case, two subjects choose A and six subjects choose B. Typical examples of evasion games are the Hawk-Dove game and the Snowdrift game (Smith & Price, 1973).

Payoff matrices, follow-up experiment

In the follow-up experiment, the interaction contexts were characterised by the following payoff matrices: best choice: \( \begin{pmatrix} 100 & 100 \\ 100 & 100 \end{pmatrix} \), social dilemma: \( \begin{pmatrix} 400 & -200 \\ -200 & 400 \end{pmatrix} \), coordination game \( \begin{pmatrix} 500 & -300 \\ -300 & 500 \end{pmatrix} \), evasion game \( \begin{pmatrix} -300 & 500 \\ 500 & -300 \end{pmatrix} \). As in the primary experiment, we chose the parameters such that at \( p = 0.5 \), the payoff differences between A and B are equal \((\text{i.e. } 200)\) in each of the interaction contexts. In the coordination game, the unstable equilibrium was situated where three players choose A and two players choose B. The Nash equilibrium of the one-shot version of the evasion game was situated where two players chose A and three chose B. All other equilibria were the same as in the primary experiment.
Noise
Payoffs were noisy, reflecting the fact that the outcome of behaviour is often influenced by exogenous factors. This noise made it harder for the subjects to find out individually which choice was optimal, and as a consequence, made social information more valuable. Noise was implemented by adding a stochastic term to the deterministic component of the payoffs of each subject separately. This stochastic component was a number drawn from a normal distribution with mean 0 and standard deviation $\sigma$.

In the primary experiment, we set $\sigma = 175$, so that at $p = 0.5$, choosing the option with the lower expected payoff nevertheless lead to a higher payoffs in 16% of the cases. In the follow-up experiment, the stochastic component on the subjects’ payoffs was relatively larger than in our primary experiment ($\sigma = 200$). This implies that at $p = 0.5$, choosing the inferior option nevertheless lead to higher payoffs in 24% of the cases.

Simulation details
Details of the model of cultural evolution can be found in the Appendix.

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Appendix

This appendix contains eight supplementary figures, and a detailed description of the simulation model.

1. SUPPLEMENTARY FIGURES

**Figure 5.A1. Decisions in the absence (top) and presence (bottom) of social information.** To investigate how the presence of social information affected behaviour, we ran control sessions in which subjects could not collect information from their peers before making their decisions. Otherwise, the setup was identical to the setup of our primary experiment. We ran four independent sessions with sixteen subjects each ($n = 64$), for a total of eight replicate groups of eight participants each. The top row of panels shows frequencies of choices for option $A$ over twenty rounds of the four interaction in four control sessions, where social information was not available (eight replicate groups in grey, averages in colour). As a reference, the bottom row of panels shows the decision data from our primary experiment (where social information was available), also presented in Figure 5.1 of the main text. Over time, groups tended to approach the Nash equilibria of the one-shot version of the games (indicated by the arrows and the dashed lines). The presence of social information led to a more rapid convergence to the superior option in the best choice context and the dominant strategy in the social dilemma; in fact, two separate binomial generalized linear mixed models (GLMM) with subject nested in group as random factor, and with ‘information present/absent x round’, ‘previous decision x previous payoff’ and ‘difference between payoffs in round $t - 1$ and $t - 2$’ as fixed factors, detected significant effects of the presence of information on the probability that an individual chooses option $B$ ($n = 3840$ decisions for each model; t-test, $P < 0.001$ and $P = 0.047$).
In line with earlier findings (Morgan et al., 2012), information request rates were negatively related to previous payoffs ($n = 9728$, t-test, $P < 0.001$), indicating that subjects tended to request social information when their current behaviour had unfavourable returns. Moreover, information request times decreased over time ($n = 9728$, t-test, $P < 0.001$), confirming the observations from Figure 5.1 of the main text. Data on previous payoffs were pooled in cohorts of 100 points to obtain the symbols reflecting request rates. Error bars represent 1 standard error of the mean (SEM). Total number of observations per context was 2432. Cohorts with fewer than five observations are not shown as a data point. P-values are based on a binomial GLMM relating the request probability to previous payoff, using ‘subject’ as random factor, and ‘round’ and ‘interaction context’ as fixed factors.

**Figure 5.A2. Information request rates as a function of individual payoff in the previous round.** In line with earlier findings (Morgan et al., 2012), information request rates were negatively related to previous payoffs ($n = 9728$, t-test, $P < 0.001$), indicating that subjects tended to request social information when their current behaviour had unfavourable returns. Moreover, information request times decreased over time ($n = 9728$, t-test, $P < 0.001$), confirming the observations from Figure 5.1 of the main text. Data on previous payoffs were pooled in cohorts of 100 points to obtain the symbols reflecting request rates. Error bars represent 1 standard error of the mean (SEM). Total number of observations per context was 2432. Cohorts with fewer than five observations are not shown as a data point. P-values are based on a binomial GLMM relating the request probability to previous payoff, using ‘subject’ as random factor, and ‘round’ and ‘interaction context’ as fixed factors.
Figure 5.A3. Effects of payoff information on switching behaviour. Panels show proportions of decisions to switch behaviour as a function of the difference in own previous payoff and the observed average payoff of the alternative option. We consider only those decisions that were preceded by requests for others’ previous decisions and previous payoffs. Open and solid symbols represent rates of switching (±1SEM) from B to A and from A to B, respectively. Payoff differences were pooled in cohorts of 200 points to obtain the data points shown (cohorts with fewer than five observations were omitted). In all cases, a subject’s probability to switch behaviour is positively associated with the difference between the payoff of another player and the subject’s own payoff. This conclusion, which is a clear indication of payoff-based learning, is based on four separate binomial GLMM (one per context) and an overarching GLMM. Each separate GLMM (where subject nested in group was treated as a random factor, while ‘round’ and ‘previous decision x previous payoff x observed payoff difference’ were entered as fixed factors) revealed a significant effect of the observed payoff difference on the probability of switching ($P < 0.001$ in BC, CO and EV, and $P = 0.023$ in SD). Similarly, the overarching GLMM (with the same error but ‘interaction context’ being added to the interaction terms) leads us to conclude that the observed payoff difference has a highly significant effect ($P < 0.001$) on switching behaviour.
Figure 5.A4. Effects of observing behaviour of group members on own behaviour. Panels show proportions of decisions (± 1SEM) for option A as a function of the observed frequency of A. Data points were pooled in cohorts of 1/6; cohorts with fewer than five observations are not shown. The solid symbols show the information requests where information about at least one decision of a group member was requested (so information about payoffs may have also been requested within the same information request). The open symbols show decisions that were preceded by requests purely for the decisions of fellow group members (so, no payoff information was requested). For each interaction context separately, we fitted binomial GLMMs to all decisions in which any decision information was requested (data corresponding to the solid symbols). In these regression models, we used ‘subject nested in group’ as random factors, and ‘round’, ‘previous payoff’ and ‘previous decision x observed frequency of A’ as fixed factors. In BC, SD and CO we find positive effects of the observed frequency of A on the probability of also choosing that option (t-tests: n = 523, \( P = 0.002 \); n = 587, \( P = 0.039 \); n = 472, \( P < 0.001 \), for BC, SD and CO, respectively). The GLMM fitted to the SD data detected a strong negative effect of ‘round’, which may explain why the slightly positive influence of observing A (cooperation) on the probability of also choosing A is not visible from the solid dots. In the evasion game, we find negative effects of the observed frequency of A on the probability to choose it (t-test: n = 722, \( P = 0.009 \)), suggesting that subjects reacted to the underlying structure of the game. For SD, CO and EV, the findings of the models were confirmed by a GLMM fitted to data in which only decision information was requested (data corresponding to the open symbols). In these cases, we observe in the SD a stronger positive influence of the observed frequency of cooperation on the probability of an individual to also cooperate (t-test: n = 175, \( P = 0.002 \)).
Figure 5.A5. Follow-up experiment: decisions and information requests in four interaction contexts. This figure corresponds to Figure 5.1 in the main text, which presents the corresponding outcomes in the primary experiment. The top row of panels shows the fraction of subjects choosing A over twenty rounds of the four contexts (40 replicate groups of five subjects in grey, averages in colour). Dashed coloured lines indicate Nash equilibria of the one-shot version of the four games. In the best choice context, dynamics were similar to the primary experiment. In the social dilemma, levels of cooperation tended to be higher than in the primary experiment, possibly due to the smaller group size. In the coordination game, a higher proportion of groups ended up at the equilibrium where all group members choose A, which is Pareto inferior to the equilibrium where all group members play B (i.e. all players would obtain higher payoffs in the latter equilibrium). This may be explained by the fact that the Pareto inferior equilibrium had a larger basin of attraction in the follow-up experiment, since the unstable internal equilibrium was closer to 0.5 than in the primary experiment. In the evasion game, groups were attracted to the internal equilibrium (as occurred in the primary experiment). The bottom row of panels shows counts of combinations of information types requested in corresponding rounds. Colours indicate specific (combinations of) information requested: only the payoff (green), only the decision (red), or both (blue). Information requests tended to decrease over time in each of the contexts. We observe that fewer decisions were based on social information in the best choice context, compared to the other interaction contexts. Also, we find that most requests were for either a combination of previous decision and associated payoffs (blue bars), or for previous decisions only (red bars). In the best choice context, requests for both decision and payoffs are the dominant type of information request. In the other contexts, most requests were for previous decisions only. These observations are in line with those from the primary experiment.
Figure 5.A6. **Follow-up experiment: social learning strategies vary between individuals.** This figure corresponds to Figure 5.2 in the main text, which presents the corresponding outcomes in the primary experiment. 

- **a,** Distribution of subjects’ reliance on social learning in decision making, measured as the fraction of decisions in which subjects chose to collect peer information. 
- **b,** Distribution of subjects’ reliance on payoffs in social learning, measured as the fraction of requests for group member information that included at least one request for previous payoffs. The strong overrepresentation of extreme strategies – some individuals always requested payoff information, and others disregard it altogether – confirms the findings our findings in the primary experiment.
Figure 5.A7. Follow-up experiment: social learning strategies tend to be consistent across contexts. This figure corresponds to Figure 5.3 in the main text, which presents the corresponding outcomes in the primary experiment. 

a. The observed fraction of individuals with consistent (high or low) reliance on social learning is significantly larger than expected on the basis of independence across contexts ($\chi^2 = 29.551, n = 200, \text{d.f.} = 1, P < 0.001$). 

b. The observed fraction of individuals with consistent reliance on payoffs is significantly larger than expected on the basis of independence ($\chi^2 = 13.673, n = 200, \text{d.f.} = 1, P < 0.001$). ‘Sensible switchers’ (that tended to rely on payoff information in the best choice context only) occur at a high frequency, but this frequency is not significantly larger than expected on the basis of independence ($\chi^2 = 2.801, n = 200, \text{d.f.} = 1, P < 0.094$). For each of the four contexts, we categorized subjects’ reliance on social learning as ‘low’ or ‘high’ (requesting information in < 25%, or > 25% of the rounds, respectively). Similarly, subjects’ reliance on payoffs in social learning was categorized as ‘low’ or ‘high’ (with < 50%, or > 50% of the requests including payoff information, respectively) for each of the contexts separately. Next, we calculated the expected percentage of consistent individuals, assuming independence of behaviour in the different contexts.
Figure 5.8. Effects of individual variation in social learning strategies on the dynamics of cultural evolution. Arrows indicate the expected direction of change due to social learning in a group of eight individuals. Individuals learn based on frequencies (white arrows) or based on payoffs (blue arrows). The top row of panels represents the possible dynamics in a group that is homogeneous with respect to social learning strategies: each individual updates its behaviour based on either frequency- or payoff-based learning with a 50-50 probability. The bottom row of panels represents the possible dynamics in a group that is heterogeneous with respect to individual social learning strategies: four individuals always learn based on frequencies, and the other four always learn based on payoffs. Closed and open circles indicate dynamically stable and unstable equilibria of the systems, respectively. See Appendix, part 2 for a detailed description of the simulation model.
2. IMPLICATIONS OF INDIVIDUAL VARIATION IN SOCIAL LEARNING STRATEGIES FOR CULTURAL EVOLUTION: DETAILS OF THE SIMULATION MODEL

Here we give more detailed information about the simulation model presented in the main text. This model is a conceptual ‘toy model’, providing a first theoretical investigation on whether individual variation in social learning strategies influences the dynamics and outcome of cultural evolution. We do not intend to make any testable predictions or accurately mimic reality. Rather, we aim to provide a proof of principle that individual differences in social learning strategies potentially have a strong effect on the outcome of cultural evolution.

For simplicity, we focus on two different kinds of learning: payoff-based learning (in which individuals tend to imitate individuals with higher payoffs) and frequency-based learning (in which individuals tend to imitate the majority of the group). In our simulations, we compare groups that are homogeneous with respect to social learning strategy (i.e. all individuals employ the same mixed learning strategy that consists of both payoff-based learning and frequency-based learning) with groups that are heterogeneous in this respect (i.e. each individual uses either only payoff-based learning or only frequency-based learning, but individuals differ with respect to which type of learning they use).

The basic structure of the model closely follows the setup of our primary experiment. We consider groups in which individuals are involved in social interactions. Individuals have a trait (A or B) that determines their behaviour in these interactions. Payoffs of A and B are \( pa + (1 - p)b \) and \( pc + (1 - p)d \), respectively, where \( p \) denotes the fraction of the group playing A. Individuals have pure strategies (either playing A or B), but their strategy can change over the course of time due to social learning.

For each of the four interaction contexts presented in Figure 5.4 of the main text, we simulated a process of cultural evolution in \( 10^5 \) replicate groups. In each of these replicates, individuals interacted in groups of eight and obtained payoffs according to the same payoff matrices as were used in the primary experiment (see Methods section of the main text). After each interaction, one individual was randomly drawn to update her strategy (see below). This cycle was repeated for 160 iterations (loosely according to the number of potential strategy updating events in the experiment, in which eight individuals could update their strategy in each of 20 rounds). At the beginning of each simulation, seven individuals played A and one played B. This setup of our simulation mimics the introduction of a deviant behaviour in a resident group of which all individuals have adopted the same behaviour. Simulations were programmed in C++ and the code is available upon request from the corresponding author.

We implemented updating of traits through social learning is such a way that individuals used the same amount of information as was allowed in the primary experiment. In the event of frequency-based learning, behavioural updating was based on the previous decisions of a sample of six group members. The behaviour was updated to the behaviour exhibited by the majority of
the sampled group members (if both behaviours were observed in equal proportions, the behaviour was not changed). For payoff-based learning, behavioural updating was based on both the previous decision and the previous payoff of a sample of three group members. The behaviour was updated to the behaviour that was associated with the highest payoff in this sample (but only if this payoff exceeded own payoff). In the simulation model, we do not allow for spontaneous switching between A and B (cf. mutation or innovation), neither do we add a stochastic component to the payoffs. These assumptions are made for simplicity. We documented the number of simulation runs that fixated for A and for B (recall that there is no spontaneous strategy switching in our model, so a fixated group cannot change anymore).

In Figure 5.A8, we illustrate how frequency- and payoff-based learning affect the expected change in the abundance of A and B in each of the four interaction contexts, in groups that are homogeneous and heterogeneous with respect to their social learning strategies. This graph aims to give insight into the dynamics that lead to the outcomes of cultural evolution presented in the panels in Figure 5.4 of the main text. In the best choice context and the social dilemma, the individually inferior behaviour A is more likely to fixate in a group in the absence of individual variation. The arrows in Figure 5.A8 offer an intuition for this result: if a payoff-learner in the heterogeneous group has adopted the individually superior behaviour B, this individual will never switch back to A. This guarantees the eventual fixation of B. However, in heterogeneous groups, fixation in A always remains possible, particularly when B is initially rare and is disfavoured by frequency-based learning. In the coordination game, there are no differences between homogeneous and heterogeneous groups in terms of the outcome of cultural evolution. This is because any learning event (payoff-based learning or frequency-based learning) will lead to choosing A, so the fixation of A is the only possible outcome.

