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Evolution of confrontation and cooperation in simple organisms as a function of environmental resources and cost of a conflict

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Abstract. The root cause of human conflict needs to be understood but it is currently unknown whether the decision to engage in conflict is an inherited or acquired trait. This article reports two experimental simulations which demonstrate that the level of confrontation in a population of simple organisms can be explained by the evolution of a simulated gene pool. Game theory and evolutionary algorithms were combined in a novel way to examine how six variables influenced the decision to confront in the competition for resources. The main variable was how the genetically determined rate of confrontation evolved as a function of environmental resources and cost of a conflict. The additional modulatory effects of four other variables were also considered in the first round of simulations. Two variables were responsive to the difference between resources and cost. Two other variables were responsive to the organism's health status. Taking a systematic approach, we examined how a population of 1000 organisms were evolving in environments with different levels of reward and punishment. During each cycle, each organism was paired with another organism and thus needed to decide whether to confront or cooperate. We used a genetic algorithm to simulate the evolution of the gene pool over 500 cycles. The first series of simulations demonstrated that the baseline rate of confrontation was very responsive to environmental conditions. Our results also indicate that the decision to confront or cooperate depended not only upon the immediate competitive conditions, in which the organisms evolved, but were also responsive to their own health status. The second series of simulations used zero-sum games to explore how risk levels varied as a function of the potential cost of engaging in a confrontation. In the second round of simulations, a simple form of memory was implemented. The results indicated that memory had a limited, but significant effect, while the cost of a conflict was highly predictive of the level of risk taken by the organisms. Our two series of simulations show that AI could contribute to answering psychological and societal questions. Our unique combination of techniques has brought to light several new insights into the mechanisms that drive the population towards cooperation and confrontation. The degree of generalizability of our results and future avenues for deepening our understanding of these evolutionary dynamics are discussed.

Keywords: evolutionary game theory, evolutionary algorithm, confrontation and cooperation, Monte-Carlo

1 Evolution of cooperation and confrontation

1.1 A competition for resources

Natural selection is the force that shapes organisms and the variety of their traits [1]. Competition for resources sharpens these traits making them increasingly adaptive in stable environments. For many species the competition for resources results in direct confrontation with potentially lethal consequences. In this context, most available research indicates that cooperation has emerged to increase our chances of survival in the face of competition [2-4]. To maintain cooperation, cognition has increased, and this is the main driver behind the brain's expansion, particularly in the frontal cortices [5]. Despite this, confrontation between individuals and/or groups has not been eliminated. The passing on of successful genes to the next generation is often dependent upon repeated confrontations with other (same-sex) members of the same species. There is ample evidence that confrontation has been part of human evolution as indicated by the numerous prehistoric sites documenting intentional (collective) violence [6-8]. Much of human history illustrates this principle at both the individual and group levels. A classic example is Thucydides explaining the reasons for war between Sparta and Athens [9]. The rise of one power was challenging the dominant position of another and thus threatening to reduce its resources as per Intergroup Threat theory [10]. In the 21st century, access to resources is still a common driver behind individual and group conflicts. In this context, violence is often triggered when individuals estimate that the minimum amount of resources necessary for surviving and thriving will not be reached. As recently as 2018, the yellow vest movement in France was triggered by an increase in petrol taxes [11]. In this case, one single issue afforded a social movement to form from the collection of individual interests that were ready to confront the government. Throughout recorded history, and long before it, confrontations for resources have taken place. Investigating the factors that dictate the decision to confront or cooperate is thus essential to understanding violence between and within groups.

A question that the biological sciences faced in the 20th century was how selfish organisms came to cooperate. A naïve interpretation of why confrontation is used to acquire more resources is that animals benefit from being aggressive. However, the gains from aggression are only fitness enhancing if the competitor does not retaliate. Retaliation leads to a potential cost that might endanger the aggressor's life. The balance between benefit (reward in the simulation) and cost (punishment in the simulation) is axiomatic for determining the conditions underpinning cooperation or confrontation. It is at this stage that game theory started to play a crucial role in the investigation of cooperation in animals and humans. The paradigm has been widely used to explore and describe human decision making in several academic disciplines. In its most basic setting, the so-called game refers to two individuals, A and B, facing a situation that involves two options, for example cooperating or confronting. Each individual organism decides independently but is aware of the potential outcomes and that the same options are available to the other individual. Traditionally the game is represented as a matrix of choices, see Table 1.

