

Honest Signalling: from Microbes to Humans – Conference

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Abstracts

The Handicap Principle: How it became a scientific principle and why it can be rejected

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The Handicap Principle is the most widely cited explanation for honest signals, but its acceptance was a mistake and it can be fully rejected. Zahavi argued that honest signals evolve because and not despite of their costs, and that this idea provides a general principle for honesty and biological communication. He assumed that signals are wasteful, and that they evolve through a non-Darwinian 'signal selection' that favors waste rather than efficiency. Zahavi's radical proposals became accepted after Grafen (1990) published a signalling model, which he proposed validated the Handicap Principle. This model shows how sexual signals can be honest indicators of quality if high-quality males pay lower viability costs for signalling than low-quality ones. Grafen's model is more limited than has been assumed, and more importantly, it is not a model of the Handicap Principle (e.g., signals are efficient rather than wasteful and they evolve despite and not because of their costs). There are several reasons why these very different ideas became completely confused, but regardless, the Handicap Principle can be fully rejected.

The balance model of honest sexual signalling

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Costly mating signals are often described as wasteful 'handicaps', which only high-quality males can afford bear. Here I advocate an alternative interpretation based on efficiency rather than wastefulness. First, I show that the multiplicative nature of fitness selects for roughly balanced investments in mating success and viability under broad conditions. Then, I show how this balancing tendency manifests in signals that reveal their bearer's quality.

Do costly signals assort cooperators during inter-group competition?

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People around the globe participate in activities that involve self-harm, squandering of resources, and investment of time and energy. These activities are often part of cultural ceremonies and supposedly demonstrate commitment to the group. Researchers from various fields believe that these activities evolved to promote cooperation within groups by selecting individuals committed to collective action. Specifically, costly practices serve as indicators of a hidden cooperative phenotype, and only individuals with high phenotypic quality can afford them. Notably, previous research has shown that the frequency of costly signaling behaviors increases during times of war, presumably due to the need to reassure fellow group members of cooperative intentions. However, the direct relationship between costly signaling and increased cooperation during conflict has not been experimentally tested. In this presentation, I will discuss our efforts to answer this question through multiple studies using experimental manipulation to examine the effects of costly signals on cooperative selection, group cooperation, and resource sacrifice during inter-group competition. I will also discuss the limitations of costly signaling when applied to humans and our ongoing work on differential cost perception that may shed light on the human-specific form of signaling.

Ecce Homo Moralis: How people care about doing the right thing beyond its monetary consequences

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Abstract: Decades of experimental research show that people often incur costs to help others, even in one-shot anonymous interactions, where no direct or indirect rewards seem to be at play. Standard theories of social preferences explain this pro-social attitude by assuming that people care not only about their own payoff, but also about the payoff of others. However, in the past decade, this social preference framework has faced challenges. A number of experiments have demonstrated that behavior in games such as the Dictator game, the Prisoner's dilemma, the Ultimatum game, the Sender-Receiver game, and the Trade-Off game does not necessarily stem from social preferences. Instead, it is better explained by a general preference for doing what is morally right. According to this moral preference hypothesis, people are partly motivated by a desire to do what they believe is morally right, regardless of the economic consequences. In this presentation, I will provide an overview of the literature in this field, with a particular emphasis on recent developments and ongoing questions.

Talk about your altruism, it makes you cool and sexy – Competitive altruism as a reputation-enhancing costly signal in a real-life situation

