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Coordination, Cooperation, Collaboration

Three Studies on Human Capacities for Coaction

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Contents

1	Introduction	3
2	The puzzle and its pieces: a literature overview	4
2.1	The wider frame: main topics in the literature	5
2.1.1	The classics: relatedness, repetition, and reputation.....	7
2.1.2	Newer sprigs: networks, multi-level processes, and markets.....	10
2.2	Zooming in: more closely related literature	12
2.2.1	Darwinian gradation and ‘the’ problem of cooperation	13
2.2.2	Nearest neighbors in the literature.....	14
3	Original studies: coordination, cooperation, collaboration.....	17
3.1	What Niche Did Human Cooperativeness Evolve In?.....	17
3.1.1	Publication details.....	17
3.1.2	Extended abstract.....	17
3.2	Spillovers from Coordination to Cooperation: Evidence for the Interdependence Hypothesis?.....	18
3.2.1	Publication details.....	18
3.2.2	Extended abstract.....	18
3.3	The Evolution of Collaboration in Symmetric 2×2-Games with Imperfect Recognition of Types	19
3.3.1	Publication details.....	19
3.3.2	Extended abstract.....	19
4	Discussion	21
5	Conclusion	23
	Acknowledgements	24
	References	25

“In the distant future [..., p]sychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation.”
(Darwin, 1859, p. 488)

1 Introduction

For the 125th anniversary of the journal in 2005, the editors of *Science* surveyed the scientific community. They asked a broad range of colleagues to submit questions that mark critical gaps in our knowledge. From these suggestions the editors then compiled a list of the 125 most important questions facing science at the time and published it in the anniversary issue. The editors also shortlisted 25 questions that they deemed especially ‘big’, i.e. fundamental, broad-ranging, and interdisciplinarily relevant (Kennedy & Norman, 2005). “How did cooperative behavior evolve?” was selected as such a big question (Pennisi, 2005).

The fact that a topic which had already been occupying mathematicians, economists, biologists, psychologists, and scholars in other disciplines for more than fifty years at the time could make it into the ‘top 25’ scientific problems in 2005 is noteworthy. It certainly indicates that the problem poses a non-trivial challenge. Yet, it also shows how inspiring and fruitful the question is. Correspondingly, the literature dealing with cooperative behavior and its evolution was already extensive in 2005. And it has continued to grow steadily ever since.

This dissertation consists of three papers adding to that literature. While each paper comes with a motivation of its own, of course, all three are connected by a common theme. They all draw on the following rationale: if evolutionary processes usually progress incrementally, through small variations that spread in case they represent improvements relative to the status quo, can we not expect such processes to discover adaptive solutions to simpler problems first and solutions to more complex problems only later? If so, can we not expect many of those more complex solutions to be derivatives and combinations of the simpler ones? Thus, when this is so, should we not take it into account in our attempts to realistically reconstruct the paths that the evolution of human cooperativeness has taken?

The remainder of this document is organized as follows. Section 2 outlines relevant branches of the literature in order to contextualize the contributions made by the papers of this dissertation. Section 3 briefly summarizes the three original papers. Section 4 puts their results in a more general perspective and points out some directions for future research. Section 5 concludes.

2 The puzzle and its pieces: a literature overview

There is probably no doubt that, as humans, we are highly cooperative animals. We are equipped with a toolbox packed full of cooperative behaviors and possess the cognitive prerequisites to carry them out. Arguably, cooperation with other humans is so essential for us that we cannot survive more than a handful of days on our own (Tomasello, 1999, 2009).

From the perspective of a basic economic analysis, the fact that humans are able to exploit opportunities for mutual benefit is not particularly surprising, though. For rational agents inefficiency is hard to endure. Thus, if the ‘cooperative’ in ‘cooperative behavior’ is interpreted as simply meaning that agents avoid inefficient outcomes by coordinating their behaviors if needed, human cooperativeness may not appear as such a grand achievement. Instead, one may wonder why it contrasts so starkly with the behavioral repertoires of other animals. But indeed, comparative research in anthropology and other disciplines suggests that the human abilities to detect opportunities for mutualistic benefits and to coordinate in order to take advantage of them are quite unique in the animal world (Bowles & Gintis, 2011; Tomasello et al., 2005).

Thus, whether one is intrigued by the broadness of humans’ abilities to cooperate or by the apparent narrowness of the scope of other animals’ cooperative capabilities is reference-dependent. In both cases, however, the question of why we observe such remarkable differences between species seems justified (Pennisi, 2005).

Over the last decades, countless theoretical and empirical ‘pieces’ have been collected from which an army of authors has assembled potential solutions to this ‘puzzle’ of human cooperativeness (Boyd & Richerson, 2006; Gintis, 2003; Henrich & Henrich, 2006). The available pieces range from specific theoretical contributions, e.g. concerning competing concepts of equilibrium stability in evolutionary game theory (like van Veelen, 2012), to illuminating experimental results, e.g. on how chimpanzees’ behavior in the ultimatum game compares with that of humans (Jensen et al., 2007). Suggested solutions include comprehensive accounts of entire trajectories of human evolution, e.g. as presented by dual inheritance theory (e.g. Chudek & Henrich, 2011), as well as more narrowly bounded theories, e.g. of the formation and dynamics of networks of cooperating individuals or of cooperative strategy choice in repeatedly played games (e.g. Rand et al., 2011).

The following subsection, Section 2.1, provides an overview of the more general topics that the literature on the evolution of human cooperativeness is revolving around. In light of the extent of this literature, the aim of this overview cannot be completeness, of course. Instead, the goals are to briefly sketch this literature’s historic development, to recapitulate its most important concepts, and to locate those strands of the literature to which the papers of this dissertation connect. After that, Section 2.2 zooms in at selected places and surveys those works more closely that are directly relevant to the papers of this dissertation.

2.1 The wider frame: main topics in the literature

In his ‘*Descend of Man*’ Darwin (1871, p. 75) already mentions three key examples of cooperative behaviors in animals that became paradigmatic later on: joint defense against predators and other threats, pack hunting, and mutual grooming. Although all three examples are fitting illustrations of how cooperative behaviors may manifest, it is interesting to note that Darwin does not directly refer to these behaviors as cooperation. It is only in the index of this famous book that the term ‘co-operation’ can be found. Instead, when listing his examples, Darwin speaks of ‘services’ that animals render to each other (*ibid.*). The custom of implicitly presupposing a common understanding of what ‘cooperative behavior’ is that Darwin follows here, although likely not intentionally, is characteristic for much of the subsequent early literature.

It probably was not until the advent of game theory in the 1940s and 1950s that somewhat more precise semantics gained foothold in the scientific community. Particularly the development of the 2×2 prisoner’s dilemma game (PD) by RAND Corp. scientists Merrill Flood and Melvin Dresher and its popularization by their colleague Albert Tucker (cf. Kollock, 1998) advanced more systematic analyses of problems of cooperation.

		Column Player	
		<i>Cooperate</i>	<i>Defect</i>
<u>Row Player</u>	<i>Cooperate</i>	<i>R : R</i>	<i>S : T</i>
	<i>Defect</i>	<i>T : S</i>	<i>P : P</i>

Table 1: The 2×2 prisoner’s dilemma game in strategic normal form; payoffs are $T > R > P > S$.

To briefly recapitulate: in the PD two players simultaneously face the decision to either ‘cooperate’ or ‘defect’. When both cooperate, they earn a payoff of R each which is more than what they earn, P each, if both defect. However, each of the

players can be even better off, earning T , if she manages to unilaterally defect while the other cooperates, who then earns S . The resulting ordering of payoffs, $T > R > P > S$, renders a symmetric two-by-two game with a unique Nash-equilibrium, ('defect', 'defect'), which is inefficient as both players would be better off in ('cooperate', 'cooperate'). The PD thus yields a definition of 'cooperation' as strategy choice or behavior that (i) forgoes tempting benefits that might be attainable through non-cooperation, (ii) is vulnerable or exploitable through defection by others, and (iii) yields efficiency gains relative to an uncooperative status quo.

One of the upsides of defining the meaning of 'cooperation' using this dilemma is that doing so facilitates quantitative analyses of the costs and benefits that players incur when playing one of the strategies available to them. Another advantage is that the basic game is so simple that extensions in many directions become apparent immediately – in fact, the bulk of the literature on the evolution of cooperation deals with such modifications of this basic setup.

A downside that arises from defining 'cooperation' against the backdrop of the PD, however, is that it may instigate interested researchers to try to come up with solutions of 'the puzzle' that are effectively tailored to this particular – and arguably peculiar (Rusch, 2013) – simultaneous one-shot 2×2 game. Put more theatrically, the beauty of this simple game paradigm may distract valuable attention away from the complexities of real-world cooperative behavior, resulting in ahistorical solutions of an absorbing theoretical problem but not in a reconstruction of where humans are in terms of their cooperative capabilities and how they arrived there.

Still, as it reflects the historical development of this field of research rather well, there is little doubt that tracing the main strands of the literature that grew out of the PD paradigm coined by Flood, Dresher and Tucker is a viable approach to sketching what we currently know about the many mechanisms that are able to foster and sustain cooperative behavior. Eminent researchers of the field have written their books following this approach (e.g. Bowles & Gintis, 2011; Henrich & Henrich, 2007; Nowak & Highfield, 2011), and we will follow these well-trodden paths here as well. Complementary reviews of the literature are provided, for example, by Nowak (2006, 2012), West et al. (2007a, 2011), Rand & Nowak (2013), and Kurzban et al. (2015).

2.1.1 The classics: relatedness, repetition, and reputation

The branch of studies that likely started developing first solves ‘the problem of cooperation’, that we reduce to the one-shot PD for the time being, by factoring in that the two players might not be fully self-interested, but may have some stakes in each other’s welfare instead. The probably most natural motivation for doing so is the observation that players might be related, meaning that copies of a fraction, $0 \geq r \geq 1$, of one player’s genes are also carried by the other. Under the assumptions that evolutionary processes, at least in the long-run, favor behavioral strategies that maximize the expected number of copies of own genes in the population and that the costs, $c > 0$, and benefits, $b > c$, of cooperating are the same for both players and independent of the other player’s behavior, we can then ‘solve’ the PD as follows (see, e.g., Nowak, 2006).

	<i>Cooperate</i>	<i>Defect</i>
<i>Cooperate</i>	$(b - c) + r \times (b - c)$	$-c + r \times b$
<i>Defect</i>	$b - r \times c$	0

Table 2: The symmetric 2×2 prisoner’s dilemma game with genotypes who are related with coefficient $r \geq 0$; only the row type’s payoffs are shown; benefits and costs of cooperation are, respectively, $b > c > 0$.