--- Insert Table 1 around here ---

The two-number vector in each cell represents the outcome for each of the two organisms. In the example shown in Table 1, we have the following outcomes. If both individuals decide to cooperate, they equally share the 6 points so each individual gets 3 points. If one individual decides to confront and the other one to cooperate, then the aggressor is rewarded with all 6 points, and the cooperative individual gains nothing. In cases where both decide to confront then a fight ensues, and they only get 1 point each. The objective of both individuals is to maximize their gain. The choice or combination of choices that an individual will adopt to maximize gain is termed the strategy of that individual. Decisions, such as the one presented in Table 1, have been used to explore the conditions for cooperation [12].

One of the best-known thought experiments is the prisoner's dilemma where the outcomes are penalties rather than gains. The paradigm has been instrumental in demonstrating that selfishness can drive individuals to make suboptimal decisions [13]. Later, work by Robert Axelrod significantly advanced our understanding of cooperation [13, 14]. Axelrod noted that the prisoner's dilemma, like many other experiments within the paradigm, requires only one decision but in the real-world individuals repeatedly interact with the same people. Therefore, it is important to observe how the strategy evolves when decisions are repeated. In such cases, constant confrontation by both parties leads to penalties in the long run, so systematically confronting is not a viable strategy. Axelrod and Hamilton have tested the efficiency of various strategies and demonstrated that the best one was a strategy of offering cooperation in the first instance and then mirroring the behavior of the opponent. Since Axelrod's pioneering work, the evolutionary game theory paradigm has been immensely successful in answering questions in numerous disciplines interested in cooperation and/or confrontation [15-17]. The present paper aims to investigate the decision to confront or cooperate with the same approach but will introduce further refinements into the modelling of the evolutionary process.

In this paper, we used evolutionary genetic algorithms to investigate how the amount of resources and the cost of a conflict would affect confrontation rates in a virtual population of agents. The main manipulation was the use of different genes to code for different factors that may play a role in the decision to confront. This approach permits estimating the relative importance and responsiveness of each component that may play a role in the choice of a behavioral strategy. The first and main ‘genetic’ trait we implemented was the inclination to confront. Though confrontational reactions are often triggered by environmental stimuli, the literature also suggests that confrontation has a genetic component [18]. The choice to confront is a multidimensional decision and many of its contributing factors, such as aggression and impulsivity, also include a genetic component [19]. Dysfunctional psychological traits, such as psychopathy, involve behavioral strategies incorporating systematic confrontation.

In this context, although observed behavior probably results from a gene x environment interaction, for the purposes of this study we treated it as an inherited trait. The second manipulation was a set of genes coding for our reactivity to the environment. How humans react to different conditions of gain and loss has been extensively studied in behavioral/micro economics [20]. It has been demonstrated that individuals tend to be risk tolerant in the domain of losses. For example, they usually prefer a 50% chance of losing £120 rather than losing £60 for certain. Individuals are also risk avoidant in the domain of gains so they would prefer to gain £60 for certain rather than a 50% chance of winning £120. When individuals face a situation where the outcome could be either positive or negative (so-called ‘mixed gambles’) they tend to be more risk tolerant. These responses result from evolutionary processes that promote the conservation of one’s own assets. Thirdly, the last manipulation was genes that code for sensitivity to health status. Weakened individuals will tend to take less risk and avoid engaging in confrontation when compared to those with a high health status who might be more inclined to confront.

In the present paper, we have implemented an evolutionary version of the experimental paradigm used in game theory to investigate how the amount of resources in the environment and the cost of engaging in a conflict influence the gene pool that determines the choice of confronting or cooperating. The primary aim of the simulations was to establish how the confrontation rate, defined as the number of confrontations per hundred decisions, varied as a function of the outcome. The second aim was to investigate moderating factors on our model of confrontation and cooperation. Finally, we investigated whether introducing a simple form of memory would enhance the ability of organisms to survive in their environment.

This paper is structured as follows. First, we introduce our model of confrontation and describe how we implemented natural selection in our virtual environment. Second, we report a series of simulations where rewards and punishment vary in the environment and estimate how these variations impacted the confrontation rate of the organisms as determined by their genetic profile. We show that the rate of confrontation impacts other genes, which are sensitive to health or risk. We then report a second series of simulations that explored how organisms evolve in zero-sum game environments. In these simulations, we show how punishment is key in determining the profile of genes that control the basic rate of confrontation. Finally, we discuss the impact of our results on the current conceptualization of the evolution of risk taking in potential confrontations.