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Altruism functions as a reputation-enhancing costly signal consequently communicating the cost of it affects the reputation of the actor. This phenomenon was studied in a real-life situation in a fundraiser community. The members enter running races and call upon their friends to donate through them to a therapeutic camp for seriously ill children. The reputation of the fundraiser increases because of their costly act for a highly appreciated aim and their friends support the fundraisers by donating to the camp. The communication of the costs of altruism for both the donors and the fundraiser, and also the reaction of the peers was studied. Donors preferred to follow egalitarian norms and communicate the cost of their altruism only in the case of an average donation but masked the cost if the donation was below or above average. To maximise their reputation increase, fundraisers signal honestly, matching the communicated cost with the objective cost, and draw attention to their subjective cost if they run a marathon or half-marathon. Fundraisers, who emphasize the subjective cost of running collect more donations, and this strategy works better for long-distance runners. Not just the communication of the cost but emphasizing the good goal of altruism enhances the reputation of the fundraiser, as talking about how they work for the children also results in more donations. We found that the communication of the cost of fundraising is under sexual selection, as fundraisers emphasizing their cost have a higher ratio of opposite-sex donors. Overall, if you want to be cool and sexy, be altruistic and talk about it. In the case of outstanding altruism, tell everybody how challenging it was. If your altruism is less outstanding, be average, and make sure all your friends know it.

Religion as a hidden topic in family communication.

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In Hungary, many people practised their religion in secret for decades after 1945, even publicly claiming the opposite of their true beliefs. They felt the need to do so because of the communist regime's anti-religious stance and sanctions that reached down to the micro-communities. In addition to common rituals, another important element in the transmission of religion within the family is communication about religion. Several studies have shown that communication about religion has an important influence on religiosity at later age (Myers 1996, Flor & Knapp 2001, Baumbach et al 2006, Fife et al 2014). There are several reasons why religion as a topic may disappear from family communication. Perhaps the most obvious of these is the decline in the importance of religion itself, the weakening and disappearance of religion within the parental or grandparental generation. Another possible reason is fear of the possible consequences of talking about religion. In our paper, we examine the lack of religious communication and its impact on religiosity in Hungary on the basis of survey data, on the one hand, and on the other hand, through the

examples of two family cases where, for different but similar reasons, fear played an important role in making religion a taboo in family communication. In one family this was triggered by the Shoah, in the other by the prevailing communist-atheist ideology. Our analysis is based on survey data and family interviews with members of three generations conducted within the international research project “The transmission of religion across generations: a comparative international study of continuities and discontinuities in family socialization“, funded by the John Templeton Foundation.

How Does Moral Self-Concept Affect Fraudulent Behavior? A Randomized Field Experiment

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We conducted a large-scale pre-registered randomized experiment among Hungarian university students to establish the causal relationship between moral self-concept and fraudulent behavior. In doing so, we tested the conflicting predictions of two prominent social psychology theories that posit different relationships between self-concept and fraudulent behavior. While self-concept maintenance theory posits a positive relationship, the moral balance theory assumes a negative relationship between self-concept and fraudulent behavior. This study contributes to experimental research on the causes of fraudulent behavior in two ways. First, we aim to synthesize conflicting theories. Second, we propose a new methodology using an instrumental variable approach where a randomized treatment is used as an instrumental variable for self-concept. Our findings show that our treatment decreased moral self-concept, resulting in a decrease in fraudulent behavior, thus supporting the prediction of the moral balance theory. We conclude that more experiments should test the sometimes conflicting predictions of social theories and advocate for more scrutiny to explore the scope conditions of the relationship between self-concept and fraudulent behavior.

On the importance of social cues in prey communication

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Organisms must gather information about their surroundings to overcome challenges such as finding resources and avoiding danger, and for optimal decision-making, individuals often complement their personal information with the use of social information. One type of social information is associated with inadvertently produced social cues that include the presence or the behaviour of others, or the product of their behaviour such as scent marks, excretions or food remnants, all of which may provide relevant updates about current environmental conditions. Inadvertent social information (ISI) use is known to occur in many ecological contexts, including predator avoidance, foraging and habitat choice, and may lead to correlated behaviours and space use among nearby animals. Predator-related social information is often transmitted from alarmed group members to naïve ones through inadvertently produced social

cues that include fright responses, changes in posture or sudden movements. Although such cues are thought to be inherently honest, the occurrence of non-induced responses (i.e., false alarms) may act against their exploitation especially if the associated antipredator response is costly. Using individual-based models, we showed that ISI use based on risk-related social cues can be adaptive in both group-living and non-grouping prey populations, facilitating population stability and persistence under high predation pressure. Additionally, we proved that prey with an imperfect predator detection ability may benefit from the occurrence of false alarms due to an increase in the number of social cue producers when the predation risk is high. Finally, simulation results indicated that the access to and use of risk-related social information not only result in more prey individuals exhibiting the antipredator response but also leads to strong non-consumptive predator effects with substantial consequences on prey consumption. Our findings extend the predictions of recent theoretical works and provide new insights into the complex phenomenon of ISI use by exploring the boundaries under which ISI use is most likely to influence the population dynamics of group-living and non-grouping prey.

