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TESIS DOCTORAL

A neuroimaging study on how experience shapes the investor's brain

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To my family…

Acknowledgments

Steve Jobs said, “Great things in business are never done by one person: they’re done by a team of people,” and I could not agree more. Although this is not a business per se, it was the most important venture I had undertaken so far, but I was never alone. This thesis would not have been possible without the support of many people who have helped me turn an idea into a research project.

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Contents

Summary

Background:

Economics have failed to create theories of choice that allow us to accurately predict human behavior under all circumstances. To answer the question on how investors decide, we need to go beyond abstract models based on what is rational given that our rationality is computationally bounded. For this reason, studies in Neuroeconomics have begun to gain knowledge into what are the underlying neurobiological processes of decision-making that guide a person to make some economic decisions and not others. In most cases, these researches have been based on regions of interest, ruling out all the information that whole-brain analyses can bring. This thesis tries to approach the understanding of investment decision-making from a slightly different perspective. As our brain is plastic and it can change according to our experiences, we are going to analyze the investor's brain to find differences in their decision-making process and if there are any, determine which brain areas are responsible for their investment behaviors.

Methods:

In order to determine the brain structures specialized in responding to investments, the following methods have been used. For the first study published in *Brain Sciences*, an activation likelihood estimation (ALE) meta-analysis using GingerALE software has allowed us to establish which brain areas tend to be activated when an investment decision is made. For the second study published in *Journal of Neuroscience, Psychology and Economics*, an electroencephalography (EEG) along with a recording of the motor response, has enabled us to analyze anticipatory processes in terms of the decision preceding negativity (DPN) latencies, brain activations, response times and gambling decisions between investment bankers and a control group. And for the third study accepted for publication in *Scientific Reports*, a magnetic resonance imaging (MRI), whole-brain transcriptome data from Allen Human Brain Bank and functional annotations from PANTHER pathways, has made it possible to detect those areas of the brain with an increase in volume, a strengthening in their connections and their associated gene expression.

Results:

We found that, in the first study, the ventral striatum, the anterior insula, the amygdala, the anterior cingulate cortex and the occipital cortex are activated when we make an investment decision. For the second study, the prefrontal and orbitofrontal cortex under risky conditions and the prefrontal cortex under ambiguous conditions were activated streamlining anticipatory processes, while decreasing their response times and the number of gambling decisions. And for the third study, dopaminergic-related areas increased in volume and strengthened their connections with a higher gene expression of SLC6A3, TH and SLC18A2, whose pathways have been associated with the biosynthesis of catecholamines (dopamine, adrenaline and noradrenaline).

Conclusions:

In conclusion, investors have shaped their brains to survive in the financial markets by training the areas responsible for investment decision-making through their daily experience playing the market. They have higher gray matter volume and increased structural brain connectivity in dopaminergic-related pathways, which has led to a decrease in the anticipatory processes that precede a risky decision while regulating cognitive and emotional functions on the basis of the amount of available information. This plastic change has been mediated by catecholamines in areas of the brain previously identified with investment behaviors in the scientific literature.

Resumen

Antecedentes:

La Economía todavía no ha logrado crear teorías de decisión que nos permitan predecir el comportamiento humano. Para poder responder a la cuestión de cómo deciden los inversores, tenemos que ir más allá de los modelos abstractos basados en lo que es racional, dado que nuestra racionalidad es limitada. Por este motivo, los estudios en Neuroeconomía han comenzado a comprender cuáles son los procesos neurobiológicos subyacentes a las decisiones económicas. En la mayoría de los casos, estas investigaciones se han basado en el estudio de regiones cerebrales concretas, descartando la utilidad que el análisis de todo el cerebro puede aportar. Esta tesis trata de profundizar en el entendimiento de las decisiones de inversión desde otra perspectiva. Dado que nuestro cerebro es plástico y cambia en función de nuestras experiencias, vamos a analizar el cerebro del inversor para encontrar diferencias en su proceso de toma de decisión y en caso de que las hubiese, determinar qué áreas cerebrales son responsables de sus comportamientos de inversión.

Métodos:

Se han utilizado los siguientes métodos para determinar las estructuras cerebrales entre cuyas funciones se encuentran las decisiones de inversión. Para el primer estudio publicado en *Brain Sciences*, se ha llevado a cabo un meta-análisis usando el software de GingerALE, lo que nos ha permitido establecer las áreas que tienden a activarse cuando se toma una decisión de inversión. Para el segundo estudio publicado en *Journal of Neuroscience, Psychology and Economics*, hemos empleado electroencefalografía (EEG) y registro de la respuesta motora para analizar los procesos anticipatorios en términos de latencia y activación cerebral, así como los tiempos de respuesta y las decisiones entre un grupo financieros y un grupo control. Para el tercer estudio aceptado para su publicación en *Scientific Reports*, hemos usado resonancia magnética (RM), datos del transcriptoma generado por el Allen Human Brain Atlas y anotaciones funcionales provenientes de PANTHER, para detectar aquellas áreas del cerebro que han aumentado su volumen y fortalecido sus conexiones, así como la expresión genética asociada a dichos cambios.

Resultados:

En el primer estudio hemos encontrado que el estriado ventral, la ínsula anterior, la amígdala, la corteza cingulada anterior y la corteza occipital se activan cuando tomamos la decisión de invertir. En el segundo estudio, se activaron en condiciones de riesgo la corteza prefrontal y orbito-frontal y en situaciones de ambigüedad la corteza prefrontal, agilizando los procesos anticipatorios a la toma de decisión, a la vez que disminuyeron los tiempos de respuesta y las decisiones arriesgadas. Para el tercer estudio, las áreas relacionadas con la dopamina aumentaron de volumen y fortalecieron sus conexiones, con una mayor expresión genética de SLC6A3, TH y SLC18A2, genes que han sido asociados con la biosíntesis de las catecolaminas (dopamina, adrenalina y noradrenalina).

Conclusiones:

En conclusión, los inversores han moldeado su cerebro para sobrevivir en los mercados financieros, entrenando las áreas cerebrales responsables de las decisiones de inversión a través de su experiencia profesional. El aumento de volumen de la materia gris y de sus conexiones en áreas dopaminérgicas ha provocado una disminución de los procesos anticipatorios que preceden a una decisión arriesgada, al tiempo que regulan los procesos cognitivos y emocionales en función de la cantidad de información disponible. Este cambio plástico se ha visto mediado por las catecolaminas en áreas del cerebro previamente identificadas en la literatura con comportamientos de inversión.

Chapter 1

Introduction

Making an investment decision is like formulating a scientific hypothesis and submitting it to a practical test. The main difference is that the hypothesis that underlies an investment decision is intended to make money and not to establish a universally valid generalization.

George Soros

Introduction

***Motivation for this Research Study*:**

I have always thought that economics was guided by rational rules designed to maximize profit and as such, everything was formerly discovered and everything was already understood. However, after graduating in Business Administration, when family and friends approached me with questions such as "Should I invest in these stocks?" "Which pension plan would you recommend?" "How can I make these savings profitable?" I realized that no rule, as logical as it may be, will enable me to give an accurate response because no certainty is guarantee when it comes to money. What I did not realize back then was that all this uncertainty starts with the brain.

When I joined the neuroscience laboratory lead by Professor Tomás Ortiz, I found out that neurons retain their plasticity for most of their life. This means that our brain adapts itself according to our demands, or to put it in another way, our experience becomes the molder of our brain. Within the scientific projects that I was able to observe, the case of a girl who was born with half of her brain was the starting point of the beginning of this thesis. This little girl, whose doctors had given up all hope that she would be able to lead a normal life, found a hard-to-believe possibility in this optimistic professor. To cut a long story short, after several years and countless hours of stimulation, this girl discovered an almost ordinary life, just like the rest of the children of her age. Hard to believe? yes, impossible to achieve? no.

At that moment it hit me. If this has been accomplished with an "incomplete" brain, what can be done with a whole healthy brain and a proper stimulation program? Perhaps this could be a solution to the constant blunders of the economists, as most of the doctors at the University have previously stated. But, if this is so obvious, why has not been done before? I found the answer when I started my PhD. You cannot properly train a brain without knowing how that brain works in that specific field. Trying to train economists to make better economic decisions without knowing how the brain lands to this kind of choice, is like trying to strike a bull´s eye in the dark. You know you have to hit the target, but you do not know where it is.

The lack of knowledge on how the brain process and come to an economic decision is mainly due to the fact that this field, widely known as neuroeconomics, is just starting out in

science. The articles published to date are based on decision tasks where most of them focus on regions of interests (ROIs), brain areas that have been previously studied in the medical literature. The reason lies in that not all researchers are able to get whole-brain analyses off the ground given its complexity. Therefore, this scarce knowledge makes it almost impossible to understand as of today the complicated nature of this decision-making process and all the variables that influence it. Despite this, I was not discouraged.

Seeing that, for the time being, we are only able to envisage glimpses of how our brain makes economic decisions, I decided to go back to the idea of neuroplasticity. It was around this time when I came across an article that showed how the volume in a brain area called hippocampus, involved in memory and spatial processing and navigation, correlated with the amount of time spent as a taxi driver (Maguire, et al., 2000). Could it be more than just a metaphor the saying that the brain is like a muscle that grows with exercise? If those taxi drivers have increased the volume of a brain region key to enable them to drive through the streets of London, why not do the same with the investors? The interest that this question awakened, led me to the Spanish researcher Ramón y Cajal who, more than 100 years ago, had already intuited the importance of neuroplasticity. So much so that he even said that "Any man could, if he were so inclined, be the sculptor of his own brain." The idea that an intentional effort can modify the brain is the opposite approach to what has been done so far in neuroeconomics. If we can unveil the brain structures that have increased in volume as a consequence of constant stimulation due to their work experience, we will be one step closer to understanding this decision process. This is the history behind the motivation that has led me to carry out this research work.

***State of the Art*:**

Every investor wants to obtain the maximum amount of return for the minimum amount of risk. Therefore, they optimize their portfolio trying to maximize the likelihood of realizing sustainable gains while minimizing the chances of bearing irreversible losses (Zweig, 2006). However, this is not always achieved because the art of investment is not based on a mathematical formula alone. Although economic prescriptive theories along with psychological descriptive models have been able to gain a better understanding of investment behavior, it is still unknown

why investors frequently deviate from rationality when making financial decisions. In an attempt to understand and hence predict optimal and suboptimal investment strategies, neurobiological models can fill in the knowledge gap between what investors are expected to choose and what they actually decide. This new pursuit of knowledge is possible thanks to a cutting-edge communication between neuroscience, psychology and economics known as Neuroeconomics.

Neuroeconomics is defined as "the study of the biological microfoundations of economic cognition and economic behavior" (Camerer, Cohen, Fehr, Glimcher, & Laibson, 2017). By focusing on brain systems, neurotransmitters and genes involved in the cognition of economic perceptions, preferences and beliefs (Laibson, 2021), this new field aims to understand economic decisions by analyzing how the brain works.

Within this new field, the study of investment decisions has drawn the attention of researchers. What is interesting about this decision-making process is that it is all about expectations learned from experience. A decision, whether risky or safe, begins with fluctuations of dopamine within the reward circuit (Chew, et al., 2019). Nevertheless, to come to a decision, this process must integrate information coming from reward circuits as well as brain regions involved in cognition (Haber, 2017). Although activity in dopaminergic brain areas has been shown to occur with both immediate and delayed rewards, in 2004, McClure et al. demonstrated that there are two distinct systems involved in choices between monetary reward options available at different moments in time (McClure, Laibson, Loewenstein, & Cohen, 2004). On the one hand, decisions that entail immediate rewards involve the ventral striatum, the medial orbitofrontal cortex and the medial prefrontal cortex (McClure, Laibson, Loewenstein, & Cohen, 2004), all of which are activated by the receipt of rewards (Diekhof, Kaps, Falkai, & Gruber, 2012). On the other hand, intertemporal choices of delayed rewards engage the lateral prefrontal cortex and the parietal cortex (McClure, Laibson, Loewenstein, & Cohen, 2004). These latter areas of the brain are known to be implicated in the control of cognitive functions and goal-directed behavior, including the modulation of working memory information through rewards (Kennerley & Wallis, 2009) and the representation of task-reward associations (Wisniewski, Reverberi, Momennejad, Kahnt, & Haynes, 2015).

Investors choose between different types of rewards by using a common scale of values. Thus far, neuroimaging studies in humans have highlighted the ventromedial prefrontal cortex/orbitofrontal cortex as the key brain area for representing the subjective values of all reward

types on a neural common scale and, to a much lesser extent, the ventral striatum (Levy & Glimcher, 2012). The most feasible explanation is that the ventromedial prefrontal cortex computes these values by trading off costs and benefits from the amygdala and the ventral striatum, respectively (Basten, Biele, Heekeren, & Fiebach, 2010). Other areas, such as the anterior insula, engage with rewards by having a negative correlation with increasing anticipated monetary reward (Kim, Shimojo, & O´Doherty, 2011) as well as a positive correlation, mainly with the anterior cingulate cortex when a decision conflict arises between options of competing value (Pochon, Riis, Sanfey, Nystrom, & Cohen, 2008). Therefore, the brain appears to be equipped with a unified valuation network to compare between rewards.

On the contrary, risk is determined by the probabilities of possible outcomes, which are estimated by individual perceptions based on previous experiences. How these evaluated probabilities influence investors' decisions depends on the amount of information available (risk) or, rather, the information that is unknown to the investor (ambiguity). This is of high importance because financial decision-making may require the activation of distinct circuits to take or avoid risks (Kuhnen & Knutson, 2005), as applications such as risk limits, portfolio optimization, and trader performance-based compensation depend on the measurement of risk (Holton, 2004). The brain distinguishes between risk and ambiguity (Hsu, Bhatt, Adolphs, Tranel, & Camerer, 2005) in real-time analysis of financial risks (Lo & Repin, 2002), seeing that experts know how to accurately calculate risks and what factors cause those risks (Fischhoff & Kadvany, 2011). Professionals working within the field become familiar and comfortable dealing with risk, showing less emotional responsiveness over the years (Lo & Repin, 2002). Several studies have associated activation between risk and ambiguity with distinct brain areas. Usually, risk activates the insula, the striatum and the parietal cortex, whereas ambiguity involves the lateral prefrontal cortex, the medial prefrontal cortex, the cingulate cortex and the amygdala (Miendlarzewska, Kometer, & Preuschoff, 2019).

As opposed to rewards, there is no unified neural system for evaluating decisions at all levels of uncertainty, despite the fact that the anterior insula is thought to encode changes in the amount of variability (risk) as well as risk prediction errors (Preuschoff, Quartz, & Bossaerts, 2008). In 2005, Hsu et al. suggested a common neural circuit which was positively activated in the amygdala and the orbitofrontal cortex and negatively in the striatum as uncertainty increased (Hsu, Bhatt, Adolphs, Tranel, & Camerer, 2005). However, in 2019, FeldmanHall et al. ruled out these

areas and stated that only the lateral prefrontal cortex played a key role in processing high levels of uncertainty (FeldmanHall, Glimcher, Baker, NYU PROSPEC Collaboration, & Phelps, 2019), despite its correlation with individual ambiguity preferences (Huettel, Stowe, Gordon, Warner, & Platt, 2006). Nonetheless, all these areas are involved in the regulation of emotional responses, whether evoked consciously or automatically by the stimulus itself (Etkin, Büchel, & Gross, 2015; Viviani, 2014).