While the resulting game as seen from the perspective of the individuals’ *phenotypes* remains a PD, with $T = b > R = b - c > P = 0 > S = -c$, the game played by the individuals’ *genotypes* becomes a different one. Table 2 shows that modified game. For appropriate values of the coefficient of relatedness of the genotypes, r , ‘cooperate’ becomes a dominant strategy in this modified game, namely precisely when $r \times b - c > 0$ and $(b - c) + r \times (b - c) > b - r \times c$ hold. It is easy to check that both conditions resolve to $r \times b > c$, which is known as Hamilton’s rule (Hamilton, 1964). Once this insight had been formulated by Hamilton, it set off a wave of studies on cooperation and altruism among kin, often subsumed under the label ‘inclusive fitness theory’ (Gardner & West, 2014; Rushton, 2009).

A question that immediately arises when inclusive fitness benefits are suggested as an explanation for cooperative behavior is that of kin recognition (Krupp et al., 2012). The ‘solution’ of the PD through relatedness critically hinges on the condition that relatives are benefitted while non-relatives are not, or not as much, at least on average. Otherwise, if such cooperation was fully non-discriminatory, uncooperative genotypes could gain foothold in populations of cooperative ones and eventually drive them to extinction. Reliable cues of kinship or other mechanisms ensuring that relatives benefit more than non-relatives, thus, are important

for inclusive fitness based altruism and cooperation to evolve (for more comprehensive accounts of inclusive fitness theory and related discussions, see, e.g., van Veelen, 2009; van Veelen et al., 2017; West et al., 2007b).

While altruism and cooperation among relatives are wide-spread in the animal world (Dugatkin, 1997, 2002) and in *homo sapiens* (Bowles & Posel, 2005; Rush-ton, 2009), humans appear to be an outlier in terms of their ability to also form and sustain cooperative relations with unrelated others (e.g., Henrich, 2006; Nowak & Highfield, 2011, but also see Clutton-Brock, 2009). The second branch of literature on the evolution of cooperative behaviors, correspondingly, rests on the idea that any two individuals playing a PD, no matter if they are related or not, can be incentivized to refrain from giving in to temptations to defect when the potential long-term benefits of doing so offset the short term benefits from defecting. This can happen, e.g., when players face a potentially infinite time horizon allowing for directly reciprocal behavior, i.e. punishment in form of the cessation of own cooperative behavior and reward in the form of its continuation (Trivers, 1971).

To illustrate the general idea: assume that the PD is repeated with a continuation probability of $1 > \gamma > 0$. Also assume that players discount payoffs in future periods by a factor $0 < \delta \leq 1$ per time period t . Then we can compare the (expected) payoffs of two strategies of this potentially infinite game, shown in Table 3. The first strategy is unconditional defection. The second, called ‘trigger grim’, cooperates until it is defected against once and then defects forever.

	<i>Trigger Grim</i>	<i>Always Defect</i>
<i>Trigger Grim</i>	$R + \sum_{t=1}^{\infty} (\gamma\delta)^t \times R$	$S + \sum_{t=1}^{\infty} (\gamma\delta)^t \times P$
<i>Always Defect</i>	$T + \sum_{t=1}^{\infty} (\gamma\delta)^t \times P$	$P + \sum_{t=1}^{\infty} (\gamma\delta)^t \times P$

Table 3: The repeated symmetric 2×2 prisoner’s dilemma game with a continuation probability of γ and players with constant discount factor δ .

Writing, shorthand, $f := \sum_{t=1}^{\infty} (\gamma\delta)^t$, we obtain that trigger grim is a best response to itself when $f > (T - R)/(R - P)$ holds, i.e. the game then has two Nash-equilibria (both of which are subgame perfect). Thus, when sufficiently patient players mutually expect each other to be playing the trigger grim strategy and the game to go on with a sufficiently high probability, perpetual cooperation becomes a viable equilibrium – note that this is just one way of formulating the so-called ‘folk theorem’

explaining how mutual cooperation can become an equilibrium in the repeated PD; for a more comprehensive account see, e.g., Binmore (2007).

The probably most famous strategy for repeated PDs is ‘tit-for-tat’ (Axelrod, 1984; Axelrod & Hamilton, 1981). This strategy always copies its opponent’s previous action and thus cooperates if its opponent did in the round before and defects if it was defected against. Tit-for-tat has repeatedly been shown to be successful against a plethora of opponent strategies (see, e.g., Nowak, 2012). However, like any other strategy for repeated games, it is susceptible to ‘indirect invasions’ (van Veelen, 2012): populations dominated by tit-for-tat can be invaded through random drift by mutants showing the same behavior when tit-for-tat is very frequent but being vulnerable to defective types on their own. The simplest example is the case of tit-for-tat being invaded by unconditional cooperation (‘All-C’), being invaded, in turn, by unconditional defection (‘All-D’). Therefore, when mutations and drift are possible, the long-term dynamics of (very large) populations playing repeated games are usually characterized by stochastic cycles between cooperative and uncooperative phases (García & van Veelen, 2018; van Veelen et al., 2012). Nevertheless, direct reciprocity undoubtedly is a powerful solution to many instances of ‘the problem of cooperation’, emerges early in childhood (Leimgruber, 2018), and is common in many cultures (Callaghan & Corbit, 2018; Gächter et al., 2010), albeit to varying degree (Falk et al., 2018).

Apart from cooperation with relatives and with strangers in repeated interactions, an integral part of modern human life is formed by one-shot interactions with unrelated strangers, online trade probably being the prime example here. It might not be a coincidence, thus, that parallel to rapid growth of the WWW the 1990s witnessed a sharp rise in the theoretical interest in how populations of players can solve cooperation problems when these players are rematched after every round, such that they never play twice with the same opponent (e.g., Ellison, 1994; Kandori, 1992; Nowak & Sigmund, 1998; Okuno-Fujiwara & Postlewaite, 1995). One solution that gained acceptance and now forms the foundation of a third mainstream literature is canonically labeled ‘indirect reciprocity’ (for a review see, e.g., Nowak & Sigmund, 2005). The central idea here is that information about a player’s past behavior is, at least to some minimally useful extent, available to that player’s current opponent such that this opponent can condition her behavior on the type of player that she believes to be facing. In other words: there need to be mechanisms

of sufficiently reliable reputation formation and transmission such that ‘defective’ behavior can be punished by future interaction partners.

The concrete ways in which reputations are actually formed and transmitted have been subject to debate in the literature. For example, reputation can be concretized as an observable ‘image score’ that decreases when a player defects and increases when she cooperates (Nowak & Sigmund, 1998) or as binary ‘standing’ that marks a player irrevocably as ‘bad’ as soon as she defects once (Milinski et al., 2001) or as compromises between these two extremes (see, e.g., Ohtsuki & Iwasa, 2004, 2006). The different ways of operationalizing the mechanisms by which reputations are formed and transmitted all have their individual advantages and downsides (see, e.g., Albert & Rusch, 2013, for further discussion).

More generally, though, comprehensive empirical work has shown that humans are sensitive to reputational information about others and to possible damages to their own reputation potentially caused by their own wrongdoing (Engelmann & Fischbacher, 2009; Resnick et al., 2006; Seinen & Schram, 2006). These insights have also already been successfully applied in the improvement of real-world institutions (e.g., Yoeli et al., 2013).

2.1.2 Newer sprigs: networks, multi-level processes, and markets

In their beginnings, the three ‘R’-branches of the literature just outlined – relatedness, repetition, and reputation – developed somewhat independently and partially in different disciplines. Repeated games, e.g., were studied in economics quite intensively, while theoretical biologists initially focused more on relatedness. However, certainly assisted by the development of evolutionary game theory by Maynard Smith and others that formally connects theoretical economists and biologists (Maynard Smith, 1972, 1974; Maynard Smith & Price, 1973; Sandholm, 2011), research on cooperative strategy choice and behavior became a genuinely interdisciplinary field of research later on (see, e.g., van Lange et al., 2014; for a recent review of evolutionary game theory see Newton, 2018).

Parallel to continued work in the ‘R’-branches, the literature has been complemented by the addition of at least three younger arms in recent years: ‘network reciprocity’, ‘multi-level selection models’, and ‘market models’. The former two classes of solutions to the PD mainly work through more sophisticated assumptions about population structure, while ‘markets’ work through conditional partner choice combined with possibilities to signaling cooperative intentions.

Network models modify a common characteristic of the ‘R’-solutions: they do not assume that every individual potentially interacts with every other individual in the population. Instead, they explicitly describe who can interact with whom by modeling individuals as the nodes of a network whose edges then represent that agents interact. In such networks, selection can favor even unconditional cooperators under certain circumstances – the intuition being that cooperators can form clusters that become stable against invasion by defectors because of the efficiency gains of cooperation that are realized within those clusters (see, e.g., Lieberman et al., 2005; Ohtsuki et al., 2006). More complex network models allow, for example, for link-breaking and the establishment of new links by individuals (Rand et al., 2011; Wu et al., 2010). Research on network models requires time-consuming numerical simulations and thus has substantially benefitted from the advancement of computational power in the last decades, making it one of the most active new branches of contemporary cooperation research (Perc et al., 2017).

Multi-level selection models go even further than network models in terms of assumptions about population structure: they assume that individuals are parts of groups and that some non-negligible component of differential selection applies at this group level. In such models, individuals are often assumed to face competition at the individual level, i.e. within groups, and groups to be in some form of competition with each other (e.g., Traulsen & Nowak, 2006). Under the assumptions that internal cooperation makes groups more successful in the group-level competition, but that, at the same time, non-cooperation is individually beneficial, a tension between group-level and individual-level selective pressures arises. Depending on which component of selection is stronger, groups of cooperative individuals can then prevail in such multi-level selection scenarios (van Veelen, 2009). Applied to the human case, but also more generally, multi-level selection models have sparked quite lively debates (e.g., Lehmann et al., 2007; Leigh, 2010; van Veelen et al., 2012). When applied to humans in order to explain why we wage wars and at the same time behave cooperatively in interactions with our compatriots (e.g., Bowles, 2009; Choi & Bowles, 2007), the proposed group-level selection models do not fit the available historical and anthropological data very well (Glowacki et al., 2017; Rusch, 2014). In other cases, however, multi-level selection approaches have been found to have some explanatory value (e.g., Biernaskie & Foster, 2016).