The most striking effects of individual variation in social learning strategies occur in the evasion game. The probability of fixation of either A or B is much higher in groups that are homogeneous. Note that in the evasion game, average payoffs are higher when A and B coexist (cf. the payoff matrices in the Methods). As illustrated by the bottom right panel of Figure 5.A8, the dynamics of cultural evolution in the heterogeneous group will lead to a group composition where all frequency-based learners play B, whereas the payoff-based learners play A and B in equal proportions. When at this equilibrium, frequency-based learning events can no longer lead to the fixation of the most common strategy (B), because the only individuals that are playing A are payoff-based learners. In contrast, in a homogeneous group in which two players are playing A and six are playing B, fixation of B (through two consecutive frequency-based learning events) is still possible, and even likely to occur at some point. The emerging role differentiation in the heterogeneous group, in which all frequency-based learners play A and the payoff-based learners play A or B with equal probability, ensures that the group retains behavioural polymorphism. In this particular interaction context, individual variation in social learning strategies increases average payoffs in a group.
Focus on the success of others leads to selfish behavior

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It has often been argued that the spectacular cognitive capacities of humans are the result of selection for the ability to gather, process and use information about other people. Recent studies show that humans strongly and consistently differ in what type of social information they are interested in. While some individuals mainly attend to what the majority is doing (frequency-based learning), others focus on the success that their peers achieve with their behavior (success-based learning). Here we show that such differences in social learning have important consequences for the outcome of social interactions. We report on a decision-making experiment where individuals were first classified as frequency- and success-based learners and subsequently grouped according to their learning strategy. When confronted with a social dilemma situation, groups of frequency-based learners cooperated considerably more than groups of success-based learners. A detailed analysis of the decision-making process reveals that these differences in cooperation are a direct result of the differences in information use. Our results show that individual differences in social learning strategies are crucial for understanding social behavior.
INTRODUCTION

Acquiring information about others is a prominent feature of the human behavioral repertoire (Dunbar, 1998; Mesoudi et al., 2006; Dunbar & Schultz, 2007). Observing the behavior of others can allow individuals to improve their own knowledge and skills, but it can also be instrumental in anticipating how others will behave in future social interactions. Clues that help to predict how others will behave can allow for better coordination, or for being able to outsmart others for personal gain (Byrne & Whiten, 1988; Whiten & Byrne, 1997). Indeed, the ability to keep a mental tab about the past actions of others has been put forward as one of the main mechanisms that allowed for the evolution of cooperation in humans (Nowak & Sigmund, 1998; Wedekind & Milinski, 2000).

This focus on social information comes with a spectacular capacity to imitate. Imitation and other forms of social learning govern the spread of information between individuals and are therefore at the basis of cultural change. Indeed, it has been argued that these mechanisms of transmission underlie a process of cultural evolution, which is in many ways analogous to genetic evolution (Dawkins, 1976; Cavalli-Sforza & Feldman, 1981; Boyd & Richerson, 1985). Social learning has allowed humans to rapidly adapt to all kinds of environmental circumstances, and is ultimately responsible for the wide variety of languages, habits, forms of organization, and social norms that are found across cultures (Gintis, 2000; Boyd et al., 2011a; Mesoudi, 2011a; Whiten & Erdal, 2012). Because of this, social learning and its group-level consequences have been the object of considerable scientific scrutiny. Laboratory studies and theoretical models have gone hand in hand in respectively identifying the social learning strategies that people use (Traulsen et al., 2010; Morgan et al., 2011; Atkinsson et al., 2012; Hoppitt & Laland, 2013), and determining how these different strategies are shaped by selection (Laland, 2004; Kendal et al., 2009; Nakahashi et al., 2012) and affect the outcome of cultural evolution (Henrich, 2001; Sigmund et al., 2010; Rendell et al., 2011; Molleman et al., 2013a; Molleman et al., 2013b). The framework of cultural evolution has been successfully applied for a range of purposes, such as understanding the spread and the loss of technologies in human societies (Henrich, 2004; Henrich & Henrich, 2010) and inferring the ancestry of cultural traits such as language and political organization (Gray et al., 2009; Currie et al., 2010; Dunn et al., 2011).

Although there has been extensive focus on identifying the rules that humans use to learn from each other, the possibility that people may differ in the way they learn from others has long been ignored. Only recently, several studies (Efferson et al., 2008; Mesoudi, 2011b; Molleman et al., 2014; Toelch et al., 2014) have suggested that there is substantial individual variation in how much social information people use, and in the type of information they are interested in. Some focus on information about the success of others (paying attention to both their decisions and the associated payoffs), whereas others are only interested in the frequencies with which behaviors occur in their social group (disregarding information about the payoffs others obtained). Moreover,
individuals tend to use the same social learning strategy across different (social and non-social) contexts (Molleman et al., 2014). However, it is unclear how the focus on different types of social information might affect the outcome of social interactions.

In this study, we examine the consequences of individual variation in human social learning strategies on the outcome of cooperative interactions. For this, we conducted a decision-making experiment that consisted of two parts that took place one month apart. In Part 1, subjects were divided in groups and confronted with a number of different interaction settings. In each interaction round, they were allowed to view a limited amount of information about their peers’ previous behavior and earnings. In Part 2, we assorted the same subjects in groups based on the social learning strategies they had employed in Part 1, creating groups of success-based learners and frequency-based learners. These groups were confronted with a cooperation setting, in which each subject had to decide between a selfish option and an option that benefitted the group. We analyze the outcome of the interactions in these groups and investigate whether, and to what extent, differences in cooperation can be traced back to differences in social learning style.

RESULTS

In Part 1 of the experiment, 200 subjects were divided in groups of five and confronted with four different interaction contexts in randomized order (non-social, cooperation, coordination and evasion). In each context, they made decisions between two options for 20 consecutive interaction rounds. Each decision resulted in a payoff that depended on the interaction type, the decisions of fellow group members, and also included an element of random noise. Before making a decision, subjects were given the opportunity to view up to four ‘pieces of information’ about their fellow group members at a small cost, where one piece of information consisted of either a previous payoff or a previous decision of a fellow group member. The four interaction contexts we offered are consistent with those considered in our earlier study (Molleman et al., 2014), but here we focus on the three social contexts.

The results of Part 1 fully confirm the earlier observation that there are marked individual differences in both the amount of social information that individuals request, and the type of information they are interested in (Molleman et al., 2014). A large majority of information requests (86.7%) were of two types: individuals either requested the decisions of the four fellow group members in the previous round (henceforth referred to as frequency-information), or they requested both the decision and the payoff of two fellow group members (success-information). Figure 6.1a classifies all individuals with respect to what type of information they requested in each social context. In all contexts, we find U-shaped distributions, indicating that most subjects consistently focused on either frequency-information or success-information. Figure 6.1b demonstrates that most
Focus on success leads to selfish behavior

Chapter 6

Figure 6.1. Consistent individual differences in social learning strategies. In Part 1 of the experiment, 86.7% of all information requests fell into two categories: subjects either asked for frequency-information (i.e. the decisions of all four group members in the previous round) or they asked for success-information (i.e. the combination of decision and corresponding payoff for two group members in the previous round). (a) Classification of individuals with respect to the fraction of requests an individual targeted at success-information in Part 1 of the experiment. In each social context, the histogram reveals a U-shaped distribution: most individuals had extreme social learning strategies, either requesting mainly success-information or requesting mainly frequency-information. (b) Consistency of social learning strategies across the three social contexts in Part 1 of the experiment. For each context, individuals were classified as either focused on frequency (more than 50% of their requests used for frequency-information) or focused on success (more than 50% used for success-information). The graph depicts the 8 possible combinations of frequency- and success-focus across the three social contexts; the size of the circles indicating the number of individuals falling in each category. The individuals that were consistent over all social contexts are highlighted; consistent frequency-based learners (69) in orange and consistent success-based learners (23) in purple. 92 of the 145 subjects (63.4%) that requested information in at least one round of each social context were consistent across all three contexts. (c) Consistency in the number of information requests over time (between Part 1 and Part 2 of the experiment, summed over all social contexts) and (d) consistency in type of information requested between Part 1 and Part 2 (the fraction of information pieces requested that were used for success-information, over all social contexts). In both c and d, the size of the dots indicates number of individuals (the smallest dots representing single individuals), and the red lines represent linear regressions (in both cases, $R^2 = 0.454, P < 0.001$).
subjects were also consistent across the different contexts; almost two thirds of individuals always focused on the same type of information in all three social contexts.

In Part 2, 160 of the subjects that had participated in Part 1 were assorted in groups of five based on their social learning strategies, resulting in 16 groups of frequency-based learners, 8 groups of success-based learners, and 8 mixed groups (consisting of individuals with varying social learning strategies) as a control. These groups were confronted with the same interaction settings as in Part 1, again for 20 consecutive rounds, but the settings were presented in a different way (see Materials and Methods for details). Figure 6.1c and 6.1d show that individual information use was strongly correlated between Part 1 and Part 2. Subjects were consistent in both the extent to which they requested social information (Figure 6.1c) and the type of information that they focused on (Figure 6.1d). Apparently, subjects stuck to their social learning strategy for the one-month period separating Parts 1 and 2. In conclusion, the experiment provides independent confirmation for individual variation in social learning strategies and their consistency across different contexts, and it suggests that these differences are stable over longer time periods.

Here we provide a detailed analysis of the effect of group assortment with respect to social learning on the subjects’ behavior in the cooperation setting (see Appendix Figure 6.A1 for the two other types of social interaction). The cooperation setting was a social dilemma; a situation in which individuals have to choose between their own interest (defection) and the interest of the group they are in (cooperation). In our experiment, cooperation raised the payoffs of all fellow group members, but came at a cost to the cooperating individual. Accordingly, it is advantageous to be in a group of cooperators, but defection is associated with an individually higher payoff irrespective of the behavior of the others. Also in this part, there was some random noise added to each payoff, so that it could occur that cooperation paid off better than defection (see Materials and Methods for details).

As shown in Figure 6.2, the group composition with regard to learning strategy had a systematic and significant effect on the level of cooperation achieved in the group (One-way ANOVA, $F = 4.772, P = 0.016$). Particularly, cooperation levels were significantly higher in groups of frequency-based learners than in groups of success-based learners (Tukey-Kramer test, $P = 0.013$), while cooperation levels in mixed groups (mostly composed of individuals with inconsistent learning strategies) were intermediate. Due to the higher cooperation levels, average payoffs were significantly higher in groups of frequency-based learners than in groups of success-based learners (One-way ANOVA, $F = 5.083, P = 0.013$; Tukey-Kramer test: $P = 0.014$). These results strongly suggest that differences in social learning strategies affect the outcome of social interactions.

How do the observed differences in cooperation level arise? One possibility is that frequency-based learners simply have a stronger tendency to cooperate. Our data do not support this: in the first round of the interaction, when decisions were not yet influenced by social information, cooperation levels did not differ between frequency-based learners and success-based learners (respectively 0.362±0.054 and 0.350±0.076; Fisher’s exact test, $P = 0.839$). Another possibility is
that the different cooperation levels are the direct result of the different social learning strategies. To investigate this in more detail, we zoom in on how different types of social information affect subsequent behavior.

Figure 6.3a shows how subjects behaved after viewing success-information (both the decisions and the payoffs of two fellow group members in the previous round). Subjects were most likely to switch behavior (from cooperation to defection or vice versa) if they observed that others achieved substantially higher payoffs with the opposite behavior. Interestingly, this effect was equally strong for subjects that defected in the previous round and subjects that cooperated. In addition, subjects were generally conservative; if the observed payoff difference in favor of the other behavior was small, they tended not to change their behavior. Apart from this tendency to conservatism, the observed patterns are consistent with success-based learning as it is often implemented in models of cultural evolution (Henrich, 2001; Molleman et al., 2013a).

Figure 6.3b illustrates how subjects behaved after viewing frequency-information (the decisions of their four fellow group members in the previous round). In this case, the response to information was strongly affected by an individual’s own previous behavior. After having defected in the previous round, subjects were relatively likely to switch to cooperation (35% of the cases). Interestingly, this switching rate did not depend on the social information they just viewed; it was the same irrespective of the number of fellow group members that cooperated in the previous round.

**Figure 6.2.** Groups of frequency-based learners achieved higher levels of cooperation than groups of success-based learners. Bars show average cooperation rates (± 1 SEM) over all rounds of the social dilemma context in Part 2. Data are based on 16 groups of frequency-based learners, 8 mixed groups and 8 groups of success-based learners. The $P$-value shown in the graph refers to a Tukey-Kramer test.
In contrast, subjects who had cooperated in the previous round were responsive to the information they received. The more cooperators they observed among their fellow group members, the more likely they were to continue cooperating themselves. Although this latter pattern has an element of conformism, frequency-based learning as observed in our experiment is quite distinct from conformism as it is generally represented in models of cultural evolution (Boyd & Richerson, 1985; Molleman et al., 2013a; Molleman et al., 2013b). In such models, conformism is typically modelled by a symmetric S-shaped function indicating that copying a behavior becomes disproportionally more likely the more common the behavior is in the population, causing the common behavior to become even more common over time.

Could the differences in cooperation level between groups of frequency-based learners and groups of success-based learners (as shown in Figure 6.2) be fully explained by the response patterns to both types of information (Figure 6.3)? To investigate this, we implemented simplified cartoon versions of the observed learning strategies in a simulation model. In the simulations,
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we used the same payoff functions (and payoff noise level) as in the experiment, and assumed that individuals are equally likely to request information as observed in the experiment. The probability of cooperating after not requesting information was also parameterized from our experimental observations. As illustrated in Figure 6.4, the differences in social learning rules can indeed account for the observed differences in cooperation.

**DISCUSSION**

The results of our study can be summarized in three main points. First, our study confirms with an independent experiment that individuals differ systematically and consistently in their social learning strategies. Second, we show for the first time that the differences in learning strategies are stable over a longer time period, much like aspects of personality. Third, we demonstrate that individual differences in social learning strategies can strongly affect the outcome of social
interactions. In particular, groups of success-based learners reach lower levels of cooperation than groups of frequency-based learners.

Our experiment was designed to investigate the effect of social learning strategies on the outcome of social interactions. Accordingly, we consider the finding that the cooperation level achieved in groups of success-based learners is considerably lower than cooperation in frequency-based learners the main result of this study. There were no differences in cooperation between frequency-based learners and success-based learners levels in the first interaction round. This suggests that the diverging cooperation levels do not result from differences in general cooperation tendencies, but are a direct result of how the learning strategies affect behavior. This is also supported by our simulation model. Intuitively, the effect of an individual’s social learning strategy on their cooperative behavior can be understood as follows. In a social dilemma, defection yields individually higher payoffs than cooperation, so success-based learning is likely to lead to low levels of cooperation. Frequency-based learners are not as focused on information about payoffs and are therefore less inclined to adopt the individually better-paying option (in this case, defection). Additionally, high levels of cooperation can be sustained by a positive feedback in groups of frequency-based learners: the more fellow group members are observed to cooperate, the higher the inclination of individuals to continue cooperation themselves.

Although this was not the main focus of our study, we provide strong support for our earlier finding (Molleman et al., 2014) that humans differ consistently in their social learning strategies. On purpose, we modified the set-up of our experiment in several ways from that of our earlier study: groups were smaller, payoffs and information cost were different, the degree of random noise on payoffs was higher, and subjects were allowed to request fewer pieces of information. Despite these differences, the vast majority of subjects in both studies consistently used one of two social learning strategies, irrespective of the social context. This strongly suggests that individual differences in social learning strategies are a robust phenomenon. This conclusion is further strengthened by the finding that the subjects of the present study tended to use the same learning strategy in Part 2 of the experiment as in Part 1. In other words, differences in social learning strategy seem to be stable over time, at least over a period of one month. Model studies suggest that such time-stability can have important implications, e.g. for signaling intentions and for coordinating behavior within groups (Wolf & Weissing, 2010; McNamara & Leimar, 2010; Wolf et al., 2011; Wolf & Weissing, 2012). Yet, such time-stability is rarely investigated in experimental studies. Our study is a first step, but experiments spanning a longer time period and specifically designed to study time-stability are required to really judge the stability of differences in social learning strategies.

The finding that individuals differ systematically and consistently in their learning strategies has important implications for the design and interpretation of empirical studies, irrespective of whether they are conducted in the lab or the field. For example, an interesting recent study on social learning strategies in a social dilemma in 14 Indian villages neither found support for
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Conformism, nor for success-based learning (Lamba, 2014). This conclusion is based on statistical analyses (one to test for the use of conformist learning, and one to test for the use of success-based learning) that implicitly assume that the population is homogeneous with regard to social learning strategies. However, even if neither conformism nor success-based learning can be detected at the aggregate level, it is well possible that the population is heterogeneous, harboring significant variation in social learning strategies.

The idea that humans differ fundamentally in the way they gather information was already suggested by Jung (1971), but has received relatively little attention in modern systems of personality categorization such as the Five Factor Model (Digman, 1990; McCrae & John, 1992). This may be an important shortcoming; if individuals differ systematically in the way they collect, interpret and respond to information, they will also differ systematically in their behavior. This insight can have important implications for the interpretation of individual differences. Observed behavioral variation need not reflect differences in mental, physiological, or motivational states, but may instead result from differences in social learning strategies. Experimental studies designed to distinguish between these potential causes can help provide proximate explanations of how consistent individual differences in behavior come about.

From where do individual differences in social learning strategies originate? Recent evidence suggests that social learning strategies are at least partially culturally determined (Mesoudi et al., 2015), but this does not explain the variation in social learning strategies found in the culturally homogeneous sample in this study. Are these differences perhaps ‘adaptive’; have they been shaped by evolution? Such questions currently play a central role in animal behavior studies (Wolf et al., 2007; Wolf & Weissing, 2010), where consistent individual differences have been described in hundreds of species across the entire animal kingdom (Gosling, 2001; Sih et al., 2004). Theoretical studies show that individual differences in social responsiveness (or ‘social sensitivity’) can arise through frequency-dependent selection, leading to the stable coexistence of responsive types (that condition their behavior on social information) and unresponsive types (that do not use social information) (Wolf et al., 2008). Differences in social learning strategies may also be the result of evolution; modelling studies could elucidate whether and how evolution could lead to this outcome.

In the cooperation setting investigated in our study, groups of frequency-based learners achieved higher payoffs than groups of success-based learners. If frequency-based learning generally leads to superior payoffs, how can we explain that success-based learning still occurs in a social dilemma? This may be an ill-posed question. The fact that individuals consistently employ the same social learning strategy in different social contexts suggests that learning rules have not been tailored to perform optimally in every single context. This is in line with the view that evolution does not produce perfect behavior for every circumstance, but rather leads to the emergence of general-purpose strategies, or heuristics, that perform relatively well across the whole range of circumstances that an organism may face (Gigerenzer et al., 1999; Fawcett et
al., 2014). It is conceivable that frequency-based learning is superior under some circumstances, while success-based learning is superior under other circumstances. Moreover, learning strategies might complement each other, leading to a faster spread of insights and technologies in groups harboring different learning strategies (Molleman et al., 2014).

The link between frequency-based learning and cooperation has received quite some attention in the literature around the topic of ‘cultural group selection’. This literature discusses the spread of cooperation through competition between groups, when individuals use conformist learning: the disproportional tendency to copy the majority behavior. Since this type of frequency-based learning reduces variation within groups relative to variation between groups, it makes selection between groups more effective. Some argue that this increases the scope for the cultural evolution of group-beneficial traits (Boyd & Richerson, 1985; Henrich & Boyd, 1998; Boyd et al., 2003; Guzmán et al., 2007; Scheuring, 2009; Boyd et al., 2011b). However, conformism is neutral with regard to behavioral content – it makes it very difficult for any behavior, including cooperation, to spread when initially rare (Molleman et al., 2013a; Lehmann et al., 2008). Our experiment does not consider competition between groups, but measures the consequences of different learning strategies for the spread of cooperation within groups. Although many of our subjects used frequency-based learning, it was quite distinct from conformism as it is often modeled. In fact, the frequency-based learning we observed did not reduce variation within groups; it led to intermediate levels of cooperation. Also, our results suggest that frequency-based learning in a social dilemma is not neutral with respect to behavior; subjects that defected in the previous round responded to information differently from those who cooperated. It would be interesting to develop models of cultural group selection including individual differences in social learning strategies and more refined versions of frequency-based learning (as observed in our experiment). Such models may help explain both the evolutionary stability of cooperation due to cultural group selection, and the spread of cooperation when initially rare.

**MATERIALS AND METHODS**

A total of 200 subjects (mostly students, mean age: 22.9, 68.5% female) participated in the study in a laboratory at the University of Groningen. Part 1 and Part 2 consisted of respectively ten and eight sessions of 20 subjects each. In both parts, subjects were confronted with four interaction contexts (in random order) of 20 rounds each, in groups of five. At the start of each session, subjects received written general instructions that were also read aloud by the experimenters. Before each interaction context, groups were reshuffled randomly, and subjects received specific instructions on their computer screens (see the Supplementary Information of the original article for screen shots and the general instructions of both parts). After this, subjects completed a short questionnaire to ensure they had understood the payoff-structure of the following context. In
Part 1, decision-making was framed in a context of a choice between planting different crops on a farm. In Part 2, the context of decision-making was framed as investment choices in a stock market. The basic payoff structures of the contexts were the same between both parts, but the payoffs, noise on payoffs, and information cost in Part 2 were scaled with a factor 1.5 compared to Part 1 (here, values for Part 1 are given). Subjects were not aware of the identity of their group members, and were unable to see the computer screens of other participants. The experiment was run with the experimental software z-Tree (Fischbacher, 2007; code available upon request).

In each context, subjects decided between two options that remained the same in all rounds of that context (we used actual crop names (Part 1) and fictitious company names (Part 2), but here we will refer to the options as A and B). All subjects made their choice simultaneously, and were then shown the resulting payoff. Before each decision, subjects could choose to collect information about the members of their group, at a cost of 2 points. At the end of Part 2, subjects were paid in private proportional to the payoffs they had accumulated over both parts (100 points = 1 euro; mean earnings of subjects that participated in both parts: € 69.93; max earnings: € 94.30; min earnings € 50.40). We ensured that participants could not end with a negative point total, by giving them a large enough endowment at the start of the experiment. Sessions lasted for approximately 90 minutes.

In the social dilemma (see Appendix for other contexts), payoffs of choosing respectively A and B in Part 1 were given by \( \pi_A = 40p - 20(1-p) + \epsilon \) and \( \pi_B = 60p + \epsilon \), where \( p \) denotes the fraction of subjects in the group that chose option A, and \( \epsilon \) is a stochastic component, drawn from a normal distribution with mean 0 and standard deviation \( \sigma \) (\( \sigma = 20 \)). The one-shot version of this game has a single Nash equilibrium at \( p^* = 0 \), even though all subjects obtain a higher payoff at \( p = 1 \). This shows that collective interests and individual interests are opposed to each other in this context.

Simulations were programmed in C++ (code available upon request). We tracked the cultural evolution of cooperation through 20 rounds for groups consisting either of only frequency-based learners or only payoff-based learners. In each round, individuals received payoffs for cooperation and defection as in the experiment (including noise on payoffs). Individuals used social information with a 36% probability (as in the experiment). If they did not request information, they had a 63% or 16% probability to cooperate, depending on whether they cooperated or defected in the previous round (as in the experiment). If they did request information, the probability of cooperation was determined by the logistic regressions shown in Figure 6.3. Success-based learners viewed two randomly chosen peers – if both these individuals had the same behavior as the focal individual in the previous round, the focal individual was assumed to stay with their previous behavior (with a probability of 1% to switch).
ACKNOWLEDGEMENTS

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Appendix

This appendix contains two supplementary figures and a detailed description of the interaction contexts considered in this study.

1. SUPPLEMENTARY FIGURES

Figure 6.A1. Decisions over time in Part 2 of the experiment. Panels show the fraction of decisions that were made for option A in all social contexts, for all three types of assorted groups. Replicate groups are shown in grey (8 in the case of success-learners and control, 16 in the case of frequency-learners), colored lines show averages. In case of the social dilemma and the evasion game, the dotted line indicates the Nash-equilibrium of the one-shot version of the game; in case of the coordination game, it indicates the unstable internal equilibrium.
2. INTERACTION CONTEXTS

The basic payoff structures of the contexts were the same between both parts, but the payoffs, noise on payoffs, and information cost in Part 2 were scaled with a factor 1.5 compared to Part 1 (here, values for Part 1 are given). In each interaction context, payoffs of choosing respectively A and B were given by $\pi_A = pa - (1 - p) b + \varepsilon$ and $\pi_B = pc - (1 - p) d + \varepsilon$, where $p$ denotes the fraction of subjects in the group that chose option A, parameters $a$, $b$, $c$, and $d$ determine the structure.

Figure 6.A2. Non-pooled data for the response to social information. Both the top row and the bottom row correspond to Figure 6.3 from the main text, but contain only data from Part 1 and Part 2, respectively. Graphs show probability of cooperation after viewing success-information (a and c) and frequency-information (b and d).
of the interaction context, and $\varepsilon$ is a stochastic component, drawn from a normal distribution with mean 0 and standard deviation $\sigma$ ($\sigma = 20$). The stochastic component reflects the fact that the outcome of behavior is often influenced by exogenous factors, and made it harder for the subjects to find out individually which choice was optimal, and as a consequence, made social information more valuable.

The four interaction contexts can be described as follows. In the non-social context, payoffs did not depend on the behavior of fellow group members ($a = b = 10$ and $c = d = 30$). In game theoretical terms, $B$ dominates $A$ in this situation, and is the Nash equilibrium of the one-shot version of the ‘game’ (technically, it is not a game, since the payoffs do not depend on the actions of others). In the social dilemma context, cooperation ($A$) is dominated by defection ($B$): $a = 40 < c = 60$ and $b = −20 < d = 0$. Also in this case, there is a single Nash equilibrium at $p^* = 0$ - even though all subjects obtain a higher payoff at $p = 1$. This shows that in this context, collective interests and individual interests are opposed to each other, like in the famous (two-player) Prisoner’s Dilemma game. In the coordination game, the payoff of choosing one of the two options increased with the number of others also choosing it ($a = 50 > c = −30$ and $b = −30 < d = 90$). In this case, both $p^* = 0$ and $p^* = 1$ are Nash equilibria. However, the Nash equilibrium at $p^* = 0$ is Pareto superior; the payoff to all players is higher compared to the equilibrium at $p^* = 1$. There is a (dynamically unstable) equilibrium located at $p^* = (d – b)/(a – b – c + d) = 0.6$. In this equilibrium (in the experiment, when three subjects chose $A$ and two subjects chose $B$), the expected payoffs of choosing $A$ and choosing $B$ were equal, but any deviation from this equilibrium leads towards either of the Nash equilibria. In the evasion game, the payoff of choosing one of the two options decreased with the number of others also choosing it ($a = −30 < c = 90$ and $b = 50 > d = −30$). In this case, there was a Nash equilibrium at $p^* = (d – b)/(a – b – c + d) = 0.4$ (when two subjects choose $A$ and three choose $B$).

The reason for the different presentation of the decision context and differently scaled payoff matrices between Part 1 and Part 2 was to get a more robust measure of consistency. If we would have offered exactly the same games, subjects may only be consistent because they remember the exact same contexts from Part 1, and fall back on routine play.
Human cooperation in groups: variation begets variation

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Lucas Molleman
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Franz J. Weissing

Many experiments on human cooperation have revealed that individuals differ systematically in their tendency to cooperate with others. It has also been shown that individuals condition their behaviour on the overall cooperation level of their peers. Yet, little is known about how individuals respond to heterogeneity in cooperativeness in their neighbourhood. Here, we present an experimental study investigating whether and how people respond to heterogeneous behaviour in a public goods game. We find that a large majority of subjects does respond to heterogeneity in their group, but they respond in quite different ways. Most subjects contribute less to the public good when the contributions of their peers are more heterogeneous, but a substantial fraction of individuals consistently contributes more in this case. In addition, we find that individuals that respond positively to heterogeneity have a higher general cooperation tendency. The finding that social responsiveness occurs in different forms and is correlated with cooperativeness may have important implications for the outcome of cooperative interactions.
INTRODUCTION

Scientists of various disciplines have since long been interested in cooperation (Bornstein, 2003; Dietz et al., 2003; Molleman et al., 2013a; Van den Berg & Weissing, 2015a). For biologists, it is a major challenge to explain why natural selection sometimes favours behaviour that benefits other individuals (cooperation), especially when it is costly to perform (Hamilton, 1964; Axelrod & Hamilton, 1981; Lehmann & Keller, 2006; West et al., 2007). The biological world is rife with examples of such behaviour (from birds and social insects to bacteria), and humans are no exception. In fact, human cooperation is in many ways more extreme than cooperation in most other animal species: we cooperate with non-related strangers and on enormous scales (Henrich et al., 2001; Fehr & Fischbacher, 2003; Warneken & Tomasello, 2009). Not surprisingly, scholars from the social sciences also have a long tradition in studying cooperation (Messick & McClintock, 1968; Kuhlman & Marshello, 1975; Charness & Rabin, 2002; Smeesters et al., 2003; Levitt & List, 2007).

Studies using a range of methods have consistently shown that there is considerable individual variation in human cooperative behaviour. This is true for the general propensity to cooperate (cooperation tendency) (Messick & McClintock, 1968; Kuhlman & Marshello, 1975; Smeesters et al., 2003; Balliet et al., 2009), but also for the ways people condition their cooperation on the cooperation of others (cooperation strategy) (Fischbacher et al., 2001; 2012; Kurzban & Houser, 2005; Van den Berg et al., 2015). Importantly, the presence of those individual differences can significantly impact the outcomes of cooperative interactions in groups (Kurzban & Houser, 2005; de Oliveira et al., 2014). Recent theoretical studies have shown that the presence of even small amounts of variation in cooperative behaviour can be decisive for the evolution of cooperation (Mcnamara et al., 2008; McNamara & Leimar, 2010; Wolf & Weissing, 2012; Wolf & Krause, 2014). Interestingly, also environmental variation in cooperation has been found to favour cooperative and forgiving strategies (Bendor et al., 1991; Wu & Axelrod, 1995; McNamara et al., 2004; Hruschka & Henrich, 2006). The success of cooperative and forgiving strategies in the presence of environmental variation stems from their ability to uphold profitable interactions even when partners mistakenly fail to cooperate, or when a cooperative act is mistakenly perceived as defection.

Given the prevalence of individual differences in cooperative behaviour, and the importance of variation for determining outcomes of cooperative interactions, it is surprising that little is known about how people condition their own cooperation on variation in cooperative behaviour in their social group. In studies designed to assess individuals’ cooperation strategies, response to heterogeneity is often disregarded. Many of these studies are based on the public goods game (PGG), where individuals are grouped and endowed with a sum of money, and then have to decide how much of the money to contribute to an account that benefits all members of their group. In this set-up, the total earnings of the group increase with increasing group member contributions, but individuals maximize their earnings by contributing nothing. To get an idea of the cooperation strategies employed by different individuals, subjects are asked how much they would contribute
given various hypothetical average contribution levels of their fellow group members (Fischbacher et al., 2001; Fischbacher & Gächter, 2010). Such studies generally find that a large proportion of individuals is willing to contribute about equally much (or slightly less) as the average contribution of their fellow group members (they are often classified as ‘conditional cooperators’); others contribute nothing, regardless of the average peer contribution (‘free-riders’); still others contribute most when the average cooperation level of their interaction partners is intermediate.

One might expect that people take this variation in cooperation strategies into account when making decisions on their own degree of cooperation. In fact, some studies (Croson, 2007; Cheung, 2013; Hartig et al., 2015) have reported that, on average, individuals tend to reduce their contribution to a public good if the contributions of their peers are more heterogeneous. However, it is not clear how this effect arises. Does the response to heterogeneity reflect a specific conditional strategy or a more general cautiousness in a variable environment? Do all individuals respond to heterogeneity in the same way, or are there consistent differences between individuals? If there are differences, how are they related to general cooperation tendency?

To answer these questions, we conducted an experiment that consisted of two parts. In the first part, subjects played ten rounds of a PGG in groups of four, where group composition changed in every round. In each round, subjects decided how to distribute an endowment of 20 points between their personal account and an account that benefitted all group members (see Methods for details). We interpret the average contribution of a subject to the group project in these ten rounds as a measure of the subject’s general ‘cooperation tendency’. In the second part, the same individuals decided how much they would contribute in a PGG, for ten hypothetical scenarios concerning the contributions of their fellow group members. In these scenarios, the hypothetical group member contributions were always either 0, 10 or 20 points, yielding a total of ten possible combinations of peer contributions. Six of these ten combinations were pairs of cases within which the average contribution of fellow group members was the same, but their heterogeneity was different. Comparing subjects’ conditional contributions between these scenarios allowed us to investigate how subjects respond to heterogeneity in peer contributions.

RESULTS

Figure 7.1 shows a detailed breakdown of the conditional contributions made in the second part of the experiment, for each combination of peer contributions. Overall, response contributions increased with peer contributions. If all fellow group members contributed nothing (leftmost bar), 95% of individuals also contributed nothing in response. Conversely, if all fellow group members contributed the maximum (rightmost bar), 72% of subjects also contributed the maximum in response. The grouped bars show pairs of scenarios where the average contribution of fellow group members is the same, but the heterogeneity in contributions differs. For example, the
two middle bars (the 5th and 6th bar) show two cases where the average contribution is 10, but where the contributions are either heterogeneous (0, 10 and 20; bar 5) or homogeneous (three times 10; bar 6). From now on, we will focus on these pairs of scenarios. For all three pairs, Table 7.1 systematically compares the low- and the high-heterogeneity case concerning the average contribution of the subjects, the standard deviation of these contributions, and the frequency of extreme contributions (both minimum and maximum).

On average, individuals tended to contribute less when there was more heterogeneity in peer contributions (linear mixed model with subject as random factor, $P < 0.001$; see Appendix, section 3 for a detailed overview of statistical methods). This is in accordance with earlier studies (Croson, 2007; Cheung, 2013; Hartig et al., 2015). In addition, we observe that in two of the three comparisons the variation in response contributions was higher in case of more heterogeneity in peer contributions (for averages 10 and 13.33, Brown-Forsythe test: $P < 0.001$; for average 6.67, Brown-Forsythe test: $P = 0.733$). Finally, subjects were more likely to make extreme contributions when there was more heterogeneity in peer contributions – this was the case for both contributing the minimal amount 0 (logistic generalized mixed model with subject as a random factor,
Generally speaking, more heterogeneity in peer contributions caused subjects to make more extreme contributions themselves. Figure 7.2 reveals that individuals responded to heterogeneity in different ways. We classified subjects by comparing their contributions within each of the three pairs of scenarios that had the same average peer contribution, but different heterogeneity in peer contributions. If they contributed more in the cases with more heterogeneity, they were classified as ‘positive’ responders to heterogeneity. If they contributed less, they were classified as ‘negative’ responders to heterogeneity. If they contributed equally within all three comparisons, they were classified as ‘neutral’ responders to heterogeneity. If they contributed less in some of the cases and more in others, they were classified as ‘inconsistent’.

\( P = 0.001 \) and the maximal amount 20 \( P < 0.001 \). Generally speaking, more heterogeneity in peer contributions caused subjects to make more extreme contributions themselves.

Figure 7.2. Response to heterogeneity in peer contributions. The bar shows a breakdown of subjects in how they responded to increased heterogeneity in peer contributions. We considered the three cases where the average of peer contributions was the same, but heterogeneity in peer contributions was different (grouped bars in Figure 7.1). Subjects that contributed less when there was more heterogeneity in peer contributions in at least one of those cases, and never contributed more, were categorised as ‘negative’ responders to heterogeneity. Whether they contributed less in response to increasing heterogeneity in one, two, or all three cases is indicated with increasingly darker shading. ‘Positive’ responders to heterogeneity were classified similarly. If individuals contributed exactly the same for high and low heterogeneity in all three cases, they were classified as ‘neutral’ responders to heterogeneity. If individuals contributed less in some of the cases and more in others, they were classified as ‘inconsistent’.

Figure 7.3 shows that there is a clear relation between the response to heterogeneity as measured in the second part of the experiment, and the general tendency to cooperate as determined in the first part. Specifically, average contributions in the first part were 72% higher for individuals that responded positively to heterogeneity when compared to individuals that responded negatively; individuals that had a neutral or inconsistent response to heterogeneity were in between. This association cannot be explained by ‘spill-over’ effects (Fischbacher et al., 2001) between the
Table 7.1. Contribution to the group project in response to peer contributions differing in their mean and heterogeneity. The table shows averages, standard deviations, and percentage of minimum and maximum contributions (respectively 0 and 20). In each row, two situations are compared where the peer contributions were equal on average, but differed in heterogeneity (see Fig. 7.1).

<table>
<thead>
<tr>
<th>Peer contributions mean</th>
<th>Heterogeneity</th>
<th>Mean</th>
<th>S.D.</th>
<th>% min</th>
<th>% Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>6.67</td>
<td>low</td>
<td>4.32</td>
<td>4.61</td>
<td>41.7</td>
<td>0.5</td>
</tr>
<tr>
<td></td>
<td>high</td>
<td>3.74</td>
<td>5.07</td>
<td>53.2</td>
<td>1.8</td>
</tr>
<tr>
<td>10.00</td>
<td>low</td>
<td>7.65</td>
<td>4.58</td>
<td>14.7</td>
<td>1.8</td>
</tr>
<tr>
<td></td>
<td>high</td>
<td>6.90</td>
<td>6.20</td>
<td>30.3</td>
<td>6.9</td>
</tr>
<tr>
<td>13.33</td>
<td>low</td>
<td>9.42</td>
<td>6.32</td>
<td>14.2</td>
<td>13.3</td>
</tr>
<tr>
<td></td>
<td>high</td>
<td>8.30</td>
<td>7.66</td>
<td>31.6</td>
<td>20.6</td>
</tr>
</tbody>
</table>

Figure 7.3. Response to heterogeneity in peer contributions is associated with cooperation tendency. Bars show the average and SEM of contributions over ten rounds of a public goods game, where group composition was randomised before every round, for negative, neutral, positive, and inconsistent responders to heterogeneity. Statistically significant differences between types are indicated (Tukey Honest Significant Differences), except for differences between inconsistent responders and any of the other groups. Numbers at the bottom of each bar indicate the number of subjects falling in this category.
two parts of the experiment; it is still observed when controlling for peer cooperation in the first part of the experiment (see Appendix, section 3). Moreover, we still observe this clear difference when only considering the first interaction round of the first part, or the ‘unconditional contribution’ of the second part (see Methods) to determine general cooperation tendency. In these cases, contributions of individuals that positively responded to heterogeneity were respectively 50% and 40% higher than those of individuals that responded negatively; those differences were highly significant in both cases (see Appendix, section 2 for graphic representations and details).

**DISCUSSION**

The results of our experiment can be summarised in three points. First, we confirm earlier observations that when the contributions of fellow group members to a public good are more heterogeneous, people on average respond by contributing less. However, this is not the whole story; more heterogeneity in peer contributions also leads to more variable (and more extreme) contributions in response (‘variation begets variation’). Second, we observe substantial individual differences in how people respond to the degree of heterogeneity in peer cooperation. Some individuals consistently contribute more when there is more heterogeneity, whereas others consistently contribute less. Smaller fractions were either neutral or inconsistent in their response to increased heterogeneity in peer cooperation. Third, we find a clear relation between general cooperation tendency and conditional responses to heterogeneity in peer contributions. Individuals that respond positively to heterogeneity in peer contributions tend to be more cooperative in a public goods game than individuals that respond negatively. Individuals that respond neutrally or inconsistently are intermediate in their cooperation tendency.

At first sight, it may seem that the classification of the individual variation that we made in our experiment (between positive, neutral, negative, and inconsistent individuals) does not reflect very clear differences between individuals. For example, an individual that was classified as ‘positive’ may in fact only have responded positively to heterogeneity in one of three comparisons, and neutrally in both others. Sure enough, our experiment should be considered as a first step in charting the individual differences in how people respond to heterogeneity in the cooperative behaviour of their peers; further studies will be needed to come to a more comprehensive account. Having said this, we observed that even individuals that responded marginally positively (the lightest blue shade in Figure 7.2) to heterogeneity have a significantly higher cooperation tendency than individuals that responded marginally negatively (the lightest red shade in Figure 7.2; see Appendix, section 1 for details). The fact that even small differences in response to heterogeneity are associated with large differences in general cooperation tendency suggests that these differences cannot simply be regarded as random noise. In this study, we found an association between self-assessed competitiveness and response to variation; this link could be
more thoroughly investigated (for instance, by measuring competitiveness experimentally rather than through self-assessment). Associations with other factors, such as aspects of personality, may also be interesting to explore.

Individual variation is currently attracting much attention in all the behavioural sciences, including biology (Gosling, 2001; Sih et al., 2004; Wolf & Weissing, 2010; 2012) (including cultural evolution research (Efferson et al., 2008; Molleman et al., 2014; Van den Berg et al., 2015)), psychology and neuroscience (Engler, 2008; Kanai & Rees, 2011; Van den Berg & Weissing, 2015b), and economics (Fischbacher et al., 2001; Akerlof & Kranton, 2010; Fischbacher & Gächter, 2010). Biologists have shown that consistent individual differences in behavioural tendencies often have an adaptive explanation, and are likely to emerge in the course of evolution under a broad range of circumstances (Wolf et al., 2007; Wolf & Weissing, 2010). Moreover, various theoretical models (Mcnamara et al., 2008; Wolf et al., 2008; 2011) show that the presence of consistent individual variation in social behaviour will induce the evolution of sensitivity and responsiveness to this variation. In line with the results reported here, these models predict that individuals differ consistently not only in their behaviour, but also in their response to the behaviour of others, and that both are correlated.

Our empirical results demonstrate that individuals vary not only in the degree of responsiveness, but also in the type of response to the social environment (i.e., there are positive and negative responders). This suggests that there exists a previously unrecognised dimension to social responsiveness. The observed link between the type of response and cooperation tendency can have important implications for the performance of cooperation strategies. For example, if cooperators typically assort together (Fletcher & Doebeli, 2009; Rand et al., 2011; van Veelen et al., 2012), a positive response to heterogeneity may help in maintaining cooperation by ‘forgiving’ occasional non-cooperation by a member of the group due to mistakes or temporary inability (Bendor et al., 1991; Wu & Axelrod, 1995; Wedekind & Milinski, 1996; McNamara et al., 2004; Hruschka & Henrich, 2006; Fudenberg et al., 2012; Irwin et al., 2014). The types of responsiveness we observe might be related to personality characteristics, such as differences in ‘lifestyle’. Theory predicts that evolution will often result in ‘pace of life’ syndromes, with individuals with a ‘fast’ and a ‘slow’ lifestyle coexisting in a population (Wolf et al., 2007; Réale et al., 2010b). ‘Fast’ individuals are focused on short-term benefits, while ‘slow’ individuals are willing to take short-term losses if this is likely to result in longer-term benefits. One might speculate that cooperativeness and a positive response to variation are both facets of a slow lifestyle; ‘slow’ individuals are more cooperative, since they hope to elicit long-term cooperation, and they respond more positively to variation, since they interpret heterogeneity as an opportunity for longer-term cooperation rather than as a threat. Similar arguments may be used to interpret non-cooperativeness in a social dilemma and a negative response to variation as facets of a fast lifestyle. Formal evolutionary models have to be developed to check if these verbal arguments can be substantiated. Quite obviously, the
implications of individual differences in type of responsiveness for the dynamics of social interactions and performance of cooperation strategies merit further empirical and theoretical scrutiny.

**METHODS**

A total of 240 subjects (71% female, mostly students) participated in experimental sessions consisting of 16 subjects each, at the University of Groningen (the Netherlands). Participation was by informed consent, and the experimental setup was approved by the Sociological Laboratory of the University of Groningen. The experimental sessions were carried out in accordance with the approved guidelines. During the sessions (lasting approximately one hour), subjects made a number of simultaneous and anonymous decisions on computers. Subjects earned points (50 points = €1) with the decisions they made, and were paid accordingly in cash at the end of the session (mean payoff: €14.87 ± 1.90; ranging from €10.60 to €19.30; subjects were unaware of the earnings of others). Subjects received written instructions, which were also read out loud by the experimenters at the start of each session (see Supplementary Material of the original article for instructions). Each session consisted of two parts that were separately explained on the computer screen before they started, after which subjects filled out a short quiz to check their comprehension. This experiment was conducted in conjunction with another experiment; see Appendix, section 4 for details. The experiment was run with the experimental software z-Tree (Fischbacher, 2007) (code available upon request).

In the first part of the experiment, individuals played ten rounds of a PGG, in groups of four. Individuals were grouped randomly at the start of every round, and were made explicitly aware of this in the instructions before this part, as well as at the start of every new round. At the beginning of each round, subjects were allocated 20 points to distribute between a group project and their personal account. After all subjects had made their decision, the total contributions to the group project were doubled and divided equally among the group members (irrespective of their contributions), and subjects were shown their earnings (as well as the contributions and earnings of their fellow group members).

In the second part of the experiment, subjects were asked how much they would contribute (0-20 points) depending on the contributions of their fellow group members. We confronted them with ten hypothetical scenarios (on a single screen, in fixed order), where the contributions of their fellow group members were always 0, 10 or 20 points (see Figure 7.1). Out of these ten scenarios, we pay particular attention to those pairs of cases that have the same average peer contribution, but differ in heterogeneity in peer contributions. Comparing subjects’ conditional contributions within these paired cases allowed us to determine how individuals respond to heterogeneity in peer contributions. In addition to the ten conditional contributions, each subject also entered one ‘unconditional contribution’ (where the choice was limited to 0, 10 or 20 points).
This unconditional contribution was simply the contribution that individuals would make to the group project in case they did not know the contributions of their fellow group members. After this, one round of a PGG was played in randomly formed groups of four. From each group, three randomly chosen subjects automatically made their unconditional contribution, and the remaining subject made their corresponding conditional contribution. A total of 22 subjects (8.8%) contributed the same amount regardless of the peer contributions; all except one of these individuals were unconditional free-riders, contributing 0 for every scenario (the remaining individual was an unconditional cooperator, always contributing 20). Under our classification, these individuals would have been labelled as neutral responders to variation, but they are in fact completely unresponsive to peer contributions altogether. Therefore, these individuals were excluded from the analysis. Their exclusion did not affect the main results presented in this paper (see Appendix, section 3).

ACKNOWLEDGEMENTS

We thank the Department of Sociology at the University of Groningen for access to their recruitment system and laboratory facilities. We thank Stephen Heap and Simon Gächter for helpful discussions.
Appendix

This appendix consists of four sections. First, we present additional results using a more refined subcategorization of response to heterogeneity (rather than only ‘positive’, ‘neutral’, ‘negative’, and ‘inconsistent’). Second, we present additional analyses of the relation between response to heterogeneity and general cooperation tendency, using alternative measures of the latter. Third, we give an overview of the statistics employed in our study. Fourth, we describe the experimental set-up in detail.

1. RESULTS FOR ALL SUBCATEGORIES OF RESPONSE TO HETEROGENEITY

It may be argued that the classification of ‘response to heterogeneity’ in the main text of our experiment is somewhat crude. Even individuals that only contributed more in case of more heterogeneity in peer contributions in one of the three comparisons (and contributed equally in the other two cases) are classified as ‘positive responders’. Similarly, an individual that only contributed less in case of more heterogeneity in peer contributions in one case, was classified as a ‘negative responder’. To investigate to what extent these seemingly small differences between weakly negative and weakly positive individuals are meaningful, we analysed the relationship between response to heterogeneity and cooperation tendency when considering all subcategories of individuals (as they are shown in Figure 7.2 in the main text). Figure 7.A1 shows that even the marginally positive and negative individuals have quite different cooperation tendencies.
Figure 7.A1. Response to heterogeneity in peer contributions is associated with cooperation tendency, even when the response to heterogeneity is weak. Bars show the average and SEM of contributions over ten rounds of a public goods game, where group composition was randomised before every round. The same data as in Figure 7.3 of the main text are shown, but the ‘negative’ and ‘positive’ categories are further subdivided by degree of negativity or positivity, as in Figure 7.2 of the main text. Negative responders to information are further subcategorised by whether they contributed less in response to increasing heterogeneity in one, two, or all three situations. Similar subcategories were made for positive responders to heterogeneity. The darker bars (furthest removed from the ‘neutral’ bar) show the most extreme responders, whereas the lighter bars (next to the ‘neutral’ bar) show the individuals that only responded positively or negatively to increased heterogeneity in one case, and responded neutrally in both other cases. Letters (a and b) indicate significant differences (Tukey HSD test); all bars indicated with a are significantly different from all bars indicated with b, whereas bars indicated with ab are not significantly different from either. Numbers at the bottom of each bar indicate the number of subjects falling in this category.
2. RESULTS USING OTHER MEASURES OF GENERAL COOPERATION TENDENCY

In our experiment, we measure general cooperation tendency by taking the average of subjects' contributions in ten consecutive one-shot rounds of a PGG. This is in principle a valid way to measure general cooperation tendency, because individuals are playing one-shot games; information from earlier rounds is not relevant when deciding how much to contribute. However, one may argue that the outcomes of earlier rounds may still have influenced subjects in their decisions. Therefore, we here check whether our results still hold when only considering the first interaction round (when individuals have no information whatsoever about the decisions of others). Figure 7.A2a shows that this is indeed the case.

An alternative (and independent) measure of general cooperation tendency is the ‘unconditional contribution’ that individuals entered in the second part of the experiment. This unconditional contribution was used in the single round of PGG that was played in groups of four after the second part of the experiment. From each group, three randomly chosen subjects automatically contributed their unconditional contribution, and the remaining subject made their corresponding conditional contribution. Figure 7.A2b shows that if this measure is used, the same pattern still emerges. This strongly suggests that the observed pattern is robust.

Figure 7.A2. Response to heterogeneity in peer contributions is associated with cooperation tendency, also when using other measures of cooperation tendency. Bars show the average and SEM of contributions when considering (a) only the first PGG in the first part of the experiment, and (b) ‘unconditional contributions’ in the second part of the experiment. Statistically significant differences between types are indicated (Tukey HSD), except for differences between inconsistent responders and any of the other groups. Numbers at the bottom of each bar indicate the number of subjects falling in the respective category.
3. OVERVIEW OF STATISTICS

This section gives an overview of the statistical methods that were used in the study.

Factors affecting average contribution

We constructed a linear mixed model to determine which factors influence the response contribution levels when only considering the three pairs of cases that have equal average peer contribution, but different heterogeneity in contributions. We used a stepwise backwards elimination approach (Zuur et al., 2009), starting with a full model that contains as predictor variables the average peer contribution (the three levels are modelled as categorical factors), heterogeneity in peer contribution (including 'high heterogeneity' and 'low heterogeneity' as factors), and their interaction. Also, we included ‘individual’ as a random factor. The final model included both average peer contribution and heterogeneity in peer contribution as predictor variables, but not their interaction. We conclude that both average peer contribution and heterogeneity in peer contributions have a significant (respectively positive and negative) effect on response contributions. A summary of the final model is given below:

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>Std. error</th>
<th>t-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>4.7951</td>
<td>0.3428</td>
<td>13.989</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>heterogeneity in peer</td>
<td>-0.9021</td>
<td>0.2348</td>
<td>-3.842</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>contributions</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>average peer contribution (10)</td>
<td>3.5711</td>
<td>0.2876</td>
<td>12.418</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>average peer contribution (13.33)</td>
<td>5.3142</td>
<td>0.2876</td>
<td>18.479</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

In summary, average response contributions increase with average peer contributions, but decrease with increasing heterogeneity in peer contributions. This is consistent with earlier results.

Recent experiments indicate that the outcome of past social interactions in an experimental session may affect unrelated future cooperation decisions (Peysakhovich & Rand, 2015). For our experiment, this may lead to the expectation that subjects who experienced higher average levels of cooperation in the first part of the experiment would contribute more to the public good in the second part. However, an extended regression analysis including peer cooperation levels in part 1 of the experiment reveal that they had no significant effect on public good contributions in part 2. There was a small yet significantly positive effect of the average cooperation levels in the stable groups (rounds 11-25; see Section 4 of this Appendix), but including this factor in the regression analysis did not alter our main conclusions; both average peer contribution and heterogeneity in peer contributions have on average a significant (respectively positive and negative) effect on response contributions.
Factors affecting the incidence of extreme contributions

To determine which factors influence the incidence of extreme contributions we constructed a mixed-effects logistic regression model both for the incidence of contributions of 0 and the incidence of contributions of 20. We used a stepwise modelling approach, as described for the linear mixed model above, and included the same predictor variables in the first step. The final model for contributions of 0 contained average peer contribution, heterogeneity in peer contributions, and their interaction as predictors:

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>z-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-0.6805</td>
<td>0.2617</td>
<td>-2.600</td>
<td>0.009</td>
</tr>
<tr>
<td>heterogeneity in peer contributions</td>
<td>0.8905</td>
<td>0.2718</td>
<td>3.276</td>
<td>0.001</td>
</tr>
<tr>
<td>average peer contribution (10)</td>
<td>-2.5345</td>
<td>0.3317</td>
<td>-7.642</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>average peer contribution (13.33)</td>
<td>-2.5948</td>
<td>0.3346</td>
<td>-7.754</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>average (10) * heterogeneity</td>
<td>0.7127</td>
<td>0.4164</td>
<td>1.712</td>
<td>0.087</td>
</tr>
<tr>
<td>average (13.33) * heterogeneity</td>
<td>0.8907</td>
<td>0.4179</td>
<td>2.131</td>
<td>0.033</td>
</tr>
</tbody>
</table>

The final model for contributions of 20 contained average peer contribution and heterogeneity in peer contributions as predictors:

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>z-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-14.3402</td>
<td>1.5627</td>
<td>-9.177</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>heterogeneity in peer contributions</td>
<td>1.9519</td>
<td>0.4378</td>
<td>4.458</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>average peer contribution (10)</td>
<td>2.5724</td>
<td>0.7352</td>
<td>3.499</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>average peer contribution (13.33)</td>
<td>6.4348</td>
<td>0.8979</td>
<td>7.166</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

In summary, heterogeneity in peer contributions affects the incidence of extreme contributions in both ways; it has a positive effect on both the frequency of contributions of 0 and the frequency of contributions of 20. Average contribution also had an effect in both cases, but in opposite directions.

Effect of exclusion of unresponsive individuals

For the results presented in this study, individuals that were completely unresponsive (always made the same contribution, regardless of peer contributions) were excluded from the analysis. These were in total 22 subjects (8.8%); 21 unconditional free-riders (always contributing 0), and one unconditional cooperator (always contributing 20). The exclusion of these individuals from our analysis does not affect our conclusions. Their inclusion would increase the frequency of response contributions of 0 and 20 with the same amount for each combination of peer con-
Human cooperation: variation begets variation

Chapter 7

Figure 7.A3. Response to heterogeneity in peer contributions is associated with cooperation tendency, also when including unresponsive individuals in the analysis. Bars show the average and SEM of contributions. Statistically significant differences between types are indicated (Tukey HSD), except for differences between inconsistent responders and any of the other groups. Numbers at the bottom of each bar indicate the number of subjects falling in the respective category.

4. DETAILS OF THE EXPERIMENTAL SET-UP

The current experiment was part of a larger experiment that was designed to test the effects of positive assortment on cooperation in human groups. Here, we give a full description of the entire experimental set-up.

At the start of each session, all subjects received written instructions that were also read aloud by one of the experimenters (full instructions are included in the Supplementary Materials of the original article). Individuals did not know that the experiment was designed to test the effects of assortment or information about assortment in the first rounds of the experiment, or that the first rounds were used to measure general cooperation tendency for the current study.
As described in the main text, subjects first anonymously interacted in a Public Goods Game (PGG) for 10 rounds in groups of four, with changing group compositions in each round. The average contribution in these ten rounds was used as a measure of individual cooperation tendency in this study.

After the first 10 rounds, subjects played another 15 rounds of the PGG. This part was designed to test the effects of assortment and information about assortment. Each session was assigned to one of three treatments: i) assortment with information, ii) assortment without information, and iii) no assortment. Prior to this part, subjects received new instructions relevant to the treatment of their session. In the assortment treatments (i and ii), subjects were assorted in groups of four based on their decisions in the first 10 rounds of the PGG; the individuals that contributed most were grouped together, as were the individuals that contributed least, and the individuals that were in between. Individuals then played 15 more rounds of the PGG in these assorted groups, with fixed group membership over all rounds. In treatment i, individuals were made aware of the assortment regime, and were told in which group they were to be assorted (i.e., they had information about the general cooperation tendency of their fellow group members). In treatment ii, individuals did not have this information, and were only told that they would now interact in fixed groups. In treatment iii, individuals were grouped randomly, and were only told that they would now interact in fixed groups.

After these 15 rounds, the second part of the current study ensued: individuals were asked how much they would contribute in various situations with different contributions of fellow groups members (as explained in the main text).

To demonstrate that the results described in the main text of this study were not affected by the assortment regimes described above, we show our results separately for each treatment in Figure 7.A4 below.
Figure 7.A4. Response to heterogeneity in peer contributions is associated with cooperation tendency independent of experimental treatment. Bars show the average and SEM of contributions over 10 rounds of a public goods game, where group composition was randomised before every round, separately for individuals who had earlier experienced treatments i (assortment with information), ii (assortment without information) and iii (control: no assortment). All three graphs show the P-value of a Tukey HSD test, comparing the cooperation tendency of negative and positive individuals. Only for the subset of individuals that were in treatment i, response to heterogeneity does not significantly predict general cooperation tendency, but even in this case the effect is in the same direction as the overall pattern. Numbers at the bottom of each bar indicate the number of subjects falling in the respective category.
Afterthoughts

Pieter van den Berg
“One is tempted to define man as a rational animal who always loses his temper when he is called upon to act in accordance with the dictates of reason.”

–Oscar Wilde, Intentions (1891)

“The credit which the apparent conformity with recognized scientific standards can gain for seemingly simple but false theories may, as the present instance shows, have grave consequences.”

In this thesis, I have presented studies that each consider the evolution of human social behaviour, employing a number of different approaches. In the first half, I discuss theory and simulation, although the simulation models presented in Chapters 3 and 4 are quite different in both their subject and their approach. Chapter 3 focuses on the specific context of parental influence on offspring mate choice, providing a potential explanation how conflict between parents and offspring over mate choice can evolve. Chapter 4 makes a much more general point, using highly stylized social contexts (the Iterated Prisoner’s Dilemma game and the Iterated Snowdrift game) to show that underlying mechanisms matter for the evolution of cooperation. In the second half of this thesis I discuss experimental studies, all based on similar methods but again making quite different points. Chapters 5 and 7 reveal consistent individual differences in (respectively) social learning strategies and cooperation strategies, whereas Chapter 6 focuses on the consequences of such differences for the outcome of social interactions. Although not very explicitly, Chapter 2 can be regarded as a connection between these two parts; it gives an overview of models of the evolutionary emergence as well as the evolutionary consequences of individual differences.

I will not focus too much on drawing direct connections between the studies presented in this thesis. This is partly because the studies are only loosely connected. As indicated in the title of this thesis, my PhD project has been an exploration, rather than a systematic approach towards a synthesis of its constituent parts. However, through reading articles and books, gaining experience with concepts and methods from various fields, writing, presenting, and talking to people, I have gradually developed a perspective on the study of human social behaviour over the four years in which I produced this thesis. The methods used in this thesis are mostly derived from the disciplines of evolutionary biology on the one hand, and decision theory (or more specifically, game theory) from economics on the other. Through working with these methods, and going to interdisciplinary conferences where people from these different fields meet, I started noticing some parallels between their mother disciplines. In particular, I realized that both are strongly driven by functional thinking, a perspective with which I grew increasingly uneasy. Because of this, I gradually started developing my personal perspective on what future of the study of human social behaviour and cultural evolution could look like. This process is by no means completed, but I will relate some of those thoughts here.

In this chapter, I will first discuss what I think are similar developments in the study of evolutionary biology and the study of human decision making. I will start with a discussion of the dominant formal frameworks used in both these disciplines, and explain how they have come under increasing criticism. Then, I will sketch how rapid technological advances in both fields have led to an increased appreciation for the mechanisms that underlie evolution and decision making. I will argue that even though these new techniques provide us with a wealth of information, there are questions they cannot be used to answer. In line with this, conceptual modelling remains indispensable for gaining a mechanistic understanding of complex processes in general, and for the evolution of human social behaviour in particular. In the last part of this chapter, I will
outline what I think is a promising approach for developing such models. Specifically, I will argue that modelling behaviour in more heterogeneous social environments and grounding models in empirically identified cognitive building blocks can go hand in hand to advance our understanding of the evolution of human social behaviour. Throughout, I will have special attention for cultural evolution, one of the main topics of this thesis, and a field in which evolution and social behaviour are closely intertwined. I hope the expert reader will forgive me if I have made some naïve mistakes here and there; the nature of interdisciplinary research is that I am not an expert in all fields that I presume to discuss. Rather, I invite the reader to point those out to me; this is how interdisciplinary research progresses.

FUNCTIONAL EXPLANATIONS AND REAL MECHANISMS

The interdisciplinary character of the study of human decision making in social contexts comes with a varied package of theoretical frameworks and at least as many different types of empirical methods. At the time of writing of this thesis, two of the main involved disciplines, evolutionary biology and economics, are both going through a critical re-evaluation of the dominant theoretical frameworks in their respective fields. In both disciplines, the early- and mid-twentieth century saw a strong development of formal theory with a focus on functional arguments. In evolutionary biology, this functional perspective is embodied in the central role of fitness maximization arguments in explanations of the evolution of traits. In economics, it is demonstrated by the importance of arguments of utility maximization. More recently, in the face of more and more detailed knowledge about human decision making and the evolutionary process, the basic assumptions of these theoretical frameworks are being questioned. There is a growing appreciation that the functional perspective alone is not enough; we must also consider the actual mechanisms underlying evolution and decision making to be able understand what outcomes they will produce. At the same time, technological advances have revolutionized the detail in which we can look at these mechanisms. For example, genomic tools such as genome-wide association studies (GWAS) and brain imaging techniques such as functional magnetic resonance imaging (fMRI) allow us to make new connections between function and mechanism. However, this sudden wealth of information is mostly correlational in nature, and does not automatically provide us with conceptual advances. I think that we are living in an exciting time, in which research is strongly driven by empirical exploration and where we are unravelling the substrates of evolution and decision making in ever greater detail. However, this does not mean that conceptual models of those processes are no longer needed. To me, especially in a time of rapidly increasing knowledge modelling studies are crucial for the advancement of our understanding.
Evolutionary theory

Darwin’s theory of evolution missed the puzzle piece of inheritance. Although Darwin (1868) speculated about the nature of inheritance, it was Gregor Mendel who discovered the laws of genetic inheritance in his now famous experiments with garden peas. At first, Mendel’s laws seemed incompatible with Darwin’s theory, but in the first half of the 20th century both theories were united in the so-called ‘Modern Synthesis’ (Huxley, 1942). The Modern Synthesis was one of the greatest advances in evolutionary biology; it is a coherent framework that allows scholars to use mathematical techniques to model change in gene frequencies over time. Until today, mainstream research in evolutionary biology has been heavily indebted to the Modern Synthesis.

The formalization of the study of genetic evolution came with a number of key generalizations that became accepted as foundations of the field. One of the central conceptual distinctions is the one between the genotype (the information that can be passed on to the next generation) and the phenotype (the expressed traits that natural selection can act upon; Johannsen, 1911). The central dogma of molecular biology states that phenotypic traits are never back-translated to heritable information (Crick, 1970). Another standard assumption is that new genotypic variations (mutations) are random with respect to the direction of selection (Dobzhansky, 1970), and that they have small phenotypic effects. Furthermore, the physical environment is generally treated as a ‘background’ against which evolution takes place; although it may vary through space and time, it is often assumed that it is not affected by the organisms that reside in it. Perhaps most fundamental is the tradition in evolutionary biology to separate proximate questions (how is a trait directly caused?) from ultimate questions (how was the trait shaped by natural selection?) (Mayr, 1961; Tinbergen, 1963). The idea behind this separation is that ultimate questions can be largely answered without specific knowledge of the proximate causes (and vice versa). In line with this, models of evolution often largely ignore the genetic and physiological causation of traits, instead directly modelling the evolution of the phenotype itself (an approach referred to as ‘the phenotypic gambit’; Grafen, 1984).

By precluding many types of feedbacks between phenotype, genotype, and environment on the one hand, and function and mechanism on the other, the foundations of modern evolutionary theory allow the overwhelmingly complex evolutionary process to be boiled down to relatively simple models. Those models focus on the effect of selective forces on gene frequencies in populations, commonly assuming simple interactions between genes, a simple relationship between the genotype and the phenotype, small and selectively random mutational effects, as well as a simple and low-dimensional description of the environment. This has led to a rich and sophisticated tradition of modelling the fitness consequences of traits (based on the concept of reproductive value; Fisher, 1930) and analysing the resulting fitness function to predict evolutionary dynamics and outcomes. The theoretical frameworks that stem from this tradition, such as evolutionary game theory (Maynard Smith, 1982; Gintis, 2009; Broom & Rychtar, 2013), adaptive
dynamics (Hofbauer & Sigmund, 1990; Geritz et al., 1998), and quantitative genetics (Roff, 1997; Lynch & Walsh, 1998), have contributed greatly to our understanding of the evolutionary process. As knowledge about genetics accumulated throughout the 20th century, it became clear that the foundations of the Modern Synthesis are not universal laws. For example, it is becoming increasingly clear that characteristics acquired during the lifetime of individuals are in some cases inherited. Indeed, ‘epigenetic inheritance,’ whereby developmental variations are transmitted between individuals by means other than DNA, can occur in various ways (Jablonka & Raz, 2009). Structures inside cells, such as prions, reproduce within cells and are transmitted to daughter cells, including germ line cells. Similarly, self-sustaining loops in cell metabolism can be environmentally induced, and passed on to the next generation. Gene expression can be altered by molecules binding to stretches of DNA, and such alterations can be inherited over generations. The best known example is DNA methylation, but in more recent years the role of RNA interference with gene expression (and its heritability) has become more and more appreciated. Additionally, as discussed in the introduction (and Chapters 5 and 6) of this thesis, variations may be transmitted through social learning. Especially in humans, the resulting process of cultural evolution has had dramatic effects that cannot be seen as separate from genetic evolution (Levinson & Dediu, 2013; Richerson & Christiansen, 2013).

Increasing criticism of the tenets of the Modern Synthesis does not only centre on the distinction between genotype and phenotype, but also on other aspects, such as the role of the environment and mutation in the evolutionary process. For example, the concept of ‘niche construction’ (Odling-Smee et al., 2003) emphasizes that the relationship between organisms and their environment is not a one-way street. The environment plays a role in the development of individuals and in the selection of traits, but individuals also actively alter their environments in return. Furthermore, it has become clear that genetic mutations do not produce random phenotypic effects, but are subject to developmental bias (one of the most important topics in the now fully-fledged field of evo-devo). Moreover, many genetic mutations do not have phenotypic effects, allowing for the build-up of cryptic variation in populations. This cryptic variation can become visible in certain environments, leading to an enhanced evolvability in the population (Wagner, 2008). As I have explained in Chapter 4 of this thesis, the structuring of mutational effects can be of particular importance for the evolution of social behaviour. In the light of mounting evidence that is at odds with its fundamental principles, voices calling for a critical re-evaluation of the Modern Synthesis (some have called for an ‘Extended Evolutionary Synthesis’; Laland et al., 2014) have grown increasingly loud.

Decision theory
Scholars have used formal techniques to study human decision making for centuries, but the formulation of classic Expected Utility Theory (Von Neumann & Morgenstern, 1944) led to the firm grounding of these formal techniques in a coherent framework that is still dominant today.
Expected Utility Theory has both been used as a normative theory, for determining optimal decisions and policies, and as a descriptive theory of human behaviour, employed to explain various phenomena resulting from human decision making (Tversky, 1975). Either way, it is based on the assumption that the agents making the decisions are rational, and strive to maximise some measure of subjective value (utility). Much like the Modern Synthesis in evolutionary biology, the formal framework of Expected Utility Theory is based on a few defining principles. Examples are the axioms of transitivity (if one prefers A over B, and B over C, one must also prefer A over C) and the axiom of independence (if one prefers A over B, one should still do so when a third potential outcome C is added). These axioms ensure that models of human behaviour within the Expected Utility framework are relatively simple and mathematically tractable. Game theory, which studies decision making when multiple rational agents interact (see Chapter 2), resides within this general framework (Luce & Raiffa, 1957).

Since the later decades of the 20th century, there has been increasing discomfort among scholars of human decision making with the Expected Utility paradigm. This is mostly because of mismatches of the rationality axioms with the accumulating empirical evidence about actual human decision making. The work of Kahneman & Tversky is probably the best-known in this respect. Through a number of brilliantly designed experiments, they have shown that human decision making is subject to many biases. One example is an experiment with which they showed that the way a choice is presented (framing) can be very important to what people choose. They presented the following dilemma to a group of respondents (Tversky & Kahneman, 1981):

“Imagine that the U.S. is preparing for the outbreak of an unusual Asian disease, which is expected to kill 600 people. Two alternative programs to combat the disease have been proposed. Assume that the exact scientific estimate of the consequences of the programs are as follows:

If Program A is adopted, 200 people will be saved.

If Program B is adopted, there is 1/3 probability that 600 people will be saved, and 2/3 probability that no people will be saved.”

To another group of respondents, they posed the exact same problem, but framed in a different way. The cover story was the same, but the two options were framed as follows:

“If program A is adopted, 400 people will die.

If program B is adopted, there is a 1/3 probability that nobody will die, and a 2/3 probability that 600 people will die.”
In both versions, the two options are identical, but framed differently. This framing had huge consequences: in the first version, which was framed in terms of lives saved, a clear majority of respondents (72%) preferred the low-risk option A (72%); in the second version, which was framed in terms of deaths, the majority of respondents (78%) preferred the high-risk option B. This is a clear violation of rational choice.

Anomalies as in the example above have often been accommodated in Expected Utility Theory by extending the theory (for example, by positing that people can have different utility functions for different contexts; Thaler, 1999) or by including constraints on human decision-making (‘bounded rationality’; Simon, 1955; 1982). Despite quite some work on alternative paradigms for studying human decision making (Starmer, 2000), Expected Utility Theory has remained the dominant framework in economic approaches to human decision making. However, alternative approaches based on information processing (asking what is the available information and how it can be used by agents that have limited cognitive capacities) are slowly gaining ground. Gigerenzer and colleagues (Gigerenzer & Goldstein, 1996; Gigerenzer et al., 1999; Gigerenzer & Gaissmaier, 2011) showed that simple decision making mechanisms (‘heuristics’ or ‘rules of thumb’) can often be surprisingly effective, especially when confronted with incomplete information or heterogeneous environments. More recently, information processing theories that are grounded in empirical evidence of basic cognitive processes underlying decision making have received increasing attention (Oppenheimer & Kelso, 2015).

Functional focus in evolution and economics

There has been plenty of borrowing of formal techniques between evolutionary biology and economics in the past. Biologists borrowed and adjusted game theory from economics, introducing the framework of evolutionary game theory (see Chapter 2), which eventually found its way back into economics (Weibull, 1995; Samuelson, 1997). Other formal methods in biology, such as optimal foraging theory, are also heavily indebted to economics (Hammerstein & Hagen, 2005). This is not so surprising: both disciplines study how complex systems with many agents change over time, and the way this change is explained is strongly characterized by functional thinking. In classical economics, the assumption is that agents are maximizing expected utility. In evolutionary biology, the idea is that organisms appear designed to maximise (inclusive) fitness (Darwin, 1859; Grafen, 2002; West & Gardner, 2013). In both disciplines, this functional focus has been accompanied by a relative neglect of the mechanisms that underlie the processes of interest. This neglect is justified by the idea that proximate mechanisms are inconsequential to the eventual outcome of the process (although this argument is usually made more explicitly in evolutionary biology than in economics).

Today, the traditional functional frameworks in both disciplines are facing mounting evidence that mechanisms do matter to the outcome of the process of evolution and decision making. Voices are growing louder that the functional and mechanistic perspectives cannot be separated.
as easily as is traditionally assumed, and in fact need to be considered in concert (Gigerenzer & Goldstein, 1996; Jablonka & Lamb, 2005; Laland et al., 2014). Probably not coincidentally, our knowledge about mechanisms underlying evolutionary and economic processes is currently rapidly increasing.

**Mechanisms underlying evolution and decision making**

The increasing criticisms of the theoretical frameworks in both evolutionary biology and economics have mostly been fuelled by the accumulation of observations that are at odds with them. At the same time, at least in the case of evolutionary biology, these observations were often only possible because of the rapid technological advances in the field. Researchers are now able to study the genome and how it is expressed in much more detail than ever before. This has led to a growing appreciation for the importance of proximate mechanisms in the process of evolution. Similarly, technological advances for brain activity imaging led to the rapid growth of the new field of neuro-economics. In both cases, new techniques have allowed researchers to make new connections between mechanism and function. However, although such studies accumulate detailed information about the links between function and the underlying substrate at an unprecedented rate, this knowledge is only correlational in most cases. Consequently, the technological advance of the last few decades has also led to the realization that the wealth of new information can be very difficult to interpret, and that new technologies do not automatically lead to increased conceptual understanding of how the processes of evolution and decision making work.

The explosion in our ability to acquire genomic data is clearly illustrated by the rapid reduction of the cost of sequencing an entire genome from tens of millions of dollars to around five thousand dollars over the last 15 years. However, the rate at which we can now sequence genomes is substantially outpacing the rate at which we can annotate genes, providing a significant bottleneck for the progress of ecological and evolutionary genomics (Pavey et al., 2012). There are various methods available for inferring the functional associations of genes. Targeted genetic experiments (such as gene knockouts or targeted genome editing; Cong et al., 2013) are probably the most direct way to infer the function of genes, but those are not feasible for all organisms because of practical or ethical reasons (for example, in humans). In such cases, genome-wide association studies (McCarthy et al., 2008), where inter-individual genetic variation is statistically associated with traits, are a popular method. Although such studies (as well as other types of genomic and transcriptomic studies) give us clues about where to look for a better understanding of the causation of traits, they do themselves not give us a deeper insight in the complex causal relationships between genes and traits. Popular media often implicitly misrepresent the correlational nature of such studies as causal, by reporting that a gene ‘for’ some disease has been found, rather than a gene ‘associated with’ that disease.
Networks of interacting genes constitute only a part of the overwhelming complexity of the causation of behaviour. The brain, which implements behaviour, is the product of a complex interaction between genetic, epigenetic and cultural factors, as well as experiences throughout development (Jablonka & Lamb, 2005). The diversity and intricacy of factors involved in the recent evolution of the human brain becomes apparent when we compare it with that of the chimpanzee, with which we share our most recent common ancestor. The differences between the brains in those two species are not only due to differences in brain-associated genes, but also due to differences in levels of expression of those genes, in the extent to which they are methylated and modified by histones, and in the alternative splicing of the mRNAs that they produce (Konopka & Geschwind, 2010). Furthermore, the behavioural divergence between humans and chimpanzees has been strongly affected by cultural evolution. This shows that an account of human behavioural evolution that relies on modelling changing gene frequencies alone is missing large parts of the puzzle.

On top of the extreme complexity that underlies the development of the human brain is the extreme complexity of the neurological and physiological causation of human behaviour. Behaviour is the product of complex interactions of the billions of neurons in the brain, with each other, the physiological state of the body, and the information about the environment that is coming in through the senses. There have been enormous advances in non-evasive brain imaging techniques, most notably fMRI, which help us associate psychological constructs or processes of interest with activity in specific regions in the brain. However, just like GWAS studies in genomics, these studies provide us with correlational information and do not automatically come with an increased understanding of the psychological mechanisms that are in play. Like with the –omics-revolution, there have been those who are confident that these new tools will revolutionise our understanding of human decision making (e.g. Glimcher & Rustichini, 2004; Rangel et al., 2008), those who have been more cautious (Aue et al., 2009), and those who are outright sceptical (Miller, 2010).

I think the advances in our ability to study mechanisms in detail are exciting, and I am confident that they will contribute to our understanding of human behaviour. However, there are two kinds of pitfalls that we have to be aware of. First, I think we need to be careful not to overinterpret correlational relationships we find between functions and mechanisms. Like a detective finding a weapon at a murder scene, we must not jump to conclusions about causal relationships, but rather interpret the coincidence of a potential cause and a potential effect as a clue, a motivation to investigate further. Second, it is important to remember that even knowing all the constituent parts and relationships within a complex system such as the brain or the genome does not necessarily give us insight in how the system as a whole behaves. They provide pieces of information, but I think conceptual modelling will always be necessary to give us insight in the causation (and hence, evolution) of human social behaviour. But what is the right level of abstraction for such models, given all the layers of complex causation of behaviour described above? I think answer-
ing this question is the most important challenge of the modeller. This is by no means an easy task, but I will elaborate further on how I think we may approach this below.

**Cultural evolution**

Cultural evolution is where evolution and decision making come together. When considering the strongly functional perspectives dominating evolutionary biology and decision science, it is no surprise that research in the field of cultural evolution has been characterized by this kind of thinking. However, I think that this strongly functional perspective is particularly problematic in the case of cultural evolution. Cultural variants are transmitted through social learning, which is a complex psychological process that is much more than just copying (even though that is how it is often represented). Social learning involves the direction of attention to social information (Chapter 5 in this thesis shows that humans differ in this respect), and a subsequent change in behaviour or ideas based on the gathered information (this thesis, Chapter 6). It is a process of reconstructing expressed cultural variants rather than a process of copying hardwired information (Sperber & Hirschfeld, 2004). The fact that the transmission of cultural variants is intertwined with their expression clearly shows that any analogy of the concepts of genotype and phenotype in cultural evolution is problematic. As already discussed in the introduction of this thesis, this is not the only way in which the process of cultural evolution deviates from the fundamental principles that were introduced for genetic evolution by the Modern Synthesis. The rules of transmission are much less clear, and certainly not as straightforward as the rules of genetic transmission (for instance, cultural transmission within a single generation, and even ‘upstream’ through the generations, is possible). Also, the *de novo* generation of new cultural variants is more directed than in genetic evolution (although new genetic variation is not random either, as discussed above). Feedbacks between the development, expression, and transmission of cultural traits make the process of cultural evolution both potentially much more rapid and complex than the process of genetic evolution. Although there has been quite some theory development in the field of cultural evolution, methods are not nearly as diverse and sophisticated as theoretical models of genetic evolution.

In my opinion, the study of cultural evolution provides an ideal test-case for the development of more mechanistic evolutionary models, for at least three reasons. First, as outlined above, a one-sided functional perspective is particularly problematic for the study of cultural evolution. Second, perhaps not as weighed down by its history as genetic evolution is by the Modern Synthesis, scholars in this field may be more open to unorthodox new approaches. Third, as I will detail further below, promising approaches for modelling decision making grounded in basic psychological mechanisms are currently on the rise. I think the adoption of such approaches can substantially benefit the study of cultural evolution.
THE WAY FORWARD

It is much more easily said than done that the overwhelming complexity that underlies human behaviour ‘needs to be appreciated’ for understanding its evolution. Hidden in that imperative lies an astronomical challenge that cannot even be met during a life-time scientific career. The complexity is daunting, and in a way the technological advances that have laid bare this complexity almost discourage conceptual advances. However, I think this moment of critical re-evaluation of function-driven theory provides a great opportunity for taking some first steps towards a more mechanistic way of thinking about the evolution of social decision making processes and cultural evolution. We are still very far from understanding how genes cause the development of the brain, and, consequently, behaviour. Although we may for the foreseeable future have no choice but to keep making black-box assumptions about the genetic causation of those basic cognitive processes, I think there is scope to increase the mechanistic underpinnings of models of the evolution of behaviour on the psychological level. In this last part, I will discuss how I think more appreciation for psychological mechanisms and a more realistic idea of the environments that those mechanisms evolved in can contribute to a better understanding of the evolution of human social behaviour.

The traditionally functional focus in studies of the evolution of behaviour goes hand in hand with the tendency to study the evolution of behaviour in single isolated contexts. This is not surprising; when the world is simple (i.e., when organisms are only faced with a single type of context), it is often relatively easy to work out what their optimal behaviour should be. However, when we appreciate the fact that the world confronts organisms with many different circumstances, the challenge of understanding the evolution of behaviour is transformed. When we think about the evolution of behaviour in a complex and heterogeneous world, we are almost forced to think about the evolution of mechanisms that underlie behaviour, rather than the evolution of the behaviour itself. I fully agree with evolutionary biologists McNamara & Houston (McNamara & Houston, 2009), who wrote:

“Although behavioural ecologists have built complex models of optimal behaviour in simple environments, we argue that they need to focus on simple mechanisms that perform well in complex environments.”