Psychological and neuroscientific research has emphasized that emotions play a role in decision-making, especially because changing our emotions can change our choice (Phelps, Lempert, & Sokol-Hessner, 2014). It is probable that this nonconscious process guides our decisions prior to our conscious knowledge and provides the neurobiological evidence as to why these choices are made as they "feel right" or come "straight from the gut" (Bechara & Damasio, 2005), even with high-stakes decisions (Huang, 2019). Despite this, it remains unclear how emotions influence risk processing and risk anticipation. Anticipatory effects in distinct neural circuits can impact financial choices (Knutson & Greer, 2008). For instance, risky and safe investments are predicted by ventral striatum and anterior insula activation, respectively (Kuhnen & Knutson, 2005). It appears as if two parallel processes occur when a person makes an investment choice. On the emotional level, activity in the anterior insula assesses potential losses, while the thalamus can anticipate regret in the case of loss. On the cognitive level, the dorsomedial prefrontal cortex evaluates risk by using the information provided by the anterior insula and the thalamus (Mohr, Biele, & Heekeren, 2010). To decide, the parietal cortex and the dorsolateral prefrontal cortex must combine the information about risk with the expected reward obtained from those areas (Mohr, Biele, & Heekeren, 2010).

In an attempt to seek environmental validity for these results found in the literature, neuroeconomics has begun to connect brain areas supporting this decision-making process to real-life financial risk taking. Thus far, only the activation in the anterior insula (Häusler, Kuhnen, Rudorf, & Weber, 2018) and the ventrolateral prefrontal cortex (Raggetti, Ceravolo, Fattobene, & Di Dio, 2017) have been negatively correlated with individuals' expertise in trading stocks in real life. Furthermore, the decision to trade in active investors has recently been attributed to genes associated with catecholamine synaptic levels (Sapra, Beavin, & Zak, 2012), especially dopamine (Muda, et al., 2018; Anderson, Dreber, & Vestman, 2015) since is closely connected to reward-seeking behaviors (Arias-Carrión & Pöppel, 2007). Although economic preferences are partially

explained by genetic differences (Benjamin, et al., 2012), environmental factors, such as work experience, also mediate in this connection between genes and risk-taking (Muda, et al., 2018) shaping individuals' financial decisions and may even diminish genetic predispositions to investment biases (Cronqvist & Siegel, 2014).

***Objectives*:**

As of today, there is a major interest in understanding how we make investment decisions and what are the factors that drive these choices. It is claimed that investment decision-making should rely on rational analysis based on facts and not emotions. However, this is not always beheld due to the fact that trying to make money out of market forecasts can trigger all types of emotional responses. Although neuroeconomic studies have begun to highlight the significant role of several brain areas in this decision-making process, the scientific community is still hesitant to draw strong conclusions about which neuronal circuits actually drive these investments.

Since the structure of the brain can modify itself with every activity it performs (DeFelipe, 2006), many occupational neuroplasticity studies have been conducted (Wu, et al., 2020) where the majority of the stimuli that can cause a change in the brain comes from the heavy demands to acquire the professional skills needed to carry out the work. The changes that occur endow the person with a more well-equipped brain to better suit the task at hand in their job. Consequently, the behaviors that we observe are determined by the functioning of the brain, a muscle that has been trained steadily over the years by a combination of formal training and on-the-job experience.

According to these considerations, analyzing a person's brain, either through a task or in resting-state, can help us towards a more accurate comprehension of how investment decisions are made. Therefore, the goal of this thesis is to analyze the changes that have taken place in the investor's brain associated with their professional experience investing in the financial markets.

To accomplish the aim of this thesis, the following objectives were outlined:

Objective 1: Identify the convergence of brain regions involved in investment decisions.

Objective 2: Determine if professional experience modifies decision-making in conditions characterized by risk and ambiguity, both in terms of motor response and brain activation, between a group of investors and a control group.

Objective 3: Analyze differences in the volume of gray matter between senior and junior investors and identify its structural connectivity based on financial work experience, as well as the higher genetic expression within those structures.

***Methods and Research Plan*:**

To achieve the objectives of this thesis, we used methods from cognitive neuroscience to collect data from the investor's brain that allow us to determine what are the key structures in the investment decision-making process. The two neuroimaging methods used have been: electroencephalography (EEG), which records electrical activity on the scalp, and resonance magnetic imaging (MRI), which produces dimensional detailed anatomical images.

As neuroscience can inform economics (Camerer, Loewenstein, & Prelec, 2005), there have been an increasing number of studies connecting brain activation with economic decisions. Nevertheless, there is not enough information to draw strong conclusions about what neuronal circuits drive investment decisions. To attain objective 1, we first identified the convergence of brain regions involved in investment decisions by conducting and activation likelihood estimation (ALE) meta-analysis following PRISMA guidelines based on what has been reported in the neuroeconomic literature. By looking into how likely each individual voxel in the brain was activated by an investment task, we were able to identify four clusters of brain areas that play a key role in this decision-making process. In other words, the ALE meta-analysis that we performed

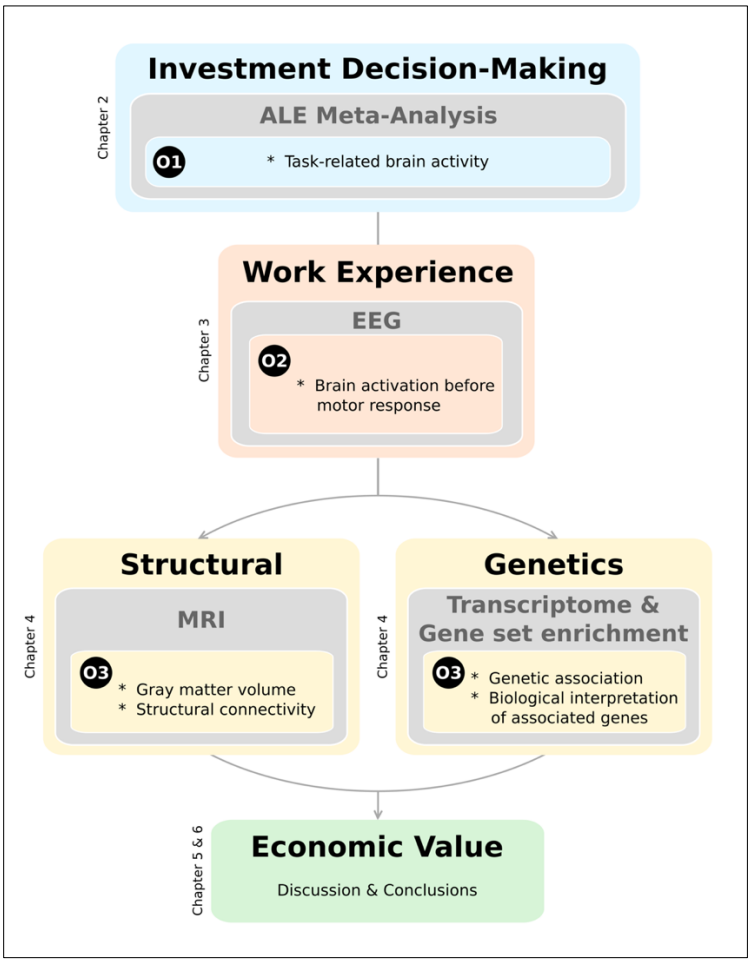
using all the brain coordinates reported in the functional magnetic resonance imaging studies, have allowed us to distinguish the spatial location that is activated when deciding whether to invest or not to. This objective is set out in the article "An ALE meta-analysis on investment decision-making" published in *Brain Sciences*.

While the previous objective focuses on healthy adults making an investment decision, objective 2 analyzes possible differences in decision making based on work experience. Providing that experience can improve decision-making (Nakamoto & Mori, 2012), we used electroencephalography (EEG) to study if financial experiences influence anticipatory processes under risky and ambiguous conditions. This technique, due to its high temporal resolution, enables us to observe a slow negative potential that precedes a decision, known as decision preceding negativity (DPN). The DPN is involved in cognitive processes associated with the elaboration of the response (Bianchin & Angrilli, 2011). Researchers have started to pay attention to the anticipatory neural activity that precedes a financial choice to see if it can be predicted (Kuhnen & Knutson, 2005). In our study, we focused on which brain areas are activated before the decision is made and if these regions differ according to one's profession. Our results support other findings of the effect of financial expertise on decision-making, reducing anticipatory processes while regulating cognitive and emotional functions on the basis of available information given to the participants. This objective is set out in the article "Neural implications of investment banking experience in decision-making under risk and ambiguity" published in the *Journal of Neuroscience, Psychology and Economics*.

After finding a distinction in the decision-making process between a group of investment bankers and a control group, we conducted a magnetic resonance imaging (MRI) study to examine the structure of the investor's brain. Objective 3 is based on the notion that our brain is plastic; therefore, it can rewire itself. This neuroplasticity process can help us understand how structures are formed and adapted to better suit a specific task. By using MRI, due to its high spatial resolution, along with approaches to link neuroimaging and genetics, we were able to investigate the influence of investment work experience on brain anatomy. These analyses are based on the knowledge that environmental factors, such as experience, can impact our gene expression, which in turn shapes our brain anatomy and our behavior (Clayton, et al., 2020). We found a higher expression of three genes associated with the biosynthesis of catecholamines in senior investors, displaying an increase in gray matter volume and structural connectivity in dopaminergic-related

pathways. Behaviorally, this implies that emotions and bodily awareness change as investors grow in maturity. This objective is set out in the article "Connectivity adaptations in dopaminergic systems define the brain maturity of investors" accepted for publication in *Scientific Reports*.

As shown in the following figure, the research plan has been developed in accordance with the objectives proposed in this thesis. Our research plan has consisted of: (i) a review of the scientific literature using an activation likelihood estimation meta-analysis with functional magnetic resonance imaging (fMRI) studies that have reported whole-brain results during an investment task, to identify the convergence of brain regions involved in the investment decision-making process, (ii) an electroencephalography (EEG) during a gambling task, to determine if work experience modifies decision-making under risky and ambiguous conditions between a group of investment bankers and a control group, and (iii) a magnetic resonance imaging (MRI) at resting-state, to analyze differences in the brain in terms of gray matter volume and structural connectivity between senior and junior investors, as well as whole-brain transcriptome data from Allen Human Brain Bank (AHBA) and functional annotations from the Protein Analysis Through Evolutionary Relationships (PANTHER) pathways to determine the higher genetic expression within those structures.



Research Plan and Methodological Framework. The thesis is divided into three *sections* (ALE meta-analysis, Work experience, Structural and Genetics), each one corresponding to an *objective* (O1, O2 and O3). O1: Identify the convergence of brain regions involved in investment decisions. O2: Determine if professional experience modifies decision-making in conditions characterized by risk and ambiguity, both in terms of motor response and brain activation, between a group of investors and a control group. O3: Analyze differences in the volume of gray matter between senior and junior investors and identify its structural connectivity based on financial work experience, as well as the higher genetic expression within those structures. The *methods* used in each section are: activation likelihood estimation (ALE) meta-analysis, electroencephalography (EEG), and structural magnetic resonance imaging (MRI) and whole-brain transcriptome data from Allen Human Brain Bank and functional annotations from PANTHER pathways, respectively. The goals of these methods are described in each box.

***The Role of Each Article within the Research Plan*:**

The three articles have set the path for us to begin to understand which brain structures and circuits are responsible for the investment decision-making process. The first article, "An ALE meta-analysis on investment decision-making" published in *Brain Sciences*, has helped us to establish those brain areas that are repeatedly activated when a person is making an investment decision according to the neuroeconomic literature. This is of high significance because knowing what these regions are, allows us to connect the changes that have taken place in the brain with their corresponding brain activity, in this case, with an investment decision-making task, in the event that those areas are the same.

Once we have reviewed the literature, the second article, "Neural implications of investment banking experience in decision-making under risk and ambiguity" published in the *Journal of Neuroscience, Psychology and Economics*, have served as a basis for the differences in decision-making during a gambling task between an investment banker group and a control group. To avoid biases in our results, the task did not consist of making financial choices that involved specific knowledge. This experiment was also essential on the grounds that no differences in decision-making may imply any neuroplasticity in the investor's brain.

As soon as we have established that there are indeed differences in the decision-making process based on work experience, the third and last article, "Connectivity adaptations in dopaminergic systems define the brain maturity of investors" accepted for publication in *Scientific Reports*, has enabled us to locate where the structural changes in the brain have taken place when comparing senior with junior investors, as well as the higher genetic expression within those changes.

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Chapter 2

An ALE meta-analysis on investment decision-making

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Review

An ALE Meta-Analysis on Investment Decision-Making

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Abstract: It is claimed that investment decision-making should rely on rational analyses based on facts and not emotions. However, trying to make money out of market forecasts can trigger all types of emotional responses. As the question on how investors decide remains controversial, we carried out an activation likelihood estimation (ALE) meta-analysis using functional magnetic resonance imaging (fMRI) studies that have reported whole-brain analyses on subjects performing an investment task. We identified the ventral striatum, anterior insula, amygdala and anterior cingulate cortex as being involved in this decision-making process. These regions are limbic-related structures which respond to reward, risk and emotional conflict. Our findings support the notion that investment choices are emotional decisions that take into account market information, individual preferences and beliefs.

Keywords: neuroeconomics; investor; stock; reward; risk; ventral striatum; anterior insula; amygdala; anterior cingulate cortex

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1. Introduction

"To invest successfully over a lifetime does not require a stratospheric IQ, unusual business insights, or inside information. What's needed is a sound intellectual framework for making decisions and the ability to keep emotions from corroding that framework" [1] (p. ix). While there is no agreement on how emotions influence these decisions, there is a common understanding that expert investors are wired to weigh expected rewards and risks while making financial decisions. We believe that this kind of knowledge, acquired by a combination of formal training and on-the-job experience, is a trait of the brain.

What is interesting about this decision-making process is that it is all about expectations learned from experience, by constantly readjusting these predictions to the actual results [2]. A decision, whether risky or safe, begins with fluctuations of dopamine within the reward circuit [3]. However, to come to a decision, this process must integrate information coming from reward circuits as well as brain regions involved in cognition [4].

Although activity in dopaminergic brain areas has been shown to occur with both immediate and delayed rewards, in 2004, McClure et al. demonstrated that there are two distinct systems involved in choices between monetary reward options available at different moments in time [5]. On the one hand, decisions that entail immediate rewards involve the ventral striatum, the medial orbitofrontal cortex and the medial prefrontal cortex (mPFC) [5], all of which are activated by the receipt of rewards [6]. On the other hand, intertemporal choices of delayed rewards engage the lateral prefrontal cortex (lPFC) and the parietal cortex [5]. These latter areas of the brain are known to be implicated in the control of cognitive functions and goal-directed behavior, including the modulation of working memory information through rewards [7] and the representation of task-reward associations [8].

How, then, do investors choose between different types of rewards? The answer lies in a common scale of values. Thus far, neuroimaging studies in humans have highlighted the ventromedial prefrontal cortex/orbitofrontal cortex (vmPFC/OFC) as the key brain area for representing the subjective values of all reward types on a neural common scale and, to a much lesser extent, the ventral striatum [9]. The most feasible explanation is that the vmPFC computes these values by trading off costs and benefits from the amygdala and the ventral striatum, respectively [10]. Other areas, such as the anterior insula (AIns), engage with rewards by having a negative correlation with increasing anticipated monetary reward [11] as well as a positive correlation, mainly with the anterior cingulate cortex (ACC) when a decision conflict arises between options of competing value [12]. Therefore, the brain appears to be equipped with a unified valuation network to compare between rewards.

On the contrary, risk is determined by the probabilities of possible outcomes, which are estimated by individual perceptions based on previous experiences. How these evaluated probabilities influence investors' decisions depends on the amount of information available (risk) or, rather, the information that is unknown to the investor (ambiguity). Several studies have associated activation between risk and ambiguity with distinct brain areas. Usually, risk activates the insula, the striatum and the parietal cortex, whereas ambiguity involves the lPFC, the mPFC, the cingulate cortex and the amygdala [13].

As opposed to rewards, the scientific community is still hesitant to draw strong conclusions about a unified neural system for evaluating decisions at all levels of uncertainty, despite the fact that the AIns is thought to encode changes in the amount of variability (risk) as well as risk prediction errors [14]. In 2005, Hsu et al. suggested a common neural circuit which was positively activated in the amygdala and the OFC and negatively in the striatum as uncertainty increased [15]. However, in 2019, FeldmanHall et al. ruled out these areas and stated that only the lPFC played a key role in processing high levels of uncertainty [16], despite its correlation with individual ambiguity preferences [17]. Nevertheless, all these areas are involved in the regulation of emotional responses, whether evoked consciously or automatically by the stimulus itself [18,19].

Psychological and neuroscientific research has emphasized that emotions play a role in decision-making, but it remains unclear how they influence risk processing and risk anticipation. Anticipatory effects in distinct neural circuits can impact financial choices [20]. For instance, risky and safe investments are predicted by ventral striatum and anterior insula activation, respectively [21]. It appears as if two parallel processes occur when a person makes an investment choice. On the emotional level, activity in the AIns assesses potential losses, while the thalamus can anticipate regret in the case of loss. On the cognitive level, the dorsomedial prefrontal cortex (dmPFC) evaluates risk by using the information provided by the AIns and the thalamus [22]. To decide, the parietal cortex and the dorsolateral prefrontal cortex (dlPFC) must combine the information about risk with the expected reward obtained from those areas [22].

It is not fully known which neuronal circuits drive investment decisions. An unbiased way to understand what leads a person to make some investments and not others is by using the coordinates reported from all task-related neuroimaging studies to determine brain activation while investing. Our aim is to summarize the structures specialized in responding to investment decision-making by conducting an activation likelihood estimation (ALE) meta-analysis from individual functional magnetic resonance imaging (fMRI) studies that have reported whole-brain analysis results during an investment task.

2. Methods

This meta-analysis was performed according to the PRISMA systematic reviews and meta-analyses guidelines [23].

2.1. Eligibility Criteria

We included studies that analyzed decision-making via investment tasks in healthy human adults without any other restrictions, such as language, publication date or text

availability. Studies were eligible if they included fMRI as the only neuroimaging technique used and if they reported original data from whole-brain analysis results. We excluded all studies whose participants had suffered brain injuries, had any diseases or had disorders. We selected those studies that assessed investment decisions using financial assets. Furthermore, we restricted our selection to peer-reviewed articles.

2.2. Information Sources and Search

Studies were identified in the following electronic databases: WOS, PubMed and PsycINFO. The only filters used were species (humans) and age (adults). The search terms included the following: investment decision making; investment risk taking; investments; financial decisions; financial risk taking; investors; traders; trading (decisions); stock market; stock exchange; portfolio; market bubbles; financial bubbles; brain; and fMRI (see Appendix A for the search strategy using the WOS database).

2.3. Data Collection Process

Information was collected using a spreadsheet under the following headlines: authors, title, year of publication, number of participants, sex, age, stimuli, aim, behavioral results, brain activation and coordinates. If a study reported Talairach coordinates, we transformed them into Montreal Neurological Institute (MNI) space using the icbm2tal algorithm implemented in the GingerALE toolbox (https://www.brainmap.org/ale: available on 7 December 2020).

2.4. Meta-Analysis of Brain Activation Coordinates

GingerALE (version 3.0.2) was used to run the activation likelihood estimation (ALE) algorithm [24–26]. GingerALE meta-analytic software reveals concordant brain regions among the provided imaging studies, using random effects analysis to test the maximum activation probabilities against a null hypothesis of spatially independent activations. Cluster-level family-wise error thresholding at $p < 0.01$ was used to correct for multiple comparisons [27] due to its increased power and compromise between sensitivity and specificity. An initial cluster-forming threshold of $p < 0.001$ (uncorrected) was used, and 1000 permutations were applied.

2.5. Visualization

We used Caret v5.65 software to project the cortical results into a three-dimensional population-average landmark and surface (PALS-B12), using an enclosing voxel algorithm and fiducial mapping [28]. The subcortical slices were generated with in-house Matlab scripts. The ALE values of the meta-analysis were projected with a threshold of 0.0025 for visualizing the trend. Black borders were used to delineate the surviving regions to multiple comparisons.

3. Results

3.1. Study Selection

The search on the WOS, PubMed and PsycINFO databases was conducted from October 2020 to November 2020 and provided a total of 495 studies. Once duplicates had been removed, 350 studies were screened on the basis of titles and abstracts. We discarded 322 articles, as they did not meet the eligibility criteria; 106 studies belonged to a different population (participants with disorders, neurodegenerative diseases and brain injuries, healthy elderly people, adolescents and children), 165 studies did not involve an investment task with financial assets, 28 studies had no original data, and 23 studies used other techniques (electroencephalography, positron emission tomography or transcranial stimulation). Then, the full text of the remaining 28 studies were examined, and 12 studies were excluded due to the fact that they did not report whole-brain analysis results. As a result of the selection criteria, 16 studies were selected for the meta-analysis (Figure 1).

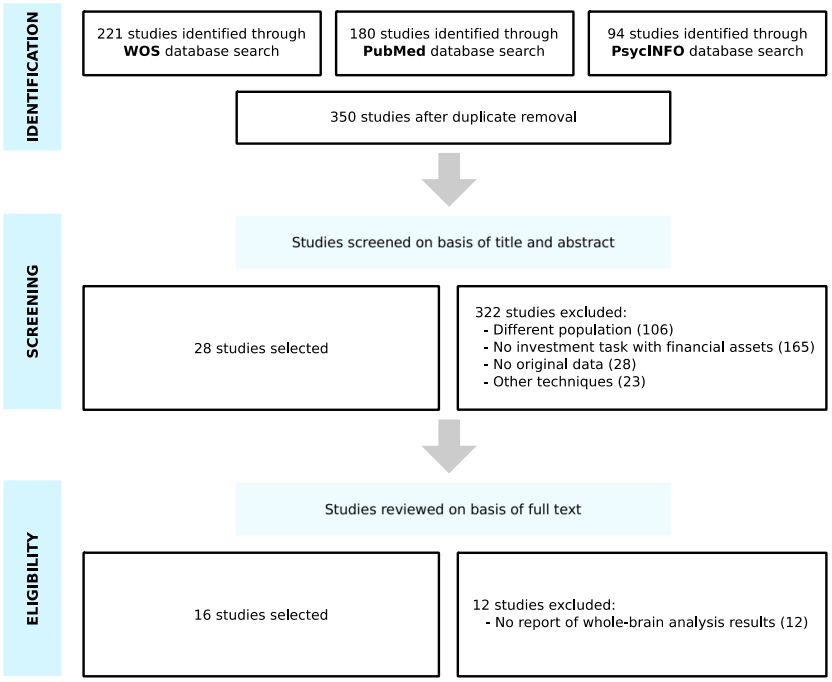

Figure 1. Search flow diagram adapted from PRISMA guidelines.

3.2. Study Characteristics

All articles employed some type of investment decision-making task. Four studies focused on the role that previous investments had on current decisions [29–32], while the rest concentrated on trading tasks.

The information presented was essentially market data. However, three studies also shared social information [33–35], and one included the responses from a computer partner as a control condition [36]. Only one study presented the stimuli under gain and loss domains [37], whereas three studies used market bubble conditions [38–40].

Eight studies focused on certain cognitive processes while choosing between investments, including sunk costs [30,31], disposition effects [41] and prediction errors [36,42,43].

Some studies included other behavioral tests with the same participants whose brains were being scanned. For example, questionnaires were conducted on the future time perspective [39], eye gaze [40] and self-assessment questions [37].

The included studies involved 594 healthy adults without any real-life experience in investing, except for one study [37]. Two studies included only males [37,40], and two did not report the sexes of the participants [29,35].

All sixteen studies were conducted with fMRI and were published between 2005 and 2018.

3.3. Study Results

Regarding studies with prior investments, it has been demonstrated that previous investments affect current decisions, making people more prone to continue investing. This is related to higher activation not only in the prefrontal and parietal cortices [29–31], but also in the anterior insula, due to its role in risky decision-making [29,32]. This latter brain area, along with the ventral striatum, has been repeatedly found to be active in tasks involving trading decisions [21,34,36–38,41–43].

Studies which included social information reported a higher activation in the ventral striatum when investors decided to follow herd buying behavior [34], as well as in the paracingulate cortex while forecasting price changes [35]. On the contrary, overweighting private information involved activity in the inferior frontal gyrus, the anterior insula [33] and the ACC to resolve social conflicts that arose from going against the group [34]. However, this does not apply if the information is non-human [34,36]. In the study on

gain and loss domains, only the former, along with the anterior insula, could be related to real-life experience in trading stocks [37]. With respect to market bubble conditions, higher levels of nucleus accumbens (NAcc) and vmPFC activity [38,40] and dlPFC and inferior parietal lobule connectivity [39] indicate a propensity to ride bubbles and lose money.

Investment decisions can be affected by certain cognitive processes, such as higher sunk costs translating into more risk-taking behaviors in the lateral prefrontal and parietal cortices [30,31]; a higher disposition effect lowering ventral striatum activity because investors held onto losing assets longer [41]; fictive errors driving investment behavior through increased activity in the ventral striatum [36,43]; and decreased activity in anterior insula and anterior insula-amygdala connectivity when reappraisal strategies regulated negative feelings [42].

Studies with behavioral tests linked the estimation of future prices with activation in the inferior parietal lobule and future time perspective scores [39]; the ability to infer other investors´ intentions with signal changes in the dmPFC and eye gaze scores; and beliefs and preferences toward risk (risk optimism index and risk tolerance index) with activation in the anterior insula and real-life trading experience [37].

3.4. Meta-analysis of Brain Activation Results

Figure 2 and Table 1 display the results of the ALE meta-analysis we conducted. The four clusters we found were (1) ventral striatum + amygdala + anterior cingulate cortex; (2) the ventral striatum; (3) the anterior insula; and (4) the occipital cortex. Table 2 shows the characteristics of the studies included in the meta-analysis with the clusters reported by each study.

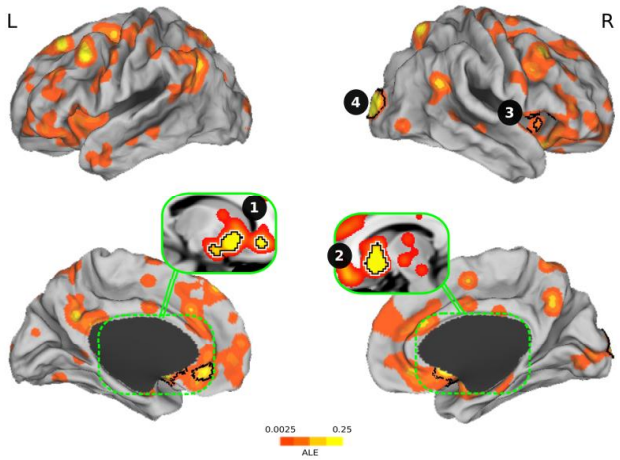

Figure 2. Overview of significant clusters resulting from the activation likelihood estimation (ALE) meta-analysis regarding investment decision-making. The four clusters found during risky and safe investments were (1) ventral striatum + amygdala + anterior cingulate cortex; (2) the ventral striatum; (3) the anterior insula; and (4) the occipital cortex. The clusters corrected for multiple comparisons are outlined in black. L = left, R = right.

Table 1. Significant clusters of the meta-analysis surviving to multiple comparisons.

Cluster #	Brain Areas	Size (mm^3)	Center Coordinate	Peak Coordinate	ALE	*P*	Z
1	Ventral striatum + amygdala + ACC [1]	6360	(−11.8, 13.3, −7.8)	(−10, 16, −4)	0.0439	$p < 0.0001$	6.59
2	Ventral striatum	3976	(11.2, 13.1, −5.8)	(10, 14, −6)	0.0748	$p < 0.0001$	9.44
3	Anterior insula	2048	(22.6, −95.3, 8.8)	(22, −96, 8)	0.0611	$p < 0.0001$	8.24
4	Occipital cortex	1544	(49.1, 18.6, −3.9)	(54, 16, −4)	0.0303	$p < 0.0001$	5.11

[1] ACC = anterior cingulate cortex.

Table 2. Investment decision-making studies included in the meta-analysis.

References	Stimuli	Brain and Behavioral Results	Cluster #
Kuhnen et al., 2005	Two stocks (one good and the other bad) and a bond	Anticipatory nucleus accumbens activity preceded risky choices, and excessive levels of activation led to risk-seeking mistakes. Anticipatory anterior insula activity preceded riskless choices, and excessive levels of activation led to risk-aversion mistakes.	1 2
Lohrenz et al., 2007	Market information in live and not live conditions, gains and losses, portfolio value and percentage already invested	Higher levels of ventral caudate activity correlated with fictive error signals, driving investment behavior.	1 2 3
Mohr et al., 2009	Streams of 10 past returns from an investment	Risk and value are represented in the brain during investment decisions in discrete (simple gambles) and continuous distributions (stocks). Risk–return models support the correlation between risk and anterior insula activation.	1 4
Bruguier et al., 2010	Replay of market experiment sessions (order and trade flow) with and without insiders	Theory of mind is involved in forecasting price changes in markets with insiders and related to increased activation in the paracingulate cortex.	
Burke et al., 2010	Stock information and social information (four human faces or four chimpanzee faces)	Higher levels of ventral striatum activity correlated with the participants´ likelihood to follow herd behavior, especially in the number of buying decisions. Going against the group involves activity in the anterior cingulate cortex to resolve the conflict.	1 2
Brooks et al., 2012	Purchase prices and asset prices (random walk)	The irrational belief in mean reversion better explains the disposition effect. Participants with a large disposition effect exhibited lower levels of ventral striatum activity in response to upticks in value when the asset price was below the purchase price.	1 2 3
De Martino et al., 2013	Portfolio value and trading prices (asks and bids) in bubble and non-bubble markets	The evaluation of social signals in dorsomedial prefrontal cortex activity affects value representations in the ventromedial prefrontal cortex. Higher levels of ventromedial prefrontal cortex activity predict an investor's propensity to ride bubbles and, therefore, lose money.	
Zeng et al., 2013	Amounts already invested in a company´s project where sunk costs and incremental costs are manipulated	Higher levels of lateral frontal and parietal cortex activity are related to higher sunk costs and more risk-taking behavior. Higher levels of striatum and medial prefrontal cortex activity are linked to smaller incremental costs and continued investing.	
Lohrenz et al., 2013	Market data and social information (other players´ bets)	Interpersonal fictive errors guide behavior and highly correlate with striatum activity.	1 2
Ogawa et al., 2014	Stock and asset information in a virtual stock exchange with two non-bubble stocks and one bubble stock	In market bubbles, brain networks switch toward dorsolateral prefrontal cortex and inferior parietal lobule connectivity, in which buying decisions are made in the former based on the information gathered by the latter region. Cash holdings were positively correlated with activation in the ventromedial prefrontal cortex, while trading during large price fluctuations were associated with superior parietal lobule activity.	

Table 2. *Cont.*

References	Stimuli	Brain and Behavioral Results	Cluster #
Smith et al., 2014	Trading prices of risk-free and risky assets (stocks) in markets where endogenous bubbles are formed and crash	Higher levels of nucleus accumbens activity are associated with buying decisions, lower earnings, and increased likelihood of a crash. Higher levels of anterior insula activity are correlated with selling decisions before the price peak and higher earnings.	1 2
Haller et al., 2014	Project costs and success probabilities	Higher levels of dorsolateral prefrontal cortex and lower levels of ventromedial prefrontal cortex activity are related to higher sunk costs and being prone to continue investing in previous investments.	1 2
Gu et al., 2014	Market prices where choices are made under two conditions: regulate and attend	Only fictive errors are susceptible to reappraisal strategies by changes in activation in anterior insula and anterior insula–amygdala connectivity, modulating subjective feelings that affect behavior directly.	1 3
Huber et al., 2015	Two stocks with social (decisions made by two fictitious traders) and private information (personal recommendation from a rating agency)	Higher levels of inferior frontal gyrus/anterior insula activity and lower levels of parietal-temporal cortex activity are correlated with overweighting private information, which can influence the probability in the formation of informational cascades.	2
Majer et al., 2016	Past returns of investments and investment choices with fixed or risky returns	Higher levels of anterior insula and dorsomedial prefrontal cortex activity correlated with risk and decision-making.	
Häusler et al., 2018	Stocks (risky option) and bonds (non-risky option) in gain and loss domains	Lower levels of anterior insula activity are connected to risky decisions in real-life stock traders. These choices are based on personal beliefs about risky choices and the willingness to bear risk.	1 3

4. Discussion

It is not surprising that the first three clusters we found included areas of the brain that are closely related to the expectation of reward and risk, as investments are based on risk–return tradeoffs. The fourth cluster, the occipital cortex, is activated during investment decisions as market information gathered via computers is perceived through the visual pathway. Nevertheless, while investors consider the need to control their emotions in order to not interfere with their investment decisions, these same brain regions are also involved in emotions when assessing the value of environmental stimuli. Although areas such as the vmPFC/OFC did not survive multiple comparisons, Figure 2 shows that there was a tendency, which confirmed a role of these regions in investment decision-making, probably as a common scale of values. These results lead us to believe that investment choices are emotional decisions.

Generally, perceived risks (AIns) and risk attitudes (lateral OFC) seemed to affect the value of the chosen investment (dlPFC and amygdala) [32]. Prior to deciding, value was correlated with mPFC, lPFC and posterior cingulate cortex activity [32], whereas distinct neural circuits involving the nucleus accumbens (NAcc) and the AIns seemed to promote risk-seeking and risk-averse choices, respectively [21] (Figure 3). However, while excessive activation in these areas may cause investment mistakes [21], reduced activation could lead to a learning process in which emotion regulation in fictive error signals (i.e., what might have happened) could guide valuation and choice [42] (Figure 3). These differences between actual returns and returns that could have been experienced if decisions had been diverse also drive investment behavior through significant ventral caudate and posterior parietal cortex activation [43] (Figure 3).

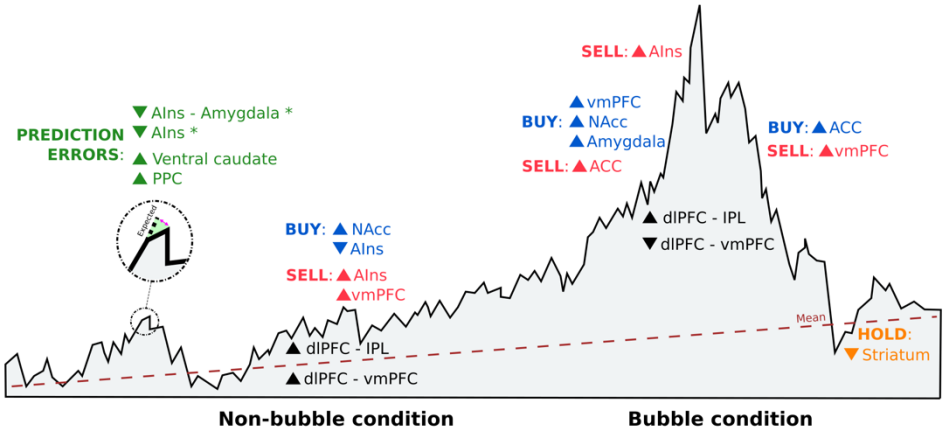

Figure 3. Schematic representation of brain activation reported in the ALE meta-analysis study during investment decision-making. Sell orders are shown in red, buy orders are in blue, and neither sell nor buy orders (hold) are in orange. Each order is accompanied by increased (▲) or decrease (▼) neural activity in certain brain areas. Prediction errors appear in green, where (*) indicates that reappraisal strategies were implemented. The location of each activation in the figure is based on the situation of the market, being under bubble or non-bubble conditions. Black indicates brain connectivity activation under both market conditions. AIns = anterior insula; PPC = posterior parietal cortex; NAcc = nucleus accumbens; vmPFC = ventromedial prefrontal cortex; ACC = anterior cingulate cortex; dlPFC = dorsolateral prefrontal cortex; and IPL = inferior parietal lobule.

Seeking environmental validity for these results, we found an attempt to connect real-life financial behavior with brain activation during an investment task. Häusler et al. [37] demonstrated that choosing between a stock and a bond involved differences in brain activation in the AIns (Figure 3). Active stock traders showed lower AIns activation when choosing the risky option (stock) compared with those who did not trade in real life [37]. This may be due to individual differences in risk attitudes [29] and the way in which investors perceive risks [32]. Therefore, this difference was not based on cognitive abilities

or financial constraints, but rather mediated by individuals´ preferences and beliefs about risky financial choices [37].

In financial markets, prices are determined by the interacting decisions of many investors. Inferring other agents´ intentions while making value judgments can lead to an increase in prices above their fundamental values, causing a market bubble. Under these conditions, social signals activate the paracingulate cortex [35] and the dmPFC [40], which affect value representations in the vmPFC [40], an area known to be associated with asset preferences [39,44]. This increased sensitivity in the vmPFC toward other investors´ intentions makes activity in this brain area a predictor of the tendency to ride bubbles [40] (Figure 3). Although investors can be predisposed to buying stocks in market bubbles, the vmPFC has also been found to correlate with cash holdings [39], probably due to its activation after monetary gains [21]. Nonetheless, functional connectivity in the vmPFC decreased as bubbles gave way to an increase in dlPFC–inferior parietal lobule (IPL) connectivity (Figure 3), since supportive information is required from the IPL to estimate future stock prices so that the dlPFC can decide [39].

Another brain area that is thought to track bubble magnitude, responding to both buying and selling outcomes, is the NAcc [38]. Increased NAcc activity is associated with lower returns [38], given the propensity to buy risky assets [21] in subsequent trading periods (Figure 3). By contrast, if the activity occurs in the AIns, it will serve as a risk detection signal that will result in higher earnings, due to a higher propensity to sell before the bubble reaches its peak [38] (Figure 3).

While there is no universally acknowledged explanation of how bubbles form, it is known that herd behavior often causes higher volatility in the stock markets [45], both up and down, as investors decide to get in or out at the same time. The reason for this behavior is that when faced with uncertainty, investors tend to imitate the actions of others. Activity in the ventral striatum is influenced by social information on other investors' decisions, making one´s decision to buy or reject more in line with the stock bought or rejected by the herd [34], even when there is no advantage in doing so [36]. One feasible reason is that the striatum engages in prediction error signals, helping us learn the value of different options [36]. Aligning with the group also activates the amygdala [34], which may reflect a social learning process [46], and the middle cingulate cortex due to its sensitivity in identifying oneself with other investors´ behaviors [36]. However, if investors do not base their decisions on the behavior of others and act against the group, activity in the ACC increases to solve the social conflict that arises [34] (Figure 3). This would imply that investors update their beliefs by overweighting private information instead of social information, which results in higher activation of the inferior frontal gyrus–AIns and lower activation of the parietal-temporal cortex, areas known to be associated with risk and uncertainty [33].

It is evident that information can alter financial decision-making, especially if prior investments have been made. Throwing good money after bad in order to avoid realizing certain losses is a cognitive bias that investors are sensitive to. This effect, known as sunk costs, demonstrates that the amount of money that has already been allocated affects the decision of whether to continue an investment or not. When sunk costs are higher, activity in the lPFC, the parietal cortex [31], the amygdala and the ACC increases [30], given the desire to not appear wasteful [47]. At the same time, investors stop tracking the expected value of new investments to focus on previous investments to guide their current decisions so that the participation of the vmPFC and the NAcc in this decision process is considerably diminished, thereby making them prone to continue investing [30]. It has been found that there is a strong negative connectivity between the dlPFC and the vmPFC after an investment is made as a way to not waste resources while overriding the commonly expected value-based decision-making [30].

According to Kahneman and Tversky [48], aversion to loss realization is one of the reasons why investors fall into sunk costs, a fallacy that may strengthen the disposition effect. The disposition effect is a behavior which leads investors to "sell winners too early

and ride losers too long" [49], based on an irrational belief in mean reversion [41]. There is a negative correlation between the disposition effect and ventral striatum activity related to rises in asset prices [41] (Figure 3). Expecting a return to the mean could be the reason behind an attenuated striatal response to upticks in value below the purchase price [41], given that dopamine neurons respond more strongly to unpredicted rewards [2].

There are three main limitations to this review. The first limitation comes from a small sample size, considering that neuroeconomics is still a new field and most of the studies to date have focused on specific regions of interest instead of whole-brain analysis. The second limitation arises from the different stimuli and aims used in all investment decision-making tasks. For example, some studies have presented stimuli in a moving display or used live trading, which resemble more closely what happens in real-life financial decisions, as opposed to static stimuli trying to evoke actual dynamic markets. The third limitation derives from the lack of active stock traders as participants, except for the study by Häusler et al. [37], given that environmental factors can shape individual financial decisions.

5. Conclusions

Investment decisions can overwhelm the brain. Trying to make sense of all information that financial markets convey while listening to one´s emotions without being overridden by them involves a coordinated effort of several brain areas in order to reach a decision. Since the question of how investors make decisions has not yet been fully uncovered, the aim of this meta-analysis is to determine the convergence of brain regions necessary for this complex decision-making process. Based on our ALE meta-analysis results, investment decisions involve limbic areas that ponder reward vs. risk, as investment portfolios are built on trying to achieve an optimal balance between return and risk. Emotions toward these two concepts, and the emotional conflicts that can arise while prioritizing among them, are an influential factor that guide this decision process. As Benjamin Graham has noted, "individuals who cannot master their emotions are ill-suited to profit from the investment process." Despite the four clusters found, we believe that investment decisions are not limited to those areas alone. In the stock market, aspects such as when to buy or sell, the market conditions or even the way in which other investors behave can affect whether an investment will result in being profitable or not. As Warren Buffet once advised, "be fearful when others are greedy and greedy when others are fearful." Every investor knows how to be fearful and greedy, but what they truly need to discover is when the right time to be one or the other is. The same investment behavior and the same brain activation could lead to different yields depending on the moment. Determining the role of a specific brain area in this decision-making process is indeed a complicated endeavor. Herein lies the difficulty in understanding how investors make decisions. Given the scarce literature, future studies should continue addressing this decision-making process while including whole-brain analysis in their methods.

Author Contributions: E.O.-T. searched in all databases using the terms cited above to identify all fMRI investment decision-making studies in healthy adults. Titles were screened by E.O.-T. to remove duplicates. E.O.-T. and I.D. independently assessed the studies by title and abstract to exclude all articles that did not meet the eligibility criteria. Full text articles were reviewed independently by E.O.-T. and I.D. based on the inclusion and exclusion criteria. In case of disagreement, E.O.-T., I.D. and J.L.-P. had to reach a consensus. E.O.-T., I.D. and J.L.-P. wrote and reviewed the entire manuscript. All authors have read and agreed to the published version of the manuscript.

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Appendix A

Search strategy using the WOS database:

Financial decisions AND fmri

(Search results: 94)

Financial risk taking AND fmri

(Search results: 29)

Investments AND fmri

(Search results: 75)

Stock market AND fmri

(Search results: 8)

Trading AND investors AND brain

(Search results: 12)

Market bubbles AND fmri

(Search results: 3)

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Chapter 3

Neural implications of investment banking experience in decision-making under risk and ambiguity

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Neural Implications of Investment Banking Experience in Decision-Making Under Risk and Ambiguity

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Financial decision-making is governed by cognitive and emotional processes. However, it is possible to learn how to manage both before making a decision based on experience. Electroencephalography might provide some insight into what is behind these choices by analyzing the slow negativity preceding a risky decision, known as the decision preceding negativity (DPN). The DPN is involved in cognitive processes associated with the elaboration of the planned response as well as the anticipation of the affective motivational stimuli. Using monetary gamble under risk (outcome probabilities are known) and ambiguity (outcome probabilities are unknown), we studied the DPN in a group of investment bankers, to see if individual financial experience influences anticipatory potentials that precede choices. Our results showed that investment bankers are able to shorten their anticipatory decision-making process by having a DPN closer to motor response. As this occurs, the prefrontal and orbitofrontal brain areas under risk were activated due to the role that emotions play in financial decision-making. On the other hand, under the ambiguity condition, activation of the prefrontal areas was caused by cognitive regulation of emotion. Our conclusion is that financial experience also influences risky choices by shortening the decision-making process while balancing cognitive and emotional processes, which depend on the amount of missing information.

Keywords: financial decision-making, lateral and medial prefrontal cortex, orbitofrontal cortex, emotional regulation

According to Bossaerts (2009),

> financial decision making is the outcome of complex neurophysiological processes involving, among others, constant re-evaluation of the statistics of the problem at hand, balancing of the various emotional aspects, and computation of the very value signals that are at the core of modern economic thinking. (p. 383)

First, these complex neurophysiological processes are due to how the brain distinguishes between risk and ambiguity (Hsu, Bhatt, Adolphs, Tranel, & Camerer, 2005) and how it encodes risks and rewards separately (Bossaerts, 2009). Second, decision-making is supported by emotions that significantly influence our reasoning processes (Bechara, Damasio, Tranel, & Damasio, 1997) in real-time analysis of financial risks (Lo & Repin, 2002) through risk perception and risky decision-making (Dillenberger & Rozen, 2015; Loewenstein, Weber, Hsee, & Welch, 2001). Emotions form part of value computation, which is within our control (Sokol-Hessner, Camerer, & Phelps, 2013), and is important because changing emotions can

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change choice (Phelps, Lempert, & Sokol-Hessner, 2014). Third, the computation of value signals, which the brain constructs when subjects make economic choices (Padoa-Schioppa, 2011), is "not merely retrieved from memory, but recomputed every time" (p. 397; Bossaerts, 2009).

Neural activity related to decision-making under risk, ambiguity, and financial risk-taking has been found in several brain areas, including the orbitofrontal cortex (OFC; represents value and is associated with reward-seeking behavior), the amygdala (reacts to emotional information), the dorsolateral prefrontal cortex (dlPFC; manages cognitive control), the ventromedial prefrontal cortex (vmPFC; represents value), the ventral striatum (represents value prediction errors and anticipation of monetary gains), and the inferior frontal gyrus (risk signals and risk aversion), among others (Bossaerts, 2009; Camerer, 2013; Padoa-Schioppa, 2011; Hsu et al., 2005; Kuhnen & Knutson, 2005). The OFC, the amygdala, and the dorsomedial prefrontal cortex are more active when a person is making decisions under ambiguous conditions (Hsu et al., 2005). In addition, the representation of subjective values takes place within the prefrontal regions, precisely in the OFC and the vmPFC (Padoa-Schioppa, 2011).

Financial decision-making may require the activation of distinct circuits to take or avoid risks (Kuhnen & Knutson, 2005), as applications such as risk limits, portfolio optimization, and trader performance-based compensation depend on the measurement of risk (Holton, 2004). Professionals working within the field become familiar and comfortable dealing with risk and are ready to make quick decisions when necessary (Buehler, Freeman, & Hulme, 2008). Financial experts know how to accurately calculate risks and what factors cause risks (Fischhoff & Kadvany, 2011) because they assess them by training their mind to run "what-if" scenarios (Smith, Sanchez, & Lawrence, 1996). Due to this, they reduce and control risks, therefore showing less emotional responsiveness over the years (Lo & Repin, 2002). As a result, risk analysis is an exercise of judgment based on risk perceptions shaped by experience.

Learning and experience are factors that streamline decision-making processes by reducing event-related potential (ERP) latencies (Nakamoto & Mori, 2012). Nonetheless, there is no general agreement about the effect of expertise on decision-making due to ambiguous results (Lambert, Bessière, & N′Goala, 2012). Electroencephalography (EEG) might provide some insight into what is behind these decisions, considering that individual experience influences anticipatory potentials that precede risky choices (Bianchin & Angrilli, 2011). Albeit, only a few investigations have delved into the anticipatory components of decision-making (Breiter, Aharon, Kahneman, Dal, & Shizgal, 2001; Fukui, Murai, Fukuyama, Hayashi, & Hanakawa, 2005) and even fewer into the negative ERPs closer to motor response, such as negative shift potential (Duncan et al., 2009; Ortiz, Goodin, & Aminoff, 1993) or decision preceding negativity (DPN; Bianchin & Angrilli, 2011). DPN is the last pronounced slow negative potential before a willed risky decision (Bianchin & Angrilli, 2011).

Using EEG, the volunteers' brain activity was recorded while playing a monetary game under risky and ambiguous conditions. Our research focuses on the processes that precede gambling decisions in both conditions with a group of investment bankers (IB) by investigating the immediate slow negative potential that precedes motor response. The analysis of the EEG data focused on DPN latencies and its shortening, as well as the interaction of prefrontal and orbitofrontal brain areas related to cognitive and emotional processes due to their financial experience.

Method

Sample

Thirty-one healthy volunteers, 16 IBs (12 men and four women of mean age 32.75 ± 6.914 years) and 15 controls (10 men and five women of mean age 34.07 ± 6.250 years), were studied. Two volunteers reported being left-handed (one from each group). The rest were all right-handed. The investment banking group volunteers were chosen by the Chartered Financial Analyst Institute Spain and the Instituto de Estudios Bursátiles Spain, whereas volunteers from the control group worked in different disciplines, except finance. All volunteers had a similar education level, cultural characteristics, and no history of neurological illness, psychiatric disorders, or substance abuse. All volunteers

provided written informed consent and were in full compliance with the Declaration of Helsinki. The study was conducted with the approval of the Ethics Committee of the Rey Juan Carlos University.

Experimental Task

The study consisted of sequential presentation of two types of stimuli: risk and ambiguity (Wang, Zheng, Huang, & Sun, 2015). Both stimuli displayed a monetary value, which was a random number between 40 and 200. The probability of gain and loss was shown together with the risk stimuli, but it was concealed with the ambiguity stimuli. The two conditions were presented in a random order, each occurring 50% of the time (114 risk stimuli and 114 ambiguous stimuli). Risk and ambiguity stimuli had three probabilities (0.25, 0.50, and 0.75; 38 stimuli each). The duration of both stimuli was 2,000 ms, followed by the outcome for 500 ms (Figure 1). They were informed to respond exclusively when they chose to bet ("gambling decisions"). The total duration of the task was 9.5 min.

Procedure

Volunteers were tested on an individual basis in a small, dimly lit room. Subjects sat in an armchair, 1 m in front of a 19" LCD screen (refresh rate = 100 Hz) that displayed the stimuli, and were provided with a motor response device connected to the EEG amplifiers to monitor their answers. They were instructed to keep their eyes open, blink as little as possible, and avoid sudden movements.

Electrophysiology System

High-density EEG recordings were obtained using a custom-designed 128-channel electrode Neuroscan cap with an ATI-Pentatek EEG system (Advantek SRL CABA, Argentina). Data were processed to an average reference following acquisition with a bandpass filter of 0.05–30 Hz and a sample rate of 512 Hz. Impedances were kept under 5 kΩ. We used electrodes in both mastoids as online references. Noisy channels were replaced with linear interpolations from clean channels sparingly. DPN latency around 150 ms before motor response was obtained separately for each condition and each subject by the last negative wave closest to motor response at the Cz electrode (Figure 2).

Motor Response

The motor response was recorded continuously from a channel that connected the EEG amplifiers to a device placed in the right hand of

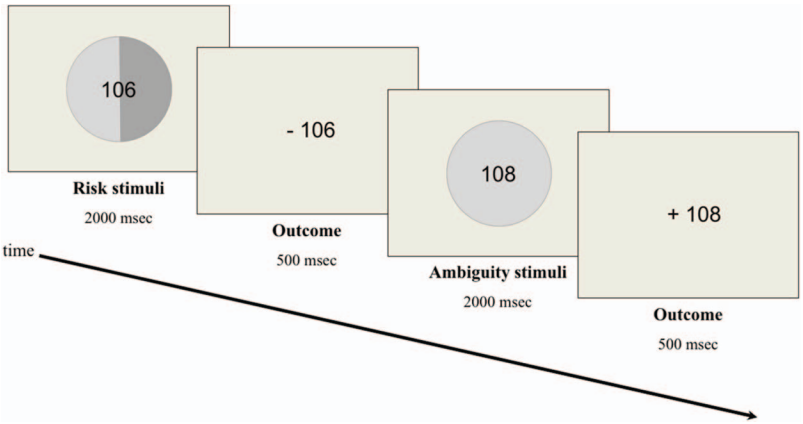

Figure 1. Decision-making task. Risk stimuli were represented as a pie chart with the probability of winning (dark gray) or losing (light gray) all the money that appeared in the center of the chart. This was followed by either a positive outcome (winning) or a negative outcome (losing). Same for the ambiguity stimuli, with the exception that no probabilities were shown and the pie chart appeared all in light gray color. See the online article for the color version of this figure.

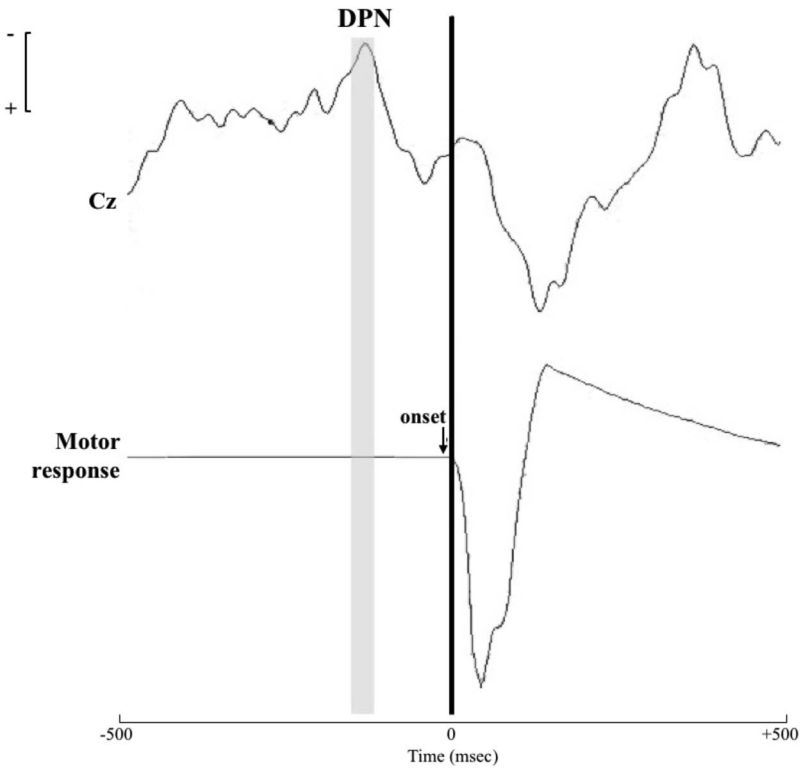

Figure 2. Example of motor response-synchronized cerebral evoked potentials. Decision preceding negativity (DPN) from the Cz scalp location and motor response from pressing a button with the right index finger.

the volunteer. The data were analyzed off-line by alignment of both cerebral and motor response channels on each stimulus of the task. Motor response was defined by the positive deflection when the subject pressed the button on the device (Figure 2). We measured response times from onset stimuli as well as the number of gambling decisions for each condition.

Source Localization Reconstruction

The sources of the DPN component were estimated from 123 electrode recordings in the 31 volunteers and located through the solution of the EEG inverse problem using the Bayesian model averaging (BMA) approach (MacKay, 1992; Penny, Mattout, & Trujillo-Barreto, 2007; Trujillo-Barreto, Aubert-Vázquez, & Valdés-Sosa, 2004), and individual models were solved with low-resolution electromagnetic tomography (Pascual-Marqui, Michel, & Lehmann, 1994). The BMA analysis was done by opening a time window of −20 to + 20 ms, starting from the highest negative amplitude peak measured in the Cz electrode (Figure 2). The primary current density was estimated, using the BMA method described earlier, for each subject's DPN component in the two conditions. Statistical parametric mapping was used to make population-level inference over the calculated sources of the DPN. Subsequently, statistical parametric mappings were computed based on a voxel-by-voxel independent Hotelling's *T*-squared test to estimate the statistically significant sources for DPN for risk and ambiguity conditions between groups. The resulting probability maps were thresholded at a false discovery rate q ¼ 0.05 (Lage-Castellanos, Martínez-Montes, Hernández-Cabrera, & Galán, 2010) and were depicted as three-dimensional activation images overlaid on the Mon-

treal Neurological Institute average brain (Evans et al., 1993). Anatomical structures according to the anatomical atlas label (Tzourio-Mazoyer et al., 2002) and Brodmann areas were identified, and local maxima were measured and located according to the Montreal Neurological Institute coordinate system.

Statistical Analyses

Kolmogorov–Smirnov and Shapiro–Wilk tests were used to assess the normality of all variables of a continuous nature, age, response times, and latencies, in both groups. Homogeneity for the IBs and controls at baseline was analyzed using the two-sample t test (age) and the chi-squared test (gender). Pearson correlation coefficients were used to examine the relationships among response times, latencies, and number of gambling decisions, in each group and condition. To explore possible underlying interactions, a repeated-measures analysis of variance (ANOVA) was used to investigate condition and group effects. The between-subjects factor was group (IB and control), whereas the within-subjects repeated measures were DPN latency, response times, and gambling decisions in each condition (risk and ambiguity). Statistical analyses were performed using the SPSS 22 statistical package.

Results

Kolmogorov–Smirnov and Shapiro–Wilk tests showed that all variables satisfied the normality assumption in both conditions (both $p >$ .15). This includes the number of gambling decisions.

Homogeneity for the Investment Bankers and Controls at Baseline

None of the comparisons between demographic variables reflected statistically significant differences between groups. Results for age and gender were respectively, $t(29) = -0.555$, $p = .583$, and $\chi_1 = 0.261$, $p = .609$.

Decision Preceding Negativity Latencies, Response Times, and Gambling Decisions

A preliminary question must be analyzed; it refers to the appropriateness or efficacy of repeat univariate ANOVAs for different variables, gambling decisions, response times, and DPN latencies, but with the same subjects. A multivariate generalized linear model would be the right choice, if it was not for the small sample size, 16 and 15 per group. Moreover, there was no empirical evidence of relationship between these variables in our data: A previous Pearson correlation analysis between these variables, in each group and condition, showed the low linear relationship between them. Only correlation between response times and DPN latencies was significant in the risk condition for the control group, with $r = -0.611$ and $p = .016$. For the remaining comparisons, p values $>.3$ were obtained. Therefore, the analysis of each variable separately seemed more reasonable. The analysis was carried out using a repeated-measures ANOVA for each variable. As a general result of the analyses, we can emphasize the statistical significance of the three effects, condition, group, and group $\times$ condition interaction, in the three variables.

Decision Preceding Negativity Latencies

When the plot of the means for DPN latencies was analyzed (Figure 3A), it appeared that the IB and control groups exhibited divergent behavior when the condition changes. The three effects were significant, condition ($p = .004$), group ($p < .001$), and group $\times$ condition interaction ($p = .003$).

Statistical analysis highlighted the significant differences between DPN latencies in both groups, $F(1, 29) = 6.453$, $p = .017$ in the risk condition and $F(1, 29) = 32.125$, $p < .001$ in the ambiguity condition. The 95% confidence intervals for both differences, control–IB, are, respectively, [4.28, 39.68] and [50.48, 107.48]. Finally, there were also significant differences between DPN latencies in both conditions in the control group, $t(14) = 3.98$, $p = .001$, with 95% confidence interval, ambiguity–risk, [25.82, 86.18].

Response Times

When the means of response times were plotted (Figure 3B), it seemed that the IB and control groups exhibited a similar behavior when the condition changes. Now, only group $\times$ condition interaction ($p = .035$) was significant. Statistical analysis highlighted the significant differences between response times in both conditions in the IB group, $t(15) = 4.019$, $p = .001$. The 95% confi-

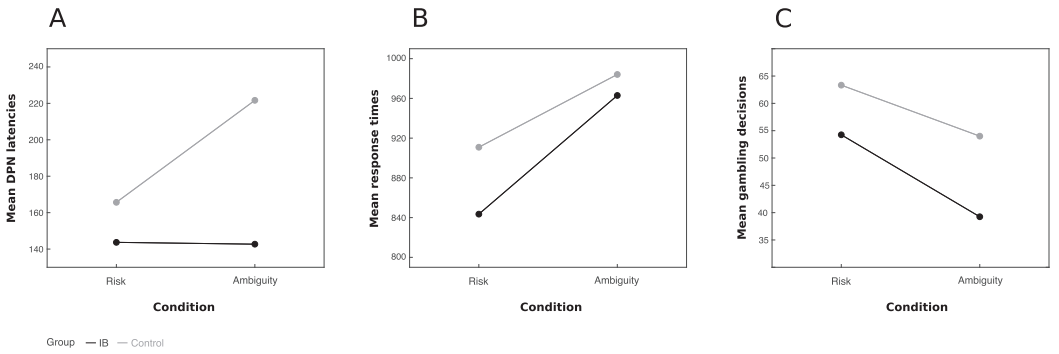

Figure 3. Standardized means plot of decision preceding negativity (DPN) latencies (A), response times (B), and gambling decisions (C) according to groups (investment bankers [IB] and controls) and conditions (risk and ambiguity).

dence interval for the mean difference of response times, ambiguity-risk, was [56.11, 182.82].

Gambling Decisions

Finally, Figure 3C shows the plot of the means for gambling decisions. Now, group ($p = .042$) and group × condition interaction ($p = .016$) were significant. There are significant differences, in the IB group, between gambling decisions in both conditions, $t(15) = 2.983$, $p = .009$, with 95% confidence interval, risk–ambiguity, [4.28, 25.72].

Source Localization

Using independent Hotelling's *T*-squared test, we found significant differences in brain activation in frontal areas in the IB group during both conditions. In the control group, those activations were located in temporal and superior medial frontal areas during the ambiguity condition (Table 1 and Figure 4).

Discussion

Our results support the hypothesis that IBs are able to shorten their anticipatory decision-making process by having a DPN closer to motor response in gambling decisions under risk and ambiguity due to their financial experience. In the risk condition, prefrontal and orbitofrontal brain areas were activated, confirming the idea that emotions have a role in

Table 1
Summary of Statistically Significant Differences in Maximal Intensity Projection Areas (Independent Hotelling's T-Squared Test) at $p < .05$

AAL	BA	MNI coordinates			T^2 Hotelling's test $df = 3, 29$; univariate $p < .05$	IB vs. C
		X	Y	Z		
Risk						
Frontal middle L	46	−30	46	12	12.69620037	IB > C
Frontal superior orbital R	11	10	63	−20	10.95732975	IB > C
Frontal middle orbital R	10	2	50	−6	10.47997475	IB > C
Frontal middle R	45	46	43	5	10.30744839	IB > C
Ambiguity						
Frontal inferior opercular L	48	−54	14	0	13.18717003	IB > C
Frontal superior medial L	10	−2	64	20	10.85658455	IB > C
Temporal pole superior L	38	−58	6	−7	10.39766312	IB < C
Frontal superior medial R	10	3	62	12	9.64823246	IB < C

Note. AAL = anatomic label corresponding to probabilistic brain atlas; BA = Brodmann areas; X, Y, Z = Montreal National Institute coordinates; L = left; R= right; IB= investment bankers; C= controls. IB versus C indicates which group has higher activation in each brain area.

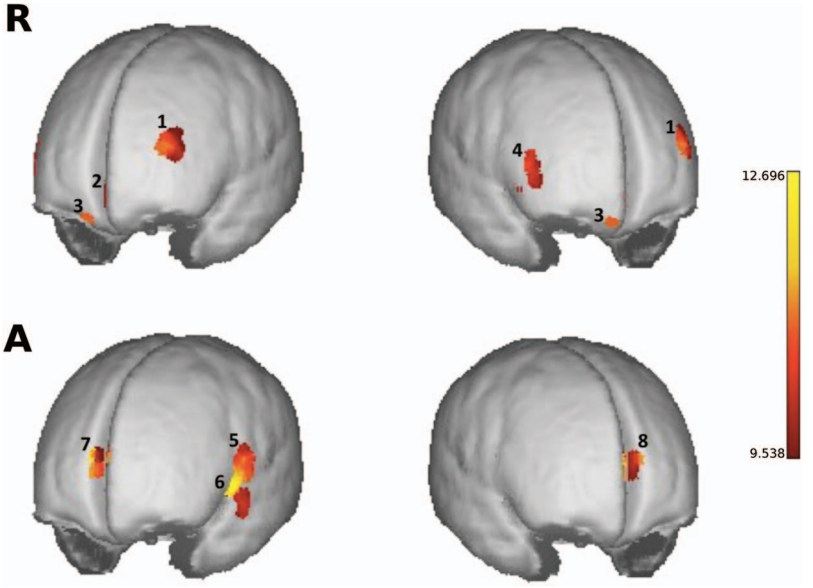

Figure 4. Statistical mapping using independent Hotelling's *T*-squared test showing significant differences in maps between investment banker and control groups in decision preceding negativity latencies at $p < .05$ from results in Table 1. R = risk; A = ambiguity; (1) = frontal middle left; (2) = frontal middle orbital right; (3) = frontal superior orbital right; (4) = frontal middle right; (5) = frontal inferior opercular left; (6) = temporal pole superior left; (7) = frontal superior medial right; (8) = frontal superior medial left. See the online article for the color version of this figure.

financial decision-making, whereas under the ambiguity condition, only the prefrontal areas were activated, thus indicating a more logically reasoned behavior due to cognitive regulation of emotion.

Risk Condition

In the risk condition, the DPN of the IB group was significantly closer to motor response (Figure 3A). Considering that most risk analyses are managed quickly (Slovic, Finucane, Peters, & MacGregor, 2004) when they occur in daily life, learning and experience are factors that streamline decision-making processes by reducing ERP latencies (Nakamoto & Mori, 2012).

We found activation of brain areas related to cognitive and emotional processes in the IB group (Table 1 and Figure 4). All lateral prefrontal and orbitofrontal brain areas were activated in favor of the IB group during the risk condition (Table 1 and Figure 4). The lateral prefrontal cortex (lPFC) is responsible for how to achieve goals and outcomes using plans and coordinating behavior by managing top-down control of cognitive processes (Wallis, 2007). Here the dlPFC activity shows cognitive control during risk-taking decisions, through the inhibition or reevaluation of responses, rewards, and emotions (Figner et al., 2010; Reyna & Huettel, 2014), because higher dlPFC activity is related to lower risk-taking (Gianotti et al., 2009), as we can see in the decreased number of gambling decisions in the IB group compared with the control group (Figure 3C).

Decision-making also involves neural processes in the vmPFC and OFC (Carter, Meyer, & Huettel, 2010), which respond to gains, losses, and their probabilities (Rushworth, Noonan, Boorman, Walton, & Behrens, 2011). The OFC is related to experiential or emotional processes, like the integration of cognitive and emotional information (De Martino, Kumaran, Seymour, & Dolan, 2006; Hsu et al., 2005), but is also activated by abstract rewards and punishments, such as gambling (Breiter et al., 2001). We agree with other researchers that

emotions play an important role in the assessment of subjective value (Phelps et al., 2014) and that they affect risk perceptions by how they direct attention (Fischhoff & Kadvany, 2011). Moreover, higher activation of the OFC indicates how much information is unknown (Hsu et al., 2005).

In other words, the OFC plays a role in calculating "how rewarding a reward is" by combining multiple sources of information to obtain a value signal (Wallis, 2007). This value of choice outcome is passed to the dlPFC, which controls behavior to achieve the goal (Wallis, 2007).

We suggest that the significant differences in favor of the IB group (Table 1 and Figure 4), due to long- and short-term training (Meshulam & Malach, 2016; Patel, Spreng, & Turner, 2013), have an impact on emotions that improve early attentional processes. Combining these results, we believe that the IB group shortened their risky decision-making process because they learned risk assessment and developed decision strategies to be able to manage emotions and control risks through years of financial experience.

Ambiguity Condition

In the ambiguity condition, the difference between groups increased, with the DPN of the IB group remaining significantly closer to their motor response (Figure 3A). IBs used lateral and medial prefrontal regions (Table 1 and Figure 4) to cognitively regulate emotional responses to avoid making rash decisions, as we see in the significant differences from this group with increased response times and decreased number of gambling decisions between conditions (Figure 3B and 3C).

In addition to the aforementioned functions of the dlPFC (Figner et al., 2010; Reyna & Huettel, 2014; Wallis, 2007), this brain area also plays a role in the regulation of emotion (Ochsner, Bunge, Gross, & Gabrieli, 2002) and has been suggested to support regulation in financial situations (Sokol-Hessner et al., 2013). One feasible explanation is due to working memory processes, localized in the lPFC, deciding the strategy to cognitively view an emotional stimulus in unemotional terms (Ochsner et al., 2002).

The vmPFC encodes subjective value (Padoa-Schioppa, 2011) of immediate and delayed rewards (Kable & Glimcher, 2010) and is activated during decision-making under ambiguity when there is feedback information after each trial, implying an anticipatory fear of the choice's outcome (Stout, Rock, Campbell, Busemeyer, & Finn, 2005). The vmPFC helps the value-based decision-making process by triggering affective responses in hypothetical gambles (Pujara, Wolf, Baskaya, Koenigs, & Program, 2015), but more importantly, this brain area has been identified with emotion regulation (Ochsner et al., 2002).

Usually, interactions between the lPFC and the medial prefrontal cortex (mPFC) are thought to be involved in cognitive control. The lPFC uses the value signal to plan and coordinate behavior, whereas the mPFC determines if it is worth following a given action path (Wallis, 2007). Nevertheless, lPFC and mPFC have been found to increase their activity during emotion regulation (Ochsner et al., 2002).

Using cognitive regulation of emotional responses helps to reduce loss aversion and physiological arousal to market volatility in senior stock traders (Lo & Repin, 2002), which means that one has some control over their affective state (Sokol-Hessner et al., 2009). By cognitively regulating one's emotions, one increases activity in the lPFC and the mPFC, as the activity in the amygdala and the OFC decreases (Ochsner et al., 2002). We suggest that IBs have developed strategies, gained from years of financial experience, that allow them to cognitively regulate the emotional impact caused by changes in market dynamics and risk exposures while making decisions.

There were two main limitations in this study. First, the sample was modest; perhaps a larger number of participants would help us to better understand any possible behavioral differences between groups, especially in the ambiguity condition. Second, the participants did not experience "real" gambling because we used hypothetical payoffs. However, the same affect-driven context dependency that takes place in real payoffs can also appear in games (Bateman, Dent, Peters, Slovic, & Starmer, 2007).

In conclusion, financial markets are governed by both rational and emotional processes (Lo & Repin, 2002); however, it is possible to "change

the way we feel by changing the way we think" (p. 1215; Ochsner et al., 2002). We believe that knowing how to balance both processes can only be attained from experience. Nevertheless, better knowledge about brain connectivity may shed light on risky decision-making based on financial experience and could possibly show us what this entails for risk management.

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Chapter 4

Connectivity adaptations in dopaminergic systems define the brain maturity of investors

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Connectivity adaptations in dopaminergic systems define the brain maturity of investors

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Investment decisions rely on perceptions from external stimuli along with the integration of inner brain-body signals, all of which are shaped by experience. As experience is capable of molding both the structure and function of the human brain, we have used a novel neuroimaging connectomic-genetic approach to investigate the influence of investment work experience on brain anatomy. We found that senior investors display higher gray matter volume and increased structural brain connectivity in dopamine-related pathways, as well as a set of genes functionally associated with adrenaline and noradrenaline biosynthesis (SLC6A3, TH and SLC18A2), which is seemingly involved in reward processing and bodily stress responses during financial trading. These results suggest the key role of catecholamines in the way senior investors harness their emotions while raising bodily awareness as they grow in investment maturity.

Humans have a tendency to predict future events not only in foreseeable scenarios, but also in the midst of randomness. Obviously, not all predictions are accurate, especially in the financial markets. It is sometimes claimed that the stock market is a game of chance, where no amount of knowledge of past performance data can help to predict future market trends[1]. However, instead of seeing random variability in market movements, our brain is designed to impose a pattern[2] in pursuit of allocating money advantageously. In this context, neuroscientists have found that investment decisions may be driven by signals triggered in dopamine-rich subcortical areas of the brain[3], where more unconscious processes are expected to take place.

AQ1

It has been postulated that dopamine neurons help to predict rewards by detecting subtle patterns that we would otherwise not immediately comprehend. However, this perception only comes from experience, by a learning process of constantly readjusting expectations based on actual results[4]. Once these predictions are converted into internal feelings, perceived somatic signals appear in anticipation of those expected outcomes[5–6]. It is probable that this nonconscious process guides our decisions prior to our conscious knowledge and provides the neurobiological evidence as to why these choices are made as they "feel right" or come "straight from the gut"[5], even with high-stakes decisions[7].

Notwithstanding that interoception may influence cognitive and affective processes involved in risky decision-making[8], individuals differ in their ability to generate and sense physiological responses to emotional situations[9]. Experienced traders, for instance, have lower heart rate variability[10], but also a better acuteness for discerning their own heartbeat, a sensitivity that has been connected to their profitability as well as their survival in the financial markets[11]. Considering their connection to the dopaminergic reward system, it is not surprising that the brain areas involved in what has been termed "brain-gut" neural communication[12–13] happen to be what the literature is highlighting as some of the key regions responsible for risk taking in economic investments[14].

In an attempt to reveal the success of the intelligent investor, neuroeconomics has begun to connect brain areas supporting this decision-making process to real-life financial risk taking. Thus far, only the activation in the anterior insula[15] and the ventrolateral prefrontal cortex[16] have been negatively correlated with individuals' expertise in trading stocks in real life. Furthermore, the decision to trade in active investors has recently been attributed to genes associated with catecholamine synaptic levels[17], especially dopamine[18–19] since is closely connected to reward-seeking behaviors[20]. Although economic preferences are partially explained by genetic differences[21], environmental factors, such as work experience, also mediate in this relationship between genes

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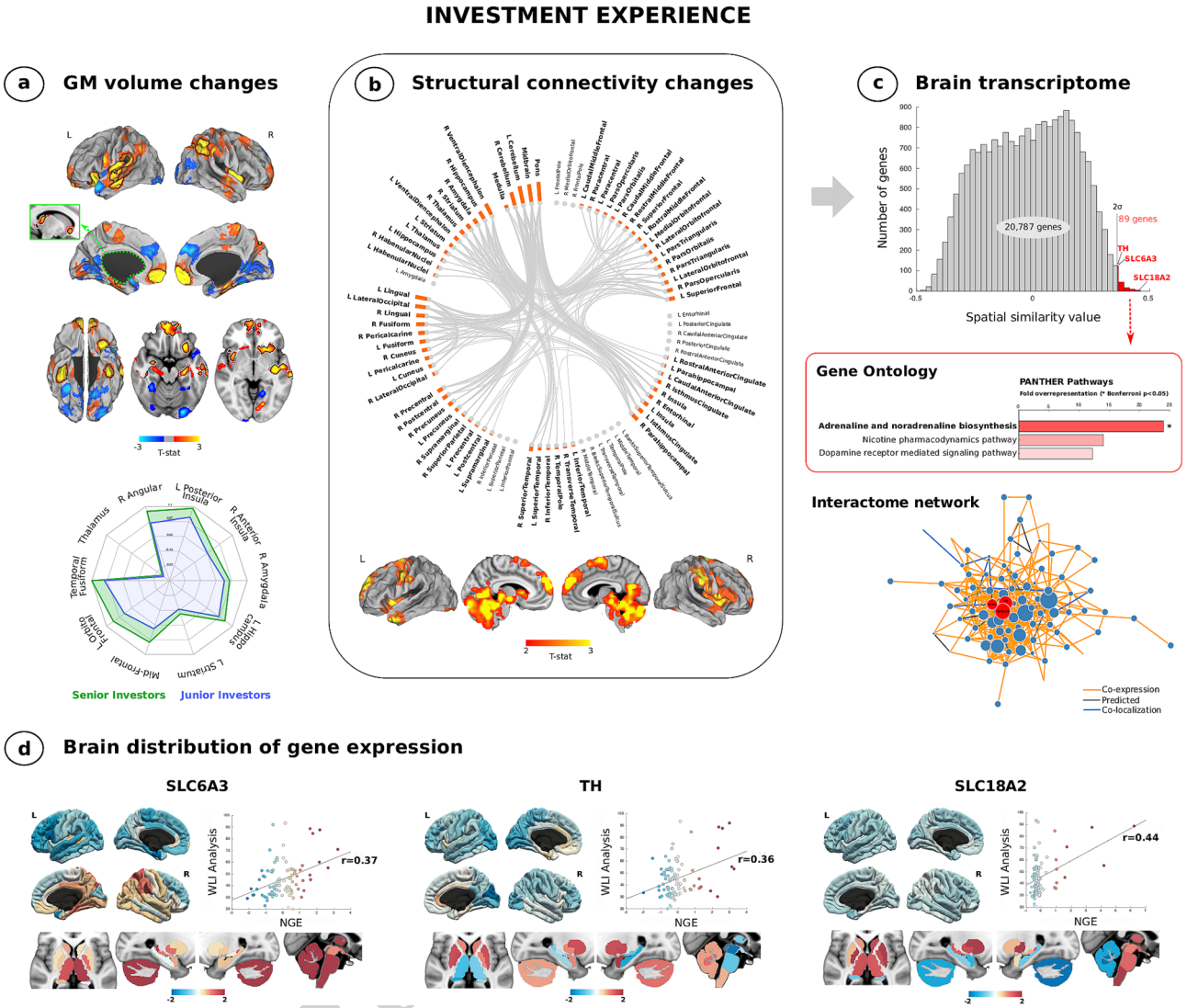

Figure 1. Structural brain changes and cerebral gene expression related to investment experience. (**a**) Cortical and subcortical maps of gray matter volume in senior investors. Red-yellow colors represent higher volume and blue colors lower volume. The results corrected for multiple comparisons are outlined in black (*Top*). Radar plot is shown (*Bottom*). (**b**) Connectogram of structural connectivity and brain projections of the weighted-degree of link-level interaction analysis related investment work experience. (**c**) Genes whose similar spatial distribution correlated with brain connectivity maps shown in b (*top*). Genetic pathways associated with these 89 genes (*middle*). Genetic functional network exhibiting the centrality of SLC6A3, TH and SLC18A2 (*bottom*). (**d**) Projections of cortical and subcortical areas of the distribution of these genes in the brain. SLC6A3 ($p = 0.00029557$), TH ($p = 0.00043982$) and SLC18A2 ($p = 0.00001728$). *WLI analysis* weighted-degree of link-level interaction analysis, *NGE* normalized gene expression, *R* right, *L* left.

and risk-taking[18] shaping individuals' financial decisions and may even diminish genetic predispositions to investment biases[22].

