K 132250: Signalling games: honesty and reputation

Project summary

The project had two main lines of investigation: the first about the general conditions of honest signalling, the second about the role of gossip in maintaining reputation systems in humans. In the first line of research we were able to show both theoretically and experimentally that honesty is maintained by condition-dependent trade-offs and not by equilibrium cost (Számadó et al., 2022, 2023). We described the conditions of honest signalling in a Trust game with fitness interdependence (Barclay et al., 2021) and we were able to show that fitness interdependence within gossip triad promotes honest gossip (Wu et al., 2021). We investigated the role marginal cost and marginal benefit in a simple signalling game experimentally (Samu et al, in preparation). In the second line our results show that intense competition for reputation promotes cooperation more than cross-checking of gossip or social bonding (at least under lab settings, Samu & Takács, 2021). Furthermore, we were able to show that a perspective taking reputational strategy can promote cooperation in the Prisoners' dilemma (Righi & Takács, 2022). We found that gossip as a tool is more frequently used to negotiate differing opinions instead of attacking a shared enemy (Estevez et al., 2022). Last but not least, investigating gossip in disconnected groups we found more gossip when the sender and receiver are part of the same group and more positive gossip about in-group rather than out-group targets. Individuals in broker positions (links between groups) are more likely the senders and targets of negative gossip (Estevez & Takács, 2022).

We published 4 reviews, two of them in in the prestigious journal of the *Philosophical Transaction of the Royal Society B* (IF: 6.237). The first consist a brief classification of reputation systems (Számadó et al., 2021), the second is on the role of networks in maintaining reliable reputations and cooperation (Takács et al., 2021), the third review was on the role of gossip in maintaining reliable reputations (Giardini et al., 2022), last but not least is a review of reputation based cooperation (Takács, 2022).

Experimentation was impossible during most of the project due to the Covid pandemic. We still published three experimental papers (Samu & Takács, 2021, Számadó et al., 2022; Estevez et al., 2022), the fourth is under preparation (Samu et al, in preparation).

We have published two papers on microbial cooperation (Zachar & Boza, 2022; Boza et al., 2023).

Szabolcs Számadó (leading editor) and Károly Takács participated as editors in organizing and publishing a special issue on gossip –called 'The Language of Cooperation:' – in the prestigious journal of the Philosophical Transaction of the Royal Society B (IF: 6.237).

We organized a workshop in Budapest (14-15th, September, 2023) titled "Honest Signalling: from Microbes to Humans" with Szabolcs Számadó (lead organizer) and Károly Takács part of the organizing team.

We published 14 papers and 2 commentaries during the project; of those 14 papers 11 were published in Q1 and 3 in Q2 journals.

The sum of impact factor of the journals where these papers were published: **82.37**

We have two more papers submitted (to BMC Biology and Royal Society Interface) and four more papers under preparation (all credited with the OTKA number K132250).

Summary of the papers

Honesty and dishonesty in gossip strategies: a fitness interdependence analysis.

Wu*, J., Számadó*, S., Barclay, P., Beersma, B., Dores Cruz, T. D., Iacono, S. L., ... & Van Lange, P. A. (2021)

* shared first authors

(*Philosophical Transaction of the Royal Society B*, IF: 6.237)

Previous models utilizing gossip (e.g. indirect reciprocity models) assumed that gossip will be honest. However, there is plenty of empirical evidence to show that humans need not honest, gossip can be misleading. Analysing the honesty of gossip proved to be a difficult enterprise for two reasons. First of all the cost of producing gossip (i.e. speaking) assumed to be negligible, thus traditional costly signalling models could not be used. Second, there can be many, hard to specify, indirect cost of producing dishonest gossip. We use fitness interdependence theory to handle these potential indirect costs and benefits of dishonest vs. honest gossip. Fitness interdependence theory assumes a fitness interaction between players, such interaction can be described with a parameter called 'valuation'. Valuation can range from -1 to 1. On the one hand, -1 denotes conflict of interest between players, i.e. players are interested in the demise of the other player. On the other hand, 1 denotes complete shared interest where players want the best for each other. We investigated a gossip triad with a gossiper, a receiver and the target. The receiver and the target plays a two person social dilemma game (e.g. snowdrift or stag-hunt game). There are two options (two types) in these games: cooperate or defect. The signaller knows the type of the target and she may or may not communicate this type honestly to the receiver. We investigated the conditions where such communication (gossip) where honest by writing up the fitness of the gossip triad using fitness interdependence terms between players. We have shown that the signaller will be always honest if the effect of sharing honest gossip on the receiver and on the target has the same sign (negative or positive) as her valuation of receiver and the target. For example, if the effect of sharing honest gossip is positive for both the receiver and the target, the signaller will be always honest if her valuation of the receiver and target is positive for both. If there is a conflict in one of the effects vs. valuations (e.g. the effect is positive but the valuation is negative) then the cost/benefit ratio (coming from fitness effects) will decide honesty. If there is a conflict in both effect valuation then the signaller will be always dishonest. A key assumption of our model is that the receiver is always trustful. An important next step is to relax this assumption and investigate the co-evolution of trust and honesty.

Samu F. & Takács K. (2021) Evaluating mechanisms that could support credible reputations and cooperation: cross-checking and social bonding.

(*Philosophical Transaction of the Royal Society B*, IF: 6.237)

Gossip is believed to be an informal device that alleviates the problem of cooperation in humans. Communication about previous acts and passing on reputational information could be valuable for conditional action in cooperation problems and pose a punishment threat to defectors. It is an open question, however, what kind of mechanisms can make gossip honest and credible and reputational information reliable, especially if intense competition for reputations does not exclusively dictate passing on honest information. We propose two mechanisms that could support the honesty and credibility of gossip under such a conflict of interest. One is the possibility of voluntary checks of received evaluative information from different sources and the other is social bonding between the

sender and the receiver. We tested the efficiency of cross-checking and social bonding in a laboratory experiment where subjects played the Prisoner's Dilemma with gossip interactions. Although individuals had confidence in gossip in both conditions, we found that, overall, neither the opportunities for cross-checking nor bonding were able to maintain cooperation. Meanwhile, strong competition for reputation increased cooperation when individuals' payoffs depended greatly on their position relative to their rivals. Our results suggest that intense competition for reputation facilitates gossip functioning as an informal device promoting cooperation.

Barclay et.al. (2021). Cooperating to show that you care: costly helping as an honest signal of fitness interdependence.

(*Philosophical Transaction of the Royal Society B*, IF: 6.237)

There are situations where it is beneficial for the ego to know the valuation the other player has about the ego. We investigated this idea with the help of a two-step social dilemma game where players played a helping game followed by a trust game. It is important to know how the partner values the ego in the trust game, since this will determine whether the partner cooperates or not. Helping the ego in the helping game can serve as a signal for the ego that the partner has a high valuation of the ego, thus the partner will repay the trust in the second game. We investigated the conditions where such helping behaviour could serve as a honest signal of valuation. At equilibrium, helping is a costly signal of stake: helping is worthwhile for those who value the recipient (and thus will repay any trust), but is not worthwhile for those who do not value the recipient (and thus will betray the trust). Recipients demand signals when they value the signallers less and when the cost of betrayed trust is higher; signal costs are higher when signallers have more incentive to defect.

Networks of reliable reputations and cooperation: a review

Károly Takács, Jörg Gross, Martina Testori, Srebrenka Letina, Adam R. Kenny, Eleanor A. Power and Rafael P. M. Wittek

(*Philosophical Transaction of the Royal Society B*, IF: 6.237)

Reputation has been shown to provide an informal solution to the problem of cooperation in human societies. After reviewing models that connect reputations and cooperation, we address how reputation results from information exchange embedded in a social network that changes endogenously itself. Theoretical studies highlight that network topologies have different effects on the extent of cooperation, since they can foster or hinder the flow of reputational information. Subsequently, we review models and empirical studies that intend to grasp the coevolution of reputations, cooperation and social networks. We identify open questions in the literature concerning how networks affect the accuracy of reputations, the honesty of shared information and the spread of reputational information. Certain network topologies may facilitate biased beliefs and intergroup competition or in-group identity formation that could lead to high cooperation within but conflicts between different subgroups of a network. Our review covers theoretical, experimental and field studies across various disciplines that target these questions and could explain how the dynamics of interactions and reputations help or prevent the establishment and sustainability of cooperation in small- and large-scale societies.

The language of cooperation: reputation and honest signalling

Számadó, S., Balliet, D., Giardini, F., Power, E.A. and Takács, K.

(*Philosophical Transaction of the Royal Society B*, IF: 6.237)

Large-scale non-kin cooperation is a unique ingredient of human success. This type of cooperation is challenging to explain in a world of selfinterested individuals. There is overwhelming empirical evidence from different disciplines that reputation and gossip promote cooperation in humans in different contexts. Despite decades of research, important details of reputation systems are still unclear. Our goal with this theme issue is to promote an interdisciplinary approach that allows us to explore and understand the evolution and maintenance of reputation systems with a special emphasis on gossip and honest signalling. The theme issue is organized around four main questions: What are the necessary conditions for reputation- based systems? What is the content and context of reputation systems? How can reputations promote cooperation? And, what is the role of gossip in maintaining reputation systems and thus cooperation?

Commentary: why are no animal communication systems simple languages?

Dustin J. Penn & Szabolcs Számadó (2021).

(*Frontiers in Psychology*, IF: 2.99)

Pre-hunt charade as the cradle of human musicality.

Szabolcs Számadó. (2021).

Behavioral and Brain Sciences (IF: 17.33)

Four Puzzles of Reputation-Based Cooperation: Content, Process, Honesty, and Structure

Francesca Giardini, Daniel Balliet, Eleanor A. Power, Szabolcs Számadó, Károly Takács

(*Human Nature*, IF: 2.75)

Research in various disciplines has highlighted that humans are uniquely able to solve the problem of cooperation through the informal mechanisms of reputation and gossip. Reputation coordinates the evaluative judgments of individuals about one another. Although reputation and gossip might consequently support large-scale human cooperation, four puzzles need to be resolved to understand the operation of reputation-based mechanisms.

Condition-dependent trade-offs maintain honest signalling

Szabolcs Számadó, Flóra Samu and Károly Takács

(*Royal Society Open Science*, IF: 3.653)

How and why animals and humans signal reliably is a key issue in biology and social sciences that needs to be understood to explain the evolution of communication. We present the results of a laboratory decision-making experiment with human participants to test the role of equilibrium signal cost and signalling trade-offs for the development of honest communication. We found that the trade-off manipulation had a much higher influence on the reliability of communication than the manipulation of the equilibrium cost of signal. Contrary to the predictions of the Handicap Principle, negative production cost promoted honesty at a very high level in the differential trade-off condition.

A Reputation-Centered Theory of Human Cooperation and Social Organization

Károly Takács

(*Sociologica*, IF: 0.86)

While all species are unique, only humans have been able to develop complex tools and technology, and to place energy and their environment under control. Our argument is that human uniqueness lies in human sociality. Namely, largescale and widespread cooperation, the establishment and maintenance of social order, the use of language as a communication tool, advanced social cognition, and large social complexity built on social norms are characteristics of unique human sociality. Here we claim that reputation is a human invention that could have largely contributed to the development of these characteristics.

Brokering or Sitting Between Two Chairs? A Group Perspective on Workplace Gossip

José Luis Estévez and Károly Takács

(*Frontiers in Psychology*, IF: 4.232)

Brokerage is a central concept in the organization literature. It has been argued that individuals in broker positions—i.e., connecting otherwise disconnected parts within a firm's social network—can control the flow of information. We find more gossip when the sender and receiver are part of the same group and more positive gossip about in-group rather than out-group targets. Individuals in broker positions are more likely the senders and targets of negative gossip. Finally, even if both the brokers and the boss(es) are the targets of their colleagues' negative gossip, the combination of the two categories (bosses in broker positions) does not predict more negative gossip anymore.

More than one's negative ties: The role of friends' antipathies in high school gossip

José Luis Estevez, Dorottya Kisfalusi, Károly Takács

(*Social Networks*, IF: 3.140)

Gossip is universal, and multiple studies have demonstrated that it can have beneficial group-level outcomes when negative reports help identify defectors or norm-violators. We contrast two theoretical accounts. According to the first, gossip brings closer individuals who have "enemies" in common. Based on this, we infer that gossip appears in triads where both the sender and receiver share their antipathy against the target. The second position argues that gossip is used to compromise different opinions of friends towards the target. Thus, what predicts gossip is direct antipathy against the target or being friends with someone who dislikes the target (indirect antipathy) rather than the combination of the two antipathies. We test these two lines of reasoning, we found support for direct antipathy in 13 (nine unique) classrooms and indirect antipathy in five. No evidence for shared antipathy is found.

Gossip: Perspective Taking to Establish Cooperation

Simone Righi and Károly Takács

(*Dynamic Games and Applications*, IF: 1.290)

Problems of cooperation are frequent among living organisms, but they are difficult to solve. We confirm that it is difficult to obtain cooperation among agents playing the Prisoner's Dilemma when reputations are individually assigned. We propose that third-party communication (gossip) can overcome this difficulty, but only under specific conditions concerning its content, amount and persistence. We show that—in order to sustain cooperation—gossip should not only be about private evaluations of others but should also include perspective taking and exchange of information about tolerance thresholds to support cooperation. This perspective taking reputational strategy can propagate and establish cooperation in the population independent of gossip frequency and

population size, under various selection mechanisms of communication partners and targets, and assumptions concerning agents' memory.