The cost of the past: Do trade-offs rather than handicaps maintain honest signalling?

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Animal communication depends on signal reliability, which presents a central challenge, as low-quality cheaters may fake signals of high-quality individuals. The Handicap Principle suggests that signals are honest only when they are costly. However, the Handicap Principle, be it as popular as it is, lacks both theoretical and empirical support. In our recent paper (Számadó et al. 2023 *BMC Biology*), we have devised a method to calculate a general trade-off function at the evolutionary equilibrium for any pairwise asymmetric signalling game with a conflict of interest. This trade-off transforms the signaller's fitness such, that it becomes adaptive for any signaller to remain honest, despite any equilibrium cost. We have calculated this trade-off both for additive and multiplicative fitness cases. As it turns out from our model, signalling costs and the reliability of signals are independent, and the equilibrium cost of signals does not affect honesty: it may even be negative, benefiting the signaller regardless of the receiver's response. Honesty is rather maintained by the trade-off between fitness components, with different trade-offs applying to signallers of different qualities. A low-quality individual therefore has its optimum fitness at a different signal level than a high-quality signaller. At the equilibrium, it is the various signaller's best interest to stay in their respective optima, investing into signalling according to their different qualities. Our results refute Zahavi's claim that signals must be costly at the evolutionary equilibrium for reliability, thereby rejecting the Handicap Principle.

Introduction to the Structural Microfoundations theory

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The Microfoundations theory predicts that some demographic processes alter the social network structure in a way that the benefit from following a cooperative strategy falls. When this happens, social trust decreases, frequency of violating social norms increases, crime increases. At this point, implementing an institution that alters the payoff structure of the society in a way that cheating behaviour becomes more costly. In this sense, legal institutions are more similar to mutualistic cooperation than to strategic one. The behaviour that is 'honest' in the pre-demographic transition societies due to network reputation logic, becomes an 'honest-seeming' institutionally enforced individual act.

Signalling trade-offs provide a unified theory to explain honest and dishonest communication

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The Handicap Principle (HP) has long dominated explanations for honest signalling. Yet, the theoretical models cited as validating the HP were misinterpreted, and its central tenet – the claim that signals must be costly in order to be honest – has been refuted theoretically and empirically. A new general theory is thus needed to explain honest and also dishonest signals. Recent studies show that honesty is maintained by condition-dependent signalling trade-offs. Signalling trade-offs can provide this unification, as a growing number of studies indicate. High vs. low quality signallers face different trade-offs at the honest equilibrium therefore they are bound to invest differently. Such differential trade-offs, or lack of, can explain both honest and dishonest signalling. Moreover, these signalling trade-offs translate investments into fitness benefits, thus they provide the link between proximate and ultimate explanations, bridging over biological and economical interpretations. One strong prediction of this theory is that condition-dependent signalling trade-offs are to be found in case of every single honest communication system in nature.

Cue-driven microbial cooperation and communication: evolving quorum sensing with honest signalling

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Background: Quorum sensing (QS) is the ability of microorganisms to assess local clonal density by measuring the extracellular concentration of signal molecules that they produce and excrete. QS is also the only known way of bacterial communication that supports the coordination of within-clone cooperative actions requiring a certain threshold density of cooperating cells. Cooperation aided by QS communication is sensitive to cheating in two different ways: *laggards* may benefit from not investing in cooperation but enjoying the benefit provided by their cooperating neighbors, whereas *Liars* explicitly promise cooperation but fail to do so, thereby convincing potential cooperating neighbors to help them, for almost free. Given this double vulnerability to cheats, it is not trivial why QS-supported cooperation is so widespread among prokaryotes.

Results: We investigated the evolutionary dynamics of QS in populations of cooperators for whom the QS signal is an inevitable side effect of producing the public good itself (cue-based QS). Using spatially explicit agent-based lattice simulations of QS-aided threshold cooperation (whereby cooperation is effective only above a critical cumulative level of contributions) and three different (analytical and numerical) approximations of the lattice model we explored the dynamics of QS-aided threshold cooperation under a feasible range of parameter values. We demonstrate three major advantages of cue-driven cooperation. First, laggards cannot wipe out cooperation under a wide range of reasonable environmental conditions, in spite of an unconstrained possibility to mutate to cheating; in fact, cooperators may even exclude laggards at high cooperation thresholds. Second, lying almost never pays off, if the signal is an inevitable byproduct (i.e., the cue) of cooperation; even very cheap fake signals are selected against. And thirdly, QS is most useful if local cooperator densities are the least predictable, i.e., if their lattice-wise mean is close to the cooperation threshold with a substantial variance.

Conclusions: Comparing the results of the four different modelling approaches indicates that cue-driven threshold cooperation may be a viable evolutionary strategy for microbes that cannot keep track of past behavior of their potential cooperating partners, in spatially viscous and in well-mixed environments alike.

Contextual flexibility of honest signalling in dogs

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A review of scientific results on honest signalling in dogs reveals that dogs readily alter their honest signals to dishonest ones when dishonest signalling is more advantageous for them. Dogs adjust their signalling to the context or by relying on previous experience with the partner. Dogs are capable of altering their honesty both in conspecific and interspecific interactions. I will unravel this flexibility in various types of interactions: body size communication, playful interactions, reactions to a threatening opponent and interspecific ostensive communication. Size communication by vocalization was thought to be honest because of anatomical constraints within the vocal production system. But many species are able to signal a larger body size in agonistic and competitive contexts. Dogs are held to communicate their body size reliably with their growls, where formant dispersion correlates with their weights. These growls are interpreted by the receiver correctly, as it is demonstrated in cross-modal matching tests, where dogs were able to connect size related acoustic information to visual size information. This indicates that dogs cumulate multimodal information into one mental representation of the signaller. Although dogs are able to modify the formant dispersion characteristics of their growls, dogs body size signalling seems to be honest in conspecific agonistic contexts. Where do they use modulated, dishonest body size signalling then? Growls signal larger body size in playful situations. Exaggeration is a common feature of mammalian play behaviour. In the case of dogs, body size communication by growls usually happens in visible distance of the partner. This means, on the one hand, that larger body size communication in agonistic situation may lead to more severe fight, on the other, it means that exaggerated body size is not misunderstandable during play. Moreover, larger body size growls in playful situations are always complemented by other honest play signals, most importantly with the relaxed-open-mouth signal. According to previous findings, dogs communicate their body sizes honestly in conspecific agonistic situations. But they dynamically alter the acoustic parameters of their growls in interspecific threatening contexts, by adjusting their signalling behaviour to the fighting potential of their actual human opponent. Female-owned or partly female-owned dogs growled signalling a larger body size if the threatening human was a man. This raises the question if dogs may also alter their body size signalling in conspecific agonistic situations depending on the emotional-motivational background of the growls. Or dogs may have different conspecific and interspecific communication strategies. During competitive interactions with humans dogs show tactical deception to mislead the noncooperative human. In a test situation dogs were trained to lead a human to a hidden food. Among the human participants two were cooperative and gave the food to the dog. The third type of human participants however put the food away into their pockets. Dogs consistently led the non-cooperative, competitive human to an empty hideaway. This performance may be explained by rule-based learning or may suggest that dogs have acquired a simple theory of mind. Flexible alteration of honest signals to dishonest ones, and the use of tactical deception pinpoint the complexity of dogs' social behaviour and social cognition. These achievements are even more remarkable if we take into account that primates needed twenty to several hundred trials before they started to withhold information or mislead a competitor. This is in line with the findings of comparative language research with dogs, that also shows that when human-related social behaviour or

linguistic abilities are tested, it is not lineage that underlies abilities, but accumulated experience with human social behaviour or language.

Reputation: A device to facilitate the honesty of human communication – that is subject to strategic manipulation itself

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Safeguards of honest communication among humans lie in the social and structural embeddedness of our interactions. Embeddedness offers opportunities for cross-checking information in third-party interactions, developing and discussing evaluations of trustworthy sources and of the reliability of information. The complexity of our social world and the amount of information, however, makes it unfeasible to carefully check and validate all information we process. As a handy device for orientation, humans assign reputations to others that offer guidance of who are good interaction partners, and of who can be trusted as communicators. Individuals having a reputation of being trustworthy communicators are compensated in different ways, for instance, by social approval and receiving special treatment once resources are distributed.

Consequently, due to its benefits, the reputation of being a trustworthy communicator is subject to competition. Individuals, for instance, often share information when it is not desired and exaggerate to color information content. They do so as these could improve their assessments as communicators. The fundamental puzzle is therefore apparent: once the reputation of a communicator can be improved by coloring, inflating, or even strategically manipulating content, how can it ensure honest communication? What correction mechanisms could improve the chances that the right people are trusted as communicators? We suggest that such mechanisms can be identified in the contexts of the informal social network structure, social bonding, and cognition. These mechanisms ensure that trustworthy communicators are rewarded, and idle gossipers are mostly discredited. We highlight the importance of cross-checking the validity of information received through trusted (well-embedded) third-party interactions, the development of bonding trust to those who provided reliable information in the past, and the use of epistemic vigilance and third-party explorations to figure out the intentions of communicators. We use agent-based models and controlled laboratory decision-making experiments to demonstrate the validity and relevance of these correction mechanisms for honest communication.

Salience of Partisan Identity and Social Attitudes

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Many assume that elite polarization raises the salience of conflicts between political communities, increasing the role of identity in expressing opinions in social issues. This paper, however, argues that the current experimental paradigm of political research on attitude formation makes it hard to distinguish the effect of the salience of partisan identity from learning processes. As an alternative, we apply a method of social psychological research on identity to the study of partisanship in attitudes. The results of a series of survey-experiments in Hungary are in line with an identity-based model of attitude formation, and clearly identify the effect of the salience of partisan identity. In contrast, there is no straightforward evidence in favor of the hypothesis that attitude polarization is driven by affective polarization. We conclude that beyond social identity theory, sociological theories of role behavior can also contribute to the better understanding of partisan identity.

The diversity of activation thresholds promotes cooperation in the Threshold Public Good Games

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Societies face various collective actions, in which a certain number of group members must act cooperatively in order to reach a collective goal. But the majority of such situations presents a social dilemma: a conflict between short-sighted self-interest and longer-term collective interests. As cooperation is costly, non-cooperation pays off if others carry out the successful collective outcome. Such social dilemmas are often modelled as a Threshold Public Good Games, in which the collective goal is reached successfully if the number of cooperative decisions reaches a threshold. Because cooperation is often a costly act, to coordinate such actions actors can attempt to communicate, to ensure that cooperative decisions are only made once the chances of reaching the goal, thus meeting the threshold, is promised. In our model, actors decide to cooperate depending on the fraction of group members indicating an intention for cooperation. In particular, we focus on the distribution of decision thresholds and other function characteristic, characterising the decision attitude of an actor, in societies. We find that a medium level of diversity of decision attitudes is the optimal for reaching a successful collective action. At very low levels of diversity, the so-called bandwagon effect may not be triggered, and coordination for collective cooperation often fail. At the other end of the continuum, too high diversity may also hinder success, as more extreme type of decision attitudes may dominate. Our results translate into the policy suggestion of setting up a slightly diverse, but not too diverse groups in order to have a successful collective cooperation.