

What can we learn from neurofinance?¹

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ABSTRACT

Neurofinance is a relatively recent field which aims to unveil the neurobiological mechanisms through which decisions are made in finance. This article investigates how neurosciences can contribute to the study of finance and the most appropriate ways for neuroscientific methodologies to be applied to financial situations. In order to examine these areas, we have produced a literature review around three axes of the main neuroscientific studies published in finance: financial risk; discounting and credit risk; information and trading decisions. One of the crucial insights offered by neurofinance is how to reconcile classic and behavioral finance by showing that emotions are critical to rational decision-making, in spite of also being part of the origin of biases. Through its unique set of techniques, neurofinance is able to pinpoint the biological and neurological explanations behind some of the common biases highlighted by behavioral finance, as well as tackle some novel questions. We conclude this review by pointing toward potentially fruitful avenues for future research and by highlighting which methods appear particularly well adapted for neurofinancial studies.

KEYWORDS: Neurofinance, risk aversion, information, emotion, time-discounting, brain, hormones, genes.

1. Introduction

Richard H. Thaler, 1999, *The End of Behavioral Finance*, *Financial Analyst Journal*.

Behavioral finance is no longer as controversial a subject as it once was. As financial economists become accustomed to thinking about the role of human

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behavior in driving stock prices, people will look back at the articles published in the past 15 years and wonder what the fuss was about. I predict that in the not-too-distant future, the term “behavioral finance” will be correctly viewed as a redundant phrase.

As evidenced by the recent Nobel prize awarded to Richard Thaler, behavioral finance is increasingly gaining recognition as a useful framework for the analysis of financial behaviors. Using insights from cognitive psychology, behavioral finance was able to describe numerous biases, anomalies, and deviations from perfect “rationality” that had previously been associated with finance (see Barberis and Thaler, 2003). “Behavioral finance” is not yet a redundant phrase, and it has clearly demonstrated its usefulness over the years. For instance, prospect theory has become “widely viewed as the best available description of how people evaluate risk in experimental settings” (Barberis, 2013), and regulatory bodies have accordingly started to gain interest in behavioral finance. In a report ordered by the Autorité des Marchés Financiers (AMF), De Palma, Picard and Prigent (2009) clearly recommend measuring the loss aversion and probability weighing of customers under the obligation to establish the risk profile of clients. MIFID 2 recently introduced the idea of the customer capacity to “bear loss” in relation to the notion of loss aversion. In the wake of regulators’ interests, several firms have been created to propose more sophisticated and accurate questionnaires to measure the risk tolerance and loss aversion of financial institutions customers⁵.

What could then constitute the “next frontier” for behavioral research in finance? In the same way that behavioral finance caused “a fuss” in the 80s, the recent emergence of the use of neuroscientific methods in finance is drawing an increasing amount of attention. “Neurofinance” stands at the crossroads of biology, neuroscience, psychology and economics. Glimcher and Rustichini (2004) go as far as saying that the above mentioned fields are converging into a unified disciplinary framework which can provide “a single general theory of human behavior”.

If neurofinance can help explain biases observed by behavioral finance, its recent findings may be able to reconcile the emotional “biases” of behavioral finance and classic finance. Contrary to what some authors have implicitly or explicitly written (Goetz and James 2008, Kalra Sahi 2012), it is now a stylized fact in neurofinance that emotions are critical for rational behavior

5. We might cite “RiskTolerance”, created by Pierre-Laurent Fleury, André De Palma and Nathalie Picard in 2010.

(Gupta et al. 2011). This central thread will be explored throughout the article. The main assumption in neuroeconomics and neurofinance was presented by Nobel Prize winner Francis Crick: “A person’s mental activities are entirely due to the behavior of nerve cells, glial cells, and the atoms, ions, and molecules that make them up and influence them” (Crick 1995). Therefore, in neuroeconomics, utility can be defined as the averaged firing rate of a population of neurons that encodes the subjective value of an object, making it directly observable (see for instance Glimcher and Fehr, 2009, p. 514).