In light of these findings, it can be hypothesized that the experienced investor unwittingly relies on the emotions or inner feelings induced by dopamine neurons while creating an investment portfolio. As the human brain is plastic throughout the entire lifespan[23–24], substantial structural changes can be found in all human beings with particular behavioral expertise[25–27]. This study investigated whether work experience investing in the financial markets could lead to brain network changes, especially in dopamine-related systems, using a neuroimaging connectomic-genetic integration approach.

Results

Investment experience and brain changes. We found that senior investors display higher gray matter (GM) volume in several brain areas compared to junior investors, namely in the bilateral medial prefrontal cortex, frontal pole, insular cortex, thalamus, fusiform cortex and inferior temporal gyrus; right amygdala, putamen, angular gyrus, superior parietal lobule and lateral occipital cortex; and left orbitofrontal cortex, ventral striatum, hippocampus, superior and middle temporal gyrus (Fig. 1a and Table S1). No regions showed sig-

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nificant decreased volume after carrying out the same analysis. Interaction analysis showed increased structural brain connectivity in the mesolimbic circuits, the cerebellum, the insular cortex and the temporal pole when comparing groups (Fig. S1). When we gathered all the participants in one group and took into consideration work experience, we observed a predominant pattern of subcortical and mesocortical connectivity, particularly involving the brainstem, such as the pons and the midbrain (Fig. 1b). All the statistical and significant link-level connections for both analyses can be found in the connectogram figures (Fig. 1b and Fig. S1).

Intersection between investor brain connectivity and cerebral gene expression. While evaluating the entire cerebral transcriptome, we discovered that the cortical expression levels of 89 genes showed significant spatial similarity with the brain connectivity associated with work experience (Fig. 1c). We identified that this set of genes is functionally related with specific genetic pathways, such as the adrenaline and noradrenaline biosynthesis, the nicotine pharmacodynamics pathway and the dopamine receptor mediated signaling pathway. Using a lenient significant threshold in overrepresentation analysis showed that after applying a Bonferroni correction ($p < 0.05$), the adrenaline and noradrenaline biosynthesis pathway survived (Fig. 1c). This catecholaminergic-related molecular pathway encompassed three specific genes, namely SLC6A3, TH and SLC18A2. The high spatial similarity of subcortical, and to a much lesser extent, cortical, expressions levels of SLC6A3 ($r = 0.37$), TH ($r = 0.36$) and SLC18A2 ($r = 0.44$) with our weighted-degree map of work experience investing in the financial markets map is displayed in surface, volume and scatterplot formats in Fig. 1d. Finally, we confirmed with an interactome genetic analysis that all three genes, SLC6A3, TH and SLC18A2, play key and interdependent roles in their overall genetic interactions beyond their mere spatial matching, based on their central position in the interactome network (Fig. 1c).

Discussion

We found a concurrent increase in the volume of certain cortical (insula, prefrontal, temporal and parietal cortices) and subcortical areas (pons, midbrain, amygdala, hippocampus, striatum and thalamus) with regard to financial experience, which leads us to believe that none of these regions in isolation are specialized in responding to investments alone. Conversely, these results demonstrated the existence of a network that is probably engaged while considering whether to invest or not, particularly the brainstem related circuitry in the pons and midbrain. The higher genetic expression of SLC6A3, TH, and SLC18A2 in these areas suggest the importance of noradrenaline, adrenaline and dopamine, also known as catecholamines, in reward processing and bodily stress responses while trading in financial markets.

Legendary investor Peter Lynch pointed out that "*In the stock market, the most important organ is the stomach. It's not the brain*"[28], although it may be the connection between them what drives this decision-making based on "gut feelings." The bidirectional communication system that closely connects the gut and the brain influences high and low-level processes[29]. In intuitive decision making, triggering interoceptive awareness of these signals as gut feelings is connected to fronto-insular activation[30] when it comes to perceived risks in decision-making[31]. On the one hand, the orbitofrontal cortex seems to be one of the brain regions representing predictive reward value[32] during economic choice[33], whereas the ventromedial prefrontal cortex also depicts inflated trading values serving as a predictor of the tendency to ride bubbles[34]. On the other hand, the anterior insula appears to code a risk detection signal[35] whose activation precedes riskless choices[36], particularly in active stock traders[15]. As a consequence of experiencing these gut sensations, interoceptive memories appear within a network connecting the medial prefrontal cortex, the anterior insula, the amygdala and the hippocampus[30]; brain areas where an increased volume was seen in senior investors (Fig. 1). Paying attention to somatic signals to ensure advantageous behavior[37] may be an ability developed by senior investors while building their portfolio.

Forecasting where the market is heading to make the most profitable investment decisions requires weighing two concepts widely used in finance: expected reward and risk. Despite the fact that reward processing involves the mesocorticolimbic dopaminergic circuit[38], which we also observed in our results (Fig. 1), trying to calculate these parameters in a changing and uncertain environment demands a trade-off between exploitation and exploration strategies[39]. When senior investors are sure about which investment path they should follow, responding to the current conditions usually implicates exploitative decision making, where the striatum and the ventromedial prefrontal cortex track the subjective value of potential rewards[40–41]. On the contrary, seeking alternative investments or acquiring new market knowledge in order to decide may be related to exploratory decisions which are mainly associated with activation in the frontopolar cortex and the intraparietal sulcus[41], raising the possibility that attentional control in the anterior part of the former region may be the switching mechanism among these learning behavioral plans[42]. The role of catecholamines in this regulation[43], probably by amplifying the neural response during reward anticipation[44] as a novelty seeking risk attitude[45], may be one of the reasons for investors' ability to adapt to fast-moving financial markets.

Investment decisions appear to be influenced by internal bodily states, expected outcome values and attentional mechanisms shaped by professional financial experience. Certain genes regulate the neurobiological system behind these functions, where individual differences in the neurotransmitter process may arise, impacting trading behavior[17,46–47]. By combining neuroimaging with genetic information, we were able to identify three highly expressed genes (SLC6A3, TH, and SLC18A2) involved in the regulation of noradrenaline and adrenaline, and dopamine release, previously linked to reward sensitivity, economic risk attitudes[44–45] and exploration strategies[41]. Although prior studies have also targeted DRD4, COMT, MAOA-L and 5-HTTLPR as genetic determinants of financial risk-taking behavior, most of these results suggest that one factor mediating the variability in financial decisions is dopamine[18,48–50], with an intermediate synaptic level associated with successful trading[17]. A feasible explanation is that by means of reinforcement learning, dopamine neurons are able to convey both positive and

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negative motivational signals[51] as a probability distribution in which numerous future outcomes can be represented simultaneously in the brain[52].

It is important to mention that our results come from a small sample size. By using neuroimaging genetics, another limitation arose from the comparison between our connectivity maps with the gene expression profiles from the Allen Human Brain Atlas (AHBA), although this represents a new approach into how environmental factors can mediate the relationship between genes with financial risk-taking in neuroeconomics. Ideally, having longitudinal MRI data could give us a more precise idea of the progression of the structural changes that occur in the brain as the years of experience increase, and whether the high rate of investors quitting their job in the early years of their career is due to factors such as a failure to develop the key circuits involved in investment decision-making.

The last limitation come from the lack of longitudinal MRI data due to the high rate of investors quitting their job in the early years of their career.

Despite the fact that investors may vary in their ability to make advantageous financial choices, our conclusion is that there is a common neurological basis gained by experience. By learning how to harness the emotional aspects of investing while raising bodily awareness, they are able to turn feelings into lessons that ultimately will guide their decisions supported by catecholamine-related brain systems.

Methods

Participants. Thirty-one healthy participants, 16 senior investors (2 women, mean age = 40.5, SD = 7.8) and 15 junior investors (1 women, mean age = 26.5, SD = 4.3), were studied. We defined a "senior"/"junior" investor as a person who has more/less than three years of professional experience investing in financial markets according to the professional categories generally used across financial companies. All participants were recruited by the Chartered Financial Analyst Institute (CFA, Spain), the Instituto de Estudios Bursátiles (IEB, Spain) and via email through contacts. No history of neurological illness, psychiatric disorders, or substance abuse were reported. The study was conducted with the approval of the Ethics Committee of Rey Juan Carlos University and all participants provided written informed consent and were in full compliance with the Declaration of Helsinki.

MRI data acquisition. Participants were scanned with a Siemens 3 T Magneton Prisma. To study volumetric changes in the brain, a high-resolution, 3D, T1-weighted magnetization prepared rapid gradient-echo (MPRAGE) sequence was used with: 1 mm isotropic voxels; 192 sagittal slices; acquisition matrix size = 256 × 256; repetition time (TR) = 2300 ms; echo time (TE) = 2.98 ms; field of view (FOV) = 256 mm. Participants were instructed to remain as still as possible and bi-temporal foam pads were used to restrict head motion.

Imaging preprocessing. MRI data was preprocessed using FMRIB Software Library v5.0.7 (FSL). The anatomical T1 preprocessing pipeline included: reorientation to right-posterior-inferior (RPI); alignment to anterior and posterior commissures; skull stripping; and gray matter (GM) segmentation. An optimized Voxel-based morphometry was used[53], carried out with FSL[54]. The partial GM volume estimations were transformed to 2 mm MNI 152 standard space using non-linear registration. The resulting images were averaged and flipped along the x-axis to create a left–right symmetric, study-specific gray matter template. Then, all native gray matter images were non-linearly registered to this study-specific template and "modulated" to correct for local expansion (or contraction) due to the non-linear component of the spatial transformation. Finally, the modulated gray matter images were smoothed with an isotropic Gaussian kernel with a sigma of 3 mm (7 mm Full width at half maximum).

Between group structural differences. A two-class generalized linear model, adjusting for age, was used to examine between-group differences in GM volume. The removed effect of age in the brain can be visualized in Figure S2. To correct for multiple comparison, a Monte Carlo simulation was used with 50,000 iterations to estimate the probability of false positive cluster sizes at each voxel with a p-value < 0.05. The analysis was repeated correcting by gender and the results remained.

Brain connectivity analysis. To identify possible brain networks related to GM volume changes, a structural connectivity analysis was implemented. To reduce the dimension of our link-level analysis, GM images were down-sampled to 6 mm. A general linear model (GLM), was used to examine the between group differences in the structural connectivity (the relationship of the GM volume changes in 2 regions), using an interaction analysis for each pair of GM voxels. A statistical network of 6220 × 6220 nodes was obtained. Whole-brain correction for multiple comparisons was computed adapting the Monte Carlo simulation method to networks[55]. To compute false positive cluster size with a p-value < 0.001, 10,000 random networks were generated with the same smoothing properties. Compared to weighted-degree maps where clusters are defined as contiguous voxels, here clusters were defined as links that connect contiguous voxel groups.

To study how work experience affect the different networks of the brain, another interaction analysis was used to examine the relationship of work experience with the structural connectivity strength (how strongly 2 regions' volumes are related between them). The interaction analysis looks for multiplicative effect of the volume of one region with work experience and how this explains the volume in another region, removing the individual effects of the volume of these regions and the work experience, using a whole-brain correction for multiple comparisons computed by adapting the Monte Carlo simulation method to networks.

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Gene expression relationship with network changes. To investigate similarities between protein-coding genetic profiles with neuroimaging phenotypes, we correlated microarray gene expression data from the Allen Human Brain Atlas (AHBA) with the weighted degrees of the links with a p-value < 0.001, while performing the interaction analysis with work experience. The AHBA provides high-resolution genome-wide expression values for six human subjects, quantifying more than 20,000 genes in 3702 samples spatially distributed throughout the brain[56]. Consistent with the latest recommendations[57], brain maps representing the spatial distribution of each gene were created by using the microarray expression data with their MRI images and the coordinates of each sample for the six donors. The following steps were performed: (i) for each gene, expression values with multiple probes were averaged; (ii) each sample was associated with an anatomical label using the 89 brain regions defined with the Freesurfer atlas (68 cortical regions defined by the Desikan–Killiany atlas, 16 subcortical regions of the Freesurfer segmentation, 2 cerebellum and 3 ROIs of the brainstem: midbrain, pons and medulla); (iii) for each subject, we computed the median of gene expressions of all the samples within the same region; (iv) finally, we computed the median gene expression value of each brain area between the six donors. After extracting the work experience weighted degree map, this was converted to the 89-region atlas and a Pearson correlation was used to assess the spatial similarity value with the expression values of all the available genes. The spatial similarity computation identified the most similarly distributed genes to our neuroimaging outcome based on weighted degree connectivity maps, using a spatial similarity value higher than 2 standard deviations of the spatial similarity distribution.

Gene ontology (GO). To study the genetic functionalities of genes with a highly similar spatial expression to our brain phenotype, we used Gene Ontology annotation resources. This overrepresentation test evaluated the Protein Analysis Through Evolutionary Relationships (PANTHER) pathways associated with the genes located in the upper bound of the tail. The list of genes was entered into a GO term enrichment analysis tool[58] (http://geneontology.org), using a binomial test with False Discovery Rate correction to perform the statistical testing (multiple comparison correction at q < 0.05 level).

Interactome analysis. We used a genetic interactome approach to validate our genetic findings beyond their spatial brain colocalizations. Genemania[59] (http://genemania.org) and Cytoscape[60] v3.8.2. (https://cytoscape.org) software was used to perform a genetic interactome analysis. A composite gene–gene network based in co-expressions, co-localizations, and predicted interactions was used to obtain the complex relationships between all genes derived from the neuroimaging-AHBA spatial intersections, and closeness centrality was used to assess the hubness of specific genes in the interactome network[59–60].

Visualization. Cortical surfaces were visualized using the population-average landmark and surface-based projections of CARET v5.65 software (http://brainvis.wustl.edu/wiki/index.php), whereas subcortical surfaces were visualized using Matlab R2018b (https://www.mathworks.com/products/matlab.html). Surface images were displayed using a color scale based on T-scores. In-volume images were added to show subcortical striatal-thalamic-limbic-midbrain findings, when present. The statistically significant links in the 6220 × 6220 matrix were projected onto a connectogram using NeuroMArVL (https://immersive.erc.monash.edu/neuromarvl/). For visualization purposes, the 6220 nodes were reduced to 85 cortical-subcortical brain regions.

Data and code availability

Neuroimaging data and code availability: The neuroimaging dataset and all codes for imaging analysis are available for the research community from the corresponding author upon request. Genetic data: The genetic data are available from the AHBA website (https://human.brain-map.org). AQ2

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Author contributions
E.O.-T., J.L.-P. and T.O. conceived the study and collected the data; I.D. and J.S. performed the data analyses; E.O.-T., I.D., J.S., J.L.-P. and T.O. participated in data interpretation; E.O.-T. and I.D. wrote the manuscript; J.S., J.L.-P. and T.O. edited the manuscript; and E.O.-T., I.D., J.S., J.L.-P. and T.O. approved the final version.

Competing interests
The authors declare no competing interests.