Market models, finally, work with combinations of pieces of theory that are also used in other branches of the literature. In particular, market models assume that some form of conditional partner choice is possible, closely resembling the mechanism of link-breaking in network models, and that some information about the opponent(s) is available to the choosing party, resembling the availability of reputational information in models of indirect reciprocity. A unique feature of market models, however, is that they allow for the information about an opponent's type to be provided by that opponent herself. The question of interest then becomes the one that other signaling models target as well (e.g. Akerlof, 1978; Spence, 1973; Zahavi, 1975): when do the respective populations end up in pooling equilibria in which both cooperative and uncooperative types signal the same intentions, i.e. information becomes useless and defection prevails, and when do they end up in separating equilibria in which signals remain meaningful and are used to maintain cooperation among cooperative types? While the details of the setups of market models vary quite widely, their workhorse mechanism of partner choice based on signals has been found to be a viable solution to problems of cooperation both theoretically and empirically (see, e.g., Barclay, 2011; Barclay & Willer, 2007; Noë & Hammerstein, 1994; Barclay, 2016, provides a review).

2.2 Zooming in: more closely related literature

As mentioned, the six branches of the literature just outlined in Section 2.1 share a common methodological characteristic. They all provide working solutions to 'the problem of cooperation' by taking the PD and adding assumptions about population structure, repetition of play, and/or information available to players. What they often leave implicit, though, is that players need to be equipped with appropriate cognitive capabilities for many of these additional assumptions to be satisfiable – some form of a memory, e.g., is a minimal requirement for both direct and indirect reciprocity. Importantly, thus, crucial additional assumptions are often introduced rather *ad hoc*, i.e. without much further reflection on the origins of the cognitive capabilities required to make these premises true (Axelrod & Hamilton, 1981 is a noteworthy counterexample).

When a cognitive ability is as useful across multiple behavioral domains as a memory is, this problem arguably is not really severe. In such a case, it seems fine to simply presuppose that players possess a memory that evolved independently earlier and are therefore able to remember all required information and to condition

their behavior accordingly. However, in cases where the cognitive capabilities required for making a certain solution to problems of cooperation viable is hypothesized to have evolved for exactly this and no other purpose, things become problematic.

2.2.1 Darwinian gradation and ‘the’ problem of cooperation

Take directly reciprocal behavior and consider a stylized example. The ability to play ‘tit-for-tat’ requires not only a (one-period) memory but at least also some form of a primitive understanding (i) that cooperation and defection in a certain social situation are possible, (ii) that the opponent also has these two options, and (iii) that one can respond to each behavior of the opponent by cooperating or defecting in the next encounter. Assuming (a) that advanced cognitive abilities are at least somewhat costly, (b) that all relevant social interaction has the characteristics of a PD, and (c) that all-out defection is the ‘original’ state of the world, then it is hard to imagine how the capabilities required for playing ‘tit-for-tat’ can evolve in parallel to ‘tit-for-tat’ play itself, because all-out defection is an evolutionarily stable state. That means: any small individual advance toward a cognitive setup allowing for ‘tit-for-tat’ play would be weeded out quickly as it induces costs but cannot realize its potential benefits as long as it is singular or rare in a population of individuals who defect perpetually.

In a discussion of this problem, Binmore (2006) trenchantly criticizes colleagues who jump from the demonstration that a cooperative equilibrium is stable to assuming that this population state can also be reached by evolutionary dynamics for making use of ‘hopeful monsters’, i.e. for assuming that the capabilities required for carrying out a certain type of cooperative behavior simply occur by chance and in sufficiently many mutants at the same time. A scenario, he argues, that is prohibitively unlikely under biologically realistic conditions.

In their seminal paper that made ‘tit-for-tat’ famous, Axelrod and Hamilton (1981) clearly identified this problem, too. They devote an entire section to the discussion of the initial viability of ‘tit-for-tat’, and suggest, in essence, that reciprocal behavior started to evolve in interactions between relatives, i.e. in a ‘safer haven’ of social interaction characterized by reduced conflicts of interests between individuals (see Section 2.1.1).

It is important to note that Axelrod and Hamilton (1981) explicitly discuss how a spin-off of unconditional altruism targeted at kin may have been gradually transformed into a separate kind of behavior – direct reciprocity – that can be used in interactions with any partner. Their suggestion, thus, is an application of Darwinian gradation and more complex than what has been referred to as a ‘mismatch’ or even ‘the big mistake’ explanation of the evolution of cooperative behavior later on (Boyd & Richerson, 2006; Burnham & Johnson, 2005; for discussions see El Mouden et al., 2014; Hagen & Hammerstein, 2006; Raihani & Bshary, 2015; for estimates of human relatedness under ancestral living conditions and their implications see Hill et al., 2011; Rusch, 2018; Walker, 2014).

The explanatory pattern assuming that a behavior that originally evolved in one context gradually expanded its scope to another context, becoming transformed and adapted underway, is not restricted to ‘spillovers’ from interactions among kin to interactions with strangers, though. As we have seen in Section 2.1.1, relatedness induces a change of the relevant payoffs of a game, e.g. transforming the PD into a situation of aligned interests for suitable values of r , c , and b . Analogously, the papers of this dissertation argue, principles of strategy choice that are adaptive in games with lower levels of conflicts of interests than PDs might have gradually ‘spilled over’ to games representing such ‘social dilemmas’, i.e. situations in which individually rational behavior results in efficiency loss at the collective level (Dawes, 1980; Hardin, 1968; Liebrand, 1983; Olson, 1965).

In recent years, a handful of senior scholars have employed explanatory patterns analogous to Darwinian gradation in their accounts of the evolution of human capacities for cooperative behavior, too (Binmore, 2007; Sterelny, 2016; Tomasello et al., 2012). Also note that Rand et al.’s (2014) theory of social heuristics includes the idea of spillovers between different behavioral domains, but assumes a cultural instead of a biological transmission of behavioral traits. Still, as the relative sparseness of the following review of directly related literature will show, much work remains to be done (also see Section 4).

2.2.2 Nearest neighbors in the literature

The first paper of this dissertation, Rusch (2013), develops the explanatory approach just laid out in more detail. Then, it points out that, at least in the limited universe of one-shot 2×2 games, PD-type social dilemmas are ‘rare’ in the sense that most other games represent situations with conflicts of interest that are less

severe. The paper then concludes by asking: in the light of this broad spectrum of possible interaction settings that are less conflictual, why should we not be interested in how principles of strategy choice that evolve in those other contexts fare when employed in more conflictual strategic settings? (A question to be taken up in the third paper of this dissertation.) This paper extensively draws on earlier work in game theory listing and classifying all 2×2 games (Fraser & Kilgour, 1986; Kilgour & Fraser, 1988; Rapoport & Guyer, 1966; Robinson & Goforth, 2005; also see Bruns, 2015) and chimes in with work taking a critical stance on the ubiquity of PD models (e.g., Alvard & Nolin, 2002; Balliet et al., 2017; Connor, 1995; Dugatkin et al., 1992; Noë, 2006; Tomasello et al., 2012).

The second paper, Rusch and Lütge (2016), presents the results of an experiment that finds evidence of behavioral spillovers between strategic contexts. Student subjects played series of 2×2 games that were either PDs or ‘Stag Hunts’, i.e. less conflictual coordination games. From a broader methodological perspective, this paper is closely related to experimental work in psychology and economics that studies strategy choice by subjects who play more than one game sequentially (Ahn et al., 2001; Albert et al., 2007; Bettenhausen & Murnighan, 1985; Bettenhausen & Murnighan, 1991; Cooper & Kagel, 2008; Devetag, 2005; Knez & Camerer, 2000; Mengel & Scubba, 2014), simultaneously (Angelovski et al., 2018; Bednar et al., 2012; Bernasconi et al., 2009; Cason & Gangadharan, 2013; Cason et al., 2012; Godoy et al., 2013; Grimm & Mengel, 2012; van Huyck et al., 1991), or in mixed ways (Liu et al., 2018) as parts of the same experiment. In the context of research on human cooperation and its evolution, though, a similar approach has only been taken by a handful of other studies so far (Duffy & Fehr, 2018; McCarter et al., 2014; Peysakhovich & Rand, 2016; Savikhin & Sheremeta, 2013).

The third paper, Rusch (2019), introduces the concept of *maxims*, i.e. principles of strategy choice that can be employed in more than one game. It then operationalizes collaboration, i.e. cooperation in the form of joint payoff maximization for mutual benefit, as such a maxim. Thereafter, it studies the performance of this collaborative maxim relative to several opponent maxims in a strategic environment that consists of randomly formed (symmetric) 2×2 games played by an entirely unstructured population of players, i.e. under structural conditions that are very unfavorable of the evolution of cooperative strategies. This paper directly builds upon work on collaboration (Angus & Newton, 2015; Newton, 2012, 2017, 2018) and also connects to recent work on team reasoning (Gold & Colman, 2018; Karpus &

Radzvilas, 2018). Somewhat more remotely, it also relates to game theoretic work studying the performance of agents who potentially play multiple games but, for one reason or the other, do not distinguish between different games too sharply (Bednar & Page, 2007; Jehiel, 2005; LiCalzi & Mühlenbernd, 2019; Mengel, 2012; Samuelson, 2001).

More detailed discussions of the respective parts of the related literature can be found in the original papers that this dissertation consists of. These original papers are listed and briefly summarized in the following Section 3.

To conclude the current broader literature review, i.e. Section 2, it may be worth noting that the number of experimental papers studying behavioral spillovers between strategic contexts and of theoretical works that propose explanations for when and why we might observe such spillovers has been increasing quite steadily over the last decade. This dissertation, thus, is part of a growing branch of the literature that is attracting a decent amount of attention. It is much to be hoped that this increased level of interest in the details of the mechanics of decision making in cooperative contexts, i.e. across multiple games, and potentially also in the evolutionary origins of these decision making routines, will not fade away too soon. Maybe this dissertation can help in sustaining or even fostering this somewhat maverick and still comparably small but quite active and very fruitful niche of the research landscape.

3 Original studies: coordination, cooperation, collaboration

This section briefly summarizes the three original studies that this dissertation contributes to the literature on (the evolution of) human cooperativeness. All three underwent peer review and are published in international journals. For each paper, bibliographic details are given, followed by an extended abstract.

3.1 What Niche Did Human Cooperativeness Evolve In?

3.1.1 Publication details

This single-authored theoretical paper, Rusch (2013), was published in *Ethics & Politics* (ISSN 1825-5167; volume XV/2, pages 82-100). The postprint version of the paper is available via URI: hdl.handle.net/10077/9678.

3.1.2 Extended abstract

The Prisoner's Dilemma (PD) is widely used to model interaction between unrelated individuals in the study of the evolution of cooperativeness. Many mechanisms have been studied that allow for small founding groups of cooperative individuals to invade and take over populations of less or non-cooperative individuals even when all social interaction is characterized as a PD (for reviews see, e.g., Kurzban et al., 2015; Nowak, 2012; West et al., 2011).

This paper critically discusses the role of the PD as the most prominent tool in cooperation research and puts forward two new objections to such an exclusive focus on PD-based models. It is highlighted that only two of the 726 combinatorially possible strategically unique ordinal 2×2 games have the detrimental characteristics of the PD and that the frequency of PD-type games in a space of games with random payoffs does not exceed about four percent.

These observations are purely *a priori*, of course. Thus, they do not compellingly imply that the empirical relevance of PDs is overestimated. However, it is proposed that, in the absence of convergent empirical information about the ancestral human social niche, the *a priori* argument put forward here can be interpreted in favor of a somewhat neglected answer to the question of how the founding groups of human cooperation themselves came to cooperate: behavioral and/or psychological mechanisms that evolved for other, possibly more frequent, social interaction situations might have 'spilled over', i.e. been applied to PD-type dilemmas only later.

3.2 Spillovers from Coordination to Cooperation: Evidence for the Interdependence Hypothesis?

3.2.1 Publication details

The coauthored experimental study Rusch & Lütge (2016) was published in *Evolutionary Behavioral Sciences* (ISSN 2330-2925, volume 10, issue 4, pages 284-296). The postprint version of the paper is available via DOI: 10.1037/ebs0000066. Author contributions are: research design H.R. & C.L., data collection: H.R., statistical analyses: H.R., wrote the paper: H.R. & C.L.

3.2.2 Extended abstract

Recent theoretical work has proposed that the evolution of human cooperativeness might, at least in part, have started as the cooptation of behavioral capacities evolved for solving problems of coordination to solve problems with higher incentives to defect, that is, problems of cooperation (Angus & Newton, 2015; Binmore, 2007; Sterelny, 2016; Tomasello, 2009; Tomasello et al., 2012). Following this line of thought, this study systematically tests human subjects for spillover effects from simple coordination tasks (2×2 stag hunt [SH] games) to problems of cooperation (2×2 prisoner's dilemma [PD] games) in a laboratory experiment with rigorous controls to rule out subject confusion or habituation. It is found that cooperation levels in PD games embedded in a sequence of SH games are significantly increased compared to a baseline sequence consisting only of PDs when subjects play in fixed pairs. No such effect is found when players are randomly rematched each round. Additional findings include that the observed spillover effect cannot prevent a decay of cooperation over time, that there is no indication of a reversed effect (i.e., no signs of negative spillovers from failed cooperation to miscoordination), and that subjects' self-reported preferences in SH games are prosocial.

It is critically discussed to which extent these findings support the interdependence hypothesis, i.e. the idea that decision making mechanisms employed in solving cooperation problems are evolutionarily rooted in, and thus partially overlapping with, decision making mechanisms used for solving problems of coordination. Attention is also given to a comparison of the explanatory power of the interdependence hypothesis with those of two alternative explanatory approaches to the experimental results: (i) the idea that subjects might be 'conditional cooperators' (Fisch-

bacher et al., 2001; Burton-Chellew et al., 2016) and (ii) the ‘social heuristics hypothesis’ (Rand et al., 2012, 2014), i.e. the idea that the decision making mechanisms that student subjects bring to the laboratory are attuned to solving the coordination and cooperation problems of everyday life rather than being the result of evolutionary adaptation.

3.3 The Evolution of Collaboration in Symmetric 2x2-Games with Imperfect Recognition of Types

3.3.1 Publication details

The single-authored game theoretical study Rusch (2019) was published in *Games and Economic Behavior* (ISSN 0899-8256; Volume 114C, pages 118-127). The postprint version of the paper is available via DOI: 10.1016/j.geb.2018.12.005.

3.3.2 Extended abstract

Ample game theoretic research on the conditions allowing for specific types of cooperative behavior to be fostered by natural and/or cultural selection exists. Nonetheless, a recent series of papers has introduced a fresh perspective on the subject within the game theoretic framework by suggesting an amendment to the concept of cooperation itself (Newton, 2012; Sawa, 2014; Angus & Newton, 2015; Newton & Angus, 2015; Newton, 2017). These authors argue that, instead of thinking of cooperation as playing a particular strategy in a specific game, usually C in the prisoner's dilemma [PD], we could also think of cooperation as coalitional strategy choice, such as jointly switching from (D,D) to (C,C) in the PD. To disambiguate play of a cooperative strategy from coalitional strategy choice, Angus and Newton (2015) suggest to refer to the latter as ‘collaboration’.

One particular strength of this concept of collaboration is its genericity, i.e. it provides a unified formal approach to describing cooperative behavior in more than one game. Correspondingly, Angus and Newton (2015) and Newton (2017) have already shown that collaboration can be positively selected for by evolutionary processes when social interaction between individuals is modeled as one of a range of specific games.

This paper complements previous work on collaboration by expanding on its genericity: conditions for the evolutionary viability of collaboration under fairly undemanding assumptions about population and interaction structure are derived.

Doing so, it is shown that collaboration is an adaptive principle of strategy choice in a broad range of niches, i.e., stochastic mixtures of games.

The model devised and analyzed here demonstrates that collaboration as a principle of strategy choice, i.e. as a maxim, can be evolutionarily viable and successful in both finite and infinite populations: it can prevail against several opponent maxims provided that the niches inhabited by the respective populations fulfill certain conditions.

Notably, collaboration's potential for evolutionary success in this model is not based on repeated encounter, population structure, information about past behavior, or any of the other previously studied factors favoring the evolution of cooperativeness. In fact, it is shown that collaboration can potentially prevail in entirely unstructured populations, even when all interaction is assumed to be one-shot. Rather, collaboration's evolutionarily fate in the model depends on whether social interaction offers sufficiently many opportunities for attaining mutual benefits, i.e. on whether a population's niche favors collaboration or not.

