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An Essay on the Emergence of Non-pathological Aggressive-like Behaviors in the Context of Social Interactions

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"So, what do you do?", "I'm into murders and executions mostly."

[American Psycho, Breat Easton Ellis]

To the Guardian of my Time.

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Two chapters of my dissertation are based on co-authored material.

Specifically, Chapter 2 is based a paper that is currently under review in *Scientific Reports* journal, with the title: "Dopaminergic and serotonergic genetic variants predict actions and expectations of cooperation and punishment" . The co-authors listed in the manuscripts are: Dr. Veronica Mariotti, Dr. Sara Palumbo, Dr. Stefano Vellucci and Professor Silvia Pellegrini (Department of Clinical and Experimental Medicine, University of Pisa), Dr. Pablo Marcos-Prieto, Prof. Emiliano Ricciardi, Prof. Ennio Bilancini and Prof. Pietro Pietrini (IMT School for Advanced Studies Lucca) and Prof. Leonardo Boncinelli (Department of Economics and Management, University of Florence).

Chapter 3 is based on an article currently under review in *Proceedings of the National Academy of Science (PNAS)* journal, with the title: "Prolonged exertion of self-control causes increased sleep-like frontal brain activity and changes in aggressivity and punishment". Additionally, the same work that this chapter is based on will be present in the Doctoral Thesis *Essays on Conflict, Aggressivity and Punishment* by Pablo Marcos-Prieto.

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Publications

1. G. Orrù, E. Ordali, M. Monaro, C. Scarpazza, C. Conversano, P. Pietrini, A. Gemignani and G. Sartori, (2023). "Reconstructing individual responses to direct questions: a new method for reconstructing malingered responses", *Frontiers in Psychology*, 14, p.1093854.
2. P. Marcos-Prieto, E. Ordali, S. Palumbo, S. Vellucci, E. Ricciardi, P. Pietrini, S. Pellegrini, L. Boncinelli and E. Bilancini, "Dopaminergic and serotonergic genetic variants and their relationships with classical economic games", *in preparation*.
3. P. Marcos-Prieto, E. Ordali, S. Palumbo, S. Vellucci, E. Ricciardi, P. Pietrini, S. Pellegrini, L. Boncinelli and E. Bilancini, "Dopaminergic and serotonergic genetic variants predict (actions and expectation of) cooperation and punishment", *under review*.
4. E. Ordali, P. Marcos-Prieto, G. Avvenuti, E. Ricciardi, L. Boncinelli, P. Pietrini, G. Bernardi and E. Bilancini, "Prolonged exertion of self-control causes increased sleep-like frontal brain activity and changes in aggressivity and punishment.", *under review*.

Presentations

1. E. Ordali, "Experience-dependent increases in low-frequency, sleep-like activity attenuate prosocial behavior," at *OHBM 2022, Organization for Human Brain Mapping 2022 Conference*, Glasgow, Scotland, June 19^{th}, 2022.
2. E. Ordali, "Dopaminergic and serotonergic genetic variants predict (actions and expectation of) cooperation and punishment", at *ESA 2022, European Economic Society Association Conference*, Bologna, Italy, September 1^{st}, 2022.

Abstract

Aggressivity is a type of widespread behavior in our society, yet its outcomes are everything but desirable. If evolutionary, being aggressive might have given some clear advantages to one to prevail (e.g., seizing resources, better mating options); nowadays, aggressive behavior held none of those advantages, being a form of prevarication where the ultimate goal is to harm another individual, either physically, emotionally, morally or materially. Why, then, is aggressive behavior still persistent despite the rise of cooperative societies? In this doctoral Thesis, with the aid of three controlled experiments and the expertise of Behavioral Economics and Neuroscience, I aim to shed more light on non-pathological aggressiveness, its genetic underpinnings, and cognitive mechanisms. Specifically, we found that some genetic variants of dopamine and serotonin are highly connected with actions and beliefs regarding cooperation and punishment, where having a particular variant makes one more prone to act and think pessimistically toward the behaviors of others or to free-ride more. In another experiment, we demonstrate that extreme exertion of self-control makes it more probable to behave aggressively in a subsequent social situation. Frontal areas dedicated to impulse control regulation are, in fact, extremely vulnerable to functional fatigue, showing signs of *local sleep*. In this neuronal phenomenon, groups of neurons fire at frequencies typical of sleep states instead of the ones of wake. Our experiment associated the prolonged exertion of self-control with the emergence of delta waves in frontal areas dedicated to impulse and emotion regulation and subsequent aggressive choices in a series of proxied social situations.

Chapter 1

Introduction

Aggressive behavior can be defined as *any behavior directed toward another individual that is carried out with the immediate intent to cause harm* (Bushman and Anderson, 2001; Anderson and Bushman, 2002; Berkowitz, 1993). From this definition, it is clear that aggressive behavior is hostile and non-cooperative and that it is exerted in order to cause damage to another individual, whether physical, mental, moral, or even material. Although aggression is typical in the animal kingdom (Hamburg, 1970; Rusch and Gavrilets, 2020; Sapolsky, 2005), so it is also among humans: the mortality rate due to homicide, the most violent and deliberate act of aggression, is 6.2 globally (per 100,000 people), with peaks of 19.2 in the American continent (WHO, 2023).

Given this data and despite its malevolent nature, why, then, is aggressive behavior so persistent in our society? What are its causes, underpinnings, and (even) benefits? What makes humans behave aggressively?

First, we must define what we mean by "aggressive behavior" and its major underpinnings. Aggressiveness is both an individual trait, that is, the level at which a person is prone to be aggressive or not independently of other factors or trait-aggressiveness, and aggression as a behavior triggered by an emotion or a situation, or state-aggressiveness (Deffenbacher

et al., 1996; Spielberger, 2010). In particular, trait-aggressiveness depends on unchangeable factors, such as genetics and personality. For example, high levels of testosterone (more often found in men) have been reported to correlate with highly expressed aggression (Mazur and Booth, 1998), as well as particular genetic polymorphisms, which can impact the overall level of interpersonal aggressivity (Caspi et al., 2002; Sokolov and Cadet, 2006; Coccaro, Lee, and Kavoussi, 2010; Moore, Scarpa, and Raine, 2002). State-aggressiveness, instead, is more linked with the situation and the person's current mental state, as described more thoughtfully below. However, the two aspects are deeply intertwined, and it is not always easy to retrace the source that provoked a certain aggressive outcome.

Then, we need to acknowledge that aggressive behavior has been classified into two subcategories, depending on different motivational roots: reactive and proactive aggression (Romero-Martinez, Sarrate-Costa, and Moya-Albiol, 2022). Specifically, reactive or hostile aggression is defined as the behavioral response to threats, real or perceived, provocations, and frustrations. As such, this type of aggressive response is characterized by impulsiveness and immediateness, and it is associated with poor emotional regulation and executive control (Berkowitz, 1993; Lickley and Sebastian, 2018). On the other hand, proactive aggression has an instrumental nature, is planned and goal-directed, and is associated in humans with callous-unemotional traits characterized by lack of empathy, guilt, and shallow affect (Frick and Viding, 2009; Dodge and Coie, 1987). Proactive aggression is more common in the animal kingdom as a way to gather food or resources, to have a higher social status, or better mating options (Hamburg, 1970; Rusch and Gavrilets, 2020; Sapolsky, 2005). In humans, this type of behavior is typical of personality disorders and Psychopathy and, as such, is not very common. It is estimated that worldwide, Psychopathy is diffuse only in the 1% to 3% of the population (APA, 2024).

Lastly, we must distinguish between aggression as a normal response

to a stimulus and pathological aggressive behavior. As the name suggests, pathological aggression derives from alterations of the processes that control the aggressive answer. These alterations can result from a lesion or a trauma in a region that is key for the control of such behavior or is due to a psychiatric illness. Studies on this type of aggressive behavior are helpful, as they permit us to better understand some of the processes involved in actualizing the normal answer. In fact, early animal research showed that monkeys with bilateral ablations of the dorsolateral prefrontal cortex exhibited enhanced aggressive behavior with respect to monkeys with bilateral ablation of the orbitofrontal cortex (Butter, Mishkin, and Mirsky, 1968). These results posit for the inhibiting and controlling role of the prefrontal cortex concerning aggressive impulses originating in subcortical areas (Giancola, 1995) and for a complex neural circuit comprising the orbital-frontal cortex, amygdala, hypothalamus, anterior cingulate cortex, and interconnected structures that was implicated in expressing and inhibiting aggression (Davidson, Putnam, and Larson, 2000). Research using fMRI techniques instead allows us to determine metabolic differences in activity in the left frontal cortex and left temporal cortex of violent psychiatric patients compared to non-patients (Volkow and Tancredi, 1987; Volkow, Tancredi, et al., 1995) and, more generally, aggressive inpatients present left hemisphere abnormalities (Amen et al., 1996). An fMRI study conducted on homicide offenders with comorbid psychiatric conditions showed that compared with controls, homicide offenders' orbito-frontal cortex was not engaged during the response inhibition of the Go/NoGo task (Joyal et al., 2007). Research on individuals showing pathological aggression also permitted to detect alterations in the electrical cortical activity; the presence of slow waves (theta and delta) in the wakeful EEG has been found in violent offenders (Mednick et al., 1981), in violent psychiatric inpatients (Volavka, 1990; Convit, Czobor, and Volavka, 1991), and in adolescents with conduct disorder, in which this indicator predicts the occurrence of aggressive acts later in life (Raine, Venables, and Williams, 1990; Scarpa and Raine, 1997). Interestingly, a PET study of visual imagery on healthy and non-aggressive individuals showed a decrease in the activity of the

medial orbito-frontal cortex of subjects who were imagining acting aggressively (Pietrini et al., 2000), once again highlighting the pivotal role of the orbito-frontal cortex in anger control. Here, the focus will be reactive aggression and, in particular, the cognitive processes underneath it, and aggression as a non-pathological answer to a stimulus. At the same time, both trait and state aggressiveness will be considered in different chapters of the dissertation.

Additionally, a behavioral economics approach will be adopted throughout the chapters. Behavioral economics perspective applies psychological insights into human behavior to explain economic decision-making, critically reviewing the neoclassical and hyper-rational notion of *homo economicus* (Mullainathan and Thaler, 2000). In this sense, behavioral economics is able to take into account complex human phenomena, such as individual selfishness leading to non-cooperative behavior and ultimately, aggressiveness. In fact, following the neoclassical economic approach, non-cooperative behavior is explained in terms of maximization of one own utility function, with the only variable considered being one's own benefit. Instead, in behavioral economics a non-cooperative act is described in terms of long-term and short-term costs (i.e., punishment) and benefits (i.e., rewards). Non-pathological aggression, then, is a non-cooperative act derived from a mishmatch between an immediate benefit, which can be classified as selfish, and a long-term consequence, such as harming another person and being punished for it. From this perspective, people keep engaging in aggressive acts because the immediate benefits outweigh the long-term costs (Rachlin, 2004; Georgiev et al., 2013).

Behavioral theoretical models of aggression provide an interesting framework for understanding this type of behavior. For example, the General Aggression Model (GAM, Anderson and Bushman, 2002) aims at taking into account while explaining susceptibility to reactive aggression as the outcome of a social encounter, individual differences, past experiences, and cognitive resources. In particular, as it can be seen by the sketch

model depicted in Figure 1, the availability of cognitive resources might represent a pivotal point in increasing or decreasing the likelihood that a hostile reaction is provoked as a response.

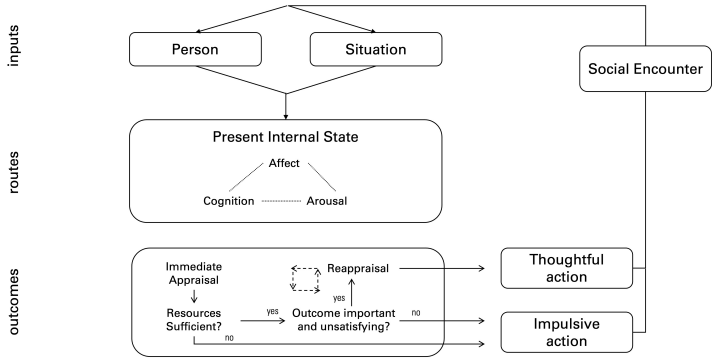


Figure 1: Graphical representation of the General Aggression Model (Anderson & Bushman, 2002).

Cognitive resources, in fact, are implied in a lot of mental processes, such as self-control, executive control, or self-regulation (Robinson, Schmeichel, and Inzlicht, 2010; Schmeichel, 2007), which is the capacity of humans to consciously inhibit a predominant response in order to maximize a long-term goal or interest (Miyake et al., 2000; Mischel, 2014). In the GAM framework, this concept is precious because it helps understand many aggressive acts led by impulsiveness, poor judgment of the situation, or non-optimal consideration of the consequences. If one's ability to control oneself is impaired or depleted, the subsequent act of decision-making will also be impaired. Numerous findings state that this is the case in general (Baumeister, Bratslavsky, et al., 2018; Vohs and T. F. Heatherton, 2000; Baumeister, Gailliot, et al., 2006), and specifically regarding aggressive acts (Gottfredson and Hirschi, 1990; DeWall et al., 2007; Muraven, Pogarsky, and Shmueli, 2006; Stucke and Baumeister, 2006; Baumeister, 2013).

In the following chapters of this doctoral thesis, we will investigate all

these aspects of aggressive behavior. In particular, non-pathological trait-aggressiveness will be explored in Chapter 2, where the extent of genes' role concerning the disposition to cooperate or to punish another individual was investigated. The chapter describes a study in which participants ($N = 104$), after having been genotyped for eight total polymorphisms from dopaminergic and serotonergic pathways, completed an online experiment comprising several economic games proxying for social situations with hostile or cooperative frameworks. Results showed that genes shape the probability of being (or not) cooperative and engaging in punishment with different intensities. In particular, the experiment showed how beliefs are essential in guiding our behavior and that beliefs are also subjected to genetic influence. Chapter 3, instead, will focus on state-aggressiveness, reactive aggressive-like behaviors, and the emergence of a Functional Frontal Fragility syndrome that might be identified as the source of suboptimal decision-making in social interactions, ultimately leading to aggressive acts. This syndrome might arise when, due to a previous predisposing condition, slow waves typical of sleep states emerge in the brain during wakefulness, impairing subsequent decision-making. In particular, with two highly controlled experiments, we aimed to investigate two phenomena (i.e., ego depletion and local sleep) that might be related and contribute to the emergence of a brain state or syndrome that affects decision-making, causing aggressive behavior to be more accessible. In the first experiment ($N = 44$), we used electroencephalographic techniques to assess brain functioning paired with depleting tasks and economic games. In contrast, in the second, we only used the same behavioral tasks on a bigger sample of participants ($N = 403$). The results of both studies go in the same direction and show that after extended practice with tasks that are designed to oblige participants to exert self-control to perform them correctly, i.e., depleting them of cognitive resources, delta waves (1-4 Hz) emerge in the local EEG, especially in a cluster of frontal neurons comprising the inferior frontal gyrus (Study 1) and that this state is linked with the behavior that subjects display in the subsequent economic games (Studies 1 and 2). Depleted subjects chose the aggressive alternative over the peaceful one

in higher proportion than their non-depleted counterparts ($p < 0.001$, Hawk and Dove game), and the use of prosocial punishment is reduced while the use of spiteful punishment increases (Public Goods Game with Punishment, $p = 0.001$). Lastly, Chapter 4 briefly concludes with some final remarks.

Chapter 2

Genetic variants, cooperation and punishment

In this Chapter, I will present a two-part research project conducted to highlight if and how much genetic variants can predict our behavior concerning cooperation, aggressiveness, punishment, and beliefs about these behaviors. Initially, we administered an online experiment made of several economic games and psychological questionnaires to a sample of participants, of which genetic information was in our possession. Then, we opted to analyze the results found only in two played games, the Public Goods Game with and without punishment, while constructing a dataset comprising all the other results found in the remaining games. The Chapter is constructed as follows: after a brief introduction about the state-of-the-art regarding genetic research in conjunction with social behaviors, the main hypothesis and aim of the within-subjects experiment that we conducted will be presented, followed by methods, results, and discussion. Lastly, I will briefly describe the part of the experimental protocol that constitutes the extended database.

2.1 Introduction

From the recent literature, we know that genes matter when talking about behaviors. Examples derive from twins and family studies, demonstrating that genetic influences are crucial determinants of both cooperation (Wallace et al., 2007) and antisocial behaviors (Brunner et al., 1993). Specifically, molecular genetic variations of neurotransmitter system functions, such as serotonin, dopamine, and oxytocin, have been studied. Contributions like the ones of Zak, Stanton, and Ahmadi (2007) and Kosfeld et al. (2005) and Crockett, Clark, Tabibnia, et al. (2008), Crockett, Clark, Lieberman, et al. (2010), and Crockett, Clark, Hauser, et al. (2010) are nowadays considered seminal in the field and highlight, for example, how much trust behavior, time preferences (e.g., time, delay, and temporal discounting, short- or long-term orientation), and moral preferences are directly influenced by neurotransmitter modulation. Serotonergic and dopaminergic systems are implicated in several cognitive processes, from motivation and mood to learning and decision-making (Cools, Nakamura, and Daw, 2011; Dayan and Huys, 2009; Bang et al., 2020). The involvement of these neurotransmitters in cognitive processes is particularly important since their regulations depend on genetic allele variants that give rise to inter-individual differences in their production, transportation, transmission, and metabolism. All these processes are known to ultimately affect behaviors, such as in the allelic variations of the MAO-A gene or receptor DRD4, to put some notable examples. Monoamine oxidase A, found in chromosome X, is responsible for the metabolization of mostly norepinephrine (NE) and serotonin (5-HT). The short allele of MAO-A, which makes the metabolization four times more inefficient than usual, has been correlated with aggressive behaviors and criminal records in male subjects (Caspi et al., 2002; McDermott et al., 2009; Simons, Beach, and Barr, 2012). Instead, dopamine receptor D4 exon 3 is a functional polymorphism often associated with altruism and risk-seeking behavior, depending on the number of repetitions of the alleles (in the mentioned examples, 4/4 or 7/7, see Bachner-Melman et al., 2005; DeYoung et al., 2006; Enge et al., 2017; Zhong et al.,

2010). Other polymorphisms of serotonin and dopamine have also been found to affect the expression of aggression and cooperation, such as polymorphisms of solute carrier-family 6 member 4 (SLC6A4), of tryptophan hydroxylase-2 (TPH2) (Gärtner et al., 2018), and of catechol-O-methyltransferase (COMT) rs4680 (Baeken, Claes, and De Raedt, 2014; Glavina Jelaš, Dević, and Karlović, 2018), although their precise influence on behavior might be more complex. Recent research shows, in fact, that genetic polymorphisms involved in the control of synaptic and metabolic functions are also sensitive to environmental experiences, whether positive or negative. As such, depending on the experiences present in a given environment, the same genetic variants might either act as risk variants in the case of adverse life events (Rigoni et al., 2010) or as plasticity variants, incrementing the probability of developing prosocial behavior in the case of positive environmental inputs (Iofrida, Palumbo, and Pellegrini, 2014; Belsky et al., 2009; Simons, Lei, et al., 2011).

To better understand how genetic variants of neurotransmitters affect decision-making and social behaviors, experimental and behavioral economics expertise was used to investigate such phenomena since stylized economic games rely on material incentives that permit the elicitation of relevant proxies of social behaviors within experimental settings (Von Neumann and Morgenstern, 1947). In this framework, findings emerged concerning genetic variants of dopamine and serotonin receptors, highlighting the link of particular genetic variants with fairness preference and altruistic punishment (Knafo et al., 2008; Israel et al., 2009; Zhong et al., 2010; Jiang et al., 2015). As such, investigating these topics is particularly interesting since it will help shed more light on the complex mechanisms in play between plasticity-susceptibility genetic variants, key human behaviors such as cooperation and punishment, and environmental influence.

In this contribution, we focused on the Public Goods Game (PGG) since it embeds the fundamental tension between individual and group benefits, capturing a typical situation in social dilemmas where individ-

uals have no personal reasons to contribute. In a standard PGG, an initial endowment, which can be either kept or committed to a joint project that benefits the group as a whole, is given to each individual in a group. Contributions are multiplied by a constant greater than one and equally divided among the group members. Therefore, individuals are strongly incentivized to keep their endowment and benefit from others' cooperation (the so-called "free-rider problem"). At the same time, the social optimum is attained when everybody contributes as much as possible. On top of that, a punishment option may be introduced, such that peers can spend part of their final profits on reducing the share of others, which is generally used to punish defectors and enhance cooperation, as in Fehr and S. Gächter (2002). Several real-life examples in which the PGG framework can be applied are climate negotiation, communal cattle management, paper co-authorship, recycling, contributions to private parties, or paying taxes. Drawing from the latter example, we can think of PGG as follows: if everybody pays taxes, the services provided in return to the whole population are better (e.g., infrastructure, health services, education). However, even those who did not contribute (e.g., evaded taxes) because their incentives prevailed over the group motives will benefit from the public services. That being the case, looking at a mechanism that will try to avoid, as a deterrent, the "free-riders problem" or, in our example, tax evaders is paramount. Peer punishment towards defectors (i.e., prosocial punishment) has been identified as such a tool, and its potential genetic roots have been extensively investigated (Crockett, Clark, Lieberman, et al., 2010; Crockett, Clark, Hauser, et al., 2010; Zhong et al., 2010; Enge et al., 2017; Gärtner et al., 2018). Other punishment modalities, such as antisocial and spiteful punishment (Herrmann, Thoni, and Gachter, 2008), have not yet been looked at in the field of behavioral genetics.

Given this, we decided to focus on introducing some novelties concerning previous related literature. Our design included multiple gene variants together with the collection of information from several games in experimental economics and their related beliefs, adding belief exploration to these types of studies. Belief exploration, that is, assessing one's

personal beliefs about a behavior or a situation, is highly relevant since beliefs are thought to play a role in guiding human behavior indirectly by forming mental associations that the person will recall before taking action. Moreover, we considered the whole set of punishment strategies (prosocial, antisocial, and spiteful punishment, as well as the option of not punishing) to assess to what extent the investigated genetic polymorphisms influence our behavior in social situations. Specifically, the role of four genetic variants of the dopaminergic pathway and four polymorphisms of the serotonergic pathway in modulating antisocial punishment behavior in PGG was investigated by considering both antisocial punishers, that is, those who punished individuals that contributed more and spiteful punishers, that is, those who punished individuals regardless of their contribution (Herrmann, Thoni, and Gachter, 2008). Subjects that had never punished and those who punished low contributors were considered the reference group to be compared with the antisocial sample. Furthermore, as little is known about the relationship between genetic variants and individual beliefs about others' behavior, we also considered beliefs about others' behaviors in the PGG to assess the general attitudes of subjects toward contributions and punishment. Interestingly, we found that specific dopaminergic and serotonergic gene variants affect both actions and expectations about others' behavior in social contexts.

2.2 Materials and Methods

2.2.1 Participants and Experimental Session

Participants were recruited from a larger sample of subjects pertaining to an ongoing project at the University of Pisa, where DNA extraction and genotypization was performed. The study was conducted in accordance with the Declaration of Helsinki and the research obtained the approval of the Ethical Committee of University of Pisa. Of that sample, one hundred and four participants (71 females) agreed to participate to this experiment, which was performed online through the platform Pro-

lific, whose interface was coded using oTree (Chen, Schonger, and Wickens, 2016). However, the results of this paper were computed using only ninety-nine subjects (67 females, mean age 32.9 years, with a standard deviation of 12.3) due to the fact that 5 subjects did not complete all the tasks in the experiment. Gender did not significantly correlate with any of the genetic variants and neither with behavior nor beliefs in the Public Goods Game. Given the strategy method nature of the experiment, we were able to schedule online sessions in the platform Prolific according to the availability of the subjects and perform the matching ex-post. Hence, we opened eight sessions throughout May and June 2020. The show-up fee was 1.5 euros, which could be increased depending on performance to 6 euros. A bonus payment of 0.4 euro was given to the subjects whose belief was accurate enough (see below), so as to ensure incentive alignment and truthfulness in the belief elicitation task. All participants gave informed consent, which was presented to them online, and could interrupt the experiment at any moment if desired.

2.2.2 Public Goods Game

Both versions of the Public Goods Game were played in a one-shot, anonymous fashion (Fig. 2). The subjects were paired in groups of four participants each and received an initial endowment of 10 points that they could either keep for themselves or devote to a joint project. The total points in the common pool were multiplied by two and then divided equally between the players. Therefore, there was an individual incentive to "free ride" on the contribution of others, e.g., contribute zero points, receiving 10 points plus the amount derived from the contributions of others. On the other hand, the social optimum, welfare, and efficiency maximizing outcome required every subject to contribute all the 10 points so that each subject could attain the result of 20 points. For the version with the punishment option, after the first stage, the subjects were allowed to assign two of their final points as "punishment points" to one player, reducing that player's final number of points by four. No feedback was provided in the second stage. Thus, the options for the

players were "punish the player that contributes the less" (prosocial punishment), "punish the player that contributes the most" (antisocial punishment), "do not punish" (second-order free-riders), or "punish a player at random" (spiteful punishment). For belief elicitation, in the case of the contributions, subjects received a bonus of two points if they could guess the actual average contribution in the sample within a margin of error of one point. Regarding the beliefs about punishment, subjects received a bonus if they could jointly guess the more and less frequent modalities of punishment indicated by the rest of the players.

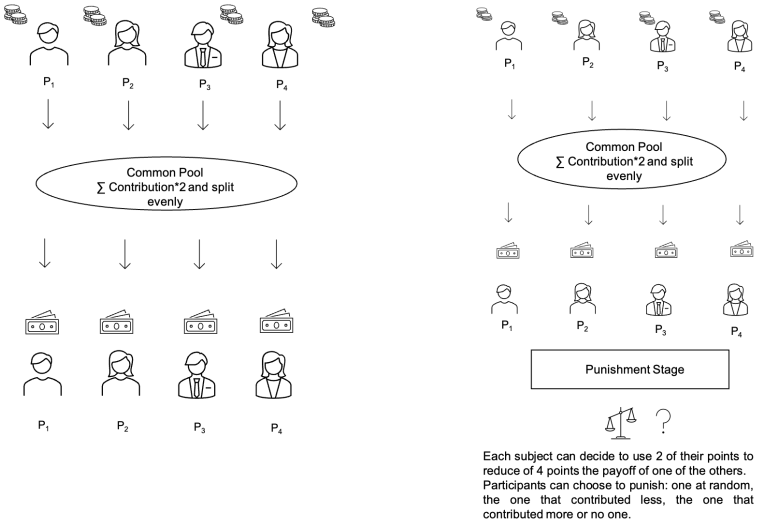


Figure 2: Visual depiction of both versions of the Public Goods Game played in the experiment.

2.2.3 Genetic Data

Each participant donated a saliva sample, collected with an Oragene collection tube (DNA Genotek Inc., Ottawa, Ontario, Canada). DNA was extracted from saliva by the prepITL2P kit following the manufacturer's protocol (DNA Genotek Inc.). Participants were genotyped for

four polymorphisms of the serotonergic pathway (TPH2-rs4570625, 5-HTR1B-rs13212041, 5-HTR2A-rs6314, and 5-HTTPLR, including both the VNTR and the SNP rs25531), and four genetic variants of the dopaminergic pathway (ANKK1-rs1800497, SLC6A3 40 bp VNTR, DRD4 48 bp exon III VNTR and COMT-rs4680). Concerning HTR1B-rs13212041, HTR2A-rs6314, TPH2-rs4570625, and ANKK1-rs1800497, homozygotes for the minor allele were grouped with heterozygotes and compared to the homozygotes for the ancestral allele (i.e., HTR1B-rs13212041 C/C + C/T vs. T/T, HTR2A-rs6314 C/C + C/T vs. TT, TPH2-rs4570625 T/T + G/T vs. G/G, ANKK1-rs1800497 C/C + C/T vs. T/T). Regarding COMT-rs4680, the genotypic groups were created based on functional data (Lachman et al., 1996). Specifically, the low activity genotype (A/A) was compared to the high and intermediate activity genotypes (G/G and G/A). The same strategy was adopted for the VNTR polymorphisms: DRD4-exon III-VNTR and 5-HTTLPR, including the functional SNP rs25531 $A > G$ (16642437). In detail, the DRD4-exon III-VNTR low activity alleles (non-4r) were compared to the high activity genotype (4r/4r) (Simpson et al., 2010; Schoots and Van Tol, 2003; Asghari et al., 1994), while the 5-HTTLPR low activity genotypes (S/S, S/LG (rs25531), S/LA (rs25531) and LG/LA) were compared to the high activity genotype (LA/LA). S (short) and L (Long) are the most common alleles of the 5-HTTLPR. Evidence shows that the S allele decreases the 5-HTT expression (Lesch et al., 1996; Heils et al., 1996), and the same effect has been reported for the LG allele (L allele with G (rs2535) nucleotide -16642437). The G nucleotide is less frequent in the S allele but does not further reduce the 5-HTT transcription compared to the SA allele (Sakai et al., 2002; Meyer et al., 2015). Regarding SLC6A3-VNTR, non-9r alleles were compared to the 9r/9r genotype.

Except for TPH2-rs4570625 and SLC6A3 40 bp VNTR, all the genetic variants are in Hardy-Weinberg equilibrium (Table 1), a principle for which the genetic variation in a population will be constant across generations, in the absence of disturbing factors (Hardy, 1908; Weinberg, 1908; Mayo, 2008). When studying genes of a restricted sample (such as in the

case of an experiment), H-W equilibrium is used to state that the distribution of allele variation in the sample is not different from the one of the general population to avoid hyper- or hypo-representation of some genetic variants, hence resulting in misleading results. In our case, although TPH2-rs4570625 and SLC6A3 40 bp VNTR were kept in the analysis, their results were not considered since these two genes were, in our sample, not distributed according to H-W equilibrium.

2.2.4 Data Analysis

Eight genetic variables and six behavioral variables were correlated for 48 simultaneous tests. Spearman correlations were used to account for violations of linearity and the presence of non-normalities in the data. Table 2 shows the correlation coefficients with their respective uncorrected p-values, P_U. Subsequently, a standard Bonferroni correction was applied to correct p-values for multiple testing, P_C, that returned four correlation coefficients (three for the serotonergic pathway and one for the dopaminergic pathway) that remain statistically significant.

All the computations were performed with Stata 16. Specifically, for the PGG, we considered the subject's contribution to the joint project, $PGGc$, for the Public Goods Game without punishment, and $PGGp$, for the version with the punishment option. Similarly, we considered the associated beliefs of the actions in the two games, $bPPc$ and $bPGGp$, respectively. Considering the punishment itself, we created a dummy variable, $ANTI$, in which we merged the antisocial and spiteful punishment choices (with value 1), as opposed to the prosocial punishment and the absence of it. Then, since the beliefs about punishment were stated as the punishment action that people believed to be more common, and not as a number, another dummy variable was created, $bmANTI$. In this case, 1 was given if the subject believed the more common punishment behavior was antisocial or spiteful, and 0 was given otherwise. The allelic distribution of each gene was transformed into a dummy variable to be comparable with the decisions taken during the experiment. The dummies were created based on previous literature that identifies pairs

Table 1: Hardy-Weinberg Equilibria of the genotyped polimorphisms

	Genotype groupings	Genotypes	Whole sample ($n = 104$)
HTR1B-rs13212041	T/T	T/T	0.711
	C-allele	C/C	0.019
		C/T	0.269
	H-W eq.	$p = 0.728$	
5HTTPLR+rs25531	L/L	L/L	0.240
	S/S	S/S	0.230
		S/L	0.528
	H-W eq.	$p = 0.555$	
HTR2A-rs6314	T/T	T/T	0.788
	C-allele	C/C	0.009
		C/T	0.201
	H-W eq.	$p = 0.786$	
TPH2-rs4570625	G/G	G/G	0.519
	T-allele	T/T	0.019
		G/T	0.641
	H-W eq.	$p = 0.018$**	
SLC6A3 40 bp VNTR	9r/9r	9r/9r	0.105
	non-9r allele	9r/non-9r	0.326
		non-9r/non-9r	0.567
	H-W eq.	$p = 0.05$*	
ANKK1-rs1800497	T/T	T/T	0.721
	C-allele	C/C	0.009
		C/T	0.269
	H-W eq.	$p = 0.355$	
DRD4 48 bp exon III VNTR	4r/4r	4r/4r	0.375
	non-4r allele	4r/non-4r	0.451
		non-4r/non-4r	0.173
	H-W eq.	$p = 0.556$	
COMT-rs4680	A/A (Met/Met)	A/A	0.192
	G-allele	G/G	0.336
		A/G	0.471
	H-W eq.	$p = 0.700$	

Table 2: Spearman correlation matrix. Uncorrected (P_U) and Bonferroni corrected p-values (P_C) are reported.

Variables	Public Goods Game		Public Goods Game with punishment			
	PGG_c	$bPGG_c$	PGG_p	$bPGG_p$	$ANTI$	$bmANTI$
Serotonin pathway						
HTR1B - T/T	0.1269	-0.0042	-0.2140	-0.1634	-0.1571	-0.3850
	(0.2108)	(0.9667)	(0.0335)*	(0.1060)	(0.1205)	(0.0002)***
p corrected	(1)	(1)	(1)	(1)	(1)	**(0.0160)***
5HTTLPR - L/L	-0.3553	-0.3440	-0.0565	-0.0377	-0.0385	-0.1820
	(0.0003)***	(0.0005)***	(0.5786)	(0.7110)	(0.7051)	(0.0743)
p corrected	**(0.0148)***	**(0.0235)***	(1)	(1)	(1)	(1)
HTR2A - T/T	0.0594	0.0803	0.1322	0.1396	-0.0508	0.1602
	(0.5589)	(0.4295)	(0.1922)	(0.1683)	(0.6173)	(0.1170)
p corrected	(1)	(1)	(1)	(1)	(1)	(1)
TPH2-T/T	-0.0468	-0.0131	0.0184	-0.0680	-0.0508	-0.0650
	(0.6453)	(0.8978)	(0.8569)	(0.5037)	(0.6173)	(0.5269)
p corrected	(1)	(1)	(1)	(1)	(1)	(1)
Dopamine pathway						
DAT-1-9r/9r	0.0006	0.0985	0.2942	0.2019	0.2488	0.3078
	(0.9953)	(0.3319)	(0.0031)**	(0.0451)*	(0.0130)*	(0.0022)**
p corrected	(1)	(1)	(0.1)	(1)	(1)	(0.2)
ANKK1-T/T	-0.1045	-0.0131	0.1083	0.0644	-0.0508	-0.0650
	(0.3034)	(0.8978)	(0.2860)	(0.5264)	(0.6173)	(0.5269)
p corrected	(1)	(1)	(1)	(1)	(1)	(1)
DRD4-4r/4r	-0.1365	-0.0959	0.0591	0.0255	0.0984	-0.0253
	(0.1778)	(0.3451)	(0.5612)	(0.8020)	(0.3326)	(0.8061)
p corrected	(1)	(1)	(1)	(1)	(1)	(1)
COMT-A/A	-0.0403	-0.0490	-0.2733	-0.3533	0.0336	0.1820
	(0.6921)	(0.6303)	(0.0062)**	(0.0003)***	(0.7411)	(0.0743)
p corrected	(1)	(1)	(0.2)	**(0.0160)***	(1)	(1)

made of some target behaviors and specific allelic combinations. Robustness checks were done depending on the nature of the variable. For example, Pearson's chi-square test, Fisher's exact test, Kendall's tau correlation, linear probability model with robust errors, and probit estimation were used with binary variables. In contrast, for roughly continuous variables, Kendal's tau correlation, two-sample Wilcoxon rank-sum (Mann-Whitney) test, linear regression with robust errors, and a tobit estimation.

2.3 Results of the Public Goods Game

2.3.1 Serotonergic Pathway

We found an association between the L/L genotype of 5-HTTLPR and smaller contributions in the PGG without punishment ($t = -3.7075$, $P_C = 0.0148$) (Figure 3a). This result was robust to Kendall tau correlation, $P_{KU} < 0.001$ and $P_{KC} = 0.0213$, and non-parametric Wilcoxon rank-sum test, $P_{WU} < 0.001$ and $P_{WC} = 0.0210$. On average, 5-HTTLPR L/L genotype was associated with a reduction in contributions of 2.4 points, accounting for about 12% of the variance. This finding survived additional correction for heteroskedasticity, $P_{RU} < 0.001$and $P_{RC} = 0.0170$, was significant to tobit estimation ($P_{TU} = 0.0011$) but was only marginally significant after multiple testing correction ($P_{TC} = 0.0541$). The L/L genotype of 5-HTTLPR was also associated with the belief that others' contribution in the PGG without punishment was smaller or null ($t = -3.2927$, $P_C = 0.0235$) (Figure 3b). This result was also robust to Kendall tau correlation, $P_{KU} < 0.001$ and $P_{KC} = 0.0322$, and Wilcoxon rank testing $P_{WU} < 0.001$ and $P_{WC} = 0.0317$. On average, 5-HTTLPR L/L genotype decreased beliefs about others' contribution by 1.65 points, explaining about 10% of the variance. This finding also survived additional correction for heteroskedasticity, $P_{RU} < 0.001$ and $P_{RC} = 0.0210$, was significant to tobit estimation ($P_{TU} = 0.0011$) but was only marginally significant after multiple testing correction ($P_{TC} = 0.0536$). Overall, these findings indicated that the high expression genotype of 5-HTTLPR

was associated with a lower contribution in the PGG without punishment and lower expectations about others' contribution in the same game.

We also found that the T/T genotype of 5-HTR1B-rs13212041 was less frequent in subjects who believed that the antisocial or spiteful punishment behavior was the most common in the group of PGG players ($t = -4.0654$, $P_C = 0.0047$) (Figure 3c). This result was confirmed by using a Pearson's chi-squared $P_{\chi^2 U} < 0.001$, $P_{\chi^2 C} = 0.0072$ and a Fisher's exact test, $P_{FU} < 0.001$ and $P_{FC} = 0.0149$, and it was robust to the use of Kendall tau correlation, $P_{KU} < 0.001$ and $P_{KC} = 0.0079$. The marginal effect of 5-HTR1B-rs13212041 T/T genotype on beliefs, obtained by using the linear probability model, was -0.3938, explaining about 15% of the variance. This survived additional correction for heteroskedasticity, $P_{RU} < 0.001$ and $P_{RC} = 0.0216$, and was confirmed by an alternative probit estimation, $P_{PU} < 0.001$ and $P_{PC} = 0.0134$. Overall, these findings suggested that the 5-HTR1B-rs13212041 T/T genotype may predispose to more optimistic beliefs about others' punishing attitudes.

2.3.2 Dopaminergic Pathway

The only result that survived Bonferroni's correction within the dopaminergic pathway was an association between the A/A genotype of COMT-rs4680 and the belief that others' contributions in the PGG with punishment was smaller ($t = 3.705$, $P_C = 0.0160$) (Figure 3d). This result was robust to the use of Kendall tau correlation, $P_{KU} < 0.001$ and $P_{KC} = 0.0229$, and Wilcoxon rank testing, $P_{WU} < 0.001$ and $P_{WC} = 0.0225$. The variance in beliefs explained by COMT-rs4680 A/A was about 12%, meaning that this gene variant was associated with the belief that the contributions of others were lower by 2.14 points on average. This finding survived additional correction for heteroskedasticity, $P_{RU} < 0.001$ and $P_{RC} < 0.001$, and was confirmed by tobit estimation, $P_{TU} < 0.001$, and $P_{TC} = 0.0072$. Overall, people with A/A genotype of COMT-rs4680 appeared to have more pessimistic beliefs about the average contribution in the PGG with a punishment option.

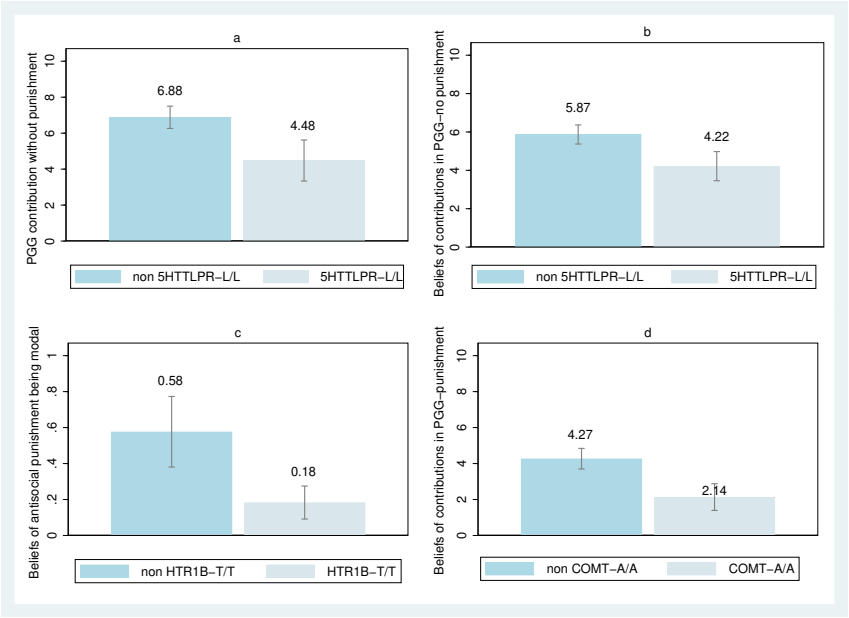


Figure 3: Plot representation of the four main results. Panels (a) and (b) show results regarding carriers vs. non-carriers of the L/L genotype of 5-HTTLPR about, respectively, the mean difference in contributions to the public good in the absence of a punishment option and the relative beliefs about that same behavior. Panel (c) shows the mean difference in beliefs about the presence of antisocial behavior for carriers vs. non-carriers of the T/T genotype of 5-HTR1B. In contrast, finally, panel (d) shows the mean difference in beliefs about the average contribution to the public good, in light of a punishment option, between carriers vs. non-carriers of Met/Met variant of COMT-rs4680 gene.

2.4 Discussion

This study explored how some genotypes may affect behaviors and beliefs about others' behaviors within social dilemmas. We analyzed, in a sample of euthymic subjects from the general population, potential associations between specific serotonergic and dopaminergic gene variants and both behaviors and elicited beliefs about others' behavior in two versions of the Public Goods Game, one with the option of punishing other participants and one without such an option. We found significant associations between two serotonergic and one dopaminergic alleles and contribution behaviors, with beliefs about others' contribution behavior and the prevalence of antisocial and spiteful punishment. Our findings suggest that genes affect behavior and expectations about others' behavior.

2.4.1 Main Findings for the Serotonergic Pathway

In line with the existing literature evidence showing that a reduction of 5-HT signaling decreases cooperative responses during the Prisoner's Dilemma game (Wood et al., 2006), we found that carriers of the L/L genotype of 5-HTTLPR, which has been associated with lower serotonin transmission due to its higher reuptake from the synaptic cleft, contributed less to the public good (i.e., they tend to free-ride) when the option of punishing others was not present (Figure 3a); furthermore, we observed that the L/L genotype carriers expected more frequently to observe free-riding behavior also from other people (Figure 3b). 5-HTTLPR is a VNTR (variable number of tandem repeats) located in the promoter region of the SLC6A4 gene, which encodes for the serotonin transporter (5-HTT). 5-HTT controls the strength and duration of serotonergic neurotransmission by regulating the serotonin transport from the synaptic cleft to the presynaptic terminal of serotonergic neurons (Montañez et al., 2014). 5-HTTLPR is characterized by two alleles: the Short (S) one with 14 repeats of a 20-23bp-long unit and the long (L) allele with 16 repeats. The L allele has been associated with more rapid serotonin reuptake, resulting in lower levels of active serotonin, whereas the S variant appears to

be associated with reduced serotonin reuptake, resulting in higher levels of active serotonin (Lesch et al., 1996; Heils et al., 1996; Greenberg et al., 1999). Homozygotes for the L allele are less anxious (Crişan et al., 2009) and more prone to risky behavior (Stoltenberg et al., 2011; Crişan et al., 2009; Kuhnen and Chiao, 2009), as compared to the S allele carriers, and have been described to have a higher sensitivity to punishment and norms on the social context (Schroeder, McElreath, and Nettle, 2013). We thus hypothesized that carriers of the L/L genotype lack the anxiety that often prevents free-riding behavior, mostly under non-threatening circumstances.

