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### On the origins of human sociality

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# Summary

The concept of *Homo economicus* constitutes a valuable benchmark for modelling economic environments. However, it regularly fails to capture human behaviour, especially in settings including interpersonal interactions. In lab experiments and field observations, it has been consistently shown that humans are not really *Homo economicus*, that they are not profit-maximizing, rational, and selfish agents, and that they knowingly and willingly share their endowments with individuals whose identities they do not and will never know. Why and under what conditions people act prosocially have therefore occupied the minds of economists, as well as scientists from other fields, for a long time.

A crucial prerequisite for understanding human prosociality is investigating its origins, and in doing so, looking for mechanisms that can explain (i) how our sociality evolved to the extent it did, and (ii) why it did not evolve to the same extent in other species. My dissertation, therefore, focuses on examining the roots of human ultra-sociality and looks for a combination of uniquely human mechanisms that would explain the evolution of our moral sentiments. In doing so, it combines methods and insights from various disciplines, since understanding the human mind and behaviour unavoidably requires an interdisciplinary approach.

Chapter 2 uses formal evolutionary modelling to examine a common critical assumption in the group selection literature. It theoretically studies how relaxing the assumption of global between-group competition affects the conditions under which cooperation can evolve by group selection. The analytical solutions and the simulation results show that the evolution of cooperation can be substantially hindered under non-global competition. This has important implications for the empirical literature on the topic, as it shows that (explicitly or implicitly) assuming global competition likely yields biased estimates. Given the importance of group selection models for explaining a wide range of social behaviours in human and other animal populations, it is crucial to take the bias generated by the global competition assumption into account and adjust one's estimates based on the competition

structure in their relevant study population.

Chapter 3 presents the results of a lab experiment that investigates how honesty can bring advantages in partner choice. In this chapter, we examine whether honesty can cause commitment to acting prosocially in a situation with asymmetric information, and whether this commitment is anticipated by others and creates a preference for honest partners. Our results show that this is indeed the case. We also test whether the connection between honesty and prosociality goes through the impact of communication, where honest individuals act prosocially to avoid lying to their partners. We find no evidence for this path. Instead, our findings suggest that honest individuals might have a hard time justifying selfish behaviour to themselves in the first place.

Chapters 4 and 5 review the literature on the evolution of social preferences, and argue that, without considering commitment as a mechanism, one cannot fully explain the empirical observations from lab experiments. Chapter 4 builds on the work of Frank (1987; 1988). It goes through the most common theoretical models on the evolution of cooperation, checks whether the predictions of these models match the behaviour in the lab, and argues that commitment is the key to explaining the empirical data. Chapter 5 also studies the role of commitment in social interactions, but restricts the attention to fairness preferences in the ultimatum game. It summarizes the most common models in the literature that explain fair behaviour in the ultimatum game with noise or mistakes, and updates them by allowing for more general mutation structures. It then compares the model predictions to empirical observations from several ultimatum game experiments. The conclusion is again that a model with commitment performs best in fitting the data. What Chapters 4 and 5 aim at doing is a shift in focus in the literature towards studying what role commitment plays in human (social) interactions, and if and how we detect true commitment.

# Türkçe Özet (Summary in Turkish)

*Homo economicus* (İktisadi insan) kavramı, bir başka deyişle, insanların sadece kâr maksimizasyonu güden, rasyonel ve bencil varlıklar oldukları varsayımı, ekonomik modellemede kullanılan değerli bir ölçüttür. Ancak, özellikle bireylerarası etkileşimleri içeren durumlarda, *Homo economicus*, insan davranışlarını öngörmek konusunda genellikle yetersiz kalır. Sosyal davranışların incelendiği laboratuvar deneylerinde ve saha çalışmalarında, insanların *Homo economicus* olmadığı, ellerindeki imkanları bilerek ve isteyerek (tanımadıkları) diğer bireylerle paylaştıkları düzenli olarak gözlemlenmektedir. Bu gözlemler, sosyal davranışların tabiatı konusunda dikkat çekmiş, ve insanların neden ve hangi koşullar altında yardımsever davranışlar sergiledikleri iktisatçıların ve diğer biliminsanlarının zihinlerini meşgul etmiştir.

Bireylerin yardımsever ve sosyal eğilimlerini anlamak bu davranışların kökenlerini araştırmaktan geçer. Bunu yaparken, iki noktaya özellikle dikkat etmek gerekmektedir: (i) sosyal davranışların evrimsel tarihimiz boyunca nasıl geliştiğini incelemek ve (ii) yardımsever eğilimlerin diğer canlılarda neden aynı ölçüde gelişmediğini açıklayabilmek. Bu nedenle, bu tez, sosyal davranışların kökenlerinin insana özgü mekanizmalarla açıklanmasına odaklanmaktadır. İnsan zihnini ve davranışını anlayabilmek kaçınılmaz olarak disiplinlerarası bir yaklaşım gerektirdiğinden, bu tezde, farklı disiplinlerin araştırma yöntemleri ve öğretileri sentezlenmektedir.

İkinci ünite, teorik modelleme yöntemlerini kullanarak, grup seçilimi literatüründe sıkça kullanılan bir varsayımı irdeler. Bu ünite, gruplar arası rekabetin küresel düzlemde gerçekleştiği varsayımının gevşetilmesinin sosyal davranışlarının evrimine elverişli koşulları nasıl etkilediği teorik olarak incelenmektedir. Sunulan analitik çözümler ve simülasyon verileri, küresel rekabete kıyasla yerel rekabetin sosyal davranışların evrimini önemli ölçüde engelleyebileceğini göstermektedir. Bu sonuç, küresel rekabet varsayımı üzerine kurulu

grup seçilimi alanındaki verisel çalışmalar için büyük önem teşkil etmektedir. Grup seçim modellerinin sosyal davranışları açıklamadaki önemi göz önüne alındığında, bu ünite, bu alanda yapılan çalışmalarda küresel rekabet varsayımının sonuçlarının hesaba katılması ve ilgili popülasyona dair rekabet yapısının göz önünde bulundurulmasının zaruriyetini göstermektedir.

Üçüncü ünite, dürüstlüğün partner seçiminde ne tür avantajlar sağlayabileceğini araştıran bir laboratuvar deneyini raporlar. Bu ünite, bireylerin bilgiye erişimlerinin asimetrik olduğu durumlarda, dürüstlüğün adaletli davranmayı taahhüt edip etmediği, bu taahhüdün diğer partnerler tarafından öngörülüp öngörülmediği ve dürüst partnerler için bir tercih yaratıp yaratmadığı incelenmektedir. Yapılan deneyin sonuçlarının bu hipotezleri desteklediği gösterilmektedir. Bu ünite, dürüst bireylerin partnerlerine yalan söylemekten kaçınmak için adil davrandıp davranmadıkları hipotezi de test edilmektedir. Deneyin sonuçları, dürüstlük ve adalet arasındaki bağlantının, dürüst bireylerin partnerlerine yalan söylemekten kaçınmasından değil, bu bireylerin adaletsiz davranmayı en başta kendilerine karşı meşrulaştırmakta zorlandıklarından ötürü olabileceğini önermektedir.

Dördüncü ve Beşinci ünite, sosyal davranışların evrimi üzerine olan literatürdeki teorik ve deneysel çalışmaları gözden geçirir. Bu ünitelerde, mevcut literatürün göz ardı ettiği taahhüt mekanizmasının ele alınmadan bireylerin sosyal eğilimlerinin tam olarak açıklanamayacağı vurgulanır. Dördüncü ünite, Robert Frank'ın çalışmalarına dayanmaktadır (Frank, 1987; 1988). Bu ünite, sosyal davranışların evrimini açıklamayı hedefleyen mevcut teorik modeller gözden geçirilmekte, bu modellerin öngörülerinin laboratuvar gözlemleriyle eşleşmediği gösterilmekte, ve taahhüt mekanizmasının sosyal davranışları açıklamanın anahtarı olduğu ileri sürülmektedir. Beşinci ünite, ulti-matom oyununa odaklanarak, sosyal etkileşimlerde taahhüt mekanizmasının rolünü spesifik bir bağlamda detaylı bir şekilde incelemektedir. Bu ünite, ilk olarak, literatürdeki ulti-matom oyunlarında gözlenen adil davranışları bireylerin hata yapma yatkınlıklarıyla açıklayan modeller özetlenmekte ve bu modeller daha genel mutasyon yapılarıyla güncellenmektedir. Ardından, bu modellerin öngörülerini ulti-matom oyunu deney verileriyle karşılaştırılmakta, ve modeller ile veriler arasında bir uyumsuzluk olduğu gösterilmektedir. Son olarak, taahhüt mekanizmasının deneylerdeki verilerle en iyi şekilde bağdaştığı ve ulti-matom oyunundaki adil davranışları en başarılı şekilde açıkladığı gösterilmektedir. Bu bağlamda, bireysel ilişkilerdeki taahhüt yeterlilikleri göz önüne alınmadan insan davranışlarının tam olarak kavranılamayacağı tartışılmaktadır. Dördüncü ve Beşinci ünite, amaçlanan, mevcut literatürü taahhüt mekanizmasının sosyal davranışlar ve etkileşimlerdeki rolü üzerine daha çok odaklanmaya davet etmektedir.

# Nederlandse Samenvatting

## (Summary in Dutch)

Het concept van de *Homo economicus* is een waardevolle maatstaf voor het modelleren van economische omgevingen. Het slaagt er echter regelmatig niet in om menselijk gedrag uit te leggen, vooral in omgevingen met interpersoonlijke interacties. In laboratoriumexperimenten en veldwaarnemingen is consequent aangetoond dat mensen niet echt een *Homo economicus* zijn, dat ze geen winst maximaliserende, rationele en egoïstische agenten zijn, en dat ze willens en wetens hun middelen delen met individuen wiens identiteiten ze niet kennen. Waarom en onder welke omstandigheden mensen prosociaal handelen, heeft daarom economen en wetenschappers uit andere vakgebieden lang beziggehouden.

Een cruciale voorwaarde voor het begrijpen van menselijke prosocialiteit is het onderzoeken van de oorsprong ervan, en het daarbij zoeken naar mechanismen die kunnen verklaren (i) hoe onze socialiteit in die mate evolueerde en (ii) waarom ze niet in dezelfde mate evolueerde in andere diersoorten. Mijn proefschrift richt zich daarom op het onderzoeken van de wortels van de menselijke ultrasocialiteit en zoekt naar een combinatie van uniek menselijke mechanismen die de evolutie van onze moraliteit zouden kunnen verklaren. Daarbij combineert het methodes en inzichten uit verschillende disciplines, aangezien het begrijpen van menselijk gedrag onvermijdelijk een interdisciplinaire aanpak vereist.

Hoofdstuk 2 gebruikt formele evolutionaire modellering om een veelvoorkomende belangrijke aanname in de literatuur over groepsselectie te onderzoeken. Het bestudeert theoretisch hoe het loslaten van de aanname van wereldwijde concurrentie tussen groepen de voorwaarden beïnvloedt waaronder samenwerking kan evolueren door groepsselectie. De analytische oplossingen en de simulatieresultaten tonen aan dat de evolutie van samenwerking aanzienlijk kan worden belemmerd door niet-globale concurrentie. Dit heeft belangrijke implicaties voor de empirische literatuur over het onderwerp, aangezien dit hoofdstuk laat zien dat het (expliciet of impliciet) aannemen van wereldwijde concurrentie

waarschijnlijk vertekende schattingen oplevert. Gezien het belang van groepsselectiemodellen voor het verklaren van sociaal gedrag in menselijke en andere dierenpopulaties, is het cruciaal om rekening te houden met de vertekening die wordt veroorzaakt door de aanname van wereldwijde concurrentie en om schattingen aan te passen op basis van de concurrentiestructuur van de relevante studiepopulatie.

Hoofdstuk 3 presenteert de resultaten van een laboratoriumexperiment dat onderzoekt hoe eerlijkheid voordelen kan opleveren bij partnerkeuze. In dit hoofdstuk onderzoeken we of eerlijkheid kan leiden tot de neiging om prosociaal te handelen in een situatie met asymmetrische informatie, en of deze neiging wordt verwacht door anderen en een voorkeur creëert voor eerlijke partners. Onze resultaten laten zien dat dit inderdaad het geval is. We testen ook of het verband tussen eerlijkheid en prosocialiteit via communicatie gaat, waarbij eerlijke individuen prosociaal handelen om te voorkomen dat ze tegen hun partners liegen. We vinden geen bewijs voor dit pad. In plaats daarvan suggereren onze bevindingen dat eerlijke individuen het in de eerste plaats moeilijk vinden om egoïstisch gedrag voor zichzelf te rechtvaardigen.

Hoofdstukken 4 en 5 geven een overzicht van de literatuur over de evolutie van sociale voorkeuren en beargumenteren dat, zonder commitment als een mechanisme te beschouwen, men de empirische observaties van laboratoriumexperimenten niet volledig kan verklaren. Hoofdstuk 4 bouwt voort op het werk van Frank (1987; 1988). Het doorloopt de meest gangbare theoretische modellen over de evolutie van sociale voorkeuren, gaat na of de voorspellingen van deze modellen overeenkomen met het gedrag in het lab, en beargumenteert dat commitment de sleutel is om de empirische gegevens te verklaren. Hoofdstuk 5 bestudeert ook de rol van commitment in sociale interacties, maar beperkt de aandacht tot rechtvaardigheidsvoorkeuren in het ultimatumspel. Het vat de meest voorkomende modellen in de literatuur samen die rechtvaardig gedrag in het ultimatumspel door middel van ruis of fouten verklaren, en updatet ze door meer algemene mutatiestructuren toe te staan. Vervolgens worden de modelvoorspellingen vergeleken met empirische waarnemingen van verschillende ultimatumspel experimenten. De conclusie is wederom dat een model met commitment het beste presteert in het omschrijven van de data. Wat de hoofdstukken 4 en 5 beogen te doen, is een verschuiving van de focus in de literatuur naar het bestuderen van welke rol commitment speelt in menselijke (sociale) interacties, en of en hoe we echte commitment detecteren.

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Economic models regularly make the assumption that individuals are rational, selfish, profit-maximizing agents. Although this provides a valuable benchmark for modeling purposes, it fails to capture actual human behavior in interpersonal interactions. Empirical studies on cooperative behaviors consistently show that most people care about the well-being of others, even if they do not know the identity of those others. This thesis contributes to the understanding of social behaviors and preferences by exploring their origins. Using a combination of formal evolutionary modeling, lab experiments and agent-based simulations, it investigates how human sociality evolved to the extent it did, while sociality in other species remained relatively restricted.

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