As such, we will mostly base this literature review of the papers in neurofinance on the most important systems underpinning our decisions-making process, the nervous system and the endocrine system. One has to note important differences between them. The nervous system is a “wired” system acting through synapses, which coordinates rapid and brief (taking milliseconds) responses. The endocrine system is “wireless”⁶, the glands composing it and hormonal receptors are dispersed throughout the body. The impact of a hormone released within the blood takes at a minimum a few seconds, but can be much longer (hours, days). It can have long lasting effects⁷ (see Sherwood, 2015, for more details concerning the differences between the endocrine and nervous systems). We will also look at genetics, which partially codes the functioning of these two systems.

One major contribution of cognitive sciences to finance lies in the use of new methodologies based on the identification of changes in brain function as well as changes in body state when a participant engages into a financial decision or situation. In neurofinance, the methodology originates from experimental methods in cognitive neurosciences. Contrary to traditional experiments in economics which are built in a collective laboratory by observing interaction between several participants, the experiments in neurofinance are generally conducted in an individual laboratory, where cognitive neurosciences techniques are processed on one single subject. The overall objective is to record changes in brain function or body state when a subject engages in a cognitive process. Two different sets of experiments have

6. The nervous system is “wired”, in the sense that all its structures are directly connected. The endocrine system is more “wireless” or “Wi-Fi” like, in the sense that its structures are not directly connected. Chemical messengers are released in the bloodstream (the air, to continue the “wi-fi” analogy), to reach their receptors.

7. Nadler and Zak (2016) differentiate the impact of hormones between genomic and non-genomic. Genomic action occurs when a hormone binds to the receptors of a cell and initiate genetic transcription. This process is long, taking hour or years. An example is the secondary sexual differentiation occurring in presence of testosterone. Non-genomic actions are all the other actions, that do not involve genetic transcription. They are faster (seconds to minutes).

been developed. Behavioral experiments with healthy subjects and based on measurement allow for the observation of brain or body when a participant is engaged in some cognitive process. Experiments based on manipulation try to explain how perturbations in brain (lesions studies for instance) entail changes in cognitive behavior. The measurement techniques are said to be correlational and the manipulation techniques are said to be causal. The reader will find in the Appendix a discussion of the methodological aspects for each one of these methods.

We organized this literature review around three main parts. The first part covers the neurofinance papers studying financial risk. In the second part, we tackle discounting and credit risk. The third part tackles information and trading.

2. How may neurofinance better explain risk-taking?

Risk is one of the core topics in finance, and is thus one of the most widely researched areas in neurofinance. The contribution of neurofinance revolves around three axes. First, some work has been carried out on the importance of emotions in risky decisions, generally using a combination of physiological measurements.⁸ The second axis of research has dealt with the impact of steroid hormones such as testosterone and cortisol. Finally, a last topic of interest in research on risk taking has been genetics.

2.1. *The role of emotions in decisions under risk*

Traditional expected utility (EU) theories generally postulate that decision-making under risk is essentially a cognitive, rational activity. But this normative approach was challenged by the unveiling of numerous anomalies, such as preferences reversal (see Tversky and Thaler, 1990 for a summary). This leads to the formulation of the more flexible and descriptive prospect theory (Kahneman and Tversky, 1979, 1992). Building on it, behavioral finance started to introduce the idea of biases, possibly stemming from emotions (see for instance Kahneman and Thaler, 2006).

8. We may cite Skin Conductance Response, a non-specific proxy for arousal or fMRI (functional Magnetic Resonance Imaging, measuring brain activity through the tracking of blood flow), a method better able to discriminate between discrete basic emotional states. See Vytal and Hamann (2010) and Gajewski et al. (2017) for example.

Theories on the topic of emotion and decision-making are blossoming in the field of behavioral economics. Taking their lead from the famous “system 1” and “system 2” popularized by Kahneman (2003, 2011)⁹, most of these theories revolve around the idea of a dual process happening in our brain. They differ on the role and interaction of these two processes, but agree that one system is more “emotional”, while the other is more “cognitive”, or rational. Slovic et al. (2004) and Slovic and Peters (2006) underline that this emotional system, through its speed, “enabled human beings to survive during their long period of evolution” (p. 311). These authors postulate that people still rely strongly on this emotional way of making decisions, when time is of the essence. This cognitive and emotional dichotomy is reflected in the triune brain theory of MacLean (1990), which has pedagogical value as a first approximation to consider the brain. MacLean theorized that the brain has evolved over history. It started from a simple “reptilian” complex only dealing with instinctual response, before the addition of a “paleo-mammalian” system (the limbic system, dealing with motivations and emotions) to arrive at the addition of the “neo-mammalian” one (neocortex, dealing with higher cognitive function). We illustrate in figure 1 the simple model of MacLean, before giving more details about the position in the brain and the functions of the main area we discuss in the paper (see Table 2 for the general functions of these areas). We also display by arrows the general pathway of the dopaminergic system (a neurotransmitter heavily involved in reward and motivation) and the serotonergic system (a neurotransmitter involved in behavioral inhibition), discussed later in this article, particularly in the genetic part.

But how important is the emotional system compared to the cognitive one in decision-making under risk? Neurofinance, with the help of neurophysiological measures, is able to underline the importance of emotions on a more solid base.

Bechara et al. (1997) posit that risk is encoded as a visceral, emotional experience. The somatic marker hypothesis (Damasio, 1994) they used postulates that emotions are a biasing and intermediate step, occurring before more declarative knowledge is used. Their sample was composed of a group of patients suffering from lesions in emotion-related centers of the brain (ventromedial prefrontal cortex). These patients had average or above average intelligence, displayed unusual rationality but were inexpressive of

9. The name was first proposed by Stanovich and West (2000).

emotions. When confronted with decision-making under uncertainty, they were able to designate which alternative was the riskiest but failed to behave in accordance with this knowledge, contrary to a control group of healthy subjects. Healthy subjects were actually displaying arousal, as measured by skin conductance response before even knowing overtly what was going on. They had what might be called a “hunch”, that patients with lesions were not having. Ironically, unemotional people were shown to be unable to react rationally in this context. In a later experiment with similar design, Crone et al. (2004) underline that these results can be extended to healthy subjects. In their experiment, some of their healthy subjects learned faster which options proposed to them were more advantageous. Moderate and good performers in the experiment displayed larger skin conductance before a disadvantageous choice. Both heart rate and skin conductance responses were larger for good performers before selecting a disadvantageous option with frequent losses.¹⁰

These papers clearly underline that emotional arousal or affect plays a role in healthy decision making under risk. There is thus an important link between rationality in decision-making and emotions as pointed out by many authors. Lo (2004) describes them as “opposite sides of the same coin”. Finucane et al. (2003) use the expression “the dance of affect and reason”, an expression also adopted by Slovic et al. (2004).

The case of most interest for finance might be decision-making under risk as conceptualized by moments of the distribution of returns. A meta-analysis by Wu et al. (2012), on 28 studies totalling more than 400 subjects, underlined that prospects differing in their means activated mainly the left and right ventral striatum, and particularly the nucleus accumbens (an essential part of the reward system). It appears to be coding mainly for anticipated gain magnitude, and tends to push individuals toward risk taking when activated. Concerning choices differing in their variance, the insula was the most activated structure. The insula is heavily involved in a wide variety of emotions. For positive skewness, only the ventral striatum and particularly the nucleus accumbens were activated. Schematically, activation of the nucleus accumbens through positive mean and skewness triggers positive arousal and approach toward a prospect, while activation of the

10. As noted by Loewenstein et al. (2001) when presenting his *risk as feelings* hypothesis, emotions will not always lead to optimal choice. In Bechara et al. (1997), the high-risk option was associated with lower expected payoff. In the experiment by Shiv et al. (2005), the high-risk option was associated to the high expected payoff, resulting in healthy subjects obtaining lower payoffs, as they took less risks.

insula through variance triggers avoidance. Perhaps even more so than the details of the brain structure involved, what comes out of this meta-analysis is that the brain structures involved in risk are almost exclusively from the limbic “emotional system”.

Another topic of interest in neurofinance is risk related biases. For instance, the disposition effect (presented in Shefrin and Statman, 1985, completed by a thorough empirical test in Odean, 1998) is the tendency to hold on to losing securities and sell securities whose price has increased. It could be driven by prospect theoretic consistent behavior, or belief in mean reversion. Alternatively, the disposition effect could also be driven by realization utility, which posits that people experience a jolt of positive utility when realizing a gain and a jolt of negative utility when realizing a loss¹¹.

Brooks et al. (2012) underlined through an fMRI study that subjects with a strong disposition effect displayed an insensitivity in the ventral striatum to an increase in the value of the asset when the value was below the purchase price. Knowing that there is evidence that the ventral striatum responds to an unexpected rise in value, this finding could be consistent with a belief in mean reversion from some subjects. The authors controlled for prospect theory preferences and found that these preferences did not explain the disposition effect. However, a limitation of their study is that subjects could only decide to sell the underlying assets in their experiment, not to buy them.

More robust studies in this regard were carried out by Goulart et al. (2013) and Frydman et al. (2014). Goulart et al. (2013) underlined in an experiment that the disposition effect was associated to a greater Skin Conductance Response, but lower body temperature and heart rate. They underlined that this could be consistent with the disposition effect being driven by an emotional automatic response from system 1, therefore providing support for realization utility. In the experiment of Frydman et al. (2014), subjects could buy and sell three assets which displayed auto-correlation in their returns. This fact was conveyed to the subject in the experiment, who could therefore not think that there would be a phenomenon of mean reversion. They found a strong and significant disposition effect in their study. Subjects’ activity in the ventromedial prefrontal cortex (see Figure 1,

11. Contrary to the classical theory, where individuals only derive utility from total wealth or from consumption (Barberis and Xiong, 2012).

an area thought to encode for decision values) was correlated with capital gain (the value of the decision under realization utility) but not with the net expected value of future returns (the value of the decision under expected utility). The strength of activation of the ventromedial prefrontal cortex for gaining stock was linked with the tendency of the investors to sell those stocks to realize the gain. They also found the ventral striatum to be more active when subjects were realizing their gains instead of holding them, a fact congruent with the hedonistic utility jolt postulated by realization utility. Therefore, the evidence gathered by neurofinance overall points to the fact that the disposition effect is driven by realization utility.

Using the same dataset, Frydman and Camerer (2016) also tested a regret theory to explain stock repurchases. Regret theory states that after having sold a stock, subjects might feel regret if the stock price went up, and conversely some form of joy if the stock price went down. In turn, this might in the first case prevent or in the second case promote stock repurchase in the future. The authors indeed found in their data set such a repurchase effect, with the foregone capital being a significant determinant of the repurchase decision. They found that when the price of a recently sold stock went up, subjects experienced a decrease in activity in their ventral striatum¹² showing regret. There was an inverse correlation between the activity in the ventral striatum and the repurchase effect. Subjects who experienced a reduced activity in their ventral striatum after having seen the price of a sold stock go up tended to take longer to repurchase this stock. They also found that the regret effect and the disposition effect were correlated in their sample, pointing to a similar psychological mechanism.

Overall, neurofinance therefore provides ample evidence of the importance of emotions in decision-making under risk, and indeed it even appears that emotions are necessary for rational decision-making under risk and uncertainty. Brain structure involved in decision-making under risk is also part of the emotional system and includes notably a number of structures from the dopaminergic system. Emotions such as the jolt of pleasure received when realizing a profitable trade or regret were directly observed in the brain by fMRI and served as the basis to explain the disposition effect, for instance.

12. See Figure 1, where the Nucleus accumbens, part of the ventral striatum, is shown.

2.2. *The role of the endocrine system in risk-taking*

Another strand of literature in finance has focused on the impact of hormones – in particular, steroid testosterone and cortisol – on the behavior of agents in finance.

There are three main methodologies to study these hormones and their links with financial behavior (see Nadler and Zak, 2016, for more details). The researcher can sample the endogenous circulating level of the hormone, generally through a non-invasive salivary sample, either to observe basal levels or change in levels after an event. The researcher can also exogenously administer the hormone, a precursor or an antagonist of it directly to the subject. Last, the researcher can attempt to observe the potential long lasting effect this hormone left in the body of the subject.

Testosterone and cortisol are thought to affect behavior through their action on the dopaminergic system. They affect the ventral striatum, and more particularly the nucleus accumbens, which are brain structures heavily involved in decision-making and reward behavior. Cortisol may also have an impact on the amygdala, a brain region involved in fear-related responses (Coates et al. 2010). Another pathway of action of testosterone on financial behaviors, such as risk-taking, could be by increasing impulsivity through an inhibition of the cognitive activity in the pre-frontal cortex (Nave et al., 2017).

2.2.1. *Circulating level of Testosterone and Cortisol and Risk-Taking*

Testosterone, popularly associated with virility, is mainly produced in testes by men and is also produced in lesser quantity (roughly 1/8) by women in the ovaries and the adrenal gland¹³ (Apicella et al. 2015). It is one of the main hormones responsible for sexual differentiation (Morris et al., 2004). Researchers have therefore tried to link this hormone to various behaviors that appear to differ between men and women, including financial risk-taking. Cortisol is secreted in the adrenal gland as well, in response to physical or physiological stress. Both hormones follow a circadian rhythm¹⁴.

13. Glands located above the kidneys, secreting a variety of hormones, including testosterone and cortisol.

14. It is therefore of particular importance to test for subjects' hormonal level at the same time of the day. Levels of testosterone are potentially more stable and therefore more reliable during the afternoon or evening (Diver et al. 2003, Gray et al. 2004).

Circulating levels of testosterone have been linked to risk-taking in numerous studies on students (see the review of Apicella et al., 2015). The relation seems rather strong, even though the exact shape of the relation remains elusive. Sapienza et al. (2009) found it to exist only for women or for low concentration in both sexes (in a study on 320 men and 140 women). Stanton et al. (2011) found it to be quadratic (142 men and 156 women, robust to separate analysis between men and women). Schipper (2012) found it to exist only for men (115 men, 93 women). Some studies involving the administration of testosterone concluded on the absence of impact on risk-taking behaviors (Boksem et al. 2013, Zethraeus et al. 2009¹⁵). Concerning cortisol, the results of externally administering the hormone were mixed. It was shown in Kandasamy et al. (2014) to heighten risk aversion and probability weighting, particularly so in men, when administered over 8 days¹⁶. On the other hand, in a recent study, Kluehn et al. (2017), underline that the exogenous administration of hydrocortisone significantly increased risk-taking in men in a modified version of the Balloon Analogue Risk Task (BART) compared to a placebo.

Of even greater relevance for finance scholars, Coates and Herbert (2008) sampled testosterone and cortisol levels of 17 traders over 8 days, twice a day at 11:00 am and 3:00 pm. They found that on days where traders had higher morning testosterone levels, they made more profits in the afternoon and had higher testosterone levels in the afternoon. The fact that testosterone rose after a “victory” is coherent with the literature on the subject (see Casto and Edwards, 2016). Cortisol was linked to the volatility of the portfolio and to the implied volatility on the main asset traded. Knowing that testosterone can have euphoric effects and lead to irrational risk-taking, while prolonged exposure to cortisol might have debilitating effects promoting a rise in anxiety, the authors concluded that a rise in cortisol might exaggerate downward movements in the market, while testosterone might have the opposite effect on bubbles. While this study used actual finance professionals in the context of their work and therefore has high ecological validity, the number of subjects (n=17) limits the scope of the results.

15. The study from Zethraeus et al. (2009) suffers from the caveat that their sample was composed uniquely of post-menopausal women, and might therefore not be transposable to other populations.

16. An acute change in cortisol was found to have no effect on risk-taking in this study.

This intuition about hormones and financial stability was tested in the context of experimental markets by Nadler et al. (2018) and Cueva et al. (2015). In Cueva et al. (2015), individual endogenous level of cortisol was linked with higher risk taking in markets. The average endogenous cortisol level in the market was positively linked to price instability. A subsample of male subjects were then administered either cortisol, testosterone or a placebo. The administration of cortisol or testosterone shifted investment towards riskier assets compared to a placebo. It is however noteworthy that in both these studies performed in the context of experimental markets, no significant impact of baseline testosterone was reported.

Overall, it would appear that higher testosterone (endogenous or exogenous) is linked to more risk taking. The relation between cortisol and risk taking appears less clear – some studies have linked it with an increase in risk taking, while others point to a reduction in risk taking. The impact of cortisol may therefore depend on other, still to be identified, factors, or may interact with testosterone (the so-called “dual hormone hypothesis”, see Mehta et al, 2015 for a review¹⁷).

2.2.2. Testosterone at critical stages of development and risk-taking

In addition to the impact of circulating testosterone, some authors have studied the longer lasting impact of testosterone at the fetal and pubertal stages, that are critical for development. Testosterone exposure at these stages leads to what is called “brain masculinization” (Morris et al. 2004), increasing the impact of circulating testosterone later on (Durdiakova et al. 2010). It also leads to some observable physical changes.

A lower ratio of the length of the index to the ring finger (2D:4D) is supposed to correlate to higher testosterone exposure during the fetal stage. Similarly, facial masculinity is correlated with exposure during puberty (Apicella et al. 2015), as testosterone exposition during puberty notably makes the bones of the jaw grow. However, it is worth noting that these measures are recognized as being inherently noisy.

Given how easy it is to measure the 2D:4D ratio, numerous studies have tried to link it to risk aversion. However, the results are mitigated, with 5

17. Recently, Nofsinger et al. (2017) underlined in a portfolio management experiment on 39 students that the ratio of testosterone and cortisol (T/C) was to be associated with the tendency to sell loser stocks, particularly in females. Past returns appeared to increase testosterone levels. Higher cortisol was associated with less risk taking.

out of 9 papers on students reporting no significant results (Apicella et al. 2015). When significant, the results are sometimes only for one sex, or in the opposite direction, overall inciting to prudence concerning an association between this ratio and behavior. We must however here mention Coates et al. (2009), who correlated the P&L of high-frequency traders over a 20 months' period with their 2D:4D ratio. They found that traders with a lower 2D:4D survived longer in the market and displayed higher profit. In their follow-up study (Coates and Page 2009), they realized studying the Sharpe ratio of these traders that this effect was largely mediated by a higher tolerance for risk.

If the 2D:4D studies should be taken with a grain of salt at the moment, Cronqvist et al. (2016) were able to use a sounder measure of testosterone exposure during the fetal stage. Testosterone exposure in utero is critical for the development of a male fetus – a male fetus is on average exposed to almost thrice the amount of testosterone of a female fetus. When both a male and a female are present in the womb, the female is exposed to a higher than usual amount of testosterone. Using this fact, Cronqvist et al. (2016) studied data from 34,000 Swedish twins, including their assets holding at the end of the year. After controlling for demographics, they found that having a male co-twin was significantly related to the fraction of securities invested in risky assets, portfolio volatility, and the proportion of stocks as opposed to mutual funds held in the portfolio for a female. Therefore, exposure to prenatal testosterone was having the effect of closing the gender gap on risk-taking in their studies, from 10% to 30% depending on the variable used to assess risk-taking.

Facial masculinity yielded somewhat more conclusive results than 2D:4D. It can be measured from a forward facing portrait of subjects taken with neutral expression. Apicella et al. (2008) found it to be a significant predictor of risk-taking in male students in the lab, even after accounting for circulating level of testosterone and 2D:4D. Facial masculinity can also be computed out of publicly available photos, which makes it particularly amenable to the study of CEOs. Two studies have used a simplified measure of facial masculinity (width to height ratio). Wong et al. (2011) found a significant positive relation between this ratio and firm performance, as measured by ROA over the period 2003-2004 on 55 CEOs from Fortune 500 companies. Jia et al. (2014) studied a larger sample of male CEOs from the S&P 1500, from 1996 to 2010. They found a significant association between this ratio

of facial masculinity and various financial misreporting proxies¹⁸. They also found a significant link between this facial masculinity measure and the likelihood of the firm to be subject to a SEC enforcement action. In addition, more masculine CEOs were more likