Game Theory as a Foundation of Evolutionary Psychology

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Synonyms

Behavioral game theory; Decision theory; Evolutionary game theory; Experimental economics; Mathematical biology

Definition

Game theory is the mathematical analysis of interdependent systems composed of fitness- or utility-maximizing "actors" (e.g., humans, animals, genes, or viruses) whose success depends on the strategies of others.

Introduction

Game theory is a useful tool for understanding interdependent systems. It is a mathematical description of how individuals should behave in contexts in which the outcomes of their actions depend on the behavior of other individuals. Game theory has been applied to topics as varied as climate change negotiations (Helm et al. 2012), the evolution of cooperation (Nowak 2006b), and viral population dynamics (Turner and Chao 1999). Game theory makes sense of different "strategies" and "payoffs" by using the mathematical logic of each individual agent's perspective. Game theory was first used to model rational, conscious actions by humans in strategic settings; however, its usefulness now extends well beyond the realm of decision-making. The interaction between "strategies" could involve individuals making choices on a playing field, phenotypic traits occurring at different frequencies within a population, or genes within a body fighting to be passed on. In all of these cases, a successful "strategy" – choice, trait, or gene – depends on what others are doing (Maynard Smith 1982). Traits of interest to evolutionary psychologists are highly suitable to game theoretic approaches, because they so often depend on interactions between individuals.

Game theory is of fundamental importance to evolutionary psychology in four domains. First, traditional game theory played a role in the historical transition of psychology away from behaviorism and Freudian thought and toward experimentalism, microeconomic methodology, and evolutionary psychology (Gintis 2009). Second, game theory provides a rigorous methodology for documenting human decision-making and understanding the evolutionary basis of seemingly "irrational" human behavior. Third, evolutionary game theory yields new insights into the development and maintenance of complicated and seemingly paradoxical traits such as cooperation,

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long-term partnership, and altruism. Finally, many small, self-interested agents compete ("play games!") within our bodies – selfish genes, microbes, viruses, and more – with demonstrable impacts on our psychology and behavior. Because of its contributions in these four areas, game theory is a valuable tool in our effort to model and understand our evolved brains.

Game Theory

> "The world" is something like a great chess game being played by the Gods, and we are observers of the game. . . . If you play chess you must know that it is easy to learn all the rules, and yet it is often very hard to select the best move or to understand why a player moves as he does. So it is in nature, only much more so – Richard Feynman.

Historical Background

Game theory, like probability theory, arose from literal games. Probability can model and interpret dice rolls and games of chance, but game theory models poker and chess – games that depend at least in part on uncertainty about other players' decisions (Sigmund 1993). John von Neumann and Oskar Morganstern are the true fathers of game theory, but their brilliant twentieth century contributions did not occur in a vacuum; more than 200 years before their work, the first game-theoretic (i.e., mathematical) analysis of strategy was proposed. In 1713, Francis Waldegrave described a mathematical "mixed strategy" solution to the two-person card game Le Her in a letter to probabilist Pierre-Remond de Montmort. Montmort, in turn, passed the solution on to the mathematician Nicolaus Bernoulli. (This ongoing web of correspondence is most famous for its analysis of the St. Petersburg Paradox, a game with mathematically infinite "expected value" but paradoxically low subjective value to humans. This paradox is an early example of our growing awareness that humans are not perfectly rational actors in a classical, economic sense.) Waldegrave analyzed which strategy would give a player the best odds of winning, taking into account card distributions as well as the opponent's strategy. A more detailed discussion of Le Her and Waldegrave's work is beyond the scope of this entry; it is sufficient to note that this was apparently the first instance of a mathematical treatment of human strategy.

Games such as Chess, le Her, and Go inspired much verbal and some brief mathematical treatment of strategy for several centuries. But game theory in its true, mathematical form is the invention of John von Neumann and Oskar Morgenstern, with significant fundamental contributions from John Nash (among others). (John von Neumann was a genius who made significant and fundamental contributions to multiple fields, from pure mathematics to physics, computer science, and statistics. His impact beyond the invention of game theory is not always fully appreciated; Nash was admitted to Princeton as a PhD student with a three-sentence letter of reference concluding "He is a mathematical genius." He went on to receive the Nobel Prize for a single-page paper.)

In 1928, von Neumann wrote a seminal paper which founded the modern form of game theory (von Neumann 1928). In the 1940s, von Neumann and Morgenstern wrote a definitive treatise on game theory, entitled *The Theory of Games and Economic Behaviour* (von Neumann and Morgenstern 1944). They described games in formal mathematical detail and proposed rigorous methods of assessing behavior. In the preface to the first edition, von Neumann and Morgenstern outline their aims as follows: to provide a rigorous analysis of games, as well as sociological and economic problems, that involve "questions of parallel or opposite interest, perfect or imperfect information, free rational decision or chance influences." (von Neumann and Morgenstern 1944). The pair's greatest contribution was a formal mathematical treatment of topics characterized by opposing or colluding interests, chance, and varying levels of information availability.

In the middle of the twentieth century, John Nash came onto the scene with fundamental contributions that led to game theory as it is today. He furthered our understanding of what is now known as a Nash equilibrium a "stable state" of a game in which no single participant can gain from unilaterally changing strategy while all other participants' strategies remain the same. Over the course of game theory's development, much attention has been given to developing robust "solution concepts," or predictions about how a game should be played to maximize payoff, against a variety of new introduced complications (such as repeated games, and errors of judgment).

Since the work of these early pioneers, game theory has been employed and expanded upon by economists, political scientists, philosophers, biologists, and mathematicians; it has been the subject matter of many Nobel Prizes and has made significant contributions to multiple fields. In particular, game theory has played an important role in the transformation of psychology over the last 70 years from a field defined by Freudian thought, behaviorism, conditioning, and proximate cause to its current formulation as an experimental, biological, and mathematically rigorous evolutionary discipline (Gintis 2009). Game theory's influence began to be felt as early as the 1950s and 1960s, when psychologists began to uncover paradoxes in supposedly rational human thought through experimentation (e.g., Allais 1953); these results – and the emerging widespread interest in game theory (perhaps most notably exemplified by Martin Gardner's famous "Mathematical Games" column in *Scientific American* from 1957 through 1986.) – soon led psychologists to analyze decision-making via game theoretical experiments. The theories that emerged – e.g., regret theory, hyperbolic discounting, risk aversion, and other modes of discovered "irrationality" – owe a clear intellectual debt to the methodologies and principles of game theory (Gintis 2009).

While psychology was undergoing this experimental revolution, leading biologists and ethologists such as Konrad Lorenz and Niko Tinbergen began to investigate seeming paradoxes between self-interested evolution and cooperative animal behaviors. E. O. Wilson applied interpretations of animal behavior to human behavior in his landmark 1975 book (Wilson 1975), while John Maynard Smith (no relation to John Maynard Keynes, founder of macroeconomics) formalized and described evolutionary game theory as a fundamental new tool of biological analysis (Maynard Smith 1982). In short, game theory has helped provide mathematical rigor and experimentation to the field of psychology and has thus paved the way (with biology) to the development of evolutionary psychology.

Traditional Game Theory

Overview

In its original and simplest form, game theory is an economic tool to model human strategic behavior. It is often used in behavioral economics, experimental economics, decision theory, psychology, economic psychology, and more. When will individuals be selfish? When does it pay to be aggressive, and when does it pay to cooperate? What circumstances give rise to altruism? As we will see below, many experimental "games" answer these questions in a lab setting, such as the commonly-described games Prisoner's Dilemma, Hawk-Dove, and more.

A "game" is an interplay of actors, each of whom rationally seeks to maximize her own preferred results (formally defined as her utility). These actors can adopt a number of "strategies," or methods of engaging with other actors, and, as time goes forward, good strategies are rewarded and bad strategies are punished.

Each person does not know what strategy the others will employ. Eventually the game may result in a stable "solution" – a solution where one best strategy rises to dominance among all the actors, or where the proportion of actors with certain strategies remains constant over time. As we will see later, such stable strategies are not always achievable – consider a game where strategy A beats strategy B, strategy B beats strategy C, and strategy C beats strategy A. Furthermore, there can be "high" and "low" peaks of stability; imagine two adjacent mountain ranges with a valley in between. Human actors seeking to climb as high as possible can only tell whether they are headed up or down; as a result, they may well continue on a path toward a "good" outcome (the lower of the two peaks) without ever catching sight of the "best" outcome. We will discuss evolutionary game theory in detail in section "Evolutionary Game Theory" below, but for now simply note that evolutionary game theory deals with "actors" that can be individual organisms, single species, or genes and with "strategies" that are quite broadly defined to include not only behaviors but also a wide range of other variables such as phenotypes and proportions of genes in a population.

Types of Strategies and Strategy Sets

Actors can adopt pure or mixed strategies from a strategy set that is continuous or discrete. Pure strategies are individual and consistent for a given actor. In traditional game theory, pure strategies are a single actor's commitment to act in a single way all the time. A prisoner could always defect (not cooperate), or always cooperate. As we will see in more detail in section "Evolutionary Game Theory" below, single-locus-determined genetic traits, such as hair color (determined by a single gene), are "pure" strategies (in the evolutionary sense).

Mixed strategies involve assigning a probability (sampled from a continuous distribution) to each element of a finite, discrete set of strategies. For example, when choosing from the strategy set "cooperate" or "defect," an individual could consistently cooperate with others at a 60% rate and defect at a 40% rate. This does *not* require that she knows what others will be doing; it simply means that 60% of the time she encounters another person in a game, she will cooperate, and 40% of the time she will defect.

In game theory, continuous strategy sets can be distinguished from discrete strategy sets. One example of a continuous strategy set would be an investor deciding *when* to sell a stock, because time is continuous. (Since we can only measure time at discrete moments, it is only an approximation to say time is continuous.) She could select any time within brackets, with a probability distribution over the range of times. Many evolutionary "strategies," or "traits," are continuous, such as height, weight, brightness of color, or neuron density.

In contrast, discrete strategy sets offer well-defined, nonoverlapping options – such as the potential behaviors "cooperate" or "defect," or a gene coding for blue eyes versus brown eyes.

Types of Games

Games can be symmetric or asymmetric. The former involves players with access to the same set of strategies: for example, in a symmetric hawk-dove game, each individual can choose to act as a hawk or a dove. Hawks in this game are aggressive: they attack whomever they encounter in order to try to claim the whole food resource. Hawks receive a bonanza if they encounter a pushover Dove, but self-destruct through fighting if they encounter another Hawk. Doves are docile; they either accept defeat (and a small payoff) if they encounter a Hawk or split the reward if they encounter another Dove. In typical formulations of the game, each actor will adopt a consistent strategy to be either a Hawk (H) or a Dove (D) for all of that actor's encounters (in most formulations of the game, actors do not know which strategy their opponents will choose). The optimal strategy ultimately depends on the relative payoffs of the four possible types of encounter (H-H, H-D, D-H, and D-D), where encounters are usually treated as being "commutative" – i.e., H-D has the same result for the Hawk and the Dove as D-H; there is no importance to the ordering of the participants in an encounter. There are circumstances where order does matter, even in symmetric games. For example, where the actor initiating an encounter has an advantage. One can imagine a scenario where in a D-H encounter the Dove and Hawk both survive and go their separate ways unscathed (because the Dove sees the Hawk and flees) while in H-D the Hawk catches the Dove by surprise and takes its bounty.

The second kind of game is asymmetric – the actors do not have access to the same strategy sets, or have unequal knowledge about opponent strategies or the environment. This is often more realistic for evolutionary games; games could play out between two sexes, two ages, two sizes, or territory owners and territory invaders (Maynard Smith 1982). Imagine again the hawk-dove game, but give an extra bonus to one of the two players – whichever player “owns” the territory on which the fight occurs (and such “ownership” is not a variable – the actors have no opportunity to choose whether they are owners or invaders – but instead are assigned one role or the other as a parameter of the game). This is asymmetric, because the players do not have equal access to strategies and knowledge.

Games can also be “zero-sum” or “non-zero-sum.” In zero-sum games, the total benefit to all players sums to zero. In other words, a player can only benefit at the expense of other(s). Non-zero-sum games do not have this restriction. Poker zero-sum game, while many games are non-zero-sum, since some outcomes result in net benefit or net loss.

Solution Concepts

> You’ve got to know when to hold ‘em, know when to fold ‘em, Know when to walk away, know when to run. The Gambler, by Don Schlitz, sung most notably by Kenny Rogers.

Solution concepts are formally described predictions of how a game should be played to maximize a player’s payoff. For example, in most classic formulations of the Prisoner’s Dilemma (described in detail in a later section), the rational solution concept is “always defect.” For a Hawk-Dove game, a solution concept could be “choose to act like a Dove 40% of the time and like a Hawk 60% of the time,” or, equivalently, “40% of the population are pure Hawks and 60% are pure Doves.” (This equivalence is explained below in section “Evolutionary Game Theory”). These percentages depend on relative payoffs. There are many variations of solution concepts in traditional game theory, depending on the motivations of the actors, whether a game is “iterated” (i.e., repeated over time between two actors or in a group of actors), whether a game is symmetric or asymmetric, and more. Any description of a solution to a game is technically a solution concept, whether or not the behavior is deemed normatively good.

Two important categories of solution concept are “Pareto-optimal solutions” and “Nash equilibria.” Pareto-optimal solutions feature a distribution of strategies such that no one actor’s lot can be improved without hurting the lot of another (Pareto 1896). On the other hand, Nash equilibrium is reached when no single player can improve her own lot by *unilaterally* changing her strategy (Nash 1951). In fact, Nash equilibria are not always Pareto-optimal. Consider the classic prisoner’s dilemma game: two prisoners accused of having jointly committed a crime are brought into a divided room; they cannot communicate with each other, but both are told the rules of the game. Each prisoner can either cooperate (with the other prisoner, not with the police!) by staying silent about the crime or “defect” by confessing and trying to gain freedom – figuratively throwing the other prisoner under the bus. If both cooperate, and neither confesses, they each get only 1 year in prison. If both “defect” by confessing, they each get 2 years in prison. And if one defects but not the other, the first goes free and the second gets 3 years in prison. Nash equilibrium is reached when both players defect; in this case, both players get 2 years of prison, and neither player can improve her own outcome by unilaterally changing her strategy to “cooperate.” If she did, she would receive 3 years in prison while her partner would go free. However, this solution is not Pareto-optimal. The Pareto is reached if both players cooperate and do not confess: here, both players get 1 year, which is collectively better than both players getting 2 years. Obviously, though, this Pareto optimum is not a Nash equilibrium, since if one player defects and confesses, they go free while the other player gets 3 years in prison. In sum, this classic prisoner’s dilemma game illustrates that solutions which are Pareto-optimal are not always examples of Nash equilibria and vice versa. Indeed, if Nash equilibria were always Pareto optimal, game theory would be a good deal less interesting than it is.

Examples and Notation

Let us take a very simple example as illustration. The “Hawk-Dove” game discussed above has also been called the “Snowdrift” game and the game of “Chicken,” names that reflect the diverse research fields which have happened upon mathematically identical games. The games vary slightly by conventional assignment of symmetry versus asymmetry and cost-benefit ratios. Although the names are lighthearted, the "Snowdrift/Hawk-Dove/Chicken" game describes the fundamental underpinnings of mutually assured destruction by nuclear war. Bertrand Russell describes the game of "Chicken" in an extended allegory (Russell 1992) (Fortunately, at least so far, Russell's fears have proven to be unfounded, possibly displaying some of the limits of game theory, or alternatively of Russell's employment of it in this context.):

> Since the nuclear stalemate became apparent, the Governments of East and West have adopted the policy which Mr. Dulles calls 'brinkmanship'. This is a policy adapted from a sport which, I am told, is practiced by some youthful degenerates. This sport is called 'Chicken!'. It is played by choosing a long straight road with a white line down the middle and starting two very fast cars towards each other from opposite ends. Each car is expected to keep the wheels on one side of the white line. As they approach each other, mutual destruction becomes more and more imminent. If one of them swerves from the white line before the other, the other, as he passes, shouts 'Chicken!', and the one who has swerved becomes an object of contempt. . . . The game may be played without misfortune a few times, but sooner or later it will come to be felt that loss of face is more dreadful than nuclear annihilation. The moment will come when neither side can face the derisive cry of 'Chicken!' from the other side. When that moment is come, the statesmen of both sides will plunge the world into destruction. (Russell 1992)

Let us imagine a game of Chicken played by two teenagers named Marty and Tory. They drive cars toward each other at high speed, and can choose at the last second to maintain course or to swerve. If both maintain course (strategy "maintain"), they collide and both cars are destroyed. Let us assume that the people inside survive unscathed, because they were wearing seatbelts and had properly functioning airbags, but the financial loss is devastating. If one swerves (strategy "swerve"), she makes it out, car undamaged – but with the label "chicken" and its associated social cost, while her opponent is the brave victor. If both swerve, they both save face. These strategies and payoffs can be represented with a simple payoff matrix:

		Tory	
		Swerve	**Maintain**
Marty	**Swerve**	*Tie, tie*	*Coward, Hero*
	Maintain	*Hero, coward*	*Crash, crash*

In italics within each box, Marty's choice is represented on the left and Tory's on the right. In the top left box, both choose to swerve and they tie. In the top right box, Tory maintains course while Marty swerves – so Tory is a hero and Marty is a chicken. We can assign numerical values to these outcomes as follows, assuming catastrophic losses if they collide and minor gains/losses if one swerves:

		Tory	
		Swerve	**Maintain**
Marty	**Swerve**	0,0	−1, +1
	Maintain	+1, −1	−10,−10

To simplify matters, let us adjust our notation by writing the payoff matrix only for Marty's expected payoffs:

		Tory	
		Swerve	**Maintain**
Marty	**Swerve**	0	−1
	Maintain	+1	−10

Brief inspection of this matrix reveals that the potential loss of swerving (at most −1) is insignificant compared with the risk of staying on course (−10). However, suppose that Tory thinks this through and realizes that Marty will probably arrive at that same conclusion. Might it not be better for Tory to assume that Marty will act reasonably, so Tory can choose to maintain and thus collect the +1 value of being a hero? Formally, this symmetric game has one Nash Equilibrium that is a mixed strategy: swerve with probability P and maintain with probability (1-P). This probability P depends on the payoff matrix; in this case, without writing out the math, P = 1/10; each player should swerve 9 out of 10 times and maintain course 1 out of 10 times. On the other hand, if one driver is gifted with the knowledge of what the other driver will do – that is, if we convert this into an asymmetric game – the Nash equilibrium is to "do the opposite of your opponent."

The "Snowdrift" formulation of the game is somewhere different. Two drivers, Tom and Sam, both get their cars caught in a snowdrift. They each can choose to cooperate by getting out of the car and shoveling in the bitter cold, or defect by relaxing in their cars listening to The Beatles. The benefit *b* is getting home, while the cost *c* is shoveling in the cold. If they both cooperate, they can split the work so the cost is c/2 while the benefit of getting home remains b.

Here is the payoff matrix, written from Sam's perspective:

		Tom	
		Cooperate	**Defect**
Sam	**Cooperate**	b – c/2	b – c
	Defect	b	0

Clearly, Sam would most like to do no work but nonetheless get home safely – the case whereby she defects and Tom cooperates. Indeed, if b > c, the best strategy is to do the opposite of your opponent assuming you have special ability to see their choice (defect if they cooperate, cooperate if they defect). But what if b < c – if the costs of doing the work alone outweigh the benefits of getting home? In that situation, both players are better off defecting.

Indeed, this unorthodox formulation of the snowdrift game wherein solo costs outweigh benefits is mathematically equivalent to the Prisoner's Dilemma. Consider such a case, where the cost of shoveling alone is 6 and the benefit of getting home is 3.

		Tom	
		Cooperate	**Defect**
Sam	**Cooperate**	0	−3
	Defect	3	0

Whether Tom defects or cooperates, Sam is better off defecting. If Tom cooperates, Sam could earn 0 or 3 by cooperating or defecting, respectively; if Tom defects, Sam could earn −3 or 0 by cooperating or defecting, respectively. Since 3 > 0 and 0 > −3, Sam should always defect. Since Tom will make the same realization, Tom will always defect as well – and we have arrived at equilibrium, sitting inside two cars in a snowdrift listening to The Beatles. (Of course, games where cooperating is the best move for both parties also exist! They just aren't very compelling.)

Conventionally, the name of a game reflects the ranking of payoffs, such that, for example, a "prisoner's dilemma" must have "defect" as the optimal strategy.

These are the building blocks of traditional game theory, which models rational actions and strategies for individuals seeking to maximize their own utility. But the astute reader may notice a flaw: humans are not rational, and utility is not easily quantified. We will discuss this and other drawbacks of game theory in section "Limitations of Game Theory."

Evolutionary Game Theory

Overview

Evolutionary game theory was founded and developed by John Maynard Smith (Maynard Smith 1982) as well as Karl Sigmund and many others. It was first introduced formally to biologists in 1973 in a *Nature* paper entitled "the Logic of Animal Conflict" (Maynard Smith and Price 1973) and has been used extensively since then. However, prior to the pioneering work of John Maynard Smith, the ideas of game theory were used in evolutionary biology in R. A. Fisher's work on sex ratio theory (what sex ratio should a female give birth to, given the current sex ratio of the population?), Bill Hamilton's subsequent work on sex ratio and his introduction of an "unbeatable strategy" (which would give rise to evolutionarily stable strategies), and Lewontin's work on populations "playing against nature" (Fisher 1958; Hamilton 1967; Sigmund 1993).

Classic game theory models conscious actions and resulting outcomes by individual players; it relies on a premise of rationality and an end goal of utility maximization. How can this method be applied to evolution, to populations of individuals with static traits? Evolutionary game theory plays with Darwinian fitness (instead of rationality) and natural selection (instead of utility maximization). Evolutionary game theory does not require rationality or even conscious thought at all. However, classical game theory does not technically require conscious thought either. The fundamental requirement for game theory is that the success of strategies depends on what others are doing; equivalently, a strategy interacts with the strategy of other actors to determine outcomes. This is perfectly suited to evolutionary systems. Strategies are just traits – phenotypes, in a population – whether the trait is physical, behavioral, or otherwise. Of course, evolutionary game theory does not presume the absence of conscious decision-making; it is equally useful when modeling traits such as cooperation and defection as it is when modeling hair color or genetic conflict.

Evolutionary game theory extends the domain of "games" to include the competition for survival among "agents" – in this case, organisms and genes. The driving force underlying classical game theory is rational utility maximization, but the driving force in evolutionary game theory is natural selection – in other words, reproductive fitness replaces utility. Finally, "strategies" in evolutionary game theory are biological traits, or phenotypes, that can arise from the interaction between the individual's genotype (i.e., genetic makeup) and the environment. For example, traits can include brain size, neuronal density, hair color, altruistic decision-making, mate choice preferences, viral deadliness, and aggression in mate competition. Evolutionary game theory models the changes in relative frequency of these traits over time (and over generations) in a population. Its crucial contribution to biological modeling is the ability to interpret situations where an individual's fitness depends on the proportions of phenotypes in a population and interactions between phenotypes (Nowak 2006a), often exemplified by the value of being a "rare" type in biological systems. For example, if a common virus sweeps through a human population, generally most humans develop an immune response; a new, rare, variant of that virus is far more successful than its precursor. In other words, evolutionary game theory helps us understand frequency-dependent fitness, and phenotypic interaction, both of which are ubiquitous in biological systems (Vincent and Brown 2005).

Like traditional game theory, evolutionary game theory has a solution concept, labeled evolutionarily stable strategies (ESS), which is closely related to the concept of a Nash equilibrium, although those who first described ESS were unaware of Nash equilibria at the time. The defining characteristic of an ESS is that it is "uninvadable" by alternative strategies: when the population is at or near an ESS, that ESS is robust against other strategies. For example, "cooperation" is only a pure evolutionarily stable strategy if the invasion of cheating at low levels would not be favored; indeed, social punishment of cheaters is often seen to be a mechanism by which cooperation remains a stable strategy. In other words, the incremental introduction of alternative strategies cannot successfully invade a population at ESS.

The definition of "pure" versus "mixed" strategies, and their involvement in solution concepts, in evolutionary game theory requires additional explanation. A gene coding for a particular phenotypic trait regardless of environmental involvement is a "pure" strategy for an individual. Imagine a gene in frogs that determines whether a male frog "sings" or "keeps quiet" in its quest to attract a mate. That gene might control with 100% accuracy whether or not a frog sings; in this case, we can describe a solution concept as being a population of "pure strategy" frogs where 30% always sings and 70% always keep quiet. That would be the exact proportion that successfully represents the proportional tradeoff between attracting unwanted attention of predators and attracting the desired attention of potential mates. It is mathematically equivalent to a different scenerio: a scenario whereby each individual frog adopts a "mixed strategy" of "sing 30% of the time and keep quiet 70% of the time." That solution is mathematically identical to a population split between two types of pure strategist frogs.

Biology: Game Theory at Many Levels

> Any modern organism is a Russian doll of actually or potentially reproducing units. – Leo Buss (1999)

Selection can act at many levels, and self-interested agents compete for their own purposes in many biological arenas. For this reason, evolutionary game theory has applications in many levels of biological organization, from proteins to populations.

Previously, evolutionary game theory has been conceptualized as two interlocking games: the inner game and the outer game (Vincent and Brown 2005). In the inner game, players interact with one another using "strategies" (phenotypes) and receive payoffs. In the outer game, evolution itself takes place: successful phenotypes ("strategies") are more frequently passed on, and population phenotypic frequencies alter in response (the inner game and outer game correspond, respectively, to Hutchinson's ecological theater and evolutionary play (Hutchinson 1965)). In the eyes of evolutionary game theory, a player can be at one of many levels: a human in a prison; a hyena in a group; a species in a community; an ant colony; cancerous cells within our body; or genes that exist at different frequencies in a population. In classical game theory, players consciously choose strategies from an available array; in evolutionary game theory, players inherit strategies as phenotypes. Further, evolutionary games can have many actors who are strategically identical: same strategies; same payoffs (this can be true of classical game theory as well). In sum, a classic conception of evolutionary game theory maximizes fitness of "agents" by looking at heritable phenotypic "strategies." In the inner game, mice compete against other mice to gather nutrients and do their best to avoid predators of other species; in the outer game, successful mice pass on their genes which vary in frequency within a population over time.

However, there is a third arena for biological games: within each individual mouse, "strategic genes" (Haig 2012) are playing chess too. As Austin Burt and Robert Trivers write in their landmark book on genetic conflict, "the genes in an organism sometimes 'disagree' over what should happen" (Burt and Trivers 2006). For example, whether a particular allele in an individual comes from its mother or father influences its evolutionary "priorities" and subsequent expression, as modulated through a process known as "genomic imprinting" (Haig 2002). (The intriguing phenomenon is too complicated to discuss further here, but refer to ▶ "Imprinting" in this volume.) Further, genes have many clever strategies to enhance their own transmission, or to change their host's behavior toward related individuals. Some genes kill off opposing genes and "drive" themselves toward high frequency levels; some genes "overreplicate" to achieve an unfair advantage (Burt and Trivers 2006). Genes interests do not always align with the interests of the organism in which they reside; sometimes they are neutral, and sometimes they even hurt an organism's fitness. Game theory, in combination with other approaches, can effectively model games between and among genes (Traulsen and Reed 2012). Genetic conflict is a third arena in which competitive or cooperative games play out, and it is one that clearly influences evolutionary psychology (as we will see below).

Genetic conflict is not the final arena. Just as our own native genes fight with one another, other self-interested players inhabit our body: gut microbes; brain microbes; foreign human cells; viruses; and more are engaged in an ongoing game with our body and each other. These dynamics are perfectly suited to game-theoretical modeling (Nowak 2006a), and these organisms demonstrably impact our psychology and behavior (Kramer and Bressan 2015). The rabbit hole goes deeper still; even proteins folding and enzymes acting in catalytic pathways can be better understood via game theoretical methods (Bohl et al. 2014). But let us not get lost too far in wonderland. Suffice it to note that game theoretical "individuals" in an arena are sometimes arenas themselves.

These interesting, and interlocking, games also complicate a more traditional approach to evolutionary game theory, where "individuals" are coherent beings with unified fitness of all of their parts, instead of arenas where genes and viruses compete for their own selfish interests. We return to this topic below, in ▶ "Frontiers of Game Theory in Evolutionary Psychology."

The Influence of Game Theory on Evolutionary Psychology

> Lord, what fools these mortals be! – Robin Goodfellow, A Midsummer Night's Dream, William Shakespeare.

Game theory has been helpful in unraveling some of the greatest mysteries in evolutionary psychology. The first and most well-known such contribution involved a series of behavioral experiments in the mid-late twentieth century revealing that our brain has been shaped by evolutionary pressures to think in ways which do not line up with intuitive predictions that our decisions would be guided by rational analysis. These experiments showed that humans are not rational thinkers in a classical sense: we greatly discount the future; are unduly influenced by striking events; exhibit loss aversion, and more. These results opened the door to questions – which are still the subject of active research – about *what* our brains work to maximize, *how* we process information, and *in what contexts* we depart from pure rationality.

Most subsequent incorporations of game theory into biology concern biological problems which are of interest to evolutionary psychologists, such as sex ratio, parent-offspring conflict (here, we refer to genetic conflict, as described in a previous section), the evolution of language, and the evolution of cooperation (Nowak 2006a). Game theory has helped to model and explain seemingly suboptimal life strategies, such as long-term pairing and cooperation between unrelated humans. It facilitates insights into the maintenance of human psychological variation, and analyses of genetic conflict and subcellular games provide insight into inefficiencies of human behavior and our own social attitudes. Any psychological trait which depends on similar traits in other humans is a good candidate for game theoretical analyses. Below are just a few examples of the wide breadth of research in the field.

Classic Applications: Humans Are Not "Rational"

Game theory's direct influence on evolutionary psychology first arose in the mid-twentieth century, when researchers brought game theory to bear on psychological experiments. This body of work, from the mid-twentieth century to today, is often known as behavioral game theory. A major contribution of behavioral game theory was the observation that human behavior does not line up with what would be expected of a rational, utility-maximizing actor. One of the earliest conducted experiments in behavioral game theory uncovered the Allais Paradox. This describes a phenomenon by which humans given a choice of different lottery conditions make seemingly inconsistent choices with what the expected payoff would be (Allais 1953). The experiment can be written simply as two choices: Test 1 = [A + X versus B + X], and Test 2 = [A + Z versus B + Z], where each letter represents a payoff and a probability. Since in Test 1, X is consistent between the choices, and in Test 2, Z is consistent between the choices, the rational expectation would be for people to consistently prefer the first option in both test cases or the second option in both test cases. This, however, is not what experiments demonstrate! Instead, the type of addition contributed by X or Z can makes humans, seemingly illogically, choose the first option in Test 1 but the second option in Test 2.

Another classic experiment, which has been repeated with twists for many years, is the "dictator" game, whereby a single player (the "dictator") can split a cash reward between herself and an assigned receiver (Bolton et al. 1998). She could be given $10 and decide to split it $5–$5, $7–$3, $10–$0, or anywhere in between. The receiver has no power to reject the split. While it would be "rational" for a dictator to assign all of the money to herself, in reality dictators usually allocate some proportion of money to their receivers. Clearly, humans are not acting solely out of self-interest!

The wealth of behavioral game theoretical studies demonstrates the ways in which humans diverge from purely "rational" behavior. We regret loss more than we appreciate an equivalent gain, we discount the future, we are concerned with building a good reputation, and we change our behavior to benefit others. We are very different than the hypothetical utility-maximizing *Homo economicus*.

Altruism, Cooperation, and Monogamy

> Purity is obscurity – Ogden Nash, Reflections on a Wicked World.

Why do humans engage in long-term, formally monogamous pairings? And what can explain our extreme levels of cooperation and altruism? It would seem that such pure actions would be costly to individuals compared with alternatives. However, game theoretical analyses can begin to unravel these mysteries.

We are one of a tiny minority of mammals who exhibit long-term mate pairings. Long-term matings seem to have many fitness costs: for example, committing to one mate means one must forego many other opportunities, and paternity uncertainty means that males risk investing years in someone else's offspring. In short, it is hard to explain why individuals with the *opportunity* to mate with many others would not do so. However, when researchers conceptualize long-term relationships as public goods and generate an appropriate game-theoretical model, the payoffs make such an investment worth it (Conroy-Beam et al. 2015). In short, long-term relationships can provide at least three types of payoff: first, mutual investment leads to fewer conflicts of interest than would arise in short-term relationships; second, two-parent investment synergistically combines for a larger resource pool overall; and third, long-term partnership allows for consistent division of labor that leads to specialization and increased efficiency (Conroy-Beam et al. 2015). Further, long-term partnership provides a mechanism to punish "romantic free-riders" who try to drink from the "mutual pool" without investing in it.

Another analysis of monogamy versus polygamy, explained in the book *The Red Queen: Sex and the Evolution of Human Nature* (Ridley 1994) and examined in detail by John Maynard Smith (Maynard Smith and Price 1973), conceives of sex as a game. Imagine a population of polygamous birds, where a new type of "monogamous male" emerges who ends up partnering with one female and raising her offspring, thus increasing the fitness of that baby. Monogamous males are selected over polygamous males. In this manner, monogamy can "invade" a population of polygamy. A more formal mathematical treatment is necessary to demonstrate conditions under which monogamy can resist an invasion by polygamous males.

Robert Trivers, Martin Nowak, Karl Sigmund, and many others have also examined the question of why humans are so cooperative from a game theoretical perspective. (The field is characterized by an ongoing debate between proponents of "inclusive fitness theory," or kin selection, and its opponents. Interested readers should investigate the primary literature for a more complete account.) Nowak evaluates five mechanisms by which cooperation might evolve, and uses game theory to generate simple rules that must hold true in order for each mechanism to be effective(Nowak 2006b). For example, one of Nowak's proposed mechanisms for the evolution of cooperation is "direct reciprocity," whereby you help someone else and they help you (as if life were a series of repeated Prisoner's Dilemma games). Although it would pay to defect in a one-off Prisoner's Dilemma, things are different in a real-life version of this game, where the dilemma can occur multiple times: over time the strategy of cooperation through direct reciprocity can emerge if the probability of encountering the same individual again exceeds the ratio between costs and benefits of a cooperative act (Nowak 2006b). Similar trade-off equations can be written down for the other four proposed mechanisms: indirect reciprocity, where cooperation buys one a good reputation that moves via gossip among a population, bringing future benefits; kin selection, whereby one's selfish genes are benefited by cooperating with a related individual; network cooperation, where spatial organization plays a role; and group selection, where groups which evolve a cooperative strategy succeed more than anti-cooperative groups (Nowak 2006b).

The evolution of cooperation has been, perhaps, the most exciting and contentious area of game theory (Maynard Smith 1982; Nowak 2006a; Sigmund 1993). It will be examined in greater detail in subsequent sections.

The Persistence of Human Psychological Variation: Rock, Paper, Scissors, Sandpiper

Consider the classic game, “rock-paper-scissors.” Rock beats scissors by smashing them; scissors beat paper by cutting it; and paper beats rock by wrapping around it. (Countless children worldwide have shaken their fists at the sky wondering how paper could *possibly* beat rock.) In other words, A beats B, B beats C, and C beats A. Intuitively, we can see that no one strategy is best; the evolutionarily stable equilibrium would be characterized by cycling or by the persistence of stable proportions of different strategies in the population. This may seem to be purely theoretical, but we have now observed many examples of multiple, coexisting strategies in nature. Here is one striking example.

The Ruff, a type of shorebird known as a sandpiper, is so-named for the male’s beautiful feather ornamentation reminiscent of Elizabethan collars. However, not all males look the same – and they do not exist on a continuum, but instead fall into one of three distinct reproductive “morphs:” independent; satellite; and “faeder” (Küpper et al. 2015). Independent males have an elaborate, colored ruff, and display to females in large groups where each male defends a small territory. Satellite males have a white ruff, and mooch off of the independent males’ display by lurking around the edges and attracting females when the moment allows. Finally, faeder males are indistinguishable from females; they sneak in and try for quick copulations when females indicate their approval for displaying independent or satellite males. None of these mating strategies is uniformly the best strategy, and the success of one often depends on the persistence of others; indeed, the highest rates of mating overall occur on display grounds which are prominently occupied both by independent and satellite males. Ruffs are Nature’s rock-paper-scissors. Intriguingly, these distinct reproductive and behavioral morphs are encoded by a “supergene,” a group of genes that are inherited together as a block (Küpper et al. 2015). This unusual genetic mechanism ensures that variation will be maintained in the population, because animals carrying two copies of this inversion cannot survive. In other words, homozygosity is lethal. This is an important genetic feature which drives persistence of multiple phenotypes, and must be taken into account – in addition to the frequency-dependent effects of behavior – in any complete model of sandpipers.

Just as evolutionary game theory helps to explain why the ruff has three consistently present male morphs, it can explain the maintenance of human psychological and cultural variation (Dall et al. 2004; Nettle 2006; Wilson 1998). Stable populations can have multiple strategies, and individual personality traits interact with different tradeoffs of costs and benefits. It is not the case that a single “best” suite of personality traits exists, and formal game theory helps researchers explain why multiple personalities persist in a population.

Here game theory was able to illuminate a truth that was lurking in the shadows, waiting to be noticed.

Frontiers of Game Theory in Evolutionary Psychology

Game theory has already made powerful contributions to evolutionary psychology, as described above. However, there are several frontiers (yet to be explored!) where game theoretical methods will undoubtedly help explain further phenomena. The two most exciting of these are: (i) game theoretical conflicts between “selfish” genes, and their impact on our psyche, and (ii) game theoretical conflicts between non-human inhabitants of our bodies, such as viruses.

The Imprint of Genetic Conflict on our Psyche

> I’m afraid that some times / you’ll play lonely games too. Games you can’t win / ’cause you’ll play against you – Dr. Seuss, Oh, The Places You’ll Go!

Genes within an organism can have different goals; conflicts within a body between self-interested genes are fertile grounds for game theoretical examination (Burt and Trivers 2006; Haig 2002). Further, this is particularly relevant to evolutionary psychology because genetic conflict is specifically and tightly connected to human behavior and psychology (Haig 2011). "Imprinted" genes, which are a representative hallmark of genetic conflict between maternal and paternal interests, are "highly prevalent" in the brain, with functions ranging from cognition and sociality to synaptic plasticity (Perez et al. 2016). Relationships between mother and child; our attitudes toward close and distant relatives; our respect affinity for and behavior towards maternal versus paternal kin; the timing and nature of sexual maturation; and other traits are all to be likely impacted by the genetic conflict present between genes of maternal and paternal origin (Haig 2011). Indeed, experimental, anthropological, and epidemiological evidence all support the connection between genetic conflict and evolutionary psychology (Haig 2011). For example, certain "imprinting" diseases, which reveal the hidden battle within our genomes, predictably affect behavior and psychology (see ▶ "Imprinting"). Beneath these psychological and behavioral patterns lie game theoretical conflicts at the level of the genome.

We can take our inference one step further back: when genes within an organism are fighting, rather than purely cooperating, they will likely lead to suboptimal functioning. War expends resources! Could competition games between genes explain "inefficiencies of mental function" and the "high frequency of pathology in human social interactions"(Haig 2011)? Imprinted genes are particularly enriched in the brain (Perez et al. 2016), and human social interaction is a major determinant of individuals' fitness. Therefore, mathematical analysis of the relative "strategies" of genes and alleles in opposition cold provide fruitful inquiry into human psychological inefficiency and pathology.

Humans: Camper Vans for Competing Microorganisms

> Curiouser and curiouser! – Lewis Carroll, Alice in Wonderland.

Humans are not coherent individuals that single-mindedly seek to improve fitness. Instead, our body plays host to a vast array of gut microbes, brain microbes, viruses, and invading human cells that compete to exert influence within the body. Further, these agents – and their game theoretical competition – impact our everyday psychology and behavior, both by accident and by design (Kramer and Bressan 2015). Anxiety, depression, schizophrenia, and more all have demonstrable connections to the small, selfish agents hitching a ride in our bodies.

Influencing the mind is like influencing the president of the USA – the mind can powerfully influence fitness, since it provides executive control (conscious and unconscious) over so many other bodily functions. For these reasons, small, selfish agents have strong motivation to hijack our brains.

A most unsettling example comes from *Toxoplasma gondii,* a unicellular protozoan parasite which passes between the brains of mice and rats and the muscles of cats (and, as it turns out, the brains of humans). *Toxoplasma*'s life cycle requires that it develops as an egg inside cat intestine; therefore, the mature organism has an incentive to manipulate rats and mice to be eaten by cats. Indeed, in rats, *Toxoplasma* demonstrably makes the rat *less afraid of cats*, slower to react to stimuli, and, in some cases, sexually attracted to cat urine (Webster et al. 2013). Though humans are not intended hosts of *Toxoplasma* (the parasite cannot complete its life cycle after entering a human host because human brains are rarely eaten by cats), *Toxoplasma* can take up residence in a human brain. Recent evidence shows that *Toxoplasma* infection is tightly connected to a wide variety of mental deficiencies, from slow reaction times to schizophrenia and depression (Kramer and Bressan 2015; Webster et al. 2013). Some evidence strongly indicates that it is causal of, not merely correlated with, mental disease (Kramer and Bressan 2015).

The evolutionary dynamics of viruses and other small, selfish agents have recently been unpacked effectively with evolutionary game theoretical methods (Nowak 2006a). Common wisdom holds that a small, selfish invader cannot be too deadly, or it will exhaust its supply of hosts and not be able to be successfully transmitted. This makes sense. But there are many virulent diseases that appear to violate this principle! What dynamics lead to the evolution of virulence? What is the "health" outcome of many small selfish agents competing within a single host? In what context can virulence paradoxically be maintained over time (as in the case of human malaria)? High virulence can be a successful strategy if the population of hosts is large or sub-divided enough that the parasite is not at risk of depleting it. Mathematical analysis indicates that evolution maintains stable proportions of viruses with different levels of virulence over time, and that linkage between ability to infect a host and virulence maintains virulence beyond what would seem to be ideal levels for the parasite (Nowak 2006a). But virulence well in excess of the transmission-viability equilibrium can be selected for as well when different parasites compete within the same "superinfected" host. When a single host is invaded by many microparasites, they compete; this competition leads to (i) coexistence of parasites with a range of virulences, (ii) higher average virulence to the host than single infection would generate, and (iii) complicated dynamics with the potential for surges in virulence (Nowak 2006a).

The connection between mental health and our microbiome is a trending topic in medicine (Foster and Neufeld 2013). Fecal transplants and oral ingestion of gut bacteria to cure gastrointestinal ills are all the rage, and gut microflora clearly affect mental state(Foster and Neufeld 2013). But in order to properly treat mental illness in connection with our microbiome, we must properly understand the evolutionary dynamics. Competing individual agents interact in complex webs within our body, with the potential for catastrophic spikes (Nowak 2006a). Some of these agents share our interests in bodily health, and some do not. Lest we interfere in the wrong manner, we must employ game theory to understand the connections between and among microorganisms in our body – and their demonstrated effect on our psychology.

V. Limitations of Game Theory

Traditional Game Theory: Poor Assumptions about Humanity?

> Man is many things, but he is not rational – Oscar Wilde, The Picture of Dorian Gray.

Many real-world phenomena interfere with our predictions about human behavior and reasonable solution concepts for a given game. Humans are not always rational in an economic sense; myriad factors can interact to influence the outcome of a game (including, for example, intangibles such as social pressure). It is possible that humans are rational, but that we cannot conceive of all perceived costs and benefits, nor quantify them. Behavior which may seem irrational, because it comes at a cost to the individual while helping a stranger, might actually serve a "hard to quantify" purpose, such as building reputation or providing a "warm glow" of good feeling to the helper. Thus, classical game theory cannot always estimate the sum of people's true utility. It has also faced some methodological criticism: for example, laboratory experiments cannot be a perfect proxy for reality (Gintis 2009). People are aware that they are in an experiment and behave in unusual ways.

Further, a "trembling hand" or "fuzzy mind" is used as shorthand for the prevalence of mistakes, behavioral or phenotypic, that might lead someone to mistakenly play the "wrong" strategy or misremember what their opponent has done so far. In more detailed examinations of game theory, theorists and experimentalists test proposed solution conceptions against "trembling hands," or occasional errors. Since the real world is filled with errors, a solution strategy must be robust against a "trembling hand" (rather than irrevocably altered by one). It is said that "close" only matters in horseshoes and hand grenades; we now know that "close" should also matter for successful game theory solution concepts!

Complications of Heritability and Individuality: A Crisis for Evolutionary Game Theory?

> In physics, every crisis is an opportunity – Richard T. McCoy, Physics of Time (The Princeton Time Project).

The aforementioned complications about genetic conflict, and the multiple hierarchies of players within a single body, raise two major criticisms of evolutionary game theory at high levels. Generally, in evolutionary game theory, we deal with "individuals" who pursue high "fitness" for themselves. Both "individual" and "fitness" encode hidden assumptions.

The maximizing principle of "fitness" assumes that selection operates on observable, heritable phenotypes in a direct and effective manner. For example, the trait of "cooperation" in a population is often modeled as a simple, consistent, and perfectly heritable trait, although in fact it can be (i) influenced by the joint action of many unlinked genes, (ii) variable in different environments and across contexts, and (iii) underpinned by complex gene-on-gene battles. In fact, a fascinating result from a type of colonial marine invertebrate, ascidians, demonstrates that apparent superficial cooperation – the fusing of two colonies – is in fact a brutal example of parasitism, where one colony becomes disproportionally represented in the germline (Buss 1999). Although the colonies seem to be fusing and sharing resources, one wins the Darwinian game and one loses. If we were to model this as a game without full knowledge, it would seem that both players benefit from the arrangement – and this is clearly not the case. This is an illustration of a now well-known theory: that the history of life is a history of "conflicts between units of selection" (Buss 1999). Characteristic features of life's organization – such as mitochondria within a cell, microbes within a body, ants within a colony, and so forth – evolve to suppress parasitism at lower levels. Is all apparent cooperation underpinned by conflict? Games are not always as they seem.

Second, "individuals" are really complicated battlegrounds for bacteria, viruses, warring genes, "chimeric" cells from distinct genetic individuals, and more. A marmoset, for example, is born as one of a nonidentical twin pair that freely swaps cells in the womb (Haig 1999). That is, an "individual" marmoset is actually a composite of two genetic individuals – a mosaic of cells with two distinct genomes, one being "itself" and the other its twin. In an evolutionary game, is an individual marmoset pursuing fitness for itself, its body? Or for a genetic individual? *Which* genetic individual? These are not simple questions. Further, humans often conflate evolutionary fitness with lifetime happiness; however, often the brain works in ways that seem counter to our day-to-day happiness but have understandable evolutionary underpinnings.

Does our richer understanding of heritability and the dynamics between levels of selection render high-level game theory useless?

In a word: no; high-level game theory is still fruitful. (Otherwise, this could have been a much shorter chapter.) Unless we have reason to suspect particularly unusual mechanisms of inheritance, the fact of heritability, rather than the details thereof, is often sufficient for game theoretical purposes (Vincent and Brown 2005). Darwin did not even know what the unit of heritability might be – he merely postulated that like begets like, organisms struggle to exist, and heritable traits influence the struggle. The mechanisms of inheritance are useful for many purposes, but they are not *particularly* essential to studies of broad evolutionary dynamics.

Nonetheless, it is worth being aware of complications of heritability, particularly those arising from genetic conflict. Indeed, these complications are more "opportunity" than "crisis:" they provide fertile ground to employ game theoretical methods at many levels, from proteins to populations.

In A Brief History of Time, Stephen Hawking relays the following anecdote: "A well-known scientist (some say it was Bertrand Russell) once gave a public lecture on astronomy. He described how the earth orbits around the sun and how the sun, in turn, orbits around the center of a vast collection of stars called our galaxy. At the end of the lecture, a little old lady at the back of the room got up and said: "What you have told us is rubbish. The world is really a flat plate supported on the back of a giant tortoise." The scientist gave a superior smile before replying, "What is the tortoise standing on?" "You're very clever, young man, very clever," said the old lady. "But it's turtles all the way down!"". Countries compete on Earth, political parties compete within countries, humans compete within political parties, and viruses compete within humans: it's game theory all the way down!

Conclusion

Game theory, and its cousin Evolutionary Game Theory, have set the stage for evolutionary psychology on multiple levels. Game theory provided mathematical tools for interpreting systems where individual success depends on the strategies of others – i.e., all human interactions. It also revealed truths about the human brain- that we are not rational according to economic definitions, and that interesting features of the mind lurk in areas where we deviate from predicted rationality. Evolutionarily game theory placed these methods and topics into a biological context, which allows us to interpret complicated phenomena such as the evolution of altruism and monogamy. Games are played in many arenas ranging from the internal wiring of our brain to complicated displays aimed at attracting a life partner to international politics. Perhaps one day games will be played among the stars. In all of these domains, the game theory will illuminate many secrets waiting to be discovered.

Cross-References

- ▶ Evolutionarily Stable Strategy (ESS)
- ▶ John Maynard Smith
- ▶ Game Theory, Economics, and Political Science

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