The 5-HTT activity is also under the regulatory control of 5-HT1B autoreceptors (Daws et al., 2000; Ase et al., 2001; Malagié et al., 2001; Hagan et al., 2012; Montañez et al., 2014). 5-HTT and 5-HT1B autoreceptors, indeed, are both located on presynaptic serotonin nerve terminals, and the 5-HT1B autoreceptors modulate the extracellular serotonin levels in serotoninergic projections by increasing the activity of 5-HTT (Hagan et al., 2012). The 5-HT1B receptor antagonist cyanopindolol, for example, has been described to inhibit the 5-HT clearance in wild-type mice (Montañez et al., 2014). As regards the 5-HTR1B-rs13212041 variant, we observed that carriers of the T/T genotype had more optimistic expectations about others' punishing behavior; that is, they expected punishment to be either less frequent or more likely to target low contributors (prosocial punishment) (Figure 3c). Since the T/T genotype of rs13212041 seems to reduce the expression of 5-HTR1B by allowing for the interaction with a regulatory microRNA (i.e., miR-96; see Jensen et al., 2009), we hypothesized that the T/T genotype might increase the serotonergic transmission by reducing the 5-HTT activity. Our finding is consistent with literature evidence showing that carriers of genetic variants that increase serotonergic transmission tend to punish less unfair behavior than carriers of variants that reduce serotonergic transmission (Enge et al., 2017; Gärtner et al., 2018). However, we cannot ignore that 5-HTR1B also acts as a heteroreceptor by reducing the release of other neurotransmitters. 5-HT1B heteroreceptors are distributed

on GABAergic, glutamatergic, and acetylcholinergic neurons and inhibit the release of GABA, glutamate, and acetylcholine (Tiger et al., 2018). Furthermore, they facilitate dopamine release by inhibiting dopamine-restricting GABAergic interneurons (Alex and Pehek, 2007; Tiger et al., 2018). Consequently, the effects of the 5-HTR1B-rs1321204 T/T genotype on social behavior cannot be restricted only to serotonin transmission.

2.4.2 Main Findings for the Dopaminergic Pathway

Concerning the dopaminergic pathway, we found that carriers of the catechol-O-methyltransferase (COMT) rs4680 A/A genotype had more pessimistic beliefs about others' contribution in the presence of a punishment option, i.e., they think other subjects contributed less to the Public Goods Game when punishment was allowed (Figure 3d). The COMT enzyme is responsible for the metabolization of dopamine. The substitution of the Val (high activity) amino acid with the Met (low activity) amino acid at position 158 (Val158Met), due to the G/A change in exon 4 of the COMT gene, reduces by about four times the activity of the enzyme, accounting for a slower catecholamine's inactivation (Bianchi, Gulotta, and Sartori, 2009). The Met/Met genotype is related to dysfunctional evaluations of risks/benefits with the result of underestimating the costs of actions (Varga et al., 2012; Soeiro-De-Souza et al., 2013), with less cooperativeness in teamwork situations (Walter et al., 2011), and with significantly lower scores in the cooperativeness scale (Baeken, Claes, and De Raedt, 2014; Glavina Jelaš, Dević, and Karlović, 2018). Furthermore, in a study where participants were asked how much of their previously earned endowment they wanted to give to a poor child from a developing country, donations from the rs4680 A/A homozygotes were about half as high as those from the G-allele carriers (Reuter, Frenzel, et al., 2011). This result could be indicative either of selfish behavior, an underestimation of costs/benefits related to the effects of punishment or that they felt more entitled to keep their earnings, in line with Goldman's hypothesis of the "warrior/worrier". In this hypothesis, the Val allele is associated with an advantage in stress resiliency (warrior strategy), while

the Met allele increases anxiety and cognitive performance (worrier strategy, see Goldman, Oroszi, and Ducci, 2006). These findings, along with studies linking the Met allele with an increased negative emotionality (Goldman, Oroszi, and Ducci, 2006; Reuter and Hennig, 2005), might explain why carriers of the A/A genotype had lower expectations of receiving a fair contribution from other people also when a punishment option existed.

2.5 Construction of a Comprehensive Database

As described in the previous paragraphs, our research question(s) about cooperation and punishment drove us to explore the results found in the two versions of the Public Goods Game in detail. However, PGGs were only a part of all the economic games the participants completed. Since the interaction between genes and complex behaviors has always been challenging to explore in detail, we believed that providing a comprehensive dataset that contains genotyping data regarding eight serotonergic and dopaminergic variants in a non-clinical sample, some psychometric measures, and environmental data of these subjects and their answers to a representative set of typical economic games extensively used in behavioral and experimental economics, would have been of use for the scientific community.

For these reasons, the last part of the project consisted of organizing all the data collected during the experiment in a dataset to be shared in an open-access platform to give insights to other researchers to design and test specific hypotheses regarding genes and behaviors. The instructions for the experiment in Italian (original), the English translation, and the gene primers utilized for the analysis are reported in Appendix A.

2.5.1 Extended Experimental Design

The sample of participants is the same one described in previous paragraphs. For the extended experiment, we adapted to our scope some of

the most classical games from the Game Theory framework, such as the Dictator Game, Ultimatum Game, Trust Game, Prisoner's Dilemma, Stag Hunt game, Hawk and Dove game, and Public Goods Game. Besides making a decision in each game, beliefs about others' behavior on every decision were elicited in an incentive-compatible way. We adapted all the games to be one-shot and the interactions anonymous, with subjects playing each game with every possible player role and being rematched after every decision. The games were created using the strategy method (Brandts and Charness, 2011; Fischbacher, Gächter, and Quercia, 2012), presenting the complete information set to the participant without depending on others' choices rather than relying on actual interaction between participants. Although it presents some limitations, this technique is essential when discussing non-simultaneous interactions, such as in this design. For payoff purposes, the pairings of the participants were created randomly, ex-post. Participants were informed that the experiment was incentivized and that one of their decisions and one of their beliefs would have been extracted randomly and paid according to the amount of points earned, potentially increasing the standard show-up fee of 1.5 euros to a maximum of 6 euros. The established conversion rate was 0.20 EUR per point, and all the games were normalized so that the maximum quantity of attainable points ranged from 0 to 20 (except for Public Goods Game, which ranged from 5 to 35 points). Lastly, according to an explicit game-specific scoring rule, a sufficiently correct stated belief translated into a bonus of two points (or 0.40 EUR) to ensure incentive alignment and truthfulness in the belief elicitation task. All participants gave informed consent, which was presented online before starting the study, and could interrupt the experiment at any moment if desired.

The experiment comprised three blocks, whose order was randomized to account for possible order problems. When correcting for multiple testing at the $Group \times Decision$ level, none of the six group dummies was significant. The first block included Dictator Game, Ultimatum Game, and Trust Game; the second block contained Hawk and Dove Game and Stag Hunt Game, and the third group comprised Prisoner's Dilemma and Public Goods Game, played with and without a punish-

ment option. At the end of the game blocks, independently of the order in which they were played, participants had to compile two psychological questionnaires and a page with personal demographic information (age, gender, and education). The majority of the self-reported tasks, such as past volunteering activities, the Altruistic Personality Scale (APS, Rushton, Chrisjohn, and Fekken, 1981), Interpersonal Reactivity Index (IRI, Davis et al., 1980), and the Traumatic Experience Checklist (TEC, Nijenhuis, Van der Hart, and Kruger, 2002) had been administered to the participants a previous study (unpublished data), while during the present experiment, participants compiled the Barratt's Impulsiveness Scale (BIS-11, Patton, Stanford, and Barratt, 1995) and the Measure of Parental Style (MOPS, Picardi et al., 2013).

Dictator Game, Ultimatum Game, Trust Game

In the Dictator Game, subjects are asked to split 20 points between themselves and another subject. The second player has no choice to make (Fig. 4a). The Ultimatum Game follows the same structure. However, this time, the second player may accept or reject the proposed split so that, if accepted, each player earns her respective price size, while, if rejected, both players earn zero. The action of the second player is presented using the strategy method, therefore stating the minimum acceptance threshold (Fig 4b). In the Trust Game, the last game of the first block, both participants receive an initial amount of four points. The first player, the investor, can send an amount of either 0, 2, or 4 points to the second player, the trustee. The points sent are then quadruplicated, and the trustee chooses how many of them, if any, to give back to the investor, conditional to the investor having sent either 2 or 4 points, relying again on the strategy method. The discretization of the strategy space of the investor, thus, is key in allowing the strategy method presentation to be easily tractable for the trustees (Fig. 4c). The beliefs in these three games are elicited in terms of average behavior in the population of experimental subjects. Hence, individuals are asked for the average split in the Dictator Game, the average offer in the first player of the Ultimatum Game, the average minimum acceptance threshold in the second player of the

Ultimatum Game, the average amount of points sent by the investor and the average amount of points sent back by the trustee.

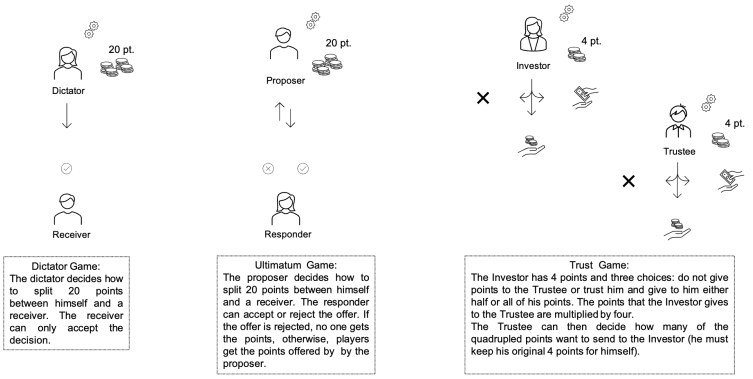


Figure 4: Visual depiction of the Dictator Game, Ultimatum Game, and Trust Game played in the experiment.

Hawk and Dove Game, Stag Hunt Game, Prisoner's Dilemma

For the second block, which includes the Hawk and Dove Game and Stag Hunt Game, and the first game of the third block, Prisoner's Dilemma, each subject on a pair may take one of two possible actions, A or B, and the combination of both actions determines the payment of each player, with the three games being symmetric. In the Hawk and Dove Game, individuals can play peacefully (option A, called Dove) or aggressively (option B, called Hawk). If both players play Dove, both earn 10 points; if a Hawk player encounters a Dove player, the Hawk earns 15 points, while the Dove only gets 5 points, thus reflecting the aggressive hoarding of resources by the Hawk and, finally, if both players play Hawk, the confrontation destroys the available resources, and both attain 0 points (Fig 5a). In the Stag Hunt Game, players can either go to location A to hunt a Stag or to location B to try to hunt a Hare. In location A, if both players are present, they can hunt a Stag, which gets them a payoff of 10 points, while a player that is alone will earn 0 points; in location B, they can individually hunt a Hare for 7 points regardless of the presence of the

other player, and hence the game reflects the tension between the payoff dominant action A, Stag, and the risk dominant action B, Hare (Fig 5b). In the Prisoner's Dilemma, an individual can play A, which stands for Cooperate, or B, which stands for Defect. If both players cooperate, they earn 10 points, while they only get 5 points if both players defect. A defector playing against a cooperator earns 15 points, while a cooperator playing with a defector gets 0 points. Therefore, the Prisoner's Dilemma shows the tension between the Pareto efficient cooperative equilibrium and the strictly dominant defective action. However, we do not use a matrix representation to explain the game, but we state by means of words the payoffs that a player can get by playing either action. Hawk and Dove and Prisoner's Dilemma are played both in the standard simultaneous way and in a sequential framework, in which each player first states her action if she plays first, and then her second action, conditional to each of the possible actions of her couple. Stag Hunt is only played simultaneously, given the coordination nature of the game (Fig. 5c).

Beliefs

The participants' beliefs about each action taken during each game were asked immediately after the participant made his/her choice and were in the form of a "make a hypothesis" question. Three different categories of such questions can be found in the experiment. Specifically, for the Ultimatum Game (proposer choice and responder choice), Trust Game (investor choice and trustee choice), and Public Goods Game (contribution without punishment, contribution with punishment), subjects were asked, in their opinion, how many points the other participants contributed on average. The incentivization of such an answer, i.e., the extra or bonus points that the participant could earn if his/her guess were correct (2 bonus points), was given to the participant if their guess (belief) about the points contributed by the lot was not further away than one point from the actual sample average. Instead, in the case in which the guess concerned the proportion of people performing an action, as in Hawk and Dove (simultaneous choice, first mover choice, second mover conditional choices), Stag Hunt (only simultaneous choice), and Pris-

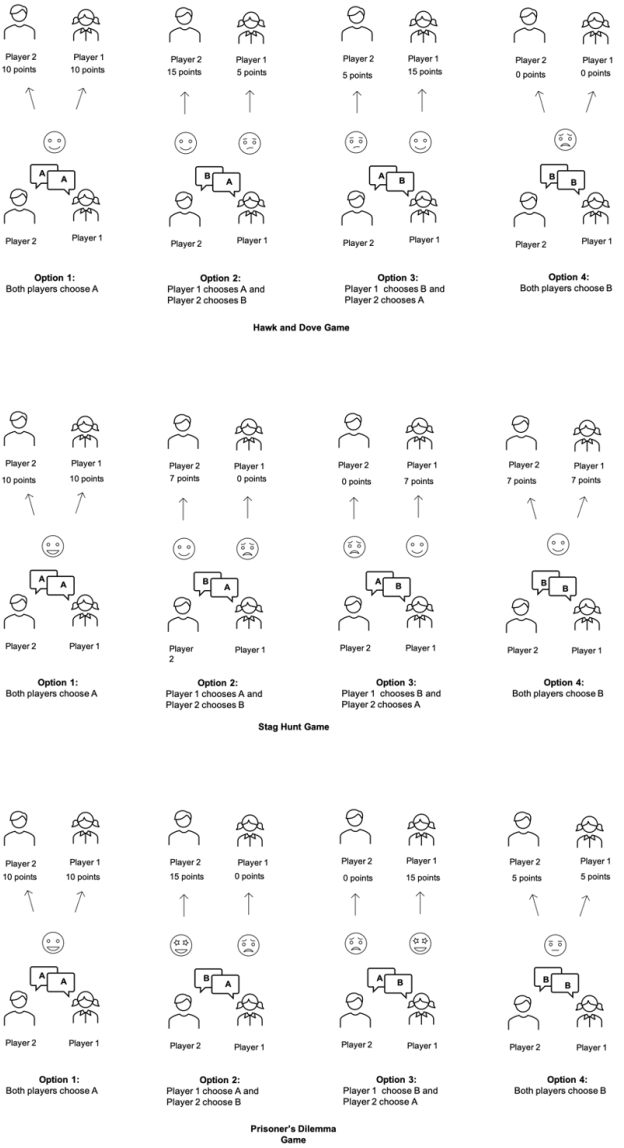


Figure 5: Visual depiction of the Hawk and Dove Game, Stag Hunt, and Prisoner's Dilemma played in the experiment.

oner's Dilemma (simultaneous choice, first mover choice, second mover conditional choices), the bonus was granted if the stated belief was not further away than five percentage points from the actual sample average. Finally, for the choice of punishment in the Public Goods Game with punishment, two bonus points were awarded to those who could simultaneously guess both the more and less frequent modalities of punishment that were performed in the experiment.

Questionnaires

The questionnaires administered to the participants in this experiment were a self-reported psychometric measure (BIS-11) and environmental data assessments (MOPS). They relied on a Likert scale answer type, where participants indicated if the statement they were reading applied or not to their life story or their personality, with a range of 1-4 for the BIS-11 and 0-3 for the MOPS. The Barratt's Impulsiveness Scale (Patton, Stanford, and Barratt, 1995) is a self-report measure of impulsivity-related behaviors and beliefs distributed along various domains such as cognition, attention, and motor behaviors that gave rise to different subscales (Attentive Impulsivity, Non-planning Impulsivity, Motor Impulsivity) and a total index. The total score of the BIS-11 can be interpreted as normal in the range between 52 and 71. In contrast, a score bigger than 72 points indicates impulsive behavior in at least one of the domains investigated. The Measure of Parental Style (Picardi et al., 2013) is a self-assessment questionnaire used to measure perceived parenting styles across three measures: indifference, abuse, and overcontrol. The participant is instructed to complete the questionnaire twice, one for each of his paternal figures. The MOPS does not have a proper cut-off score. Still, the total score for each of the three categories provides a dimensional measure showing the degree to which that individual experienced that dimension of the parenting style.

Chapter 3

Functional Frontal Fragility Syndrome and Decision-Making Processes

This Chapter will illustrate two pre-registered, between-subjects, experimental studies conducted to investigate the existence of a possible brain functional frontal fragility syndrome that can have repercussions on decision-making processes. Specifically, by mixing methodologies from behavioral economics and neuroscience, we were able to investigate two phenomena, one that is newly emerging from the neuroscience literature, namely, the local sleep phenomenon, which has promising underpinnings for explaining new avenues about the relationship between sleep and wakefulness, and a second that is more controversial and had been investigated since the '90, but with mixed results: ego depletion.

We hypothesize that the effects classically attributed to ego depletion could depend on a use-dependent increase of sleep-like episodes during wakefulness in frontal brain areas associated with executive functions and self-control exertion. With these experiments, we prove our hypothesis by showing, with EEG measures and economic games, that inducing a fatigued state in the brain can alter the behavioral response of subjects

in socially relevant situations, increasing the likelihood of choosing the aggressive alternative and engaging more often in antisocial and spiteful modalities of punishment.

3.1 Introduction

When making decisions in everyday life, we are inevitably shaped by contingent physiological, psychological, and cognitive factors. As a result, sometimes we make decisions that may appear inconsistent with our usual social behavior, even leading to unexpected aggressive behavior instead of a more desirable cooperative one (Loewenstein, Lerner, et al., 2003; Lerner and Keltner, 2001). Among the cognitive factors underpinning social behavior, the tension between intuition and deliberation plays a major role in determining cooperative or antisocial choices. Studies that investigated the role of this factor typically did so by combining cognitive manipulations and economic games (Belloc et al., 2019; Achtziger, Alós-Ferrer, and Wagner, 2015; Strack and Deutsch, 2004; Duffy and Smith, 2014; Schulz et al., 2014). Many of such studies advocated a positive effect of intuition on cooperation (Rand, Peysakhovich, et al., 2014; Rubinstein, 2007; Kieslich and Hilbig, 2014), while others supported a central role of deliberation in cooperative behavior (Achtziger, Alós-Ferrer, and Wagner, 2016; Capraro and Cococcioni, 2016), with antisocial acts (including criminal acts) assumed to have a more impulsive nature instead (Gottfredson and Hirschi, 1990).

Among the cognitive manipulations used to affect the balance between intuition and deliberation, ego depletion is one of the most popular and controversial (Baumeister, Bratslavsky, et al., 2018). In a typical ego depletion paradigm, cognitively demanding tasks requiring participants to use self-control and decision-making (so-called 'executive') functions are employed under the assumption that such an effort will deplete willpower resources (Baumeister, Bratslavsky, et al., 2018; Baumeister and T. F. Heatherton, 1996; Mischel, Cantor, and Feldman, 1996). Tasks adopted in the literature include for instance, Stroop tasks, emo-

tion suppression, and other various high-conflict decision-making tasks (Baumeister, Bratslavsky, et al., 2018; Xu, Bègue, and B. J. Bushman, 2012; Muraven, Pogarsky, and Shmueli, 2006). After such manipulations, individuals asked to complete a subsequent task requiring the same cognitive resources showed impaired executive functions and greater reliance on a more automatic and intuitive course of action (Vohs and T. F. Heatherton, 2000; Dang, Liu, et al., 2017; Boksem, Meijman, and Lorist, 2005; Van Der Linden and Eling, 2006).

However, results concerning the ego depletion effect have been strongly criticized due to inconsistent replication across studies (Friese et al., 2019). Indeed, while some investigations, including a large multi-site replication study, failed to obtain solid evidence in support of an ego depletion effect (Hagger et al., 2016), a re-analysis of the same data and other works indicated that some behavioral manipulations may be more efficient than others at inducing ego depletion (Dang, 2016; Dang, Barker, et al., 2021). Moreover, some authors noted that the literature includes little or no evidence in net contrast with the ego depletion hypothesis (i.e., reporting that manipulations improved self-control; Friese et al., 2019). Overall, these observations may be taken to indicate ego depletion as lying along a spectrum in which the strength of the effect depends on the efficacy and/or duration of the applied manipulation.

Extended task practice leads to the appearance of slow electroencephalographic (EEG) waves in task-related areas (Hung et al., 2013; Bernardi et al., 2015; Quercia et al., 2018). These waves occur in the delta (1-4 Hz) and/or theta (4-8 Hz) frequency ranges and closely resemble the slow waves that characterize human non-rapid-eye-movement (NREM) sleep. In addition to increasing locally in task-related areas, sleep-like slow waves also increase globally following sleep restriction or deprivation (Hung et al., 2013; Bernardi et al., 2015). In animal models, these waves have been shown to reflect neuronal off-periods resembling those underlying the emergence of NREM slow waves (Vyazovskiy, Olcese, et al., 2011). Crucially, sleep-like slow waves are associated with perfor-

mance impairment and loss of task focus when occurring in task-related areas (Bernardi et al., 2015; Thomas Andrillon et al., 2021). Given these observations, sleep-like slow waves during wakefulness have been suggested to represent a sign of neuronal (and cognitive) fatigue.

Interestingly, frontal brain areas involved in executive functions seem to be particularly vulnerable to fatigue and are among the first to show increases in the occurrence of local, sleep-like slow waves during extended wakefulness (Bernardi et al., 2015). In light of this, observations commonly attributed to the ego depletion phenomenon may actually reflect a form of task-dependent neural fatigue associated with sleep-like slow waves in frontal brain areas. Based on this view, the high variability in findings among previous ego-depletion studies could be due to the short duration of the tasks used in the literature, which may fail to induce sufficiently strong and consistent levels of functional fatigue in study participants.

In the present pre-registered research, we investigated whether an extended period of practice with tasks requiring decision-making and self-control could lead to local sleep-like activity within frontal areas and alterations in socially relevant behaviors, as measured by economic games. The employed tasks were selected from a previous work demonstrating their efficacy and specificity at inducing changes in self-control and frontal brain activity, in contrast to other tasks relying on different cognitive functions and brain areas (Hung et al., 2013; Bernardi et al., 2015). Here, we used two versions of the same tasks requiring or not the exertion of executive functions, to obtain different levels of efficacy in inducing task-specific slow waves and behavioral impairment.

In contrast to previous studies in the literature, we used longer fatigue-inducing tasks (~ 45 min vs. ~ 10 min). Furthermore, we collected brain activity (high-density EEG) measures that allowed us to identify the connection between ego depletion manipulations and changes in sleep-like activity. Finally, a battery of one-shot, anonymous, and incentivized

economic games was administered to assess the potential effects of prolonged task practice on behavior. We conducted two studies on a total of 447 healthy adults who were assigned to one of two experimental conditions, the No Fatigue (NF) or Frontal Fatigue (FF) groups. Study 1 included both behavioral and EEG measures ($N = 44$) to assess changes in brain activity associated with the applied behavioral manipulation, while Study 2 replicated behavioral findings on a larger participant sample ($N = 403$).

3.2 Materials and Methods

3.2.1 Ethics Approval

The whole study was conducted under two protocols defined in accordance with the ethical standards of the 2013 Declaration of Helsinki. Study 1 protocol (n.1485/2017) was approved by the Ethical Committee Area Vasta Nord Ovest, while Study 2 protocol (n.03/2022) was approved by the Joint Ethical Committee for Research of the Scuola Normale Superiore and the Scuola Superiore Sant'Anna. A fixed reimbursement ($40 euros$ for Study 1 and $10 euros$ for Study 2) was provided to each participant upon completion of the experimental procedures. In addition, participants received a bonus payment relative to their performance in the incentivized economic games presented to them, as detailed below. The experimental procedures and expected results for both studies were pre-registered on AsPredicted (Study 1 and Study 2).

3.2.2 Participants

As explained in the pre-registrations of both studies, for Study 1, the sample size was pre-determined based on similar previous investigations (Quercia et al., 2018; Avvenuti et al., 2021), assessing the effect of task-related mental fatigue on behavioral performance. Based on these studies, we expected a large effect size (> 0.9). A power calculation based on this assumption, with two independent samples, $beta = 0.8$ and $alpha = 0.05$, led to a minimum sample size of 21 subjects per

group. For Study 2, performed in less controlled experimental conditions, a smaller sample size was assumed. In particular, we estimated that a sample size of 400 subjects would allow us to identify medium-size effects of around 0.25 for the continuous variables (one tail) using a non-parametric Wilcoxon-Mann-Whitney test with two groups.

Participants were recruited through flyers, social media, and by word of mouth within the Tuscany areas of Lucca and Pisa for Study 1 and Florence for Study 2. Potential volunteers were pre-screened with an online questionnaire to exclude any medical, neurological, or psychiatric condition potentially affecting brain function and behavior. We also assessed the presence of relevant sleep-related issues (Pittsburgh Sleep Quality Index – PSQI (Buysse et al., 1989), cut-off score¡10) and extreme chronotypes (Horne-Östberg Morningness-Eveningness Questionnaire – MEQ (Horne and Östberg, 1976), scores ranging between 30 and 70). Individual preferences were measured in the pre-screening questionnaire through the "Global Preferences Survey", designed to assess a wide range of personal characteristics, such as time preferences (e.g., short-term or long-term orientation), risk preferences, positive and negative reciprocity, altruism, and trust (Falk et al., 2018). The admitted participants were subsequently contacted to schedule the experimental sessions. All volunteers signed a written informed consent form before taking part in the studies and retained the faculty to drop from the study at any time.

Together with biological sex, age, and level of education, the indexes derived from the Global Preferences Survey (positive reciprocity, negative reciprocity, altruism, patience, risk, trust) were used to divide participants into matched groups according to the mean and variance of the variables (see Table 3) the Frontal Fatigue group (FF) and the No Fatigue group (NF).

3.2.3 Structure of the Session

The experimental procedures are detailed in Figure 6. All experiments took place in the morning, from 9-10 AM to 12 PM, and involved a sin-

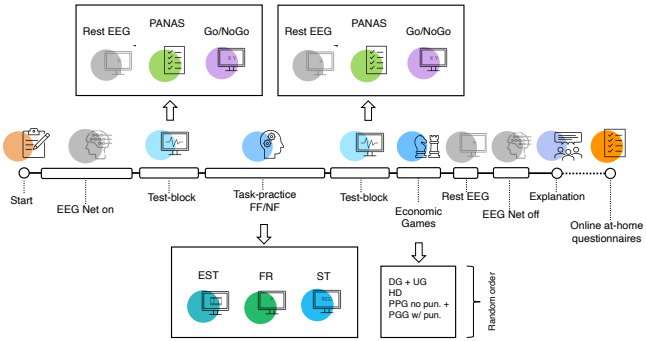


Figure 6: Visual articulation of an experimental session. Gray icons represent EEG-related operations present in Study 1 but not in Study 2. The length of the white bars reflects the relative length of each phase performed in the lab.

gle participant at a time for Study 1 and up to 20 simultaneous participants for Study 2. The time window of each session was kept fixed to avoid possible confounding factors related to time-of-day effects or the influence of daily activities (e.g., work-related fatigue). Subjects were instructed to keep their usual sleep schedule the night before the experiment and to abstain from caffeinated beverages in the morning.

Additionally, the day after the experimental session, all participants received an online set of self-report questionnaires by email, measuring impulsivity-related behaviors and beliefs (Barratt Impulsiveness Scale - BIS-11 (Patton, Stanford, and Barratt, 1995)), individual tendencies toward aggressive behavior (Buss-Perry Aggression Questionnaire – BPAQ (Buss and Perry, 1992)) and empathy (Interpersonal Reactivity Index – IRI (Davis et al., 1980)). Questionnaires were sent to the subjects the day after the experiment to avoid potential confounds related to priming effects or effects related to the different experimental protocols (FF, NF).

3.2.4 Test Block

Questionnaires

Participants were asked to self-report their mood, sleepiness, fatigue, and motivation using 10-point Likert scales and to complete the Positive Affect, Negative Affect Scale – PANAS (Watson, Clark, and Tellegen, 1988). The scores obtained from the questionnaires were compared across experimental conditions to identify potential effects induced by the different cognitive engagements in FF and NF (Appendix B Table 4).

Rest EEG Recordings

Resting-state EEG activity was recorded for 6 minutes (500 Hz sampling frequency), divided into three epochs of two minutes each. Recordings were performed three times: once in the baseline test block (T0), then at the test block after task practice and before the economic games (T1), and finally at the end of the experimental session (T2).

Go/NoGo Task

During test blocks T0 and T1, participants also completed two 5-minute trials of a classical Go/NoGo task (Garavan, Ross, and Stein, 1999; Garavan, Ross, Murphy, et al., 2002; Roche et al., 2005; Chuah et al., 2006), as in a previous work (Bernardi et al., 2015). Previous evidence indicated that extended exertion of self-control was associated with performance deterioration in this task. Here, we attempted to replicate this observation as a secondary aim of our study (see preregistration), as this would have been useful to demonstrate the efficacy of our experimental protocol in case no significant effects would emerge for the economic games. It is important to note, though, that our present study differs from previous investigations as a practice/learning session was not included to reduce experimental demands.

3.2.5 Task practice in FF and NF conditions

All participants completed three different tasks, each lasting about 15 minutes, for a total task practice time of $sim45$ minutes. In the FF condition, the tasks required high levels of impulse control, decision-making, and conflict resolution, while in the NF condition, a modified version requiring no exertion of self-control was presented (Avvenuti et al., 2021). The three tasks were always presented in the same order and included an emotion suppression task (Baumeister, Bratslavsky, et al., 2018), a false response task (Bernardi et al., 2015), and a classical Stroop task (Stroop, 1935). A detailed description of the tasks is provided below. The computerized tasks used in Study 1 were implemented using E-Prime 2 (Psychology Software Tools, Pittsburgh, PA), while a PsychoPy implementation (Peirce, Gray, et al., 2019; Peirce, Hirst, and MacAskill, 2022) was used for Study 2.

Emotion Suppression Task

In the emotion suppression task (Baumeister, Bratslavsky, et al., 2018; Dang, 2018), participants watched a series of brief video clips showing humans and/or animals in amusing situations. Participants in the FF group were explicitly requested to completely suppress their facial reactions, whereas volunteers in the NF group were left free to express their emotional responses. Compliance with the task was assessed using a camera pointing at the participant's face in Study 1 or through direct monitoring by the experimenters of the participant's computer stations in Study 2.

False Response Task

During the false response task (Bernardi et al., 2015), study participants were presented with 180 simple short questions (e.g., *What is the color of a banana?*) and two possible responses (e.g., *Yellow or Blue*). After a 300 ms delay, a green or a red sign appeared below the question, indicating whether the participant had to provide the correct or wrong response,

respectively. For participants in the FF group, the circle's color was randomly assigned for each stimulus, while it remained always green for participants in the NF group. Participants were required to respond as fast and accurately as possible. Adherence to the task requirements was verified through an a-posteriori assessment of task accuracy (50% chance level). Since some of the responses in Study 2 were not correctly recorded due to a technical issue, only the results from Study 1 are reported. Specifically, participants achieved accuracies of 60.3±18.3% (SD) and 89.9±6.2% in the FF and NF conditions, respectively ($p < 0.001$, vs. chance level, t-test).

Stroop Task

In the Stroop Task, participants were presented with color names written with the same ink color indicated by the name or a different color (Stroop, 1935). Four trials, including two different versions of the task, were presented in alternating order: in one version, participants had to indicate the color name represented by the word (ignoring the ink color), while in the other version, they had to indicate the ink color (ignoring the color name). Each trial included 64 stimuli. Responses were provided using different response buttons associated with each of the four used colors, which were blue, red, yellow, and green. For participants in the FF group, the color name and the ink color could be either congruent (i.e., color ink and color name were matched) or incongruent (i.e., the color ink and the color name did not match), while for participants in the NF group, stimuli were always congruent (i.e., color ink and color name were always matched). Adherence to the task requirements was verified through an a-posteriori assessment of task accuracy (25% chance level). Since some of the responses in Study 2 were not correctly recorded due to a technical issue, only the results from Study 1 are reported. Specifically, participants achieved accuracies of 85.7±14.3% (SD) and 98.3±1.3% in the FF and NF conditions, respectively ($p < 0.001$, vs. chance level, t-test).

3.2.6 Economic Games

All subjects completed three blocks of economic games presented in random order: Block 1 included a Dictator Game followed by an Ultimatum Game, Block 2 included a Hawk and Dove Game, and Block 3 contained a Public Goods Game without Punishment, followed by a Public Goods Game with Punishment. Instructions for the games can be found in our online repository. Participants were informed that their counterparts in the economic games were other study participants and that the pairs or groups were changed for each game so that they would not interact with the same person twice. After each decision, participants were asked about their beliefs about others' average behavior for the whole experiment in the case of Study 1 or their own experimental session in the case of Study 2. One decision in the game and one belief were picked up at random at the end, and subjects were paid according to their earned points at the ratio of €1 for each experimental point, plus a bonus of two points if the chosen belief was close enough to the actual behavior. In addition to the fixed payoffs, participants received, on average, a game payoff of €13.17 in Study 1 and of €10.74 for Study 2. The economic games used in these experiments were implemented using oTree (Chen, Schonger, and Wickens, 2016).

Dictator Game

Participants were matched in pairs and received the role of either dictator or recipient. The dictator had to decide how to split 20 points between himself and the recipient. The recipient has no action to take and just obtains the points decided by the dictator. Participants could earn two bonus points if they guessed the average split with an accuracy within one point of the actual value.

Ultimatum Game

Participants were matched in pairs and received the role of either proposer or responder. The proposer had to make an offer regarding how to split 20 points between himself and the responder. The responder was

given the choice of accepting or rejecting offers. In case the responder accepts the offer, the proposed distribution is implemented. In case the responder rejects the offer, both the proposer and the responder obtain zero points. The responder stated the minimum acceptance threshold that he was willing to accept, as done using the strategy method (Brandts and Charness, 2011). Participants could earn two bonus points if they guessed the average proposal with an accuracy within one point of the actual value. Moreover, participants could earn two bonus points if they guessed the average minimum acceptance threshold with an accuracy within one point of the actual value.

Hawk and Dove Game

Participants were matched in pairs and were both given the option of taking action either as Hawk or Dove. When both players chose Dove, they both received 10 points. When one player chose Hawk and the other chose Dove, the Hawk received 15 points, while the Dove received 5 points. If both participants chose Hawk, both received zero points. Actions were labeled as A and B. In Study 1, the action Dove was always action A, while in Study 2, the label was randomly assigned. Participants could earn two bonus points if they guessed the proportion of Dove plays with accuracy within five percentage points of the actual value.

Public Goods Game without Punishment

Participants were matched in groups of four. Each participant received a personal endowment of 10 points and was given the option to put any amount in a common pool, keeping the rest. Contributions to the common pool were then doubled and divided equally between all members of the group. Participants could earn two bonus points if they guessed the average minimum contribution with accuracy within half a point of the actual value.

Public Goods Game with Punishment

The procedure was similar to the Public Goods Game without punishment. However, in this case, participants were given the option to spend two points to reduce the earnings of another player by four points. This decision was presented using the strategy method to reduce feedback negativity. Therefore, participants decided, without receiving any feedback, whether they would like to punish the person who contributed the most ("antisocial punishment"), the person who contributed the least ("prosocial punishment"), one person at random ("spiteful punishment"), or not punish at all ("second-order free riding"). Participants could earn two bonus points if they guessed the average minimum contribution with accuracy within half a point of the actual value. Moreover, they earned two bonus points if they guessed both the most and least frequent modalities of punishment.

3.2.7 EEG data analysis

Following the procedure described in Avvenuti et al. (2021), the resting-state EEG recordings were band-pass filtered between 0.5 and 45 Hz (Kaiser-windowed finite impulse response filter; −0.01 dB passband gain, −40 dB stopband gain, 0.49 Hz roll-off) and divided into non-overlapping 4-second epochs (Avvenuti et al., 2021). The resulting traces were visually inspected to identify and mark bad channels and epochs containing clear artifactual activity. Then, an independent component analysis (ICA) was performed in EEGLAB (Delorme and Makeig, 2004) to remove signal components reflecting ocular, muscular, and electrocardiograph artifacts. Rejected bad channels were subsequently interpolated using spherical splines. Finally, for each EEG derivation, the signal was average-referenced. Power spectral density (PSD) estimates were computed using Welch's method (pwelch function) in each 4-second epoch (2-s Hamming windows, 50% overlap). Finally, as delta (1-4 Hz) and theta (4-8 Hz) frequency bands are knowingly associated with sleep states, signal power was computed for those bands and averaged across epochs.

3.2.8 Source-modeling of EEG data

Source modeling of EEG data was performed using Brainstorm (Tadel et al., 2011). Specifically, as reported in Avvenuti et al. (2021), the conductive head volume was modeled using a three-layer symmetric boundary element method (OpenMEEG BEM, Gramfort et al., 2010) and the default ICBM152 anatomical template. The forward model was constructed using a standard set of electrode positions (GSN HydroCel 64). The source space was constrained to the cerebral cortex, which was modeled as a three-dimensional grid of 15,002 vertices. The inverse matrix was computed using the standardized low-resolution brain electromagnetic tomography (sLORETA) constraint with a regularization parameter equal to $10^{-2}\lambda$. Finally, the signal power was computed for each vertex in the source space using Welch's method (1-s Hamming windows, 50% overlap).

3.2.9 Scalp and source level analyses of EEG data

Comparisons of EEG signal power across experimental conditions were performed using paired t-tests and a permutation-based cluster-mass correction (Nichols and Holmes, 2002). In brief, each contrast was repeated (10,000 permutations) after shuffling the labels of the experimental conditions, and all clusters of significant electrodes were identified ($p < 0.05$). Then, we computed the sum of test statistics across electrodes belonging to the same cluster, and the maximum obtained value was saved in a frequency table. A minimum cluster-mass threshold corresponding to the 95^{th} percentile of the resulting distribution was applied to correct for multiple comparisons. For comparisons performed at the scalp level, the analyses were restricted to 51 "internal" electrodes in order to minimize the possible impact of residual artifactual activity in channels located near the eyes or on the temporal/neck muscles (Hung et al., 2013). All statistical analyses were performed in MATLAB. At the source level, power maps were exported to MATLAB, and statistical comparisons were performed as described for scalp analyses. The obtained results were re-imported in Brainstorm for visualization.

3.2.10 Analysis Models

Appendix B Tables from 5 to 11 show regression analyses for each game using the pooled database in which three groups of control variables are added. Specifically, the demographic variables group includes age, biological sex, and education; the preference variables group includes our proxies of positive reciprocity, negative reciprocity, altruism, patience, risk, and trust; and the questionnaire variables group includes the Interpersonal Reactivity Index, Barratt's Impulsiveness Scale, and the Buss-Perry Aggression Questionnaire. Specifically, for the Hawk and Dove Game choice, probit models were used. For the split in the Dictator Game, the offer and the minimum acceptance threshold in the Ultimatum Game, and the contributions in the Public Goods Game with and without Punishment, tobit models were used. Finally, for the Punishment modalities in the Public Goods Game, probit models were used for the individual categories and a multinomial logit for the combined category.

3.2.11 Additional Analysis

We performed an additional analysis for better investigating and verifying the association between brain activity and decision-making changes. First, for each participant and EEG recording, we computed the mean delta power (1-4 Hz) across frontal electrodes (see topographic map in Figure 19). Then, we computed the average across T1 and T2, and the resulting values were used to compute the ratio with respect to baseline power levels (T0). Finally, we performed a regression analysis using all participants of Study 1 ($N = 44$) to predict behavioral results based on delta-power variations in frontal electrodes, clustering standard errors at the individual level. Our probit analysis showed a positive association between increases in frontal delta power and the likelihood of playing aggressively in the Hawk and Dove game ($p = 0.0408$).

3.3 Results

3.3.1 Delta and Theta EEG Activity

To determine whether the administration of the fatigue-inducing paradigm would lead to increases in low-frequency (delta/theta) activity, we compared the relative change in signal power induced by the experimental procedures (from T0 to T1) across the two groups (Figure 7a). The increase in delta activity (1-4 Hz) was significantly stronger in the FF group compared to the NF group in a frontal cluster of electrodes (Figure 7b). Source localization showed that the delta power difference was maximal within the left inferior frontal gyrus (IFG) and in the right middle/superior temporal gyri ($p < 0.01$, cluster-based correction, Figure 8). Instead, T0-T1 theta activity (4-8Hz) changes did not show significant differences across groups. However, a stronger increase in the FF relative to the NF condition was found after the economic games in temporoparietal and occipital electrodes (T2, corrected $p < 0.05$, Figure S1). Source-modeling identified the peak of theta power increase in the right temporal lobe ($p < 0.01$, cluster-based correction, Figure S1).

3.3.2 Economic Games

The following game decisions were collected: Dictator Game split, Ultimatum Game proposer offer, Ultimatum Game minimum acceptance threshold (MAT), contribution to the Public Goods Game without punishment, contribution to the Public Goods Game with punishment, and punishment decision in the Public Goods Game with punishment. Analyses were performed employing non-parametric tests and regression analyses. The specific test or model was selected depending on the nature of the dependent variable (binary, ordered, categorical, roughly continuous). Moreover, we performed individual tests for prosocial, antisocial, and spiteful modalities of punishment against the reference category of second-order free riding.

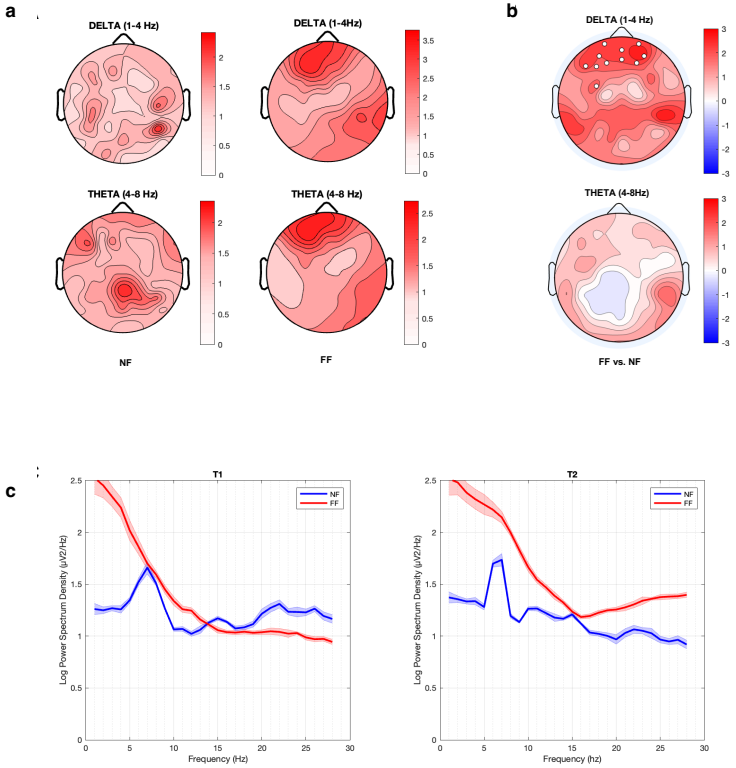


Figure 7: Changes in the low-frequency activity associated with the FF condition. Panel **a** shows low-frequency EEG activity changes associated with the FF and NF experimental conditions. Topographic plots on the left show T0 to T1 changes (ratio) in delta (top) and theta (bottom) power (from 0 to a maximum of +3) for the two experimental conditions. In panel **b**, the topographic plots show the statistical comparison between experimental conditions for the two frequency bands, with colormap indicating T-values (-3; +3). White dots mark $p < 0.05$, cluster-based correction. Panel **c** shows power spectral density (PSD) changes computed in the significant frontal cluster highlighted in Panel **a** and **b**. The left plot shows the change in PSD in the NF group (blue) and in the FF group (red) after T1, while the right plot shows the PSD difference after subjects performed the economic games (T2).

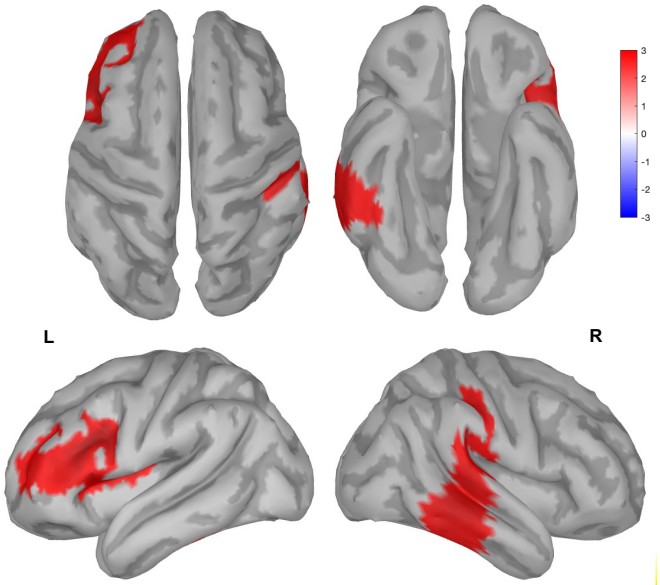


Figure 8: Source analysis of the delta EEG activity associated with the FF condition. Significant differences ($p < 0.01$, cluster-based correction) in T1/T0 delta ratios between FF and NF. Specifically, difference peaks were found in the left IFG (-36, 16, 28) and in the right Middle Temporal Lobe (70, -30, -2).

Study 1

Figure 9a shows the results of the Hawk and Dove Game and the punishment modalities in the Public Goods Game. The proportion of dovish behavior (i.e., peaceful cooperation) dropped from 86% to 41% ($p = 0.0017$, Pearson's chi-squared test), which is consistent with a tendency of the FF group to engage more often in hawkish behavior (i.e., aggressive seizing of resources). This result was robust to the use of a probit model, $p = 0.0020$. Of note, an additional probit analysis showed that delta-power variations from T0 to T1 in frontal electrodes (see Figure S11 and SI Methods) were positively associated with the likelihood of playing aggressively in the Hawk and Dove game ($p = 0.0408$; standard errors clustered at the individual level). No other significant result was found in the rest of the games (Figure 16). We performed a total of ten tests. Hence, our results were robust to concerns regarding multiple testing and would survive any suitable correction. We did not find any results regarding differences in beliefs between groups (Figure 11), and a diff-in-diff analysis did not show differences in the average accuracy and response times of subjects in the Go/NoGo task (Figure 10).

Study 2

Figure 9b shows the results of the Hawk and Dove Game and the punishment modalities in the Public Goods Game. Consistent with the results of Study 1, behavioral choices significantly differed between the NF and FF groups ($p < 0.001$, Person's chi-squared test). The result also survived the use of a probit model ($p < 0.001$). Concerning punishment, Pearson's chi-squared test showed significant differences in the distribution of punishment modalities ($p < 0.001$). Specifically, pairwise Pearson chi-squared tests showed a significant reduction in prosocial punishment ($p < 0.001$) and a significant increase in spiteful punishment ($p = 0.0019$), while total punishment was unchanged ($p = 0.2961$). These results also survived the use of probit models ($p < 0.001$ and $p = 0.0022$, respectively) and a multinomial logit (Table 11). No other significant result was found in the remaining games and beliefs (Figures 17 and 12). Diff-in-

diff regressions did not show any difference in subjects' average accuracy and response times in the Go/NoGo task (Figure 10).

3.4 Discussion

Moral precepts frequently compel individuals to engage in actions seemingly detrimental to their immediate self-interests, including core objectives like survival and reproduction. Yet, actions that benefit others have been suggested to enhance survival and reproduction through indirect means, such as integration into social groups and cultural societies (Rand and Nowak, 2013; Baumeister and Alghamdi, 2015; Sigmund, 2010; Trivers, 1971). Nevertheless, fitness is also achieved through aggressive acts, which provide the individual with immediate benefits that are often able to outweigh the long-term consequences that such behaviors might hold (Georgiev et al., 2013), explaining why aggression is a basic form of human interaction (Rusch and Gavrilets, 2020).

Aggressive behavior plays a pivotal role in the animal kingdom, and research demonstrated that, in humans, it is modulated by distinct brain structures involved in emotion regulation and inhibitory control, and its impromptu expression depends on failures of self-regulation processes (Davidson, Putnam, and Larson, 2000; Pietrini et al., 2000). Consequently, self-control, functioning as the cognitive mechanism that facilitates the inhibition of instinctual responses in favor of actions endowed with a greater value, is intimately related to aggressive behavior and punishment activities.

Here, we demonstrated that the extended exertion of self-control leads to an increased propensity to engage in aggressive choices and a shift in punishment behavior. Furthermore, individuals who engaged in cognitive tasks requiring self-control presented an increase in sleep-like (delta) EEG activity within frontal areas involved in executive functions. Such a change is consistent with a use-dependent increase in local functional fatigue and may thus explain behavioral changes as reflecting the loss of efficient top-down executive regulation.

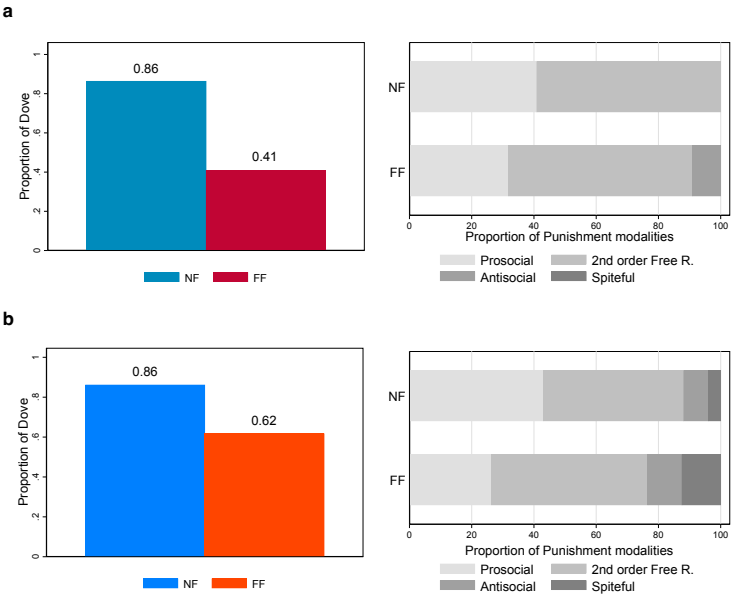


Figure 9: Results for the Hawk and Dove game and the punishment modalities. Panel **a** shows the results for the Hawk and Dove game and the punishment modalities for Study 1 (N=44), while panel **b** shows the same results for Study 2 (N=403). Left panels display the proportion of players who chose the peaceful option in the Hawk and Dove game. Players of the NF group (blue) chose the dove alternative significantly more with respect to players of the FF group (red). Right panels show the distribution of punishment modalities. In both studies, prosocial punishment and 2^{nd} order-free riding are the two most represented modalities in the NF group. In the FF group, instead, antisocial and spiteful punishment are more represented, and in Study 2, a reduction in the selection of prosocial punishment is observable.

3.4.1 Extended exertion of self-control affects subsequent socially relevant choices

Previous research suggested that humans possess a finite reserve of self-regulatory resources, which may be depleted with extended use, a phenomenon defined as ego depletion (Baumeister, Bratslavsky, et al., 2018). According to this view, experimental manipulations expected to induce ego depletion have been widely employed to investigate the role of self-control in socially relevant human behaviors. However, research produced inconsistent results. Indeed, some studies showed that when individuals experience cognitive fatigue due to prior self-regulation, they exhibit diminished empathy, reduced willingness to engage in prosocial acts, and a lowered threshold for frustration and aggression control in social interactions (Muraven, Pogarsky, and Shmueli, 2006; DeWall et al., 2007; Stucke and Baumeister, 2006). Other studies, though, failed to detect any significant effects of ego depletion on social behavior (Heatherton, Tice, et al., 1994; Achtziger, Alós-Ferrer, and Wagner, 2018). Here, we propose that a potential explanation for those discrepancies could lie in the relatively short duration of typical ego depletion paradigms, which may be insufficient to induce measurable effects in most individuals. In line with our hypothesis, we found that about 45 minutes of practice with tasks requiring self-control led to consistent behavioral changes in two independent samples studied using similar experimental paradigms and procedures. Specifically, individuals who completed tasks requiring extended exertion of self-control showed a higher propensity to fight in the Hawk and Dove game relative to those who engaged in similar tasks not requiring self-control. Thus, when confronted with a situation in which agents can decide either to resolve a conflicting situation peacefully or aggressively, depleted individuals are more likely to choose the aggressive alternative. In addition, fatigued participants showed a lower probability of selecting the option regarding prosocial punishment, that is, the act of punishing defectors, and an increased propensity in choosing to punish spitefully, that is, punishing another player at random. Nonetheless, the overall propensity

for punishment remained unchanged. Interestingly, prosocial punishment has been suggested to represent one of the potential mechanisms for the evolution of cooperation (Boyd et al., 2003; Bowles and Gintis, 2004). According to this idea, one might speculate that differences in the distribution of punishment modalities across different social groups of individuals (Herrmann, Thoni, and Gachter, 2008) could be due to differences in vulnerability to task-dependent cognitive fatigue. However, studies about potential differences in the vulnerability to (frontal) local sleep across individuals or populations are currently missing. Overall, in line with previous research (Wiehler et al., 2022; Blain, Hollard, and Pessiglione, 2016), our results indicate that the tendency of individuals to engage in aggressive-like behaviors may increase following the extended use of self-control resources.

3.4.2 Local changes in brain fatigue and sleep-need may underlie the ego depletion effect

A growing body of evidence demonstrated that contrary to long-held assumptions, sleep and wakefulness are not mutually exclusive - instead, they are locally regulated and may often coexist across distinct brain areas. During wakefulness, increases in the number and magnitude of local, sleep-like episodes characterized by slow (delta/theta) EEG waves have been reported following extended task practice and prolonged wakefulness with sleep restriction or deprivation (Hung et al., 2013; Bernardi et al., 2015; Quercia et al., 2018; Avvenuti et al., 2021; Andrillon et al., 2022). A local, use-dependent increase in the number of sleep-like episodes has been observed after prolonged practice with a variety of tasks, including self-control, visuospatial, and motor tasks (Hung et al., 2013; Bernardi et al., 2015; Quercia et al., 2018). Importantly, sleep-like episodes appear to have a negative impact on behavioral performance when they occur during specific tasks and involve task-related brain areas (Vyazovskiy, Olcese, et al., 2011). In light of these considerations, sleep-like episodes observed during wakefulness have been suggested to represent the signature of use-dependent neuronal fatigue and sleep needs (Vya-

zovskiy and Harris, 2013). Therefore, we reasoned that frontal sleep-like episodes could offer a physiological explanation for behavioral changes observed after the exertion of self-control. Consistent with this, our present results showed that extended practice with tasks requiring self-control, but not practice with similar tasks not requiring self-control, is associated with a frontal increase in low-frequency, sleep-like EEG activity. A source modeling analysis confirmed that changes in sleep-like activity involved key areas strongly associated with the exertion of self-control, such as the left inferior frontal gyrus and the right middle temporal cortex (Mitchell, 2011; Brown et al., 2012).

Given these premises, we hypothesized that the effects attributed to ego depletion might actually depend on a use-dependent increase in the incidence of sleep-like episodes involving frontal brain areas associated with executive functions. Notably, though, the present findings did not allow us to demonstrate a direct causal link between sleep-like activity and decision-making, which should be the object of future research.

3.4.3 Limitations of the Study

Some limitations of the study should be acknowledged. The behavioral manipulation adopted in the present work was based on previous investigations showing that specific tasks induce changes in local brain activity and behavior consistent with self-control-related fatigue (Bernardi et al., 2015). However, we cannot entirely rule out the potential contribution of a general (non-task-specific) mental fatigue related to cognitive demands, as we did not include a control condition requiring similar cognitive efforts but distinct cognitive functions. Notably, though, no effects of the experimental condition (FF vs. NF) or interactions between condition and time (before vs. after task practice) were found for self-reported sleepiness, fatigue, mood and positive/negative affects (Appendix B Table 4). A trend interaction was observed only for self-reported motivation but this effect did not survive correction for multiple testing ($p < 0.05$, uncorrected). Given these results, a non-specific effect of fatigue appears unlikely to explain the behavioral differences

observed in our study.

Moreover, while we tested several economic games, we found clear significant effects of task-dependent fatigue only for the Hawk and Dove game. The reason why choices in the other games, such as the Dictator or Ultimatum games, were not affected by the behavioral manipulation is unclear and in partial contrast with previous observations (Achtziger, Alós-Ferrer, and Wagner, 2015; Achtziger, Alós-Ferrer, and Wagner, 2016; Achtziger, Alós-Ferrer, and Wagner, 2018). Nevertheless, our present results were robust to corrections accounting for multiple testing and were replicated across two independent samples. We suggest that choices in distinct economic games may be differentially affected depending on the decision-making processes they reflect and the behavioral manipulation that is applied. The structure and complexity of the game may also play a role. For instance, the relative simplicity and clear-cut nature of the Hawk and Dove game may have facilitated the detection of cognitive alterations, which in contrast could be influenced by a variety of other mechanisms in more complex tasks (Mok and De Cremer, 2018).

Furthermore, while extensive research has been conducted on 'short' ego depletion and repeated games (Achtziger, Alós-Ferrer, and Wagner, 2015), our experimental protocol adopted a longer depletion strategy and relied exclusively on one-shot games. Exploring the interplay between ego depletion resulting from extended exertion of self-control and repeated interactions could unravel if, and to which extent, compensatory mechanisms could come into play to modulate individual choices that impact social life. Finally, the present study did not detect any differences in Go/NoGo performance across experimental conditions. We hypothesize that this could depend on the fact that a practice/learning period with the task was not included in the present study to reduce experimental demands. Therefore, learning and fatigue might have counteracted each other during the task, resulting in smaller and non-significant performance variation differences across experimental groups.

3.4.4 Conclusions

In conclusion, our study provides novel insights into the intricate relationship between self-control exertion, social behavior, and underlying neural mechanisms. We have demonstrated that extended exertion of self-control can lead to changes in neural activity within frontal cortical areas crucial for behavioral control and result in an increased propensity for aggressive choices in social interactions. This finding highlights the potential depletion of self-regulatory resources and its impact on prosocial behavior, shedding new light on the inconsistent results reported to date in ego depletion research. Indeed, our results support the idea of ego depletion as a spectrum in which the strength of the effect depends on the intensity and/or duration of the prior manipulation, as well as the nature of the behavior being tested. Moreover, our investigation into local changes in brain fatigue and sleep-like activity offers a novel perspective on the ego depletion phenomenon. Thus, we propose that the increased sleep-like activity in frontal brain areas associated with executive functions and self-control underlie the observed behavioral changes. This use-dependent neuronal fatigue may not only provide a physiological explanation for the effects of ego depletion but, for extension, also of the previously described effects of sleep deprivation and restriction on societally impactful behaviors (Dorrian et al., 2019). The paradigm shifts from sleep as a global phenomenon to a locally regulated one occurred in relatively recent years, and its full range of implications for our understanding of human behavior is far from being exhaustively explored. While this new perspective can offer a single and simple physiological explanation to a wide range of behavioral observations, future research will be necessary to understand the complexities of the interactions between local sleep regulation and other factors influencing human behavior.

Chapter 4

Conclusion

In this doctoral thesis, I aimed to investigate non-pathological aggressive behavior, such as why it persists in today's society, its genetic underpinnings, and the mechanisms through which it is expressed in normal individuals. To do so, I used the expertise of psychology and neuroscience, genetic insights, and behavioral economics. With three controlled experiments, non-pathological aggressive-like behaviors were investigated from various points of view, resulting in a complex but compelling puzzle. To understand this behavior, we have to abstract from what "being aggressive" means for us and treat it as any other type of behavior. In doing so, we will be free to analyze its cause and consequences, its structural mechanisms, and the ways in which it is hard-wired in our brains.

First, as with any other behavior, aggressive behavior has a hereditary component, and genes that code for it are passed from generation to generation. These genes were more important in our past, but they have become, through evolution, less and less prominent due to the rise of non-kin cooperation and more stable and non-nomad societies. However, likely, these genes did not disappear; they only had become less frequent in the general population or more specialized, as is the case for the MAOA gene, which became infamously (and somehow wrongly) known popularly as the "warrior gene" (Lea and Chambers, 2007; Gillett and

Tamatea, 2012). Hyper-represented in the New Zealander Māori population, this gene was immediately associated with aggressiveness and violence and with the overall image of Māori warriors. There is no need to say that the whole picture is far more complicated than that; the truth is that MAOA has some connections with aggressive behavior, but simply being a carrier of it is not certainly enough (Brunner et al., 1993).

From research on evolutionary psychology, neuroscience, and genetics, we know that neurotransmitters mainly initiate and control behaviors within specific brain structures. Neurotransmitters are de facto messengers that carry information through different areas of our brain (and body), and their release determines our reactions, emotions, thoughts, and, ultimately, behaviors. Some neurotransmitters have more specified tasks than others, but we know that, for example, serotonin and dopamine are related to the lash-out of aggressive and impulsive behaviors (Caspi et al., 2002; McDermott et al., 2009; Simons, Beach, and Barr, 2012). They are released in areas critical for controlling this behavior and the related emotions (such as anger and rage), so the quantity, timing of their release, and how long before they get metabolized matter when talking about the realization of a behavior. All these factors depend, ultimately, on genetics. A slight difference in the genetic sequence of a neurotransmitter, such as a different allele or a polymorphism in the pathway, could lead to an alteration in either transmission, quantity released, or metabolization of that molecule. This factor might result in no changes or a visible modification in behavior. Suppose modifications in the sequence are more than one, and all go in the "wrong" direction (e.g., transmission and metabolization less efficient, wrong timing of release). In that case, this will result in grossly exhibiting abnormal behaviors. Examples of these situations come from forensic psychology literature, where genetic anomalies created the perfect storms for peculiar expressions of aggressive behaviors (Brunner, 2007; Sartori, Pellegrini, and Mechelli, 2011; Rigoni et al., 2010). However, these cases, for how compelling, are rare, and the majority of people would have none or one of these alleles' variations. Most of the expression of aggressive behav-

ior carried by genes also depends on the environment and interaction between the two (Rigoni et al., 2010; Iofrida, Palumbo, and Pellegrini, 2014). In Chapter 2, we show when this is the case in a sample representative of the Italian population (i.e., non-forensic, non-hospitalized), where the presence of particular alleles of dopamine and serotonin leads people to think and behave in a more pessimistic and anti-cooperative fashion.

The second step we need to take to understand non-pathological aggressive behavior is to look directly at its pattern of expression within the brain. What are the areas involved, and how is it usually controlled? From neuroscience, it has been discovered that before aggressive behavior can be expressed, some areas of the brain "shut down" (i.e., are less activated; see Pietrini et al., 2000) for the said behavior to occur. Interestingly, the areas that become less active during an aggressive act usually control and inhibit all types of impulses. This fact is compelling and prompts further research, as many concerns are derived from it. What if something happens to this area, that is, it suffers a lesion? What if, after the traumatic event, it is no longer working correctly? Is a lesion the only way of causing a malfunction? Or is this area particularly vulnerable to other events, such as extreme fatigue? What if we exert self-control and inhibition for too long?

Previous research has already answered some questions, such as those in lesions and clinical studies, where it is often shown that the prefrontal cortex can no longer inhibit some types of impulsive and automatic behavior perfectly after damage (Butter, Mishkin, and Mirsky, 1968; Giancola, 1995).

However, issues remained regarding other ways in which particular areas of the prefrontal cortex might suffer from other types of events, less violent but present in everyday life. In this regard, seemingly unrelated research in the neuroscience of sleep processes found that after sleep deprivation or restriction, the waking brain suffers from episodes

of local sleep. *Local sleep* is a phenomenon in which some neurons show electrical frequencies typical of deep sleep NREM states (e.g., delta and theta waves). Instead, they should show frequencies typical of wakefulness (Vyazovskiy and Harris, 2013; Hung et al., 2013). The phenomenon has been investigated in animals and humans, with the same results: a part of the brain seems asleep, and the performance of tasks completed in this state is compromised (Bernardi et al., 2015; Quercia et al., 2018). Starting with the notion of local sleep episodes, we aimed to show that local sleep could represent a physiological marker of extended mental fatigue happening in the brain and that if this extreme fatigue was targeting the frontal cortex, it might result in an alteration of behaviors. In Chapter 3, we investigate this question using a fatigue-inducing protocol able to provoke an extreme exertion of self-control. In our hypothesis, such extended effort would have depleted the self-control resources of the individual (as per the ego-depletion theory, Baumeister, Bratslavsky, et al., 2018), making it easier for aggressive-like behaviors to take place in answer to social situations that were conveying a hostile reaction. Results prove us right: after extreme exertion of self-control for almost an hour, subjects that underwent the depleting paradigm, compared with subjects that performed the same tasks without exercising self-control inhibition for so long, showed an increase in the use of aggressive-like behavioral responses in a set of controlled behavioral situations (i.e., economic games) in which the possibility to provide an aggressive answer was given. The results we obtained prompt further investigations on the theme and shed some light on the real-life implications regarding the vulnerability of prosocial behavior to cognitive fatigue.

From a cognitive point of view, this implication is of particular relevance, as its effects might be detrimental to basic social interactions in everyday life. It is not even difficult to imagine or to put examples; each one of us had experienced at some point in his life (of his day!) being particularly wary and nervous after having experienced hours in the traffic or other activities that require our concentration, executive functions, and self-control. Somehow, when we find ourselves in this state, it

might become more accessible to get mad about something. It is easier to answer impolitely or to fight with someone close to us. We are clearly "disturbed" by this mental state, and it is certainly not the same as being generally tired. In this condition, we could engage in more impulsive answers because they are (energetically) cheaper to carry out and do not require our entire mental investment or self-control. In these cases, the rationale is simple. There is a stimulus that triggers an answer, and the answer is the quickest and cheapest in terms of energy expenditure, but it is also the one that likely might help replenish some of our resources. Impulsive answers might be a way to come back more rapidly to the "status quo", cognitively speaking. As society pushes and pushes people to work more, to work faster, and to work better, we, as a species, need to find a cognitive mechanism to survive this increase of pressure upon ourselves. It seems that frontal fatigue is a mechanism to try to regain control by losing it before. If we are depleted of resources, the ultimate goal is to rest or return to our original status. This, in the process, might lead to suboptimal answers. As we show in our experiments, when people are mentally fatigued, it is easier for them to choose a hostile reaction as the answer to social interaction, even if the long-term outcome is worse. This point might raise some concerns that will need to be investigated since, potentially, it could affect society in more than one way.

The first example that comes to mind is crime. Some individuals might commit criminal acts if people are more inclined to act impulsively when fatigued. I would speculate that the example of crimes committed out of the blue by people who never went against the law or who never showed abnormal personalities might enter this category[1].

The investigations led in this thesis seem to foster a pessimistic outlook regarding the ability of people to control aggressive behaviors; however, genetic studies, neuroscience, and experimental economics are only

[1] As in a recent crime news that happened in Brescia in 2021, a man who tried to strangulate his wife during sleep was absolved because "his brain was shut down" while in a somnambulism state.

a part of this complex picture. The goal of future research will be to counterbalance our society's demands. More studies, in fact, are needed to better understand all these phenomena and their implications.

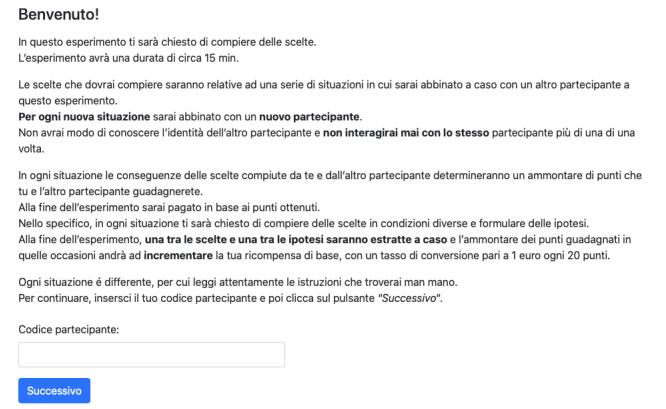
After all, don't *we all go a little mad sometimes?*[2]

[2] Anthony Perkins as Norman Bates - Psycho (1960).

Appendix A

Appendix: Genetic Variants, Cooperation and Punishment

A.1 Instructions of the Experiment - Italian



Benvenuto!

In questo esperimento ti sarà chiesto di compiere delle scelte.
L'esperimento avrà una durata di circa 15 min.

Le scelte che dovrai compiere saranno relative ad una serie di situazioni in cui sarai abbinato a caso con un altro partecipante a questo esperimento.
Per ogni nuova situazione sarai abbinato con un **nuovo partecipante**.
Non avrai modo di conoscere l'identità dell'altro partecipante e **non interagirai mai con lo stesso** partecipante più di una di una volta.

In ogni situazione le conseguenze delle scelte compiute da te e dall'altro partecipante determineranno un ammontare di punti che tu e l'altro partecipante guadagnerete.
Alla fine dell'esperimento sarai pagato in base ai punti ottenuti.
Nello specifico, in ogni situazione ti sarà chiesto di compiere delle scelte in condizioni diverse e formulare delle ipotesi.
Alla fine dell'esperimento, **una tra le scelte e una tra le ipotesi saranno estratte a caso** e l'ammontare dei punti guadagnati in quelle occasioni andrà ad **incrementare** la tua ricompensa di base, con un tasso di conversione pari a 1 euro ogni 20 punti.

Ogni situazione é differente, per cui leggi attentamente le istruzioni che troverai man mano.
Per continuare, inserisci il tuo codice partecipante e poi clicca sul pulsante "*Successivo*".

Codice partecipante:

Successivo

Descrizione della situazione

Devi **distribuire 20 punti** tra te e un altro partecipante.

Come distribuisci i 20 punti?

Tu	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Altro	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0

Successivo

Formula un'ipotesi

Nella situazione precedente, hai distribuito 20 punti tra te e un altro partecipante.
Secondo te, quanti punti **in media** i partecipanti a questo esperimento hanno distribuito all'altro nella scelta appena compiuta?

Inserisci un numero intero tra 0 e 20:

La tua ipotesi sarà considerata corretta se avrà uno scarto non superiore ad un punto rispetto alla media effettiva.
La risposta corretta ti dà un **bonus di 2 punti**.

Successivo

Descrizione della situazione

Devi **proporre come dividere 20 punti** tra te e un altro partecipante, che potrà accettare o rifiutare la tua proposta.
Se accetta, ciascuno di voi riceverà l'ammontare di punti da te deciso, ma se rifiuta, entrambi riceverete 0 punti.

Come proponi di dividere i 20 punti?

Tu	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Altro	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0

Successivo

Formula un'ipotesi

Nella situazione precedente, hai proposto come dividere 20 punti tra te e un altro partecipante.
Secondo te, quanti punti **in media** i partecipanti a questo esperimento hanno distribuito all'altro nella scelta appena compiuta?

Inserisci un numero intero tra 0 e 20:

La tua ipotesi sarà considerata corretta se avrà uno scarto non superiore ad un punto rispetto alla media effettiva.
La risposta corretta ti dà un **bonus di 2 punti**.

Successivo

Descrizione della situazione

Un altro partecipante, deve proporre come **dividere 20 punti tra te e sé stesso**. Tu potrai accettare o rifiutare la proposta dell'altro partecipante.
Se accetti, ciascuno di voi riceverà l'ammontare di punti deciso dall'altro partecipante, ma se rifiuti, entrambi riceverete 0 punti.

Devi dichiarare l'offerta minima che intendi accettare.
Se l'offerta dell'altro partecipante è maggiore o uguale a quanto da te indicato, riceverai i punti che ti sono stati offerti.

Qual è l'offerta minima che intendi accettare?

Scegli: 0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20

Successivo

Formula un'ipotesi

Nella situazione precedente hai dichiarato l'offerta minima che intendi accettare.
Secondo te, qual è **in media** l'offerta minima che gli altri partecipanti a questo esperimento hanno accettato?

Inserisci un numero intero tra 0 e 20:

La tua ipotesi sarà considerata corretta se avrà uno scarto non superiore ad un punto rispetto alla media effettiva.
La risposta corretta ti dà un **bonus di 2 punti**.

Successivo

Descrizione della situazione

Tu e un altro partecipante avete una **base di partenza di 4 punti ciascuno**.
Tu devi **decidere se dare all'altro** partecipante 4 punti, 2 punti o nulla della tua base di punti.
Se dai 4 punti, l'altro partecipante riceverà 16 punti aggiuntivi.
Se dai 2 punti, l'altro partecipante riceverà 8 punti aggiuntivi.
Se dai 0 punti, l'altro partecipante riceverà 0 punti aggiuntivi.
L'altro partecipante dovrà poi **decidere quanti punti darti**, prendendoli da quelli aggiuntivi ottenuti (16, 8 oppure 0).

Quanti punti dai all'altro partecipante?

4 2 0

Successivo

Formula un'ipotesi

Nella situazione precedente hai deciso quanti punti dare all'altro partecipante.
Secondo te, quanti punti **in media** i partecipanti a questo esperimento hanno dato all'altro partecipante nella scelta appena compiuta?

Insersci un numero intero tra 0 e 4:

La tua ipotesi sarà considerata corretta se avrà uno scarto non superiore ad un punto rispetto alla media effettiva.
La risposta corretta ti dà un **bonus di 2 punti**.

Successivo

Descrizione della situazione

Tu e un altro partecipante avete una **base di partenza di 4 punti ciascuno**.
L'altro partecipante **deve scegliere se darti** 4 punti, 2 punti o nulla della sua base di punti.
Se l'altro partecipante ti dà 4 punti, tu riceverai 16 punti aggiuntivi.
Se l'altro partecipante ti dà 2 punti, tu riceverai 8 punti aggiuntivi.
Se l'altro partecipante ti dà 0 punti, tu riceverai 0 punti aggiuntivi.
Tu dovrai poi decidere quanti punti dare all'altro partecipante prendendoli da quelli aggiuntivi ottenuti (16, 8 oppure 0).

Se l'altro partecipante ti ha mandato 8 punti, quanti punti decidi di dargli?

Tu dai:	0	1	2	3	4	5	6	7	8
L'altro ha:	2	3	4	5	6	7	8	9	10
Tu hai:	12	11	10	9	8	7	6	5	4

Se l'altro partecipante ti ha mandato 16 punti, quanti punti decidi di dargli?

Tu dai:	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
L'altro ha:	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Tu hai:	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4

Successivo

Formula un'ipotesi

Nella situazione precedente hai deciso quanti punti dare all'altro partecipante in base ai punti aggiuntivi ricevuti.
Secondo te, quanti punti **in media** i partecipanti a questo esperimento hanno deciso di dare all'altro partecipante nella scelta appena compiuta?

Se l'altro partecipante invia 2 punti, quanti punti, in media, gli vengono dati indietro?

Insersci un numero intero tra 0 e 8:

Se l'altro partecipante invia 4 punti, quanti punti, in media, gli vengono dati indietro?

Inserisci un numero intero tra 0 e 16:

Le tue ipotesi saranno considerate corrette se avranno uno scarto non superiore ad un punto rispetto alla media effettiva.
La risposta corretta ti dà un **bonus di 2 punti**.

Successivo

Descrizione della situazione

Devi scegliere tra A e B, e lo stesso dovrà fare un altro partecipante.
Ciascuna decisione è presa senza conoscere la decisione presa dall'altro partecipante.

Se scegli **A**, riceverai **10 punti** se l'altro partecipante sceglie **A** oppure **5 punti** se l'altro partecipante sceglie **B**.

Se scegli **B**, riceverai **15 punti** se l'altro partecipante sceglie **A** oppure **0 punti** se l'altro partecipante sceglie **B**.

Qual é la tua scelta?

- ○ A
- ○ B

Successivo

Formula un'ipotesi

Nella situazione precedente hai scelto tra A e B, con questi possibili esiti:

Se scegli **A**, riceverai **10 punti** se l'altro partecipante sceglie **A** oppure **5 punti** se l'altro partecipante sceglie **B**.
Se scegli **B**, riceverai **15 punti** se l'altro partecipante sceglie **A** oppure **0 punti** se l'altro partecipante sceglie **B**.

Secondo te, qual è la **percentuale** di partecipanti a questo esperimento che ha scelto A?

Inserisci un numero intero tra 0 e 100:

La tua ipotesi sarà considerata corretta se avrà uno scarto non superiore a cinque punti percentuali rispetto alla percentuale effettiva.
La risposta corretta ti dà un **bonus di 2 punti**.

Successivo

Descrizione della situazione

Devi scegliere tra A e B, e lo stesso dovrà fare un altro partecipante.
In questo caso, l'altro partecipante sceglierà **dopo aver saputo la tua scelta**.

Ricorda!
Se scegli **A**, riceverai **10 punti** se l'altro partecipante sceglie **A** oppure **5 punti** se l'altro partecipante sceglie **B**.
Se scegli **B**, riceverai **15 punti** se l'altro partecipante sceglie **A** oppure **0 punti** se l'altro partecipante sceglie **B**.

Qual é la tua scelta?

- ○ A
- ○ B

Successivo

Formula un'ipotesi

Nella situazione precedente **hai scelto per primo** tra A e B, mentre l'altro partecipante ha scelto per secondo dopo aver saputo la tua scelta. Questi gli esiti possibili:

Se scegli **A**, riceverai **10 punti** se l'altro partecipante sceglie **A** oppure **5 punti** se l'altro partecipante sceglie **B**.
Se scegli **B**, riceverai **15 punti** se l'altro partecipante sceglie **A** oppure **0 punti** se l'altro partecipante sceglie **B**.

Secondo te, qual è la **percentuale** di partecipanti a questo esperimento che ha scelto A?

Inserisci un numero intero tra 0 e 100:

La tua ipotesi sarà considerata corretta se avrà uno scarto non superiore a cinque punti percentuali rispetto alla percentuale effettiva.
La risposta corretta ti dà un **bonus di 2 punti**.

Successivo

Descrizione della situazione

Devi scegliere tra A e B, e lo stesso dovrà fare un altro partecipante.
Ora, tu sceglierai **sapendo già cosa ha scelto l'altro partecipante**.

Ricorda!
Se scegli **A**, riceverai **10 punti** se l'altro partecipante sceglie **A** oppure **5 punti** se l'altro partecipante sceglie **B**.
Se scegli **B**, riceverai **15 punti** se l'altro partecipante sceglie **A** oppure **0 punti** se l'altro partecipante sceglie **B**.

Ci sono due diversi casi:

L'altro partecipante ha scelto **l'opzione A.**

Qual é la tua scelta?

- A
- B

L'altro partecipante ha scelto **l'opzione B.**

Qual é la tua scelta?

- A
- B

Successivo

Formula un'ipotesi

Nella situazione precedente l'altro giocatore ha scelto per primo tra A e B, mentre **tu hai scelto per secondo** dopo aver saputo la scelta dell'altro giocatore. Questi gli esiti possibili:

Se scegli **A**, riceverai **10 punti** se l'altro partecipante sceglie **A** oppure **5 punti** se l'altro partecipante sceglie **B**.
Se scegli **B**, riceverai **15 punti** se l'altro partecipante sceglie **A** oppure **0 punti** se l'altro partecipante sceglie **B**.

Secondo te, qual è la **percentuale** di partecipanti a questo esperimento che **ha scelto A** dopo aver saputo che l'altro partecipante **ha scelto A**?

Inserisci un numero intero tra 0 e 100:

Secondo te, qual è la **percentuale** di partecipanti a questo esperimento che ha **scelto A** dopo aver saputo che l'altro partecipante **ha scelto B**?

Inserisci un numero intero tra 0 e 100:

Le tue ipotesi saranno considerate corrette se avranno uno scarto non superiore ad cinque punti percentuali rispetto alle percentuali effettive.
La risposta corretta ti dà un **bonus di 2 punti**.

Successivo

Descrizione della situazione

Devi scegliere tra A e B, e lo stesso dovrà fare un altro partecipante.
Ciascuna decisione è presa senza conoscere la decisione presa dall'altro partecipante.

Se scegli **A**, riceverai **10 punti** se l'altro partecipante sceglie **A** oppure **0 punti** se l'altro partecipante sceglie **B**.

Se scegli **B**, riceverai **7 punti** in ogni caso.

Qual é la tua scelta?

- ◯ A
- ◯ B

Successivo

Formula un'ipotesi

Nella situazione precedente hai scelto tra A e B, con questi possibili esiti:

Se scegli **A**, riceverai **10 punti** se l'altro partecipante sceglie **A** oppure **0 punti** se l'altro partecipante sceglie **B**.
Se scegli **B**, riceverai **7 punti** in ogni caso.

Secondo te, qual è la **percentuale** di partecipanti a questo esperimento che ha scelto A?

Inserisci un numero intero tra 0 e 100:

La tua ipotesi sarà considerata corretta se avrà uno scarto non superiore a cinque punti percentuali rispetto alla percentuale effettiva.
La risposta corretta ti dà un **bonus di 2 punti**.

Successivo

Descrizione della situazione

Devi scegliere tra A e B, e lo stesso dovrà fare un altro partecipante.
Ciascuna decisione è presa senza conoscere la decisione presa dall'altro partecipante.

Se scegli **A**, riceverai **10 punti** se l'altro partecipante sceglie **A** oppure **0 punti** se l'altro partecipante sceglie **B**.

Se scegli **B**, riceverai **15 punti** se l'altro partecipante sceglie **A** oppure **5 punti** se l'altro partecipante sceglie **B**.

Qual é la tua scelta?

- ◯ A
- ◯ B

Successivo

Formula un'ipotesi

Nella situazione precedente hai scelto tra A e B, con questi possibili esiti:

Se scegli **A**, riceverai **10 punti** se l'altro partecipante sceglie **A** oppure **0 punti** se l'altro partecipante sceglie **B**.
Se scegli **B**, riceverai **15 punti** se l'altro partecipante sceglie **A** oppure **5 punti** se l'altro partecipante sceglie **B**.

Secondo te, qual è la **percentuale** di partecipanti a questo esperimento che ha scelto A?

Inserisci un numero intero tra 0 e 100:

La tua ipotesi sarà considerata corretta se avrà uno scarto non superiore a cinque punti percentuali rispetto alla percentuale effettiva.
La risposta corretta ti dà un **bonus di 2 punti**.

Successivo

Descrizione della situazione

Devi scegliere tra A e B, e lo stesso dovrà fare un altro partecipante.
In questo caso l'altro partecipante sceglierà **dopo aver saputo la tua scelta**.

Ricorda!
Se scegli **A**, riceverai **10 punti** se l'altro partecipante sceglie **A** oppure **0 punti** se l'altro partecipante sceglie **B**.
Se scegli **B**, riceverai **15 punti** se l'altro partecipante sceglie **A** oppure **5 punti** se l'altro partecipante sceglie **B**.

Qual é la tua scelta?

- ○ A
- ○ B

Successivo

Formula un'ipotesi

Nella situazione precedente **hai scelto per primo** tra A e B, mentre l'altro partecipante ha scelto per secondo dopo aver saputo la tua scelta. Questi gli esiti possibili:

Se scegli **A**, riceverai **10 punti** se l'altro partecipante sceglie **A** oppure **0 punti** se l'altro partecipante sceglie **B**.
Se scegli **B**, riceverai **15 punti** se l'altro partecipante sceglie **A** oppure **5 punti** se l'altro partecipante sceglie **B**.

Secondo te, qual è la **percentuale** di partecipanti a questo esperimento che ha scelto A?

Inserisci un numero intero tra 0 e 100:

La tua ipotesi sarà considerata corretta se avrà uno scarto non superiore a cinque punti percentuali rispetto alla percentuale effettiva.
La risposta corretta ti dà un **bonus di 2 punti**.

Successivo

Descrizione della situazione

Devi scegliere tra A e B, e lo stesso dovrà fare un altro partecipante.
Ora, tu sceglierai **sapendo già cosa ha scelto l'altro partecipante**.

Ricorda!
Se scegli **A**, riceverai **10 punti** se l'altro partecipante sceglie **A** oppure **0 punti** se l'altro partecipante sceglie **B**.
Se scegli **B**, riceverai **15 punti** se l'altro partecipante sceglie **A** oppure **5 punti** se l'altro partecipante sceglie **B**.

Ci sono due diversi casi:

L'altro partecipante ha scelto **l'opzione A.**

Qual é la tua scelta?

- ◯ A
- ◯ B

L'altro partecipante ha scelto **l'opzione B.**

Qual é la tua scelta?

- ◯ A
- ◯ B

Successivo

Formula un'ipotesi

Nella situazione precedente l'altro partecipante ha scelto per primo tra A e B, mentre **tu hai scelto per secondo** dopo aver saputo la scelta dell'altro partecipante. Questi gli esiti possibili:

Se scegli **A**, riceverai **10 punti** se l'altro partecipante sceglie **A** oppure **0 punti** se l'altro partecipante sceglie **B**.
Se scegli **B**, riceverai **15 punti** se l'altro partecipante sceglie **A** oppure **5 punti** se l'altro partecipante sceglie **B**.

Secondo te, qual è la **percentuale** di partecipanti a questo esperimento che **ha scelto A** dopo aver saputo che l'altro partecipante **ha scelto A**?

Inserisci un numero intero tra 0 e 100:

Secondo te, qual è la **percentuale** di partecipanti a questo esperimento che **ha scelto A** dopo aver saputo che l'altro partecipante **ha scelto B**?

Inserisci un numero intero tra 0 e 100:

Le tue ipotesi saranno considerate corrette se avranno uno scarto non superiore ad cinque punti percentuali rispetto alle percentuali effettive.
La risposta corretta ti dà un **bonus di 2 punti**.

Successivo

Descrizione della situazione

In questa situazione, tu sei abbinato a caso con **tre partecipanti** all'esperimento.
Tu e gli altri partecipanti avete una **base di partenza di 10 punti**.
Tu e ciascuno degli altri partecipanti potete contribuire **con una parte** della propria base di punti.

La somma dei punti che tu e gli altri tre partecipanti avete contribuito verrà moltiplicata per due e poi divisa tra voi quattro, indipendentemente da quanto ciascuno di voi ha contribuito.
I punti che otterrai saranno dati da questa divisione più la parte dei punti della tua base che non hai utilizzato.

Quanti punti contribuisci?

◯ 0 ◯ 1 ◯ 2 ◯ 3 ◯ 4 ◯ 5 ◯ 6 ◯ 7 ◯ 8 ◯ 9 ◯ 10

Successivo

Formula un'ipotesi

Nella situazione precedente hai deciso con quanti punti, della tua base di partenza, contribuire. Secondo te, con quanti punti **in media** i partecipanti a questo esperimento hanno contribuito?

Inserisci un numero intero tra 0 e 10:

La tua ipotesi sarà considerata corretta se avrà uno scarto non superiore ad un punto rispetto alla media effettiva.
La risposta corretta ti dà un **bonus di 2 punti**.

Successivo

Descrizione della situazione

In questa situazione, tu sei abbinato a caso con altri **tre partecipanti** all'esperimento.
Tu e gli altri partecipanti avete una **base di partenza di 10 punti**.
Tu e ciascuno degli altri partecipanti potete contribuire **con una parte** della propria base di punti.

Tu e ciascuno degli tre altri partecipanti potete decidere di applicare una sanzione:
ciascuno di voi quattro può spendere 2 dei propri punti per **ridurre di 4 i punti del partecipante che intende sanzionare**.

Quanti punti contribuisci?

○ 0 ○ 1 ○ 2 ○ 3 ○ 4 ○ 5 ○ 6 ○ 7 ○ 8 ○ 9 ○ 10

Chi indendi sanzionare?

- ○ Uno a caso degli altri
- ○ Quello degli altri che ha contribuito di meno
- ○ Quello degli altri che ha contribuito di più
- ○ Nessuno degli altri

Successivo

Formula un'ipotesi

Nella situazione precedente hai deciso con quanti punti, della tua base di partenza, contribuire.
Allo stesso tempo hai deciso quale sanzione applicare.

Secondo te, quanti punti **in media** i partecipanti a questo esperimento hanno contribuito?

Inserisci un numero intero tra 0 e 10:

La tua ipotesi sarà considerata corretta se avrà uno scarto non superiore ad un punto rispetto alla media effettiva.
La risposta corretta ti dà un **bonus di 2 punti**.

Secondo te, seconde te qual è l'opzione che è stata scelta di meno?

- ○ Uno a caso degli altri
- ○ Quello degli altri che ha contribuito di meno
- ○ Quello degli altri che ha contribuito di più
- ○ Nessuno degli altri

Secondo te, seconde te qual è l'opzione che è stata scelta di più?

- ○ Uno a caso degli altri
- ○ Quello degli altri che ha contribuito di meno
- ○ Quello degli altri che ha contribuito di più
- ○ Nessuno degli altri

La tua ipotesi sarà considerata corretta se avrà uno scarto non superiore ad un punto rispetto alla media effettiva.
La risposta corretta ti dà un **bonus di 2 punti**.

Successivo

A.2 Instructions of the Experiment - English

The English translation of the instructions can be found below. For easy presentation, each game's instructions will be forerun by the game's name, while it was not shown to subjects in the experiment.

Welcome!

In this experiment you will be required to make some choices.
The experiment will be on average 15 minutes-long.
The choices you will have to make are relative to a series of situations in which you will be randomly paired with another participant of this experiment.
For every new situation you will be paired with **a new participant.**
You won't know the identity of the other participant and **you will never interact with the same participant twice.**

In every situation the consequences of the choices made by you and by the other participant will determine an amount of points that you and the other will earn throughout the experiment.
At the end of the experiment, you will be paid according to the earned points.
Specifically, in every situation you will be asked to make some choices in different conditions and to formulate some hypotheses.
At the of the experiment **one between the choices and one between the hypotheses will be extracted randomly** and the amount of points collected in those occasions will **increment** your base reward, with a conversion rate of 1 euro every 20 points.

Every situation is different, so read carefully the instructions that you will find every time. To continue, insert your participant code and click on the button *"Next"*.

A.2.1 Dictator Game

Situation's description
You have to **split 20 points** between you and another participant.

How you split the 20 points? [Radio button]

Make a guess
In the previous situation you distributed 20 points between yourself and another participant. In your opinion, how many points, **on average** participants to this experiment have distributed to the other in the choice just made?

Your hypothesis will be considered correct if it will have difference from the actual mean not larger than one point. A correct answer will give you **2 bonus points**.

A.2.2 Ultimatum Game

Proposer

Situation's description
You have to **propose how to divide 20 points** between you and another participant, that can either accept or refuse your offer. If the other accepts the offer, both of you will receive the split you decided, but if he refuses, both of you will receive 0 points.

How do you propose to split the 20 points? [Radio button]

Make a guess
In the previous situation, you proposed how to split 20 points between yourself and another participant. In your opinion, **on average**, how many points the participants to this experiment gave to the other in the choice just made?

Your hypothesis will be considered correct if it will have difference from the actual mean not larger than one point. A correct answer will give you **2 bonus points**.

Responder

Situation's description
Another participant has to **propose how to split 20 points between himself and you**. You can accept or refuse his offer. If you accept, both of you will receive the amount of points decided by the other participant, but if you refuse but of you will receive 0 points.
You have to declare the minimum offer you intend to accept.
If the offer made by the other participant will be greater or equal to what you indicated, you will receive the points that he offered to you.

Which is the minimum offer you want to accept? [Radio button]

Make a guess
In the previous situation you declared the minimum offer you intended to accept. In your opinion, which is **the average minimum offer** that the other participants of this experiment accepted?

Your hypothesis will be considered correct if it will have difference from the actual mean not larger than one point. A correct answer will give you **2 bonus points**.

A.2.3 Trust Game

Investor

Situation's description
Both you and another participant have a **starting point-base of 4 points**. You have to **decide if give to the other** 4 points, 2 points or nothing of your point-base. If you give 4 points, the other will receive 16 additional points. If you give 2 points, the other will receive 8 additional points. If

you give 0 points, the other will receive 0 additional points.
The other participant, then, will have to **decide how many points give back to you**, using the additional points just received (16, 8 or 0).

How many points do you give to the other participant?

Make a guess
In the previous situation you decided how many points give to the other participant.
In your opinion, **on average**, how many points the participants to this experiment gave to the other in the choice just made?

Your hypothesis will be considered correct if it will have difference from the actual mean not larger than one point. A correct answer will give you **2 bonus points**.

Trustee

Situation's description
Both you and another participant have a **starting point-base of 4 points**. The other have to **decide if give you** 4 points, 2 points or nothing of his point-base. If the other gives you 4 points, you will receive 16 additional points. If the other gives you 2 points, you will receive 8 additional points. If the other gives you 0 points, you will receive 0 additional points. You will have then to **decide how many points give back to him,** using the additional points just received (16, 8 or 0).

If the other gives you 8 points, how many of them you decide to send back to him?

If the other gives you 16 points, how many of them you decide to send back to him?

Make a guess
In the previous situation you decide how many point give to the other based on the points you received. In your opinion, how many points,

on average, the participants to this experiment gave to the other in the choice just made?

If the other participant sends 2 points, how many points, on average, he will receive back?

If the other participant sends 4 points, how many points, on average, he will receive back?

Your hypotheses will be considered correct if they will have difference from the actual mean not larger than one point. A correct answer will give you **2 bonus points**.

A.2.4 Hawk and Dove Game

Simultaneous

Situation's description
You have to choose between A and B and another participant will have to do the same. Every decision is made **without knowing** what the other participant picked.

- If you choose **A**, you will receive **10 points** if the other participant chooses **A** or **5 points** if the other participant chooses **B**.
- If you choose **B**, you will receive **15 points** if the other participant chooses **A** or **0 points** if the other participant chooses **B**.

Make a guess
In the previous situation you had to choose between A and B, with these possible outcomes:

- If you choose **A**, you will receive **10 points** if the other participant chooses **A** or **5 points** if the other participant chooses **B**.
- If you choose **B**, you will receive **15 points** if the other participant chooses **A** or **0 points** if the other participant chooses **B**.

In your opinion, which is the **percentage** of participants to this experiment that **chose A**?

Your hypothesis will be considered correct if it will have a difference from the actual percentage not larger than five percentage points. A correct answer will give you **2 bonus points**.

First Mover

Situation's description
You have to choose between A and B and another participant will have to do the same. In this case, the other participant will choose **after knowing which option you picked**.

Remember!

- If you choose **A**, you will receive **10 points** if the other participant chooses **A** or **5 points** if the other participant chooses **B**.

- If you choose **B**, you will receive **15 points** if the other participant chooses **A** or **0 points** if the other participant chooses **B**.

Make a guess
In previous situation **you chose first** between A and B, while the other participant chose as second after knowing which option you decided to pick.

These were the possible outcomes:

- If you choose **A**, you will receive **10 points** if the other participant chooses **A** or **5 points** if the other participant chooses **B**.

- If you choose **B**, you will receive **15 points** if the other participant chooses **A** or **0 points** if the other participant chooses **B**.

In your opinion, which is the **percentage** of participants to this experiment that **chose A**?

Your hypothesis will be considered correct if it will have a difference from the actual percentage not larger than five percentage points. A correct answer will give you **2 bonus points**.

Second Mover

Situation's description
You have to choose between A and B and another participant will have to do the same. Now, you will choose **knowing already the option that the other participant picked**.

Remember!

- If you choose **A**, you will receive **10 points** if the other participant chooses **A** or **5 points** if the other participant chooses **B**.
- If you choose **B**, you will receive **15 points** if the other participant chooses **A** or **0 points** if the other participant chooses **B**.

There are two different cases:

- The other participant picked option A.
- The other participant picked option B.

Make a guess
In the previous situation **the other participant chose first** between A and B, while you chose as second after knowing the other's choice.

These were the possible outcomes:

- If you choose **A**, you will receive **10 points** if the other participant chooses **A** or **5 points** if the other participant chooses **B**.
- If you choose **B**, you will receive **15 points** if the other participant chooses **A** or **0 points** if the other participant chooses **B**.

In your opinion, which is the **percentage** of participants to this experiment that **chose A** after knowing that the other participant **chose A**?

In your opinion, which is the **percentage** of participants to this experiment that **chose A** after knowing that the other participant **chose B**?

Your hypotheses will be considered correct if it will have a difference from the actual percentage not larger than five percentage points. A correct answer will give you **2 bonus points**.

A.2.5 Stag Hunt Game

Situation's description You have to choose between A and B and another participant will have to do the same. Every decision is made **without knowing** what the other participant picked.

- If you choose **A**, you will receive **10 points** if the other participant chooses **A** or **0 points** if the other participant chooses **B**.
- If you choose **B** you will receive **7 points** in any case.

Make a guess
In the previous situation you had to choose between A and B, with these possible outcomes:

- If you choose **A**, you will receive **10 points** if the other participant chooses **A** or **0 points** if the other participant chooses **B**.
- If you choose **B** you will receive **7 points** in any case.

In your opinion, which is the **percentage** of participants to this experiment that **chose A**?

Your hypothesis will be considered correct if it will have a difference from the actual percentage not larger than five percentage points. A correct answer will give you **2 bonus points**.

A.2.6 Prisoner's Dilemma Game

Simultaneous

Situation's description
You have to choose between A and B and another participant will have to do the same. Every decision is made **without knowing** the decision made by the other participant.

- If you choose **A**, you will receive **10 points** if the other participant chooses **A** or **0 points** if the other participant chooses **B**.
- If you choose **B**, you will receive **15 points** if the other participant chooses **A** or **5 points** if the other participant chooses **B**.

Make a guess
In the previous situation you choose between A and B, with these possible outcomes:

- If you choose **A**, you will receive **10 points** if the other participant chooses **A** or **0 points** if the other participant chooses **B**.
- If you choose **B**, you will receive **15 points** if the other participant chooses **A** or **5 points** if the other participant chooses **B**.

In your opinion, which is the **percentage** of participants to this experiment that **chose A**?

Your hypothesis will be considered correct if it will have a difference from the actual percentage not larger than five percentage points. A correct answer will give you **2 bonus points**.

First Mover

Situation's description
You have to choose between A and B and another participant will have to do the same. In this case the other participant will choose **after having**

known the option you picked.

Remember!

- If you choose **A**, you will receive **10 points** if the other participant chooses **A** or **0 points** if the other participant chooses **B**.
- If you choose **B**, you will receive **15 points** if the other participant chooses **A** or **5 points** if the other participant chooses **B**.

Make a guess
In the previous situation you **chose first** between A and B, while the other participant chose as second after knowing what option you picked.

These were the possible outcomes:

- If you choose **A**, you will receive **10 points** if the other participant chooses **A** or **0 points** if the other participant chooses **B**.
- If you choose **B**, you will receive **15 points** if the other participant chooses **A** or **5 points** if the other participant chooses **B**.

In your opinion, which is the **percentage** of participants to this experiment that **chose A**?

Your hypothesis will be considered correct if it will have a difference from the actual percentage not larger than five percentage points. A correct answer will give you **2 bonus points**.

Second Mover

Situation's description
You have to choose between A and B and another participant will have do to the same. Now, you will choose **knowing already what option the other participant picked**.

Remember!

- If you choose **A**, you will receive **10 points** if the other participant chooses **A** or **0 points** if the other participant chooses **B**.
- If you choose **B**, you will receive **15 points** if the other participant chooses **A** or **5 points** if the other participant chooses **B**.

There are two different cases:

- The other participant picked option A.
- The other participant picked option B.

Make a guess
In the previous situation the other participant chose first between A and B, while you chose as second, **after having known** what option the other participant picked.

These were the possible outcomes:

- If you choose **A**, you will receive **10 points** if the other participant chooses **A** or **0 points** if the other participant chooses **B**.
- If you choose **B**, you will receive **15 points** if the other participant chooses **A** or **5 points** if the other participant chooses **B**.

In your opinion, which is the **percentage** of participants to this experiment that **chose A** after knowing that the other participant **chose A**?

In your opinion, which is the **percentage** of participants to this experiment that **chose A** after knowing that the other participant **chose B**?
Your hypotheses will be considered correct if it will have a difference from the actual percentage not larger than five percentage points. A correct answer will give you **2 bonus points**.

A.2.7 Public Goods Game without punishment

Situation's description
In this situation you are randomly paired with **three participants** of these

experiment.
You and the others have a **starting base of points of 10 points each.** You and the others can contribute **with a part** of your starting base.

The sum of points that you and the other participants contributed will be multiplied by two and then divided between you four, independently of the amount of points that each of you actually contributed. The points obtained in the end will derived from the sum of this division plus the points of your base that you did not used.

How many points do you want to contribute?

Make a guess
In the previous situation you decided with how many points of your personal starting-base contribute.

In your opinion, with how many points, **on average**, the participants to this experiment contributed?

Your hypothesis will be considered correct if it will have a difference from the actual percentage not larger than five percentage points. A correct answer will give you 2 **bonus points.**

A.2.8 Public Goods Game with punishment

Situation's description
In this situation you are randomly paired with **three participants** of this experiment. You and the others have a **starting base of points of 10 points each.** You and the others can contribute **with a part** of your starting base.

You and the other three participants can choose to apply a **sanction**: each of you four can spend 2 of their personal points to **reduce by 4 the points of the participant that you want to sanction.**

How many points do you want to contribute?

Who you want to punish?

- A random person between the others
- The one that contributed less
- The one that contributed more
- No one of the others

Make a guess
In the previous situation you decided with how many points of your personal starting-base contribute. At the same time, you decided which sanction to apply.

In your opinion, with how many points, **on average**, the participants to this experiment contributed?

Your hypothesis will be considered correct if it will have a difference from the actual percentage not larger than one point. A correct answer will give you **2 bonus points**.

In your opinion which is the option that was chosen the most?

- A random person between the others
- The one that contributed less
- The one that contributed more
- No one of the others

In your opinion which is the option that was chosen the less?

- A random person between the others
- The one that contributed less

- The one that contributed more
- No one of the others

Your hypothesis will be considered correct if it will have a difference from the actual percentage not larger than one point. A correct answer will give you **2 bonus points.**

A.3 Genetic Primer

As aforementioned, the participants' genetic data were collected in a different moment, precedent to this experiment.
Specifically, each participant provided a sample of saliva for DNA analysis by an Oragene collection tube (DNA Genotek Inc., Ottawa, Ontario, Canada). DNA was extracted from saliva by the prepITL2P kit according to the manufacturer's protocol (DNA Genotek Inc.).

Eight genetic variants were genotyped: TPH2 - rs4570625, HTR1B - rs13212041, HTR2A - rs6314, 5-HTTLPR (including both the VNTR and the SNP rs25531), ANKK1 - rs1800497, SLC6A3-VNTR, DRD4-exonIII-VNTR and COMT-rs4680.

The following pairs of primers were designed by using the Beacon Designer v.8 software (PREMIER 128 Biosoft, Palo Alto, CA, USA) and used for Polymerase Chain Reaction (PCR) amplification:

- 5′-GCATCACAGGATTAAGAAGAAGC-3′ and 5′-TCTTATCCCTCCCATCAGCA-3′ for TPH2-rs4570625;
- 5′-AGTGACAGGTACATGAAATTAAGAGA- and 5′- AACAAACAAAC-CATTATGTGTGCTA - 3′ for HTR1B-rs13212041;
- 5′-GCTCAATGGTTGCTCTAGGAAAG-3′ and 5′-CTTTTCATTCACTCCGTCGCT-3′ for HTR2A-rs6314;
- 5′-CGTTGCCGCTCTGAATGC-3′ and 5′-GGGAGATCCTGGGAGAGGT-3′ for 5-HTTLPR;
- 5′-TGCAGCTCACTCCATCCTG-3′ and 5′-GCAACACAGCCATCCTCAAA-3′ for ANKK1-rs1800497;
- 5′-TGTGGTGTAGGGAACGGCCTGAG-3′ and 5′- CTTCCTGGAGGTCACG-GCTCAAGG -3′ for SLC6A3-VNTR;
- 5′-GCGACTACGTGGTCTACTCG-3′ and 5′-AGGACCCTCATGGCCTTG-3′ for DRD4-exonIII-VNTR;
- 5′-CAGCGGATGGTGGATTTC-3′ and 5′-TTCCAGGTCTGACAACGG-3′ for COMT-rs4680.

The 5-HTTLPR, SLC6A3-VNTR and DRD4-exonIII-VNTR were genotyped by running the PCR amplicons on 2% ethidium bromide-stained agarose gel. rs25531 was genotyped by PCR-Restriction Fragment Length Polymorphism (RFLP) by using the restriction endonuclease Msp1 (ThermoFisher Scientific, Waltham, MA, USA). TPH2 - rs4570625, HTR1B - rs13212041, HTR2A - rs6314, ANKK1 - rs1800497 and COMT - rs4680 were genotyped by High Resolution Melting (HRM)-PCR by using the CFX Connect kit (Bio-Rad, Hercules, CA, USA) and the Bio-Rad Precision Melt Analysis software.

Appendix B

Appendix: Functional Frontal Fragility Syndrome and Decision-Making Processes

Appendix of the Chapter *Functional Frontal Fragility Syndrome and Decision-Making Processes* will comprehend additional tables and figures with results that did not enter in the main manuscript, but nonetheless provide useful pieces of information regarding the study.

B.1 Matched sample characteristic

Table 3: Matching of participants

	Means			St. Deviation		
	No Fatigue	Fatigue	p t-test	No Fatigue	Fatigue	p F-test
Age	23.9777	24.0090	0.9416	4.4444	4.5806	0.6529
Gender	0.6161	0.6054	0.8172	0.4874	0.4899	0.9407
Education	13.9821	13.9283	0.7360	1.6511	1.7253	0.5122
Pos. Reciprocity	0.0163753	-0.0166556	0.643	0.7482413	0.7572825	0.8579
Neg. Reciprocity	0.0002061	0.0004495	0.9975	0.8367353	0.8085697	0.6108
Altruism	-0.0307196	0.0328269	0.404	0.8155425	0.7910178	0.6496
Patience	-0.002936	0.0027184	0.9408	0.8469781	0.7597402	0.1057
Risk	-0.0091699	0.009211	0.7997	0.7422482	0.7875032	0.3779
Trust	-0.0035312	0.0035631	0.8964	0.5940963	0.5547887	0.3086

The table shows matched characteristics of the two groups, which included biological sex, age, level of education, and the indexes derived from the Global Preferences Survey (pooled data). For these latter indices, standardized values are reported instead of raw values. Results about means are robust to the Wilcoxon rank-sum tests and results about standard deviations are robust to Levene's robust test statistic and Brown's and Forsythe robust test statistics.

B.2 Likert Scales/Moods Questionnaires

Table 4: Likert Scales - tobit estimates

	(1) Sleepiness	(2) Mood	(3) Fatigue	(4) Motivation	(5) Pos. affects	(6) Neg. affects
Condition	-0.127	-0.137	-0.189	-1.454*	-0.122	0.0827*
	[0.273]	[0.632]	[0.232]	[0.614]	[0.0672]	[0.0405]
Time	1.003***	-0.531	2.020***	-1.915**	-0.401***	-0.0968*
	[0.287]	[0.616]	[0.254]	[0.605]	[0.0670]	[0.0404]
Interaction	-0.349	-0.262	0.663	1.948*	0.110	-0.00474
	[0.399]	[0.847]	[0.359]	[0.791]	[0.0948]	[0.0571]
Demographics	YES	YES	YES	YES	YES	YES
Preferences	YES	YES	YES	YES	YES	YES
Questionnaires	YES	YES	YES	YES	YES	YES
Constant	0.233	13.00***	0.959	4.862	4.055***	0.0144
	[1.643]	[3.612]	[1.439]	[3.080]	[0.386]	[0.233]
Observations	886	886	886	886	886	886

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Standard errors in brackets.

The table displays diff-in-diff tobit estimates for the Likert Scales compiled by participants during the experiment (pooled data). The demographics group variable includes age, education, and biological sex. The preferences group variable includes Falk's et al. (2018) Global Preferences survey proxies for altruism, positive reciprocity, negative reciprocity, trust, patience, and risk aversion. Finally, the questionnaire group variable includes the Buss-Perry Aggression Questionnaire, the Interpersonal Reactivity Index, and Barratt's Impulsiveness Scale. Results are not corrected for multiple comparisons.

B.3 Go-Nogo Task

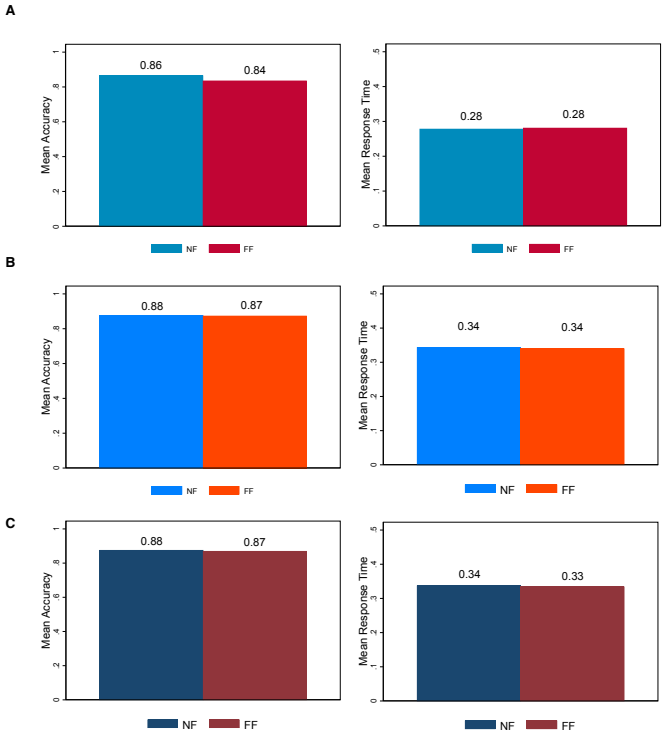


Figure 10: Results of mean accuracy and mean reaction times for the Go-Nogo Task in the two experiments. Panel A shows the results of Study 1, panel B the ones of Study 2 and finally, panel C shows the results of the two studies merged.

B.4 Beliefs

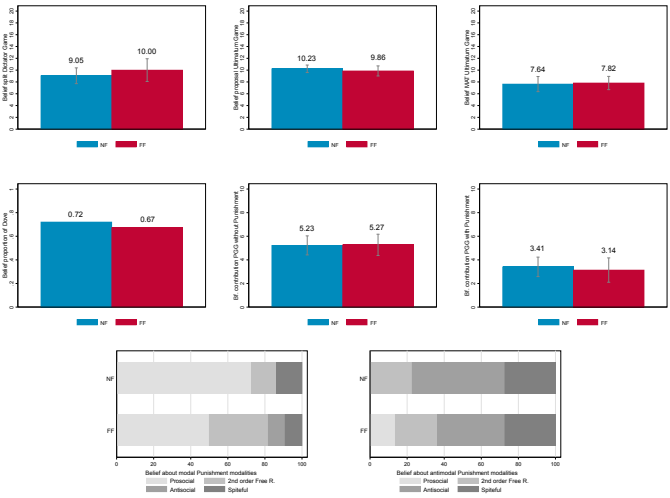


Figure 11: Results of the beliefs stated in Study 1. The order of the panel is the following: Dictator Game (average split), Ultimatum Game (average split and minimum acceptance threshold - MAT), Hawk and Dove Game (proportion of people that played "dove"), Public Goods Game without punishment (average contribution), Public Goods Game with Punishment (average contribution, most frequent and infrequent punishing behaviors). No significant results were found.

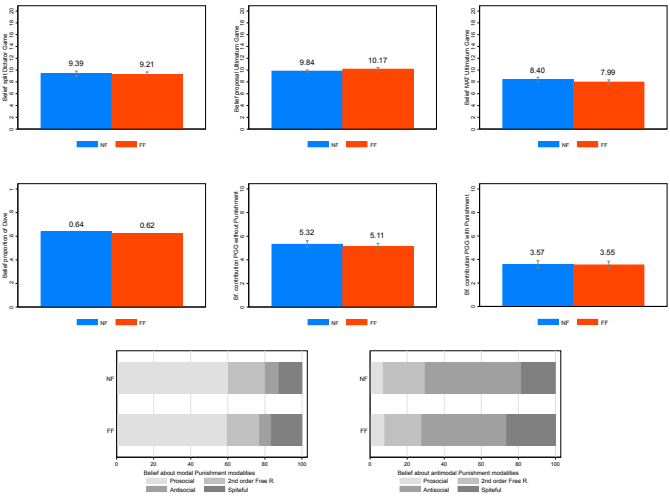


Figure 12: Results of the beliefs stated in Study 2. The order of the panel is the same as for Fig 11. A marginally significant result was found in the subjects' beliefs about the minimal proposal in the Ultimatum Game (MAT, $p = 0.0444$) but did not survive when pooling the data.

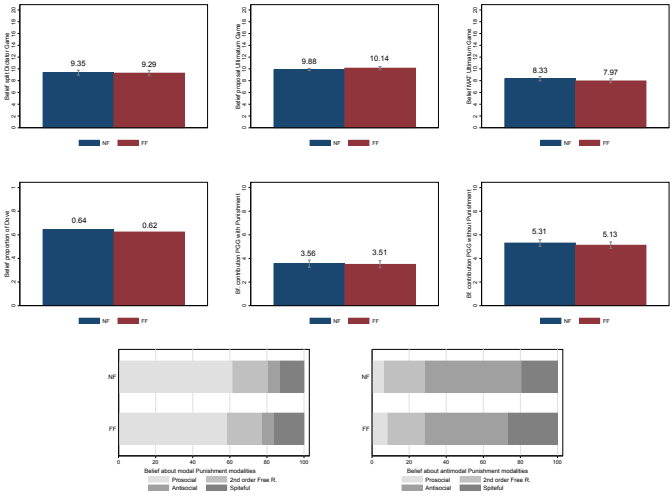


Figure 13: Results of the beliefs stated pooling the data of the two experiments. The order of the panel is the same as for Fig 11. No significant results were found.

B.5 Robustness of behavioral results

Other analysis on EEG data. Here is the graph containing the topographic plot of the analysis conducted using as a reference the period T2 as well as the source modeling results for the theta frequency band in the same period.

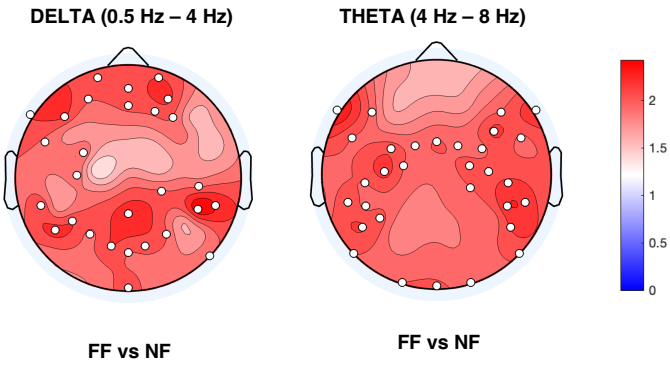


Figure 14: Differences in low-frequency activity variations after T2. The topographic plots show the statistical comparison between experimental conditions (FF vs NF) for delta and theta frequency bands at time T2 after subjects completed the economic games block. Colormap indicates T-values between +3 and -3, while white dots mark electrodes significant at $p < 0.05$ (cluster-based correction).

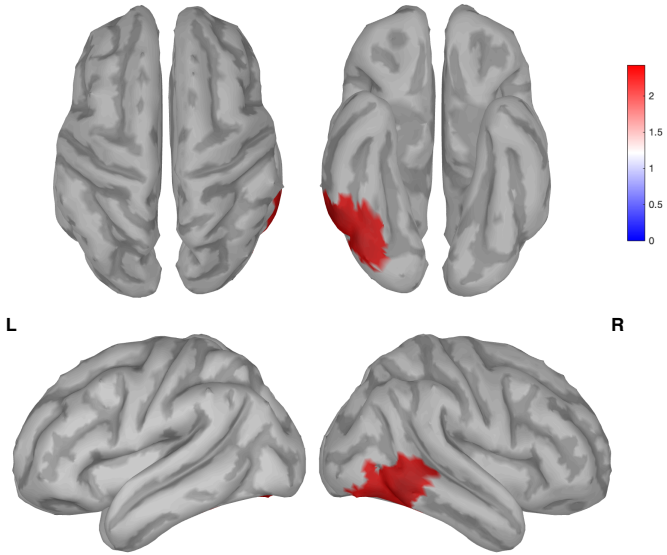


Figure 15: Source analysis of the theta EEG activity associated with the FF condition in T2. Significant differences ($p < 0.01$, cluster-based correction) in T2/T0 theta ratios between FF and NF. The difference peak was found in the right temporal lobe (64, -54, -10).

Results of the other games. All the additional results regarding the other games played that were not mentioned in the results section of the paper are reported below. Tables with regression analysis on all the results are also displayed.

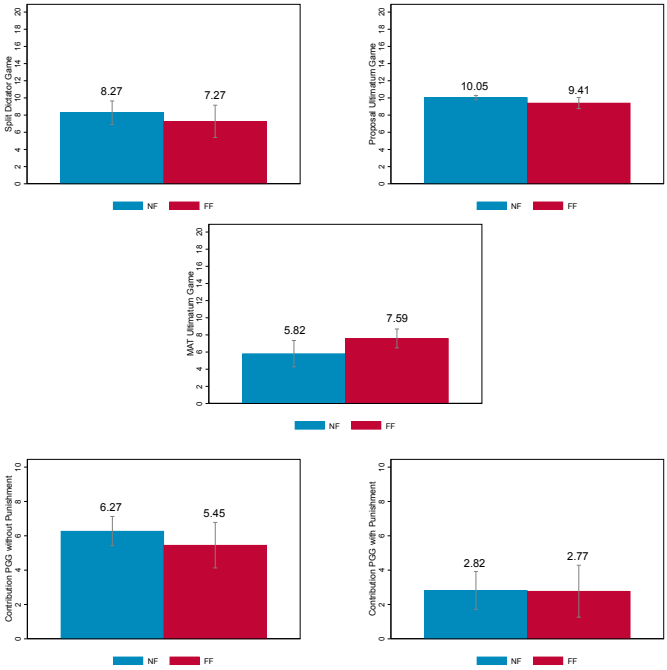


Figure 16: Results of the games of Study 1 not shown in the Results section. In order: split of the Dictator Game, proposition in the Ultimatum Game, minimum acceptance threshold for the Receiver of the Ultimatum Game, contribution in the PGG without and with punishment.

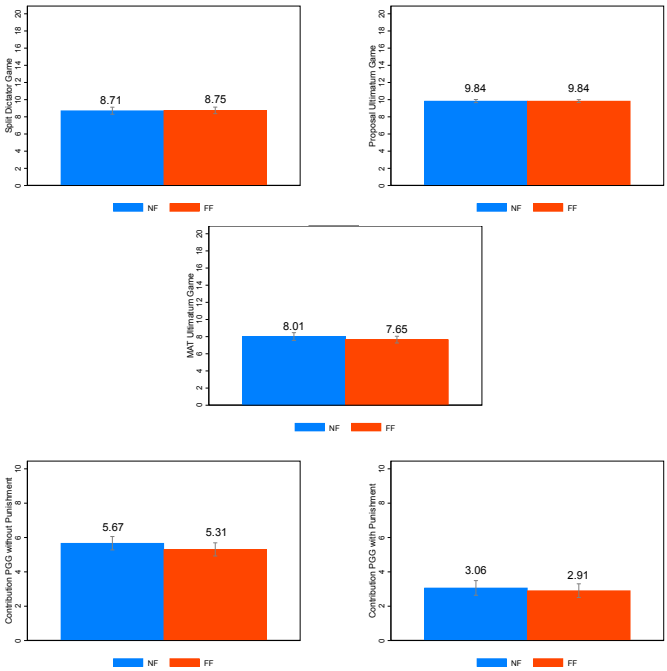


Figure 17: Results of the games of Study 2. Order of the results is the same as in Fig. 16.

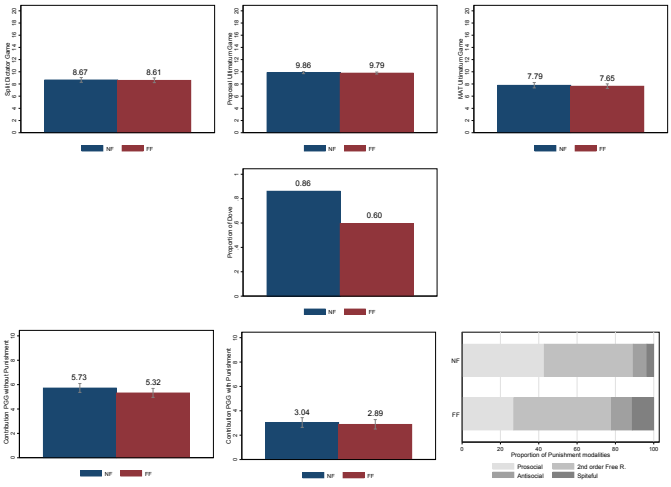


Figure 18: Results of the games (pooled data). Order of the results is the same as in Fig. 16, with the addition of the proportion of punishment modalities.

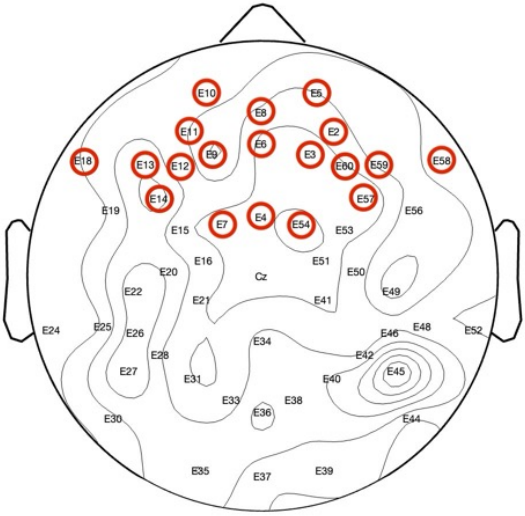


Figure 19: Cortical map of the electrodes used (red circles) to compute the additional analysis.

Table 5: Dictator Game splits - tobit estimates

	(1) Split DG	(2) Split DG	(3) Split DG	(4) Split DG
Condition	-0.0562	-0.0540	-0.0887	-0.0707
	[0.302]	[0.299]	[0.297]	[0.296]
Demographics	NO	YES	YES	YES
Preferences	NO	NO	YES	YES
Questionnaires	NO	NO	NO	YES
Constant	8.596***	9.908***	10.63***	9.567***
	[0.213]	[1.326]	[1.327]	[2.355]
Observations	447	447	443	443

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Standard errors in brackets.

The table displays tobit estimates for the dictator's split in the Dictator Game (pooled data). The demographics group variable includes age, education, and biological sex. The preferences group variable includes Falk's et al. (2018) Global Preferences survey proxies for altruism, positive reciprocity, negative reciprocity, trust, patience, and risk aversion. Finally, the questionnaire group variable includes the Buss-Perry Aggression Questionnaire, the Interpersonal Reactivity Index, and Barratt's Impulsiveness Scale.

Table 6: Ultimatum Game proposal - tobit estimates

	(1) Proposal UG	(2) Proposal UG	(3) Proposal UG	(4) Proposal UG
Condition	-0.0634	-0.0588	-0.0787	-0.0757
	[0.119]	[0.118]	[0.116]	[0.116]
Demographics	NO	YES	YES	YES
Preferences	NO	NO	YES	YES
Questionnaires	NO	NO	NO	YES
Constant	9.857***	9.301***	9.485***	8.339***
	[0.0841]	[0.523]	[0.519]	[0.923]
Observations	447	447	443	443

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Standard errors in brackets.

The table displays tobit estimates for the sender's proposal in the Ultimatum Game (pooled data). The demographics group variable includes age, education, and biological sex. The preferences group variable includes Falk's et al. (2018) Global Preferences survey proxies for altruism, positive reciprocity, negative reciprocity, trust, patience, and risk aversion. Finally, the questionnaire group variable includes the Buss-Perry Aggression Questionnaire, the Interpersonal Reactivity Index, and Barratt's Impulsiveness Scale.

Table 7: Ultimatum Game MAT - tobit estimates

	(1) MAT UG	(2) MAT UG	(3) MAT UG	(4) MAT UG
Condition	-0.147	-0.138	-0.138	-0.153
	[0.301]	[0.297]	[0.299]	[0.298]
Demographics	NO	YES	YES	YES
Preferences	NO	NO	YES	YES
Questionnaires	NO	NO	NO	YES
Constant	7.769***	8.382***	8.676***	8.218***
	[0.213]	[1.316]	[1.334]	[2.369]
Observations	447	447	443	443

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Standard errors in brackets.

The table displays tobit estimates for the receiver's minimum acceptance threshold (MAT) in the Ultimatum Game (pooled data). The demographics group variable includes age, education, and biological sex. The preferences group variable includes Falk's et al. (2018) Global Preferences survey proxies for altruism, positive reciprocity, negative reciprocity, trust, patience, and risk aversion. Finally, the questionnaire group variable includes the Buss-Perry Aggression Questionnaire, the Interpersonal Reactivity Index, and Barratt's Impulsiveness Scale.

Table 8: Hawk and Dove Game - probit estimates

	(1) Play Dove	(2) Play Dove	(3) Play Dove	(4) Play Dove
Condition	-0.843***	-0.849***	-0.877***	-0.889***
	[0.135]	[0.136]	[0.139]	[0.139]
Demographics	NO	YES	YES	YES
Preferences	NO	NO	YES	YES
Questionnaires	NO	NO	NO	YES
Constant	1.088***	0.860	1.090	1.945
	[0.104]	[0.579]	[0.596]	[1.091]
Observations	447	447	443	443

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Standard errors in brackets.

The table displays probit estimates for the "dove" action of the Hawk and Dove Game (pooled data). The demographics group variable includes age, education, and biological sex. The preferences group variable includes Falk's et al. (2018) Global Preferences survey proxies for altruism, positive reciprocity, negative reciprocity, trust, patience, and risk aversion. Finally, the questionnaire group variable includes the Buss-Perry Aggression Questionnaire, the Interpersonal Reactivity Index, and Barratt's Impulsiveness Scale.

Table 9: Public Goods Game without punishment contribution - tobit estimates

(4)		(1)	(2)	(3)
	Contribution	Contribution	Contribution	Contribution
Condition	-0.433	-0.434	-0.443	-0.432
	[0.323]	[0.323]	[0.320]	[0.319]
Demographics	NO	YES	YES	YES
Preferences	NO	NO	YES	YES
Questionnaires	NO	NO	NO	YES
Constant	5.916***	5.084***	5.508***	5.190*
	[0.229]	[1.427]	[1.426]	[0.862]
Observations	447	447	443	443

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Standard errors in brackets.

The table displays tobit estimates for contribution to the Public Goods Game without punishment (pooled data). The demographics group variable includes age, education, and biological sex. The preferences group variable includes Falk's et al. (2018) Global Preferences survey proxies for altruism, positive reciprocity, negative reciprocity, trust, patience, and risk aversion. Finally, the questionnaire group variable includes the Buss-Perry Aggression Questionnaire, the Interpersonal Reactivity Index, and Barratt's Impulsiveness Scale.

Table 10: Public Goods Game with punishment contribution - tobit estimates

	(1)	(2)	(3)	(4)
	Contribution	Contribution	Contribution	Contribution
Condition	-0.293	-0.275	-0.260	-0.250
	[0.436]	[0.432]	[0.433]	[0.432]
Demographics	NO	YES	YES	YES
Preferences	NO	NO	YES	YES
Questionnaires	NO	NO	NO	YES
Constant	2.327***	1.853	2.056	-1.048
	[0.310]	[1.928]	[1.951]	[3.437]
Observations	447	447	443	443

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Standard errors in brackets.

The table displays tobit estimates for the contributions to the Public Goods Game with a punishment option (pooled data). The demographics group variable includes age, education, and biological sex. The preferences group variable includes Falk's et al. (2018) Global Preferences survey proxies for altruism, positive reciprocity, negative reciprocity, trust, patience, and risk aversion. Finally, the questionnaire group variable includes the Buss-Perry Aggression Questionnaire, the Interpersonal Reactivity Index, and Barratt's Impulsiveness Scale.

Table 11: Punishment modalities - multinomial logit estimates

	Free Rider	Prosocial	Antisocial	Spiteful
Free Rider (base outcome)				
Prosocial punisher				
Condition	-0.562**	-0.559**	-0.579**	-0.577**
	[0.213]	[0.214]	[0.219]	[0.220]
Demographics	NO	YES	YES	YES
Preferences	NO	NO	YES	YES
Questionnaires	NO	NO	NO	YES
Constant	-0.0800	-1.295	-1.304	-2.815
	[0.142]	[0.933]	[0.964]	[1.734]
Antisocial punisher				
Condition	0.314	0.315	0.314	0.345
	[0.350]	[0.350]	[0.353]	[0.356]
Demographics	NO	YES	YES	YES
Preferences	NO	NO	YES	YES
Questionnaires	NO	NO	NO	YES
Constant	-1.872***	-2.425	-2.413	1.136
	[0.269]	[1.516]	[1.534]	[2.789]
Spiteful punisher				
Condition	1.048*	1.047*	1.097*	1.085*
	[0.428]	[0.428]	[0.437]	[0.438]
Demographics	NO	YES	YES	YES
Preferences	NO	NO	YES	YES
Questionnaires	NO	NO	NO	YES
Constant	-2.565***	-1.525	-1.460	-0.0677
	[0.367]	[1.791]	[1.865]	[3.183]
Observations	447	447	443	443

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$
Standard errors in brackets

The table displays multinomial logit estimates for each individual modality of punishment (prosocial punishment, second-order free-riding, antisocial punishment, and spiteful punishment), as compared with the reference category of second-order free-riding (i.e., not taking a punishment action). Individual probit estimates for each modality of punishment separately obtained qualitative equivalent results (pooled data). The preferences group variable includes Falk's et al. (2018) Global Preferences survey proxies for altruism, positive reciprocity, negative reciprocity, trust, patience, and risk aversion. Finally, the questionnaire group variable includes the Buss-Perry Aggression Questionnaire, the Interpersonal Reactivity Index, and Barratt's Impulsiveness Scale.

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