Honesty in signalling games is maintained by trade-offs rather than costs

Szabolcs Számadó, István Zachar, Dániel Czégel, Dustin J. Penn

(*BMC Biology,* IF: 6.59)

Signal reliability poses a central problem for explaining the evolution of communication. Here we provide a general solution to this problem and show how cost functions can be calculated for any arbitrary, pairwise asymmetric signalling game at the evolutionary equilibrium. Our model clarifies the relationship between signalling costs at equilibrium and the conditions for reliable signalling. It shows that these two terms are independent in both additive and multiplicative models, and that the cost of signalling at honest equilibrium has no effect on the stability of communication. Moreover, it demonstrates that honest signals at the equilibrium can have any cost value, even negative, being beneficial for the signaller independently of the receiver's response at equilibrium and without requiring further constraints.

The Evolution of Microbial Facilitation: Sociogenesis, Symbiogenesis, and Transition in Individuality

István Zachar and Gergely Boza

(*Frontiers in Ecology and Evolution*, IF: 3.75)

Metabolic cooperation is widespread, and it seems to be a ubiquitous and easily evolvable interaction in the microbial domain. Mutual metabolic cooperation, like syntrophy, is thought to have a crucial role in stabilizing interactions and communities, for example biofilms. We review the field of metabolic communities to identify potential evolutionary trajectories that may lead to a transition. We explore these ideas, relating to concepts of multilevel selection and of informational replication, to assess their relevance in the debate whether microbial communities may inherit community-level information or not.

Eco-evolutionary modelling of microbial syntrophy indicates the robustness of cross-feeding over cross-facilitation

G. Boza, G. Barabás, I. Scheuring & I. Zachar

(*Scientific Reports,* IF: 4.600)

Syntrophic cooperation among prokaryotes is ubiquitous and diverse. It relies on unilateral or mutual aid that may be both catalytic and metabolic in nature. Hypotheses of eukaryotic origins claim that mitochondrial endosymbiosis emerged from mutually beneficial syntrophy of archaeal and bacterial partners. However, there are no other examples of prokaryotic syntrophy leading to endosymbiosis. One potential reason is that when externalized products become public goods, they incite social conflict due to selfish mutants that may undermine any mutualistic interactions. To rigorously evaluate these arguments, here we construct a general mathematical framework of the ecology and evolution of different types of syntrophic partnerships. We do so both in a general microbial and in a eukaryogenetic context. Studying the case where partners cross-feed on each other's self-inhibiting waste, we show that cooperative partnerships will eventually dominate over selfish mutants. By contrast, systems where producers actively secrete enzymes that cross-facilitate their partners' resource consumption are not robust against cheaters over evolutionary time. We conclude that

cross-facilitation is unlikely to provide an adequate syntrophic origin for endosymbiosis, but that cross-feeding mutualisms may indeed have played that role.

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

(Submitted to *BMC Biology*)

Tamás Czárán, István Scheuring, István Zachar and Szabolcs Számadó

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.

Comment on “An evolutionary process without variation and selection” by Gabora & Steel: Hidden tautology to explain evolution without selection

(Submitted to *Royal Society Interface*)

István Zachar, Jakab Máté and Szabolcs Számadó

Gabora and Steel recently claimed that cumulative adaptive evolution is possible without variation, competition and natural selection (Gabora and Steel 2021). To support this claim, they have designed a theoretical process called self-other reorganization (SOR). SOR is a process akin to learning, involving hypothetical self-organizing and self-maintaining entities, but – according to them – it differs from Darwinian evolution in that it lacks variation, selection, birth, or death. Based on a mathematical model of SOR, they claim that it implements a cumulative evolutionary process of low

fidelity, that might be relevant in modelling adaptation of non-Darwinian pre-biological or cultural systems. However, according to our analysis, severe issues stem from the (hidden) assumptions and misinterpretation of the SOR model by the authors, leading to grossly incorrect conclusions about the capabilities of SOR under any realistic condition. The authors implement a teleological system where only beneficial changes are allowed and the interpret it as 'evolution'. To test the validity of our concerns, we have implemented an individual-based version of the SOR model, adding realistic assumptions and mechanisms that were ignored in the original paper.