Herbert Simon (father of ‘bounded rationality,’ see above) has expressed a similar view on the relationship between mechanism and environment in different words (Simon, 1990):

“Human rational behaviour is shaped by scissors whose two blades are the structure of task environments and the computational capabilities of the actor.”
In line with the previous, I think the approach towards more mechanistic modelling of the evolution of human social behaviour should be twofold. First, we may use a top-down approach by introducing more heterogeneity in the model environments in which we study the evolution of behaviour. Second, we may adopt a bottom-up approach, using and expanding our knowledge of the cognitive building blocks of human psychology, and incorporating that knowledge as the behavioural basis in our models of social evolution. Both approaches may complement each other, and should eventually lead to testable hypotheses about the evolution of human social behaviour and cultural evolution.

**More realistic environments**

In this thesis, I have shown that human social behaviour is often much less flexible than a pure functionalist might expect. In Chapter 5, I show that there are consistent individual differences in what kind of social information people focus on, and Chapter 6 shows that these differences are stable over time (and have consequences for social behaviour). In Chapter 7, I show individual variation in relatively inflexible cooperation strategies. These findings fit with a rapidly accumulating literature showing that animal behaviour is often organized in relatively rigid behavioural syndromes (see Chapter 2). Of course, psychologists have known for much longer that individual differences in psychology (and associated behavioural tendencies) are quite stable over time and contexts. The rigidity of behaviour within individuals, and its variability between individuals, can be regarded as two sides of the same coin. Also, both are a challenge for evolutionary biologists to explain, although several ways in which consistent individual differences may emerge through evolution have been put forward (see Chapter 2 for an overview). One of these ways is through heterogeneity of the environment.

As outlined above, evolutionary models often consider the evolution of behaviour in a single context in isolation. Only recently has appreciation started to grow that organisms typically live in environments in which they almost never face the exact same situation twice. In line with this, scholars have started to ask how we would expect evolution to shape the mechanisms underlying behaviour in such a heterogeneous world, rather than single dimensions of behaviour in isolated contexts (McNamara & Houston, 2009; Fawcett et al., 2014). They have argued that heterogeneous environments often lead to the evolution of ‘rules of thumb’ (Gigerenzer et al., 1999; Hutchinson & Gigerenzer, 2005), that perform relatively well on average over all the different circumstances individuals are faced with, but can also occasionally produce suboptimal behaviour. Indeed, some have argued that psychological biases such as optimism, pessimism, and even the placebo effect may be the result of natural selection in a (both spatially and temporally) heterogeneous world (Fawcett et al., 2014). In fact, it has been shown that such seemingly insensitive heuristics may in some cases actually outperform more sophisticated behavioural rules (Gigerenzer et al., 1999; Hutchinson & Gigerenzer, 2005). Some have argued that affective states (moods and emotions) may be regarded as such ‘general-purpose mechanisms’; they may be a crude but adaptive way of
changing decision thresholds in a heterogeneous but autocorrelated environment (Mendl et al., 2010; Nettle & Bateson, 2012; Fawcett et al., 2014). Although we still know relatively little about the role and function of emotion in human decision making, there are increasing efforts that combine insights from emotion research with rational choice theory (Lerner et al., 2015).

When we look at the evolution of social behaviour, very simple contexts such as the much-studied Iterated Prisoners’ Dilemma game (IPD) can lead to very volatile evolutionary dynamics. This is illustrated in Chapter 4 of this thesis, in which virtually all possible strategies eventually emerge and disappear throughout evolution of behaviour in the IPD. Considering the developments described above, it may well be that there are much fewer viable strategies in case the social context in which individuals interact is not as isolated and predictable as is usually assumed. I think an interesting future direction would be to develop models of social behaviour in an environment where a number of different social contexts may occur, and where individuals do not have an independently evolved strategy for each context separately. In such a model, the interdependence of behaviour between the different contexts may be directly imposed, for example by implementing constraints on the flexibility of behaviour. This could be achieved by assuming a fitness costs associated with flexibility, but also by assuming a behavioural architecture in which flexibility is hard to implement (e.g. consider the neural network architecture in Chapter 4, in which some strategies [such as ALLD] are much harder to reach through mutation than others [such as Pavlov]). Perhaps more interestingly, consistency of behaviour across contexts could also emerge as a product of evolution. For example, this may happen if individuals are imperfect in their assessment of the social context that they are participating in.

More realistic mechanisms

Regardless of whether we model the evolution of human behaviour in isolated contexts or in heterogeneous environments, we have to make choices about how to implement the underlying behavioural architecture. The questions how to demarcate the strategy space and what to assume about the genotype-phenotype mapping are often answered in relatively arbitrary ways. I think it makes sense to start looking for the answers to these questions by taking a closer look at the actual psychological mechanisms that underlie decision making behaviour.

Recent years in decision science have seen a rapidly increasing interest for models of human decision making that use basic cognitive building blocks of information processing as their main ingredients (Oppenheimer & Kelso, 2015). Those models are diverse in their specific set-ups, but they all start from the idea that decision making is built up from more basic cognitive elements to do with attention, memory retrieval, perception, and so on. A good example of the application of this perspective is an experiment by Johnson and colleagues (2007), in which they use an information processing framework to explain the endowment effect. The endowment effect is a well-known bias of human decision making, stating that people value objects more if they are in their possession than if they are not (Kahneman et al., 1990; Kahneman & Tversky, 2000). Johnson
et al. propose that the endowment effect occurs because individuals faced with a question such as ‘for how much money should I sell this item?’ automatically decompose it into smaller queries (memory retrievals), and the order in which they execute these queries depends on the ownership of the item. They argue that individuals will first consider the advantages of the status quo, and then the advantages of changing the current situation. Furthermore, they hypothesise that earlier queries affect decision making more strongly than later queries. Applying this reasoning to the endowment effect, they arrive at the prediction that owners should first consider positive valuations of the item, because they are arguments for retaining the status quo. Using similar logic, they predict that buyers should first consider negative valuations of the item. Indeed, participants in the experiment report positive and negative valuations of the item in opposite order depending on ownership. Interestingly, the authors show that by experimentally manipulating query order, the endowment effect can be eliminated, or even created in the absence of ownership differences.

I think it can be very useful to use similar approaches to gain a more mechanistic understanding of human social behaviour. For example, consider Chapter 6 of this thesis, in which I find that the type of social information people focus on influences their decision making in a social dilemma context. Specifically, the way people who focus on the success of others change their behaviour through ‘success-based learning’, a social learning strategy that prominently figures in the cultural evolution literature. Essentially, these individuals preferentially copy the behaviour they have observed to be most profitable. However, this does not tell the whole story of our observations. For example, we see that individuals tend to be conservative, sticking with their previous behaviour even if the opposite behaviour pays off slightly better. The response of individuals that focus on frequency-information is even further from the conformism-like learning strategies that are often considered in models of cultural evolution. If they defected in the previous round, these individuals do not seem to update their behaviour in the next round based on the social information they just viewed, although there is a significant probability that they switch to cooperation in the next round. Our experiment shows that the social learning rules that are so often emphasized in the cultural evolution literature are caricatures – there is more going on than a simple response to the social information that individuals have observed. In my opinion, we need to have a more detailed account of the cognitive processes that constitute decision making in such situations. What kind of information is used, and how is it integrated in the decision making process? I think experiments designed to unravel these cognitive processes have an important role to play in this regard.

**Integrating both approaches**

I have argued that we may gain insight in how evolution shapes the mechanisms that underlie social behaviour by considering evolution in heterogeneous social environments. I have also advocated focusing efforts at designing experiments aimed at identifying the basic cognitive building blocks that underlie human decision making in social contexts. How might both these
approaches benefit from each other? On the one hand, evolutionary models can be used as a tool to generate hypotheses about what behavioural mechanisms we may expect to find. Currently, the hypotheses that are proposed about what cognitive functions underlie decision making do not arise from a general guiding principle; I think evolutionary models could be very suitable to fulfil this role. On the other hand, we may improve our models of the evolution of social behaviour as we learn more about psychological mechanisms through experimental approaches. For example, we could incorporate elements of attention, memory retrieval and information integration in our evolutionary models as separate elements of information processing, and study the evolution of all these elements in concert. Additionally, learning more about mechanisms can give us clues about the environments that they may have originated in (‘reverse-engineering’; Fawcett et al., 2014). These intuitions may then be further sharpened through evolutionary modelling. In summary, I think we need a pluralistic approach, where theoretical models are directly inspired from empirical observations, and *vice versa*.

**Cultural evolution**

The dual approach described above, of simultaneously asking the ultimate question ‘how does evolution shape decision making mechanisms in a heterogeneous world?’ and the proximate question ‘what are the basic cognitive building blocks of decision making?’ to me seems particularly appropriate for the study of social learning (and hence, for cultural evolution). As already mentioned above, the results presented in Chapter 6 illustrate that social learning strategies are much more than just simple copying rules. Only very recently have calls arisen that we need a greater appreciation in cultural evolution research for the psychological mechanisms that underlie social learning (Heyes & Pearce, 2015); I fully agree with this. Furthermore, social learning can be regarded as a general-purpose mechanism; at least in young children, imitation is applied almost indiscriminately to various kinds of behaviour (Horner & Whiten, 2005). Also, the results presented in Chapter 5 of this thesis suggest that people tend to focus on the same type of information regardless of the social context they are in. In my opinion, this shows that it is important to regard the evolution of social learning not with respect to a single context, but as a mechanism that has been shaped in an environment in which many different circumstances occur.

I think a more mechanistic understanding of social learning strategies is the key to the development of more sophisticated models of cultural evolution. If we manage to unravel the cognitive mechanisms that underlie social learning, we may construct models that can provide us with more precise expectations on how social behaviour in groups will change over time, depending on the information focus and cooperation strategies of their constituent individuals. At the same time, understanding those cognitive processes in more detail can provide clues about the environmental circumstances that shaped them.
CONCLUDING REMARKS

The subject of this thesis, genetic and cultural change in human social behaviour, is a topic that is of interest to many scientific disciplines. The foremost disciplines that the studies presented in this thesis are indebted to are evolutionary biology and economic decision theory. In this chapter, I have tried to show that developments in both these fields have much in common. Both went through similar developments in the early and mid-twentieth century, becoming dominated by strongly functionalist formal frameworks (respectively, the Modern Synthesis and Expected Utility Theory). In both fields, those formal frameworks have recently come under increasing criticism. At the same time, revolutionary technological advances in both fields allow us to study the substrate underlying the processes of evolution and decision making (respectively the genome and the brain) in much more detail. These new techniques (such as GWAS and fMRI) allow us to connect function and mechanism in unprecedented ways. However, advancing our conceptual understanding of evolution and decision making requires more than the correlational knowledge that those techniques can provide us with. I have argued that developing conceptual models remains necessary for our understanding of the causation of human behaviour, even if brain imaging techniques advance so far that they allow us to connect function and mechanism with great resolution.

I think now is the ideal time to bring a stronger mechanistic focus to the study of the evolution of human social behaviour and cultural evolution. As I have explained, I think the approach to this should be twofold. First, we should ask what kinds of behavioural mechanisms we would expect to evolve in a heterogeneous social environment, rather than focus on the evolution of sophisticated strategies in very simple social contexts. Second, we should shift the functionalist focus in human decision theory towards models rooted in basic cognitive processes, such as information processing theory. Strides have already been in both directions, but in my view, both approaches have not yet benefitted much from each other. I think answers to both kinds of questions can help to inform the other. Knowing more about mechanisms may provide us with clues about the circumstances that have led to their evolution. Conversely, building models of evolution of social behaviour in heterogeneous environments may help us understand what kind of psychological mechanisms we should expect to emerge. As a topic that is on the crossroads of evolution and decision making, I have argued that the study of cultural evolution, and of the cultural evolution of social behaviour in particular, would be the ideal test-case for such an approach.

Generally speaking, I see an important role for (cognitive) psychology in advancing our understanding of the evolution of human social behaviour and cultural evolution. In a sense, it is strange that cognitive psychology has not played a larger role in the study of cultural evolution up to now. However, when considering the traditionally functionalist focus of the discipline, it is much less of a surprise. Now that perspectives on the study of judgment and decision making are starting to change, I think the time is ripe to make significant strides in this regard.
I am well aware that the statement ‘we need more realistic models’ may sound rather gratuitous. The power of conceptual models lies in the fact that they are abstractions of reality. By stripping the processes we are interested in to their essentials, a model gives us intuitive insight in how it behaves. However, formal frameworks that need continuous patchwork to save them from an endless stream of conflicting empirical evidence, and that need to turn every anomaly into a new model parameter, need critical re-evaluation. Our challenge is to find patterns in the realm that lies in between mechanism and phenomenon. To do this in the most meaningful way, we have to continuously ask ourselves what is the right level of abstraction for making progress in our conceptual understanding, given the knowledge and understanding that we already have. For the study of human social behaviour, my opinion is that from where we stand today, that level of abstraction lies somewhere on the road towards the more realistic end of the spectrum.
References

A


B


References


E


F


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K


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Nederlandse samenvatting
Toen u de titel van dit proefschrift las, heeft u zicht wellicht verbaasd over de breedte van het onderwerp. Menselijk sociaal gedrag is op zichzelf al een onderwerp met zeer veel facetten, en om dan ook nog zowel genetische als culturele aspecten te behandelen kan op zijn zachtst gezegd ambitieus genoemd worden. Dit proefschrift moet dan ook niet beschouwd worden als een uitputtende bespreking of een diepgravende analyse van een afgebakend onderwerp. Zoals de ondertitel getuigt, moet mijn promotieproject worden gezien als een verkenning. In dit proefschrift bestudeer ik met zowel inhoudelijk als methodologisch verschillende invalshoeken hoe menselijk sociaal gedrag door de generaties heen kan veranderen. Zoals ik hieronder in meer detail zal uitleggen, kunnen zowel culturele als genetische verandering worden beschouwd evolutionaire processen. Dit evolutionaire denken vormt de grondslag onder alle hoofdstukken in dit proefschrift. Vanuit deze biologische basis komt het onderzoek in dit proefschrift in contact met een aantal andere disciplines, zoals psychologie, economie en antropologie.

Dit proefschrift bestrijkt niet alleen een breed spectrum van onderwerpen, maar wordt ook gekenmerkt door een pluriformiteit van wetenschappelijke methodologieën. Hoofdstukken 3 en 4 zijn theoretische onderzoeken, waarin ik gebruik maak van computersimulaties om de evolutie van sociale eigenschappen na te bootsen. In Hoofdstuk 4 wordt dit nog aangevuld met een analyse volgens de evolutionaire speltheorie. Hoofdstuk 2 is een overzichtsartikel waarin ik geen eigen onderzoek bespreek, maar de besproken onderzoeken zijn ook hier voornamelijk theoretisch van aard. Hoofdstukken 5, 6 en 7 zijn experimentele onderzoeken, waarin ik mensen in een gecontroleerde omgeving gestandaardiseerde sociale interacties met elkaar heb laten hebben. Daarnaast kent dit proefschrift nog een algemene introductie (Hoofdstuk 1) en een nabeschouwing (Hoofdstuk 8), waar ik een geïntegreerde visie probeer te geven op de historie en de toekomst van de studie van menselijk sociaal gedrag vanuit een evolutionair perspectief.

**GENETISCHE EN CULTURELE EVOLUTIE**

Charles Darwin zette in 1859 in zijn boek *On the Origin of Species* het idee van evolutie door natuurlijke selectie uiteen. Twaalf jaar later, in 1871, schreef hij *The Descent of Man*, een boek dat voornamelijk de evolutie van de mens behandelt. Hij doet in dit boek een interessante observatie over taal:

*Er is een voortdurende strijd om het bestaan gaande tussen de woorden en grammaticale vormen in elke taal. De betere, kortere, gemakkelijkere vormen nemen voortdurend de overhand.*
Darwin zinspeelt hier op een idee dat pas 100 jaar later echt populair zou worden in wetenschappelijke kringen; het idee dat culturele verandering gezien kan worden als een proces van adaptieve evolutie.

Wanneer is er sprake van adaptieve evolutie? Daar is een relatief simpel antwoord op: je hebt een populatie van individuen nodig die verschillen in de eigenschappen die ze hebben (variatie); die eigenschappen moeten overdraaibaar zijn van het ene op het andere individu (erfelijkheid); en die eigenschappen moeten invloed hebben op de kans waarmee ze aan andere individuen worden doorgegeven (selectie). Net als genetische evolutie voldoet culturele verandering aan deze eisen, zij het op een andere manier. Waar genetisch bepaalde eigenschappen worden doorgegeven door middel van de biologische reproductie, worden culturele eigenschappen doorgegeven door vormen van sociaal leren (zoals imitatie of onderwijs). Dit betekent dat een gen zijn eigen verspreiding met name kan beïnvloeden door de overlevings- en reproductiekansen van zijn drager te verbeteren, terwijl het evolutionaire succes van culturele varianten hier los van kan staan. Het evolutionaire succes van cultuur hangt uiteindelijk af van de menselijke psychologie, en dus van de vraag: hoe bepalen mensen, bewust of onbewust, welke culturele varianten ze van anderen overnemen, en welke niet? Door wetenschappers in het rond 1980 geboren veld van de culturele evolutie is hier inmiddels al veel onderzoek naar gedaan. Het is duidelijk dat mensen een veelvoud van ‘sociale leerstrategieën’ gebruiken, van conformisme (het overnemen van de varianten die het meest voorkomen) tot het selectief kopiëren van varianten waar anderen succes mee hebben gehad. Verschillende leerstrategieën worden toegepast in verschillende soorten omstandigheden, maar er zijn ook duidelijke individuele verschillen in de leerstrategieën die mensen toepassen. Deze individuele verschillen in sociale leerstrategieën staan centraal in Hoofdstukken 5 en 6 van dit proefschrift.

**DE COMPLEXITEIT VAN SOCIALE EVOLUTIE**

De mens als soort valt in de eerste plaats misschien vooral op door zijn duizelingwekkend uitgebreide culturele repertoire, maar dan toch in de tweede plaats door de zeer complexe sociale relaties die het dagelijks leven kenmerken. Er is wel geopperd dat zowel onze extreme intelligentie als onze obsessie met het gedrag van anderen (zie de verkoopcijfers van de roddelpers) aanpassingen zijn om goed te kunnen functioneren in de sociale complexiteit van menselijke samenlevingen.

Een evolutiebioloog met een interesse in menselijk sociaal gedrag vraagt zich af hoe natuurlijke selectie de sociale strategieën die wij gebruiken vormgegeven heeft. Dit is een relatief ingewikkelde vraag, omdat sociaal gedrag niet alleen consequenties heeft voor het individu dat dat gedrag uitvoert, maar ook voor andere individuen in de populatie. Daardoor is het evolutionaire succes van sociale eigenschappen geen constant gegeven, maar afhankelijk van de samenstelling
van de populatie. Bijvoorbeeld, een coöperatieve houding kan zeer succesvol zijn als anderen zich ook coöperatief opstellen, maar diezelfde houding kan tot uitbuiting leiden in een populatie waarin anderen alleen oog hebben voor het eigen succes. Deze inherente interne afhankelijkheden kunnen leiden tot een dynamisch en onevenwichtig verloop van evolutie. Voorbeelden hiervan zijn te vinden in Hoofdstuk 3, waarin we zien hoe de evolutie van partnerkeuze kan leiden tot een ‘wapenwedloop’, en in Hoofdstuk 4, waar we zien hoe de evolutie van coöperatief gedrag volgens grillige patronen kan verlopen. Sociale evolutie kan in veel gevallen ook onverwachtse uitkomsten voortbrengen, zoals bijvoorbeeld individuele verschillen (in Hoofdstuk 2 ga ik hier uitvoerig op in).

De culturele evolutie van sociaal gedrag is dubbel interessant om te bekijken. We weten dat er grote verschillen tussen culturen zijn in hun sociale normen en sociale organisaties. Met simpele experimenten is aangetoond dat mensen uit verschillende culturen zich heel verschillend gedragen in situaties waar ze bijvoorbeeld hun eigenbelang tegen een gemeenschappelijk belang moeten afwegen. Daar komt nog bij dat er redenen zijn om aan te nemen dat culturele en genetische evolutie van samenwerking heel verschillend kunnen verlopen. In hoofdstukken 5, 6 en 7 bekijk ik op verschillende manieren hoe sociale informatie van invloed kan zijn op gedrag in sociale interacties.

**EVOLUTIE EN INDIVIDUELE VERSCHILLEN**

Al gaat dit proefschrift over de genetische en culturele evolutie van sociaal gedrag, er is nog een ander thema dat in elke hoofdstuk terugkeert: individuele variatie. In de laatste decennia is duidelijk geworden dat in zo goed als alle soorten consistent individuele verschillen te vinden zijn. Net als mensen, hebben dieren een persoonlijkheid; sommige koolmezen durven meer dan anderen, sommige stekelbaarzen zijn agressiever dan anderen, enzovoorts. Vanuit een evolutionair perspectief zijn individuele verschillen interessant, omdat je op het eerste gezicht juist zou verwachten dat door natuurlijke selectie variatie voortdurend zal afnemen. Daarbij de is ‘starheid’ van persoonlijkheden een raadsel: waarom leidt evolutie niet tot volledig flexibel gedrag, dat optimaal aangepast is aan de heersende omstandigheden van het moment? Relatief recentelijk zijn een aantal antwoorden op deze raadsels geformuleerd, die zich vaak bedienen van argumenten uit de sociale evolutietheorie. Tegelijkertijd is duidelijk geworden dat de aanwezigheid van individuele variatie in een populatie het verloop van de evolutie sterk kan beïnvloeden.

Zowel de evolutionaire oorzaken als de evolutionaire gevolgen van individuele verschillen worden uitgebreid besproken in Hoofdstuk 2 van dit proefschrift. In Hoofdstukken 3 en 4 speelt individuele variatie ook een belangrijke rol, zij het minder expliciet; in Hoofdstuk 3 zien we de gevolgen van individuele variatie in de context van partnerkeuze, en in Hoofdstuk 4 zien we dat evolutie kan leiden tot individuele verschillen in samenwerkingsstrategieën. Hoofdstukken

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5, 6, en 7 beslaan de hele driehoek van sociaal gedrag, cultuur, en individuele verschillen waar dit proefschrift omheen draait. Deze hoofdstukken bespreken de individuele verschillen in de type sociale informatie waar mensen in geïnteresseerd zijn (Hoofdstuk 5), en hoe die hun sociale gedrag bepalen (Hoofdstuk 6). Hoofdstuk 7 geeft een andere invalshoek op hoe mensen in een sociale interactie op verschillende manieren op sociale informatie reageren.

**DIT PROEFSCHRIFT**

Dit proefschrift bevat 8 hoofdstukken: een introductie (Hoofdstuk 1), een nabeschouwing (Hoofdstuk 8), en zes hoofdstukken die als losse artikelen zijn gepubliceerd. Hier volgt een korte samenvatting van elk van die zes hoofdstukken.

**Hoofdstuk 2** is een overzichtsartikel dat draait om de evolutionaire oorzaken en gevolgen van individuele verschillen. Ik geef in dit hoofdstuk meerdere voorbeelden van modellen uit de evolutionaire speltheorie die dit onderwerp behandelen. De speltheorie is een methode uit de economie om sociale interacties te analyseren, om zo de strategieën te identificeren die het belang van de deelnemers in die interactie het best dienen. De evolutionaire speltheorie is hier een aanpassing van; waar de ‘klassieke’ speltheorie uitgaat van de rationaliteit van de deelnemers aan een interactie, gaat de evolutionaire speltheorie ervan uit dat de strategieën van de deelnemers door natuurlijke selectie zijn vormgegeven.

In **Hoofdstuk 3** presenteer ik een evolutionair simulatiemodel waarmee ik een mogelijke verklaring geef voor het bestaan van conflict over partnerkeuze tussen ouders en hun kinderen. Grofweg samengevat komt het argument erop neer dat dit conflict geworteld is in een dieper evolutionair conflict tussen ouders en kinderen over de verdeling van de ouderlijke zorg over het nageslacht. Het model is relatief simpel van opzet, maar leidt tot relatief complexe evolutionaire patronen. Een discussie die in de wetenschappelijke literatuur ontstond naar aanleiding van dit artikel laat zien hoe snel evolutionaire argumenten ingewikkeld kunnen worden, en toont daarmee het belang van theoretische modellen voor het ondersteunen van die argumenten aan. Een commentaar op ons artikel en onze reactie daarop zijn opgenomen in Intermezzo I. Niettemin ben ik er van overtuigd dat de resultaten van deze studie voor een breed publiek zijn uit te leggen. Ik heb dit geprobeerd in een op/ed artikel voor de New York Times; deze is opgenomen in Intermezzo II.

In **Hoofdstuk 4** presenteer ik ook een evolutionair simulatiemodel, maar dit model heeft een heel ander doel dan het model van Hoofdstuk 3. In dit geval probeer ik geen potentiële verklaring te geven voor een fenomeen dat we in de echte wereld observeren, maar ik probeer een algemener punt te maken: de mechanismen die ten grondslag liggen aan gedrag zijn van belang voor de uitkomst van de evolutie van dat gedrag. In de biologie is er een traditie om ‘ultimate’ vragen (waarom is een eigenschap geëvolueerd?) van ‘proximate’ vragen (hoe wordt een eigen-
schap direct veroorzaakt?) te onderscheiden. In deze studie laat ik met een zeer simpel model zien dat de directe causatie van strategieën in twee zeer veel bestudeerde sociale interacties (het Prisoner's Dilemma game en het Snowdrift game) van groot belang zijn voor de uitkomst van de evolutie van die strategieën.

**Hoofdstukken 5 en 6** kunnen gezien worden als een tweeling-studie. Beide presenteren grootschalige gedragsexperimenten die draaien om sociaal leren, het 'erfelijkheidssysteem' van culturele evolutie. In beide experimenten heb ik proefpersonen in een computerlaboratorium anonieme sociale interacties met elkaar laten hebben. In de interacties konden ze punten verdienen, afhankelijk van de opties die zij zelf kozen, maar ook van de opties die gekozen werden door hun interactiepartners. Na iedere interactie gaf ik de proefpersonen de mogelijkheid om tegen een kleine betaling informatie over de keuzes en gescoorde punten van hun interactiepartners op te vragen. Ik zag duidelijke verschillen in de hoeveelheid en de soort sociale informatie die de proefpersonen opvroegen. Sommige proefpersonen waren vooral geïnteresseerd in welke optie door de meeste mensen gekozen werd, terwijl anderen meer oog hadden voor de hoeveelheid punten die hun interactiepartners met hun gekozen optie wisten te scoren. In Hoofdstuk 6 breng ik de gevolgen van deze verschillen in kaart; in een vergelijkbaar experiment laat ik zien dat mensen die vaak informatie over het succes (gescoorde punten) van hun interactiepartner opvragen, zich in sociale interacties zelfzuchtiger gedragen.

**Hoofdstuk 7** draait om de vraag hoe mensen reageren op individuele variatie in sociaal gedrag in hun omgeving. Dit bestudeer ik met een gedragsexperiment waarin proefpersonen deelnemen aan een 'Public Goods game'. In een Public Goods game worden proefpersonen in groepen ingedeeld, en krijgt ieder een budget van een aantal punten. Die punten mogen ze verdelen tussen zichzelf en een 'groepsproject'. Alle punten die in het groepsproject terechtkomen worden verdubbeld, en vervolgens gelijk verdeeld tussen alle groepsgenoten (onafhankelijk van hoeveel die groepsgenoten in het project hebben geïnvesteerd). Het blijkt dat mensen verschillend reageren op variatie in investeringen van hun groepsgenoten. Sommige mensen investeren zelf meer als er veel variatie is in de investeringen van hun groepsgenoten, terwijl anderen in dat geval juist minder investeren. Bovendien blijkt dat de eerste groep ook meer investeert dan de tweede groep als ze niet weten hoe hun groepsgenoten hebben geïnvesteerd.

**CONCLUSIES**

Het is niet makkelijk om tot een synthese te komen van een proefschrift dat in feite een verkenning in allerlei richtingen is. In de nabeschouwing van dit proefschrift (**Hoofdstuk 8**) heb ik mij dan ook niet gericht op het bij elkaar brengen van de individuele studies die ik in dit proefschrift presenteer, maar heb ik gekozen voor een andere insteek. Als wetenschapper in het grensgebied tussen verschillende disciplines zijn mij door de jaren heen een aantal overeenkomsten duidelijk
geworden tussen de belangrijkste disciplines waar dit proefschrift op steunt: de evolutionaire biologie, en de beslissingswetenschap (‘decision science’, geworteld in de economie). In Hoofdstuk 8 bespreek ik deze parallellen, en probeer ik een visie te geven op de toekomst van de interdisciplinaire ruimte waarin de evolutie van menselijk sociaal gedrag bestudeerd wordt.

Een opvallende overeenkomst tussen de evolutionaire biologie en de beslissingswetenschap is de ontwikkeling die beide disciplines in de vroege twintigste eeuw hebben doorgemaakt. Beide disciplines worden in die tijd gekenmerkt door een sterke ontwikkeling van het ‘functionele denken’, vergezeld door een sterke ontwikkeling van formele (wiskundige) technieken. In de biologie wordt deze ontwikkeling belichaamd door de ‘Moderne Synthese’, een formeel raamwerk waarin de natuurlijke selectietheorie van Darwin werd verenigd met de erfelijkheidstheorie. De Moderne Synthese maakte de evolutiebiologie tot een exacte wetenschap, en evolutie tot een proces waar aan gerekend kon worden. In de beslissingswetenschap kwam rond halverwege de twintigste eeuw de ‘Expected Utility Theory’ sterk opzetten, waarvan de speltheorie als een aftakking gezien kan worden. Ook dit bracht een formalisering van de studie van menselijke beslissingen met zich mee, inclusief exacte methoden om menselijke beslissingen te analyseren. Deze ontwikkelingen kenden ook een keerzijde: de sterke focus op functionele aspecten (welk gedrag is adaptief of optimaal?) heeft, in ieder geval in deze disciplines, de mechanistische aspecten (hoe wordt het gedrag direct veroorzaakt?) vaak overschaduwd. Onderzoek naar culturele evolutie wordt traditioneel ook sterk door dit functionele denken bepaald.

Ik doe de aanbeveling om in evolutionaire studies van menselijk sociaal gedrag de onderliggende mechanismes serieuzer te gaan nemen. Dit geldt zeker niet in de laatste plaats voor de studie van culturele evolutie. Ik denk dat we daarbij aan een tweeledige aanpak moeten denken. Ten eerste moeten we het idee laten varen dat evolutie leidt tot individuen die een perfect geadapteerde sociale strategie hebben voor iedere soort sociale interactie die ze tegenkomen. Mensen en dieren leven in zeer complexe omgevingen waarin ze te maken krijgen met zeer uit eenlopende omstandigheden. Daarom moeten we volgens mij nadenken over hoe evolutie vrij algemene gedragsmechanismen vormgeeft die goed kunnen presteren in een snel veranderende en heterogene sociale omgeving. Ten tweede denk ik dat we onze modellen voor de evolutie van sociaal gedrag en culturele evolutie sterker moeten wortelen in wat we weten over de basale cognitieve bouwstenen die aan dat gedrag ten grondslag liggen. Ik zie een belangrijke rol voor samenwerkingen tussen evolutiebiologen en (cognitieve) psychologen om deze stappen te gaan zetten.
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Pieter (Piet) van den Berg was born on the 30th of June 1984 in Rotterdam, The Netherlands. After the gymnasium in Leeuwarden and Deventer, he studied biology at the University of Groningen, graduating in 2008 (*cum laude*). After this, he worked as a researcher in the Evolutionary Psychology group and the Theoretical Biology group, and as a coordinator for two international M.Sc. programmes, at the University of Groningen. Next, Piet obtained a PhD grant from the Graduate Programme of the Dutch Science Foundation (NWO), allowing him to design his own PhD project at the Theoretical Biology Group of the University of Groningen, starting in 2012. The results of this project are presented in this thesis. Beside the scientific core business, Piet has engaged extensively in teaching and supervision at both the B.Sc. and M.Sc. level. Furthermore, Piet has undertaken various societal outreach activities throughout the years, including the organisation of workshops for high school students, interviews with the mainstream media in the Netherlands as well as abroad, and engagement in the development of the massive open online course “*Decision making in a complex and uncertain world*” that is open to the general public.

**Publications**


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