2 Modelling the evolution of confrontation

2.1 Introduction

The research in decision making uses many terms such as gain, loss, penalty, reward, utility, and cost that are often defined in discipline specific ways (e.g., economics, psychology, biology, and ecology). In our simulations we will use the terms reward and punishment because the organisms we simulate cannot conduct a conscious analysis of the situation and only react to these environmental incentives.

Our formal, simplified version of natural selection simulated an ecosystem of 1000 organisms. As the ecosystem was stable it systematically generated the same amount of resources and thus maintained the same number of organisms. Organisms that disappeared were replaced before the next round of decisions. Each organism had initially 100 points of health. As the healthiest individuals (i.e., the top 10%) were selected for procreating, each organism was fighting in each cycle to potentially increase its health. Organisms that were paired had to decide whether to confront or cooperate. The combined decision of the two individuals in a pair created four potential outcomes that recreated the four conditions of game theory, see Table 2. The main difference between the original study by Axelrod and Hamiton [14] and the current implementation is that the decision was probabilistic, based upon the tendency of the individual to confront, rather than being stable over time and predictable. The probability to confront is δ and to cooperate is $(1-\delta)$.

--- Insert Table 2 around here ---

We manipulated reward and punishment to evaluate how the different genes evolved and then combined to determine the value of δ. Reward and punishment were varied at each integer value between 1 and 100, which created 10,000 conditions (100 × 100). For each condition, the rate of confrontation was initially equally distributed over the population. After 500 cycles of decisions, we recorded the gene profiles, the number of survivors in the 500th generation, and their average health. We expected the genetic profile of the 500th generation to differ drastically from the equiprobable distribution used to define populations at cycle 0. The model was implemented in Python 3.7.

2.2 The organisms

The organisms in the simulation were defined by 3 properties. The first property, health, was a score that varied from 0 to 100. The organisms started with $\Gamma = 100$, when the organism reached a health of $\Gamma = 0$ it died. The second property was age, noted τ, and was set as a counter of the number of cycles the organism had survived. Aging was implemented as a loss in health that was proportional to the number of cycles past the 25th cycle. For each cycle beyond 25, the organism would lose one more health point in that cycle. The third and most important property was genotype. Genotype was defined as 9 genes that coded five traits determining the probability of confrontation as reviewed above. The first trait was the natural propensity of organisms to use aggression to get resources. This tendency was coded by five genes that had an additive effect. Each of the genes had 5 alleles (A, B, C, D, & E) that coded for 5 different levels of confrontation (0%, 5%, 10%, 15%, & 20%). The genotype could thus vary from 0% (i.e., AAAAA) to 100% (i.e., EEEEE) and could take any value between 0% and 100% that is a multiple of 5%, for example, AABCA is 15 % (0 + 0 + 5 + 10 + 0). The five genes together set the probability that an organism would decide to confront. This trait, defined by a combination of five genes termed confrontational propensity (CP), implemented the natural variance in the inclination to confront.

The other four genes implemented the context sensitive modulation of the natural tendency to undertake confrontation or cooperation. Each of the other four genes used the same five-letter coding (A, B, C, D, & E) and thus could modulate the intrinsic level of risk by up to 20%. Two modulation genes were responsive to the type of situation organisms were facing. In line with the literature reviewed above, one gene (termed risk sensitive one (RS1) was coding for whether the decision was in the reward domain. When the decision to confront and the decision to cooperate led to a positive payoff, the gene RS1 increased the rate of cooperation because a reward with no risk is favored over a reward with a risk of punishment. In agreement with the literature showing an increase in risk taking in mixed gambles, a gene termed risk sensitive two (RS2) increased confrontation rates when the decision to confront led to punishment. The two other context-dependent genes were responsive to the health status of the organism. One gene, termed health sensitive one (HS1), increased confrontation rates when the potential reward would reach maximum health. The second health-sensitive (HS2) gene was activated when the potential punishment would lead to the death of the organism. HS2 therefore increased cooperation.

Three criteria were applied to select the parameters we used in our simulations. The first criterion was the exploratory nature of our study. We wanted to estimate the degree of fit between the theoretical predictions of evolution and the implementation of our paradigm. To this end, we decided to cover as wide a range of environmental conditions as possible, even if these were not likely to happen in nature. The second criterion was the limit in computational power. Our choice for the rate of random mutations was much higher than the rate established for human genes. Implementing a rate that is similar to mutation rates in real genes would have the effect of increasing the demand in computational resources without necessarily changing the results in the long run. Even if our working hypotheses deserved empirical testing, we considered that setting a high random rate of mutation was a reasonable choice for an exploratory study. Third, in some cases, the choice was arbitrary due to the lack of evidence of a well-established value. It is not possible to establish in the human population the proportion of individuals that contribute most to the gene pool of the next generation. Our choice of 10% of the population constituting the elite reflects the fact that, in most species close to humans, genes are passed by a restricted sample of the population at each generation and there is no evidence to suggest that our early ancestors were any different. Hence, even if the exact proportion of what constitutes the elite was arbitrary to some degree it does reflect a natural process. The same logic applied to the choice of five genes for implementing the individuals' propensity to use confrontation. More than five genes enter the equation for determining the motivation to use aggression. It is also clear that an individual's propensity to use aggression is also largely determined by life experience (i.e., a genes x environment interaction). By using five genes we implemented the fact that multiple genes are involved and provided a context to explore the influence of high variance on aggression while limiting the demand for computational resources.

At initialization, the program generated the 1000 organisms and their genotypes. At this initial state, the allele distribution of each gene would allow the population to have an equiprobable distribution in each trait.

2.3 The survival cycle

The survival cycle constituted all of the events and processes that occurred between two pairings of the population, including the changes in health and the generation of new organisms. It was implemented in five steps.

In step 1 individuals were paired randomly thus creating 500 situations. The following three parameters were calculated as a function of the level of reward and punishment:

- The reward of the decision to confront.
- The reward associated with the decision to cooperate.
- The punishment associated with a fight.

In step 2 each individual organism made the decision whether to confront or cooperate. First, the probability of the organism confronting was computed using the five genes CP, RS1, RS2, HS1, and HS2 with δ the probability of confronting, or confrontation rate, being determined as shown in Equation 1.

$$\delta = CP - RS1 + RS2 + HS1 - HS2 \qquad (1)$$

Each gene that is responsive to a condition was activated if relevant and consequently modified the probability of being confrontational. That is,

- if payoff(confront) > 0 then RS1 was activated,
- if payoff(confront) < 0 then RS2 was activated,
- if health + gain > 100 then HS1 was activated,
- if health – cost $\leq$ 0 then HS2 was activated.

At the individual level, the decision was made by comparing the value of a random variable X [0,1] with equiprobable distribution, to their genetically determined value of δ. When $X < \delta$, the individual cooperated and when $X > \delta$, the individual confronted the opponent.

The third step was the encounter, where the paired organisms confronted or cooperated, and the reward and punishment were allocated to their health points.

The fourth step consisted of determining which individuals had survived the cycle. Any individual that had a health $\Gamma \leq 0$ was dead and any individual with $\Gamma > 0$ was alive for the next cycle. Individuals surviving one cycle were rewarded with one age point. The 10% of survivors with the highest health points were considered the elite who provided the genetic source for reproduction.

The fifth step consisted of generating organisms to bring the ecosystem back to its original capacity. As above, 90% of the new organisms were generated from the individuals with the highest health status. The genotype of the new individual was determined as follows: the genotype from one random individual of the elite was selected and copied. Each of the 9 genes of the parent would then be submitted to a 1% risk of being the target of a mutation. The genetic profile of the remaining 10% of the new individuals was random.

The formal framework to examine decision making is game theory as introduced by von Neumann and Morgenstern [21]. The notion of expected utility, defined as the product of the probability of an event and its outcome, is of central importance in both prescriptive theories of decision making and descriptive theories of economic decision making in humans [20]. Beyond this context, the key results have also been used to understand decision making with non-numerable outcomes such as in the political sciences [22]. According to the theory, an organism will optimize its decisions and pick the option with the highest expected utility. In this context, our organisms had the choice between two options: cooperate or confront. A perfect adaptation would lead to an optimized value between cooperation and confrontation. Table 3 presents the probability of outcome and outcomes for each of the four cases when the population had an average probability of confronting equal to p and to cooperate q, with q = 1-p.

--- Insert Table 3 around here ---

Formally, the expected utility (EU) of confronting (EU_f) and cooperating (EU_c) was defined as follows:

$$EU_f = (p \times q \times \text{Reward}) + p^2 \times (\text{Reward-Punishment}) / 2$$

$$EU_c = (q^2 \times \text{Reward} / 2) + (p \times q \times 0)$$

Critically, the environment in which the organisms evolved can be formalized by adding up the two utilities:

$$EU = EU_f + EU_c$$

The value EU thus represents the global ecology of the virtual environment in which the organisms evolved. A negative EU indicates an environment characterized by an average negative outcome, where resources are not sufficient to survive and we label this environment extreme. A positive EU, on the other hand, indicates that the number of resources available is superior to the needs of the population and we label this environment abundant. In the theoretical case of an equiprobable distribution of alleles, both p and q have a value of .5. The theoretical EUs for both confronting and cooperating can be calculated and thus the 10,000 environments can be classified on this theoretical basis as extreme ($EU < 0$), neutral ($EU = 0$) or abundant ($EU > 0$).

After the organisms have evolved, the genes determined the probability that they would choose to confront. It was therefore possible to calculate the new EU of the whole ecosystem, but this time based on the organisms that had evolved. This is the empirical EU as it was derived from the probability distribution of cooperation and confrontation that were determined by genes. The empirical EU was compared to the theoretical EU in each ecological milieu (extreme, neutral, and abundant) to establish whether an increased risk of punishment determined the organisms' choice of cooperating or confronting.

3 Results

This section reports the results of the 10,000 simulations. After evolving for 500 generations, the genes coding for confrontation rates expressed phenotypic effects that varied greatly as a function of the environmental conditions. The section is organized around each of the traits.

3.1 Genes determining confrontational propensity (CP)

The mean CP expressed by the five genes responsive to reward and punishment is presented in Figure 1. Visual inspection suggests that the genes were highly sensitive to the magnitude of punishment.

--- Insert Figure 1 around here ---

A linear regression accounted for the relationship between reward and punishment on the one hand and CP on the other. The multiple regression provides the following equation:

$$CP = 0.367048 + \text{reward} \times 0.002721 + \text{punishment} \times -0.001801 \quad (2)$$

The model is significant and accounts for 70% of the variance in the gene phenotypic effect, $r = .87$, $F(2,9997) = 11736.908$, $p < .001$. Figure 2 shows the degree of fit between model CP and the mean value of CP.

--- Insert Figure 2 around here ---

3.2 Gene sensitive to gain (RS1)

Gene RS1 was activated when the sum of the rewards of the decision to confront was superior to zero. Figure 3 shows the phenotypic effects of gene RS1 as a function of the reward.

--- Insert Figure 3 around here ---

A regression on the positive reward shows that the evolution of the phenotypic effects of gene RS1 varied as a function of the reward making the organisms less confrontational when a reward could be secured. The model, reported in Equation 3, accounts for 31% of the variance, $r = .554$, $F(1,8348) = 3704.593$, $p < .001$.

$$\text{Model RS1: RS1} = 0.121617 + \text{payoff} \times -0.000204 \quad (3)$$

3.3 Gene sensitive to Loss (gene RS2)

Gene RS2 could upregulate the confrontation rate by up to 20% in response to punishment. Figure 4 shows the relationship between the reward of deciding to confront and the mean phenotypic effect of gene RS2. The data have been fitted with a linear model, (see Equation 4), yielding a significant relationship that accounts for 17% of the variance, $r = .419$, $F(1,1615) = 342.985$, $p < .001$.

Model RS2: $\text{RS2} = 0.045159 + \text{payoff} \times 0.000427$ (4)

--- Insert Figure 4 around here ---

3.4 Gene responsive to health

Gene HS1 was responsive to situations where the gain in health from a confrontation was less than what the organism had to gain to reach maximum health. As the 10,000 simulations yielded different values on the two markers of health (i.e., number of survivors, and average health of the surviving population), we proceeded by binning the results per 10 percentile and calculated the regression model on the mean value per bin. The resulting model, reported in Equation 5, is highly significant and explains 88% of the variance, $r = .94$, $F(2,97) = 367.168$, $p < .001$, and is clearly indicative of a linear trend, (see Figure 5).

$$\text{HS1} = -1.459029 + 0.000912 \times \text{survivors} + 0.007162 \times \text{health} \quad (5)$$

--- Insert Figure 5 around here ---

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3.5 Gene responsive to death

Gene HS2 was responsive to the opposite situation and downregulated confrontation when the organism was facing death. The model, plotted in Figure 6, was calculated following the same procedure used for HS1 (see Equation 6). It yielded a significant, but marginal, effect explaining 13% of the variance, $r = .386$, $F(2,97) = 8.48$, $p < .001$.

$$\text{Model HS2: HS2} = 0.082607 + -0.000020 \times \text{survivors} + 0.000374 \times \text{health} \quad (6)$$

Further investigation indicates that gene HS2 was highly responsive to loss but could lead to either an increase or decrease in the confrontational rate.

--- Insert Figure 6 around here ---

Ad hoc analysis indicated that the evolution of gene HS2 was highly responsive to high punishment conditions, but the response of the gene (see Figure 7) suggests a bifurcation in its evolution.

--- Insert Figure 7 around here ---

The above results show the evolution of genes as a function of the environment in which they evolved. The relationship between genes was evaluated by considering the correlation between all pairs of genes. Figure 8 below is a visual representation of the correlations between genes.

--- Insert Figure 8 around here ---

As Figure 8 illustrates, even though the genes evolved independently from one another some correlations emerged between genes. If nearly all the connections are significant, we observe huge differences in the degree to which genes are correlated. Three genes CR, HS1, and RS2 are highly correlated with one another.

In addition to the effects of individual genes, it was possible to analyse the global situation as determined by the EU of the environment. As Figure 9 shows, the organisms adapted their average rate of confrontation and cooperation to each milieu. This intuition is confirmed statistically as the mean probability to confront varied with the milieu, $F(2,9997) = 10990.45, p < .001$. As the probability to cooperate mirrors the probability to confront (*i.e.*, $p = 1 - q$) it also varied with the milieu. In line with the results on probabilities, the empirical EUs (see Figure 10) differed from both the theoretical EUs, $t(9999) = 12.427$, $p < .001$, and vary with the milieu $F(2,9997) = 1377.65$, $p < .001$. These results confirm that the organisms adapted to the degree of resource scarcity of the milieu in which they evolved.

--- Insert Figure 9 around here ---

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4 Exploring risk taking through zero-sum situations

The simulations reported above afford the exploration of the natural selection of risk taking in confrontational situations. The methodological approach aimed to cover all conditions of reward and punishment that vary from zero to the life span of the organisms. Though very useful in helping us to understand how genes may react to different and extreme environments, these conditions were often not realistic. It is difficult to quantify how the rewards can be equivalent to the health of an organism. Similarly, animals tend to leave a fight before injuries become fatal. Predictably the genes in charge of determining baseline levels of risk taking are very responsive when the situation involves small rewards and a higher level of penalties. Two animals finding a water source are likely to share if there is sufficient water for both and conflict could potentially shorten their lives (as is often seen at watering holes). In this context, a second series of simulations have been carried out to further explore the sensitivity of genes to environmental conditions. However, it was designed to address the case where the average reward for cooperation and confrontation are the same but the risk, as measured by variance around the average expected return [23], is twice as high for confronting.

An important point to note about the simulations reported above is that the EU varied across conditions. In some cases, the environment was globally negative and in others it was globally positive. A particular case is when the environment is globally neutral. That is the EU of the situation is exactly zero. An interesting question thus arises when the stakes get higher while the EU remains zero for each choice. In layman's terms, the reward is equal to the punishment for each choice, but it is increasing. In theory, in these conditions, organisms should demonstrate no preference between confrontation or cooperation because they yield the same EU. From the perspective of evolutionary theory, the organisms will become sensitive to risks as the costs increase so a preference will be shown due to loss aversion. The objective of the second series of simulations was to demonstrate that organisms are biased towards environments with lower levels of risk. Though this hypothesis may seem trivial from the perspective of economic psychology, the present study will be the first one to use computer simulations to show that the biases in human thinking may stem from an evolutionary process.

To explore how genetic determinism combines with other cognitive components to provide the behavioral flexibility displayed by most organisms, we introduced a cognitive component that would modify the level of risk without being involved in the genetic coding of the risk level itself. Amongst the many cognitive functions (e.g., memory, reasoning, and consciousness) that have evolved to enhance the capability of organisms to adapt to their environment, memory is the one that plays a central role in making most species, including humans, flexible in their behavioral responses. In addition, memory can be easily implemented to test the flexibility of animal behavior for the wide range of species in this computer simulation. Based upon previous experiences, memory modifies the probability of selecting a given behavior from a repertoire of behaviors that are adaptive for responding to a given situation. Our simulations are purely Darwinian and follow the principles of natural selection. There is no modification of the code over the course of an organism's lifespan. We are not implementing a Lamarckian approach to acquiring behaviors or responses to confrontational situations. Similarly, there is no learning from experience that will modify the genetic code of the organism, and thus the Baldwin effect [24][25] is not implemented in our simulations. The present study aimed to show that genetic mechanisms on their own can explain risk taking in various conditions and thus we have limited the number of additional factors implemented. We have excluded factors that would intermingle with genetic expression or modify it over the course of a lifetime due to interaction with the environment. The addition of a simple form of memory was only done to explore how different cognitive components may generate flexibility in an organism's behavior.

5 Methods

The second round of simulations used the same model but focused on the organisms' sensitivity to risk in zero-sum games. Three aspects of the model were modified for this purpose. The first key modification was to remove the cost of confrontation for the winner and impose the full cost on the loser; this modification made the confrontation a zero-sum choice. The second modification was to control the environment so that the EU of cooperation and confrontation would always be zero. To this end, the cost of cooperating when the opponent was confronting was half the reward available. The last modification implemented a simple form of memory. The memory was limited to the last decision to confront and whether that decision led to a positive or negative health status. If the last decision was a fighting decision and led to an improvement in the health status, then the organism was 10% more likely to fight and if the decision to fight led to a loss of health, then the organism was 10% less likely to fight. These modifications, creating a more realistic environment, allowed the implementation of a zero-sum game where punishment increases while the EU for each choice remains at zero.

6 Results

The analysis of variance on the five genes as a function of both the memory status and the level of punishment is reported in Table 4.

--- Insert Table 4 around here ---

The main factors (zero-sum and memory) significantly affected the level of confrontation. Yet, as demonstrated by the η^2 values it was the punishment that was a highly significant determinant of the level of risk taken by the organisms. The interaction was also significant which demonstrates that organisms react to a combination of factors in the environment. Even if the η^2 is of limited magnitude, it illustrates the fact that the utility of memory varies as a function of the amount of potential loss. Figure 11 clearly illustrates that as potential loss increases organisms tend to be more cooperative in zero-sum games. As expected, the two genes responsive to the difference in reward and punishment were not affected in a zero-sum simulation and the two genes responsive to the health status showed a significant but limited effect in response to an increase in punishment as indicated by the low η^2 values.

--- Insert Figure 11 around here ---

7 Discussion

The simulations reported above have yielded a number of highly novel and important findings. First, a combination of genes responsive to reward and punishment determines the confrontation rate to assist the adaptation of the organisms to environments varying in reward and punishment. Our results indicate a linear relationship between loss (reward - punishment) and confrontation rate. The environmental conditions and the phenotypic effect of the CP genes are related by a linear relationship due to the simplified environment that was used to run the simulations. In this context, modelling more genes and implementing the interaction between genes might bring to light more complex relationships. The first series of simulations shows that organisms with no ability to project themselves into the future, such as with working memory, adapt their level of confrontation. In doing so our results strengthen the huge amount of research that indicates that aggression and the rate of confrontation (and by extension cooperation) evolved well before humans appeared. The confrontation rate, like any other trait submitted to evolutionary pressures, will be mechanically modified over generations if the conditions of reward and punishment change. In addition, it can be an automated reaction that does not require conscious calculation. The second series of simulations further suggests that the sensitivity displayed by the genes controlling the rate of confrontation depends upon potential loss, therefore showing that risk taking behavior emerges where the cost is relatively low.

Second, our results corroborate the idea that confrontation derives from multiple factors that act at different levels. The best evidence is from the correlation between genes that are not responsive to the same aspects of the environment. Some of the genes were directly responsive to the payoff associated with confronting but others were related to the health status of the organism. The genes modelled here constitute a simplification of reality but show that even in this simplified environment organisms develop a subtle response to variations in their competitive conditions. Our results argue against explanations based on solely social factors which have been put forth in social science [26, 27], and argue for a gene-environment interaction. It is the triggering of genes in specific conditions that might promote ancestrally acquired behaviors. Our results indicate that the willingness to confront stems from complex dynamics that involve the genetic background and the environment modulating the level of risk that organisms are willing to take. Our results suggest that individual differences in confrontation are likely to be determined by patterns of genes that have coevolved. Some of these genes are not directly involved in evaluating the outcome of a confrontation. Confrontation is thus not necessarily a primal (aggressive) response but is generated through complex dynamics.

The adaptation of the organisms to the three types of milieus in the first series of simulations is of central importance to interpreting our results. The empirical probability of engaging in confrontation has evolved so that organisms reduce their engagement rate when the conditions are extreme. It is fascinating that such a result emerges from our simulations as it clearly demonstrates that organisms develop a behavioral strategy that increases the EU even without any form of consciousness. As our implementation of evolutionary mechanisms was purely deterministic (saving the algorithm generating variance in organisms), we would interpret our results as being supportive of the idea that evolution has enabled confrontation as a natural but not systematic option in the behavioral repertoire of numerous species. It is not aggression that should be questioned, it is the milieu that makes aggression an appropriate behavior.

Our implementation of a memory mechanism in the second series of simulations has had limited success in modifying the rate of confrontation. The limited impact of memory might be due to either the limited memory span provided to the organisms or the way it was implemented. Even though limited, it has been successful in influencing genetic evolution and thus paves the way for further investigations of how high-level cognition could have emerged from low level cognitive processes. The current results suggest that organisms with even the most limited memory (i.e., of the last encounter) will change their behavior as the risk of a potential loss increases. This supports Axelrod's contention that studies of game theory should involve repeated interactions between organisms rather than the singular events that are classically discussed. A potential limit of the implementation of short-term memory is that the change in levels of risk was limited and fixed to 10%. It is possible that higher magnitudes would have had a higher impact on the behavior of the organisms and thus on their survival.

The evolutionary simulations we conducted have three limits that are worth bearing in mind when interpreting the results. First, we note that in many instances where the reward was high the organisms did not depart significantly from the initial rate of confrontation. The low selection pressure would partly explain this result and calls for more research into the topic. In natural conditions, if rewards are high and punishment is low organisms will increase in numbers up to the point where they must compete for resources. These dynamics have not been implemented in the present version and should constitute the focus of future research. Second, an important point in the intersection between the limits of the work and its novelty is the fact that the organisms simulated were not conscious. There was no planning ahead (e.g., avoiding potential confrontations) and the organisms were only reacting to situations. How consciousness influences decisions to confront was beyond the scope of this work but represents the next step in understanding the conditions that promote confrontation or cooperation. Finally, it is worth noting that the algorithm used to establish whether the situation is beneficial or not to the organisms could be interpreted as a form of cognition and thus future research should try separating basic and advanced cognition more clearly, so it is possible to draw more definite conclusions on their evolution.

In conclusion, for the first time, our study found that it is possible to simulate the impact of genes on the decision to confront or cooperate by using a unique combination of evolutionary algorithms, game theory, and Monte-Carlo simulations. Future iterations of this work may shed light on our understanding of how resource competition can lead to conflict and the potential dynamics of those conflicts.

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Table 1. Example of a theory of games

		Individual B	
		Cooperate	Confront
Individual A	Cooperate	3, 3	0, 6
	Confront	6, 0	1, 1

Table 2. Outcome matrix as a function of the decision of each individual.

		Individual 2	
		Cooperate ($1-\delta_2$)	Confront (δ_2)
Individual 1	Cooperate ($1-\delta_1$)	Reward/2, Reward /2	0, Reward
	Confront (δ_1)	Reward, 0	(Reward-Punishment)/2

Table 3. Expected utility for organism 1 as a function of the probability to confront (p), probability to cooperate (q) and the experimental parameters

		Individual 2	
		Cooperate (q)	Confront (p)
Individual 1	Cooperate (q)	$q \times q \times \text{reward}/2$	$p \times q \times 0$
	Confront (p)	$p \times q \times \text{reward}$	$p \times p \times (\text{Reward-Punishment})/2$

Table 4. Analysis of variance

Gene		Memory	Punishment	Memory * Punishment
	df	1, 4900	49, 4900	49, 4900
CP	F	375.794*	794.192*	5.666*
	η^2	0.071	0.888	0.054
RS1	F	0.041	0.771	0.891
	η^2	0	0.008	0.009
RS2	F	0.082	0.8	1.694*
	η^2	0	0.008	0.017
HS1	F	28.561*	5.878*	1.286
	η^2	0.006	0.056	0.013
HS2	F	2.165	3.957*	1.068
	η^2	0	0.038	0.011

Note: df: degrees of freedom, * significant at .01

Figure captions

Fig. 1 Mean CP per condition of reward and punishment.

Fig. 2. Relationship between the values predicted by Model CP and mean values of the phenotypic effect of CP genes.

Fig. 3. Mean phenotypic effect of gene RS1 as a function of the anticipated reward for a confrontation.

Fig. 4. Mean phenotypic effect of gene RS2 as a function of the anticipated reward for a confrontation.

Fig. 5. Plot of the multilinear model linking the number of survivors at generation 500 and the health of the population to the mean phenotypic effect of gene HS1.

Fig. 6 Plot of the multilinear model linking the number of survivors and the health of the population to the mean phenotypic effect of gene HS2.

Fig. 7 Mean value of HS2 per condition of reward and punishment

Fig. 8 Relationship between genes (only the dash connection is not significant)

Fig 9. Mean probabilities to adopt either cooperation or confrtonation for each type of milieu

Fig 10. Mean theroretical and empirical EU plotted for each milieu

Fig 11. Mean value of gene CP as a function of punishment (i.e., zero sum game) and whether the system had memory (dashed lines)