4 Discussion

Against the backdrop of the literature outlined in Section 2 and looking forward: what is the more general lesson to be learned from the papers collected in this dissertation? Which questions are the next to be addressed?

As stated at the outset, Section 1, the rationale underlying this dissertation is the application of the explanatory pattern of Darwinian gradation to the ‘puzzle’ of the evolution of human capacities for cooperative behavior. As pointed out in Section 2, this approach distinguishes the original papers collected here from large parts of the existing literature in this field of research. It mainly does so by moving away from the assumption that all social interaction relevant to the question of how these capacities may have evolved has the characteristics of a PD (see Section 2.1.1). Instead, the papers collected here

- (i) argue that, *a priori*, there is ample room for less conflictual social interaction in which crucial parts of the cognitive machinery required for well-functioning coaction with others could have evolved (Rusch, 2013),
- (ii) game-theoretically model a more generic principle of cooperative strategy choice that can be employed in multiple games, called ‘collaboration’, and investigate the breadth of the niches in which collaboration is evolutionarily viable (Rusch, 2019), and
- (iii) empirically test if student subjects in an economic experiment show behavior that is consistent with the idea that the cognitive heuristics we employ in cooperative strategy choice may not perfectly discriminate between different strategic contexts (Rusch & Lütge, 2016).

Each of these papers makes an incremental contribution of its own and all three also come with their individual limitations, of course: the arguments in Rusch (2013) remain purely *a priori*, the niches studied in Rusch (2019) are restricted to symmetric 2×2 games, as is the experimental design of Rusch & Lütge (2016), to name but a few. However, especially in the context of the recent renaissance of evolutionary game theory (Newton, 2018) and the rising interest in subjects’ strategy choice when playing multiple games in parallel, subsequently, or in more complex mixtures (see Section 2.2.2), this dissertation is timely in highlighting at least two more general directions for future research.

First, the papers collected here demonstrate how bringing the principle of Darwinian gradation – or, more generally, an evolutionary perspective – to bear on

questions of economic decision making entails the need for a deepened and more detailed understanding of the relevant parts of the cognitive machinery involved in it. The aim of understanding these components, their interplay, and their origins better, while perhaps never entirely achievable, defines a research agenda orthogonal to ‘neoclassical repair’ (Brandstätter & Güth, 1994, p. 10; also see Muthukrishna & Henrich, 2019). While many of the canonic models collected in the field of behavioral economics content themselves with proposing fitting utility functions that explain some specific empirically observed deviations from the predictions of pure neoclassical theory, the evolutionary approach, eventually, aims at explaining the origins and adaptive value of those fitting utility functions themselves. While some seminal work in economics taking this angle exists (especially: Alger & Weibull, 2013; Bergstrom, 1995; Frank, 1987), the full explanatory power of this approach still remains to be brought into effect.

Second, the papers of this dissertation line up with other work emphasizing that we should be searching for unified models that can explain human choices in more than one context. The evolutionary approach is one but certainly not the only explanatory angle yielding such models (also see the discussion in Rusch & Lütge, 2016). Recent work in psychology (Chudek & Henrich, 2011; Rand et al., 2014) and economics (Kimbrough & Vostroknutov, 2016, 2018; Krupka & Weber, 2013; Peysakhovich & Rand, 2016), e.g., emphasizes the role of norms in determining behavior: the key idea being here that humans quite actively develop and/or detect injunctive norms about how ‘appropriate’ possible behaviors in a given situation are and then decide whether to abide by these rules for ‘correct’ behavior or not. Similar to the study of maxims in game theory (Rusch, 2019), thus, the study of human ‘norm psychology’ promises to yield a better understanding of the more generic mechanics underlying human choice behavior in general and economic decision making in particular.

Today, thus, it is a very exciting open question if one of the theories describing more generic principles of decision making that are currently under consideration will prevail, or if the current explanatory plurality will endure, or if maybe even a new synthesis combining these theories will emerge.

5 Conclusion

So, to come full circle: when the editors of *Science* compile the next list of ‘big questions’ for the journal’s 150th anniversary in 2030, will the evolution of cooperative behavior still be on it?

Given the rather long list of established theories explaining varieties of cooperative behavior in a plethora of well demarcated contexts, one may at least wonder if the common parlance of ‘the puzzle of’ human cooperation is still appropriate. There is no doubt that humans do cooperate frequently and that most, if not all, theories for why they do have at least some explanatory grip in certain contexts. In that sense, human cooperativeness no longer represents a puzzle.

However, as discussed in Section 2.2, once we know that a problem can be solved in different ways in theory, it becomes all the more interesting to find out which of these potential solutions are the ones actually used in reality, and why, and since when. Today, as we have seen, we can say a lot about different possible types of cooperative behavior and why it can pay to behave cooperatively in many instances. Yet, our progress in answering the question of *how* we evolved the cognitive machinery enabling us to cooperate, i.e. to detect opportunities for mutual benefits and to exploit them where possible, has been rather slow.

Thus, the editors of *Science*’s 125th anniversary issue made a clairvoyant selection by choosing ‘How did cooperative behavior evolve?’ for their list. The literature reviewed here together with the original papers of this dissertation indicate quite clearly that this ‘how’ has the potential to occupy another generation of researchers in the behavioral sciences.

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