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SUPPLEMENTARY INFORMATION

Connectivity Adaptations in Dopaminergic Systems Define the Brain Maturity of Investors

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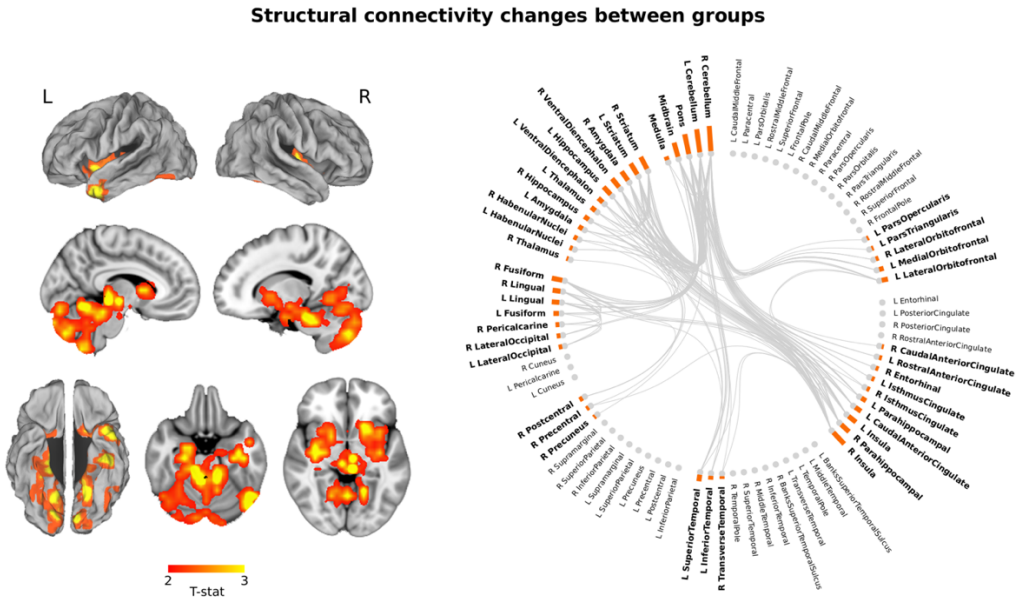


Figure S1: Connectogram of structural connectivity strength based on the weighted-degree of link-level interaction analysis maps between groups.

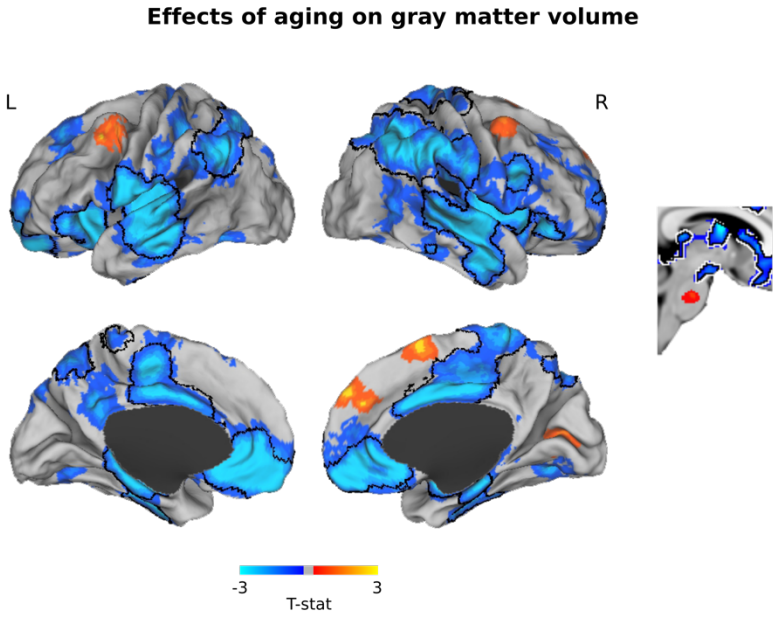


Figure S2: To control for the effect of age in our data we introduced the age as a cofounding factor in the statistical analysis. This figure shows the statistically significant effect of age in the data (lower volume in older subjects) that it was removed for all the analyses.

Table S1: Brain areas corrected for multiple comparisons, where senior investors exhibited higher gray matter volume, displayed in Figure 1A.

	HEMISPHERE	PEAK MNI COORDINATES	T-STAT
Frontal Pole	R	4, 56, -14	4.99
Frontal Medial Cortex	R	0, 54, -14	4.91
Angular Gyrus	R	52, -54, 44	4.29
Superior Parietal Lobule	R	34, -52, 52	4.16
Lateral Occipital Cortex	R	54, -60, 48	4.00
Thalamus	R	6, -28, 10	3.57
Inferior Temporal Gyrus	R	46, -26, -20	3.56
Temporal Fusiform Cortex	R	38, -22, -24	3.56
Putamen	R	34, 0, 4	3.43
Insular Cortex	R	34, 14, -8	3.28
Amygdala	R	32, -4, -20	3.13
Insular Cortex	L	-40, -14, -2	5.34
Medial Frontal Cortex	L	-10, 50, -14	4.26
Middle Temporal Gyrus	L	-66, -12, -10	4.19
Frontal Pole	L	-2, 64, -14	3.93
Putamen	L	-22, 20, -4	3.85
Thalamus	L	-20, -26, 12	3.54
Hippocampus	L	-26, -20, -18	3.40
Temporal Fusiform Cortex	L	-40, -22, -30	3.34
Superior Temporal Gyrus	L	-54, -12, -4	3.30
Frontal Orbital Cortex	L	-28, 22, -20	4.19
Caudate	L	-16, 20, -6	3.18
Accumbens	L	-14, 20, -8	3.03
Inferior Temporal Gyrus	L	-44, -16, -26	3.01

Chapter 5

Conclusions

Todo hombre puede ser, si se lo propone, escultor de su propio cerebro.

Santiago Ramón y Cajal

Conclusions

Each step of this research project has led us to the conclusion that the investor's brain has changed to adapt to the needs required by an investment job. To reach this conclusion, we have conducted three experiments that correspond to each one of the articles included in the thesis. In this section, we present the main results we have obtained in each article by discussing them according to the literature, as well as their respective conclusions, and we end with an overall conclusion drawn from all the work done.

Gone are the days when science believed that brain anatomy was fixed. As far back as the 1890s, we found that Williams James was the first to use the term plasticity as "the possession of a structure weak enough to yield to an influence, but strong enough not to yield all at once" (James, 1890) and Ramón y Cajal added that "the organ of though is, within certain limits, malleable and capable of perfection … by well-directed mental gymnastics" (Ramón y Cajal, 1894). However, it has taken several decades for researchers to be able to demonstrate that the brain can be modified beyond the critical period by factors such as the environment (Rosenzweig, Krech, Bennett, & Diamond, 1962), the things we learn (Kandel, 2012) or the mental exercises we perform (Pascual-Leone, Amedi, Fregni, & Merabet, 2005). This brain property, known as neuroplasticity, showed us that the brain changes according to our life experiences. In keeping with this notion, this thesis has demonstrated that work experience shapes the anatomy of the investor's brain.

Through learning and experience, the brain increases in volume and thickness (Valk, et al., 2017; Aydin, et al., 2007; Lazar, et al., 2005) to better suit the task at hand. For example, London taxi drivers have increased hippocampal gray matter compared to non-taxi drivers through spatial navigation (Maguire, et al., 2000). We found that investing experience has altered the structure and strengthened the synaptic connections in catecholamine-related systems to keep playing the market. Every time the stock markets open, investors analyze data and find profitable opportunities to make sound investment decisions before others beat them to it. This feeling of seizing the chance or missing out on great returns resembles the principle of use it or lose it that govern brain plasticity. This competitive nature that ruled both the brain and the markets, show us which regions or investors are ahead of the game. The analyses we conducted using magnetic resonance imaging (MRI) has enabled us to conclude that these key areas involved higher gray matter volume and

increased structural brain connectivity in dopaminergic-related pathways in senior investors (Chapter 4).

Our brain triggers dopamine when we process rewards (Schultz, 2002). Investors release dopamine in the reward circuit every time they make an investment decision, which means that experience-dependent plasticity does not happen in isolation. Following Hebb's rule of "cells that fire together wire together" (Hebb, 1949), we confirmed the strengthening of a circuit that is activated during the investment decision-making process (Chapter 4). This happens because the repeatedly chemical changes that occur in neurons that fire at the same time, tend to connect them more strongly. Once this connection is strengthened, there is a boost in communication between the different areas, which causes information to be processed at a faster speed. In our study, these chemical changes involve catecholamines (dopamine, adrenaline and noradrenaline) which help consolidate the plastic change in the pathways responsible for their investment behaviors (Chapter 4).

Advances in neuroimaging and molecular biology have made it possible to establish a relationship between neural circuits and genes (Krienen, Yeo, Ge, Buckner, & Sherwood, 2016). This is important because brain plasticity is a process that involves a variation in gene expression. Every cell in our body contains exactly the same genes, but not all of those genes are expressed inside each individual cell. For example, when we learn something new or frequently behave in a certain way, we modify which genes in our neurons are turned on or expressed (Clayton, et al., 2020). These genes are going to decide which proteins to produce, which will cause a variation in the structure and function of the neuron and in our behavior. The set of genes we found (SLC6A3, TH, and SLC18A2) are protein coding genes involved in the biosynthesis of catecholamines (Chapter 4). Therefore, it is no mere coincidence that the changes we have observed in the investors' brains are related to areas where catecholamines are one of the main neurotransmitters mediating physiologic functions. Functions that have been previously associated with reward sensitivity and economic risk attitudes (Dreber, et al., 2009; Roe, et al., 2009), two pillars (reward and risk) upon which investments are made. Therefore, using a data combination from our structural magnetic resonance imaging results with whole-brain transcriptome information from Allen Human Brain Bank and functional annotations from PANTHER pathways, has made us draw the conclusion that catecholamines (dopamine, adrenaline and noradrenaline) play an

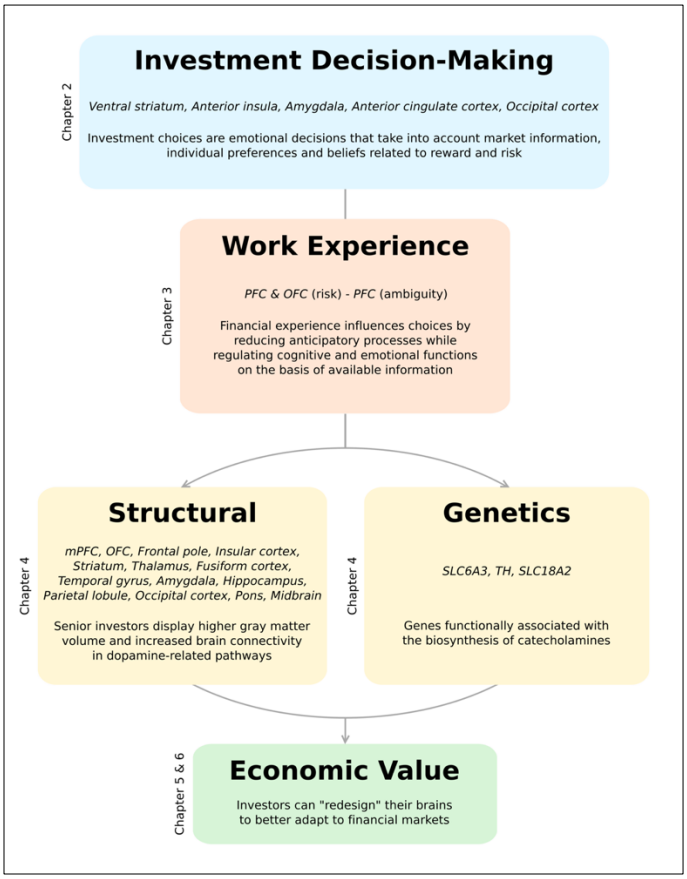
important role in investment behaviors through a higher gene expression of SLC6A3, TH and SLC18A2.

In the monetary task that we conducted prior to the magnetic resonance imaging study, we focused on decision-making under risky and ambiguous conditions. Neuronal signals produce thoughts, behaviors and perceptions of the environment by firing rapid electrical impulses, an action potential that occurs within milliseconds. In the 1950s, Vernon Mountcastle demonstrated that the nuances of the brain anatomy could be detected by analyzing the electrical activity of the brain (Mountcastle, 1957). As we were unable to place pin-shaped microelectrodes in the investors' brains, we used electroencephalography to measure changes in evoked potentials in response to external stimuli. Knowing in this task where electrical activity takes place in the brain can help us understand aspects of the decision-making process such as why investment bankers are ready to make quick decisions as they become more comfortable dealing with risk. We found that investment bankers streamline the elaboration of the response regardless of the amount of available information. The prefrontal and orbitofrontal areas lead to only prefrontal activation as available information decreases while more logically thinking increases (Chapter 3). By focusing on the decision preceding negativity (DPN) that comes before a risky choice on the electroencephalography (EEG) study, we came to the conclusion that experience reduces the anticipatory processes that lead to a decision while regulating cognitive and emotional functions on the basis of the amount of available information.

Acquiring the skill to invest in the financial markets demands time and experience. As Ramón y Cajal argued in the *Textura del Sistema Nervioso*, "… the acquisition of new skill requires many years of mental and physical practice. In order to fully understand this complex phenomenon it becomes necessary to admit, in addition to the reinforcement of pre-established organic pathways, the formation of new pathways through ramification and progressive growth of the dendritic arborization and the nervous terminals" (Ramón y Cajal, 1904 translation from Pascual-Leone, Amedi, Fregni, & Merabet, 2005). Although we cannot demonstrate from our research whether it is a reinforcement of pre-established pathways, the formation of new ones or both, we can confirm that the brain structures we found in our results are involved in investment decision-making. As stated by Merzenich, the neurons in the center of a brain area are the most committed to the task and the ones that are in the borders can vary from person to person depending on the activities they perform (Merzenich, et al., 1983). The increased volume in certain brain

areas indicates that they have been more exercised, which has caused that the neurons located at the edges engage in the same functions as these regions. What we have observed in the meta-analysis is that these areas usually correspond to different aspects of the investment decision-making process (Chapter 2). The activation likelihood estimation (ALE) meta-analysis has allowed us to identify a convergence of limbic-related brain areas that are activated when we make an investment decision. These main regions are: ventral striatum, anterior insula, amygdala, anterior cingulate cortex and occipital cortex. Our conclusion is that investment choices are emotional decisions that take into account market information, individual preferences and beliefs regarding reward and risk.

Following the outline of the flowchart presented in the introduction (Research plan and methodological framework), hereinafter are the main results and conclusions drawn from this thesis.



Main findings. Main results in italics and the conclusions in roman from the three sections of this thesis, in addition to the economic value that these results can bring about in terms of applicability outside the laboratory.

The idea that the brain is capable of shaping its structure and function as a result of every activity it performs, stems from the need to survive in a changing world. Each day, investors face the markets with an investment strategy that needs to be constantly updated. This daily practice is what led senior investors to adapt its biochemical and neurophysiologic functions to the external and internal stimuli they receive, so they change their behavior accordingly. By turning on the right genes, their brain anatomy has changed to perceive information with greater precision and speed (external stimuli) while listening to their emotions through somatic signals in their body (internal stimuli). In other words, the ability of experienced investors to adapt their behavior to the dynamic nature of the markets relies on the plasticity of their brain.

To conclude, what we do over the course of our lives is going to leave a genetic and structural mark in our brains. Gaining knowledge into these marks can pave the way to create training programs build upon neuroplasticity techniques. Be able to exercise the brain areas responsible for investment decisions outside the trading floor can have a profound effect on professional success. After all, it is more than just a metaphor the saying that the brain is like a muscle that grows with exercise.

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