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

(in preparation for *Trends in Ecology and Evolution*)

Szabolcs Számadó, István Zachar & Dustin J. Penn

The Handicap Principle (HP) has long dominated explanations for of honest signalling. Yet, the theoretical models cited as validating the HP were misinterpreted, and Iits central tenet, that – the claim that signals must be costly in order to be honest, seems to contradict the evolutionary principle of cost-saving adaptive efficiency. – As a matter of fact, the tenet of HP has been refuted both theoretically and empirically many times. , and the theoretical models claimed to validating the HP were simply misinterpreted. The fact that Grafen's model was can be used to demonstrate that honesty can exist even when signals are costless actually disproves the central tenet of the HP. A new general theory is thus needed to explain account for honest and also dishonest signals in a unified and evolutionarily consistent frame. Recent studies show that honesty is maintained by condition-dependent signalling trade-offs instead of costs. Signalling trade-offs can provide this unification, as a A growing number of studies indicate that signalling trade-offs can provide this unification. 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 according to models (including misinterpreted old ones). Moreover, these signalling trade-offs translate couple various fitness components, including both short-term investments (e.g. energetic costs) into long-term fitness benefits (e.g. reproductive success), thus they providinge the necessary link between proximate (behavioural) and ultimate (evolutionary) explanations, . They also bridging overprovide the bridge between biological and economical interpretations that have been developed disjointly for decades. 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.

The role of pay-offs in learning separating equilibria in signalling games: the higher the better

(in preparation)

Flóra Samu, Károly Takács and Szabolcs Számadó

Experimental signalling games are useful tools to understand and explore the conditions of honest signalling. In a previous experiment we found that honesty and trust reached the highest levels under the condition-dependent trade-off manipulation. Yet, a fully separating equilibria, where all signallers are honest and all receiver trust the signal, was not observed not even under the most favourable manipulation. In other words, there always was some level of mixing. There can be several factors behind this observation. First of all, the separating equilibria could be counter-intuitive thus the length of the experimental sessions might not have been long enough for everyone. Second, the players in our previous experiment randomly alternated between roles of signaller and receiver. This might have switched their focus away from optimizing for a given role. Third, the difference between being successful (in getting the reward) and unsuccessful might have been perceived as small, i.e. the

participants might have been less motivated to find the separating equilibria. In other words the ratio between the marginal benefit of signalling (getting the reward compared to not getting it) and marginal cost of signalling (the cost of using the high intensity signal compared to the cost of using the low intensity signal) might have been low. Here we test the role of these two factors by manipulating the marginal benefit and the marginal cost independently. We have found that the higher marginal cost/benefit values promote honesty.

A Darwinian model of cultural replication

(in preparation)

István Zachar & Szabolcs Számadó.

Social systems require inheritance. There is a long standing debate whether social inheritance, and thus cultural evolution, is Lamarckian or Darwinian. Here we argue that there exists a unified theory of the different inheritance systems. We provide such a unified approach. By building on the abstract requirements of replication, Darwinian evolution, and the genotype-phenotype distinction, we model informational inheritance as information transmission, involving a successive set of transformations that encode/decode information when transmitting from parent to offspring (biological or cultural). Using our model, we formally identify three topologies of information inheritance that correspond to direct, Weismannian and Lamarckian inheritance. We specify the baseline conditions, under which Lamarckian inheritance can approximate Weismannian replication. We also describe other methods, which cannot, by themselves, maintain stable inheritance of information.

Moderate Diversity of activation thresholds promotes cooperation in the Threshold Public Good Games

(In preparation)

Gergely Boza & Szabolcs Számadó

Societies face various collective actions which posits social dilemmas, in which a certain number of group members must act cooperatively in order to reach a collective goal. Such social dilemmas are often modelled as 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 secured. Here we focus on the distribution of activation thresholds in societies, which captures the dynamics of peer pressure and the interaction between different levels of selfish and cooperative behaviors. Here we show that …moderate diversity of activation thresholds favours cooperation under wide range of parameters.

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Tamás Czárán, István Scheuring, István Zachar and Szabolcs Számadó (Submitted to *BMC Biology*) Cue-driven microbial cooperation and communication: evolving quorum sensing with honest signalling.

https://doi.org/10.1101/2023.04.16.537056

István Zachar, Jakab Máté and Szabolcs Számadó (Submitted to *Royal Society Interface*) Comment on "An evolutionary process without variation and selection" by Gabora & Steel: Hidden tautology to explain evolution without selection.

Manuscripts in preparation:

Szabolcs Számadó, István Zachar & Dustin J. Penn (in preparation for *Trends in Ecology and Evolution*) Signalling trade-offs provide a unified theory to explain honest and dishonest communication.

Flóra Samu, Károly Takács and Szabolcs Számadó (in preparation) The role of pay-offs in learning separating equilibria in signalling games: the higher the better.

Gergely Boza & Szabolcs Számadó (in preparation) Moderate Diversity of activation thresholds promotes cooperation in the Threshold Public Good Games.

(deposited at bioRxiv at 30 October 2023)

Zachar I. & Számadó Sz. (in preparation) A Darwinian model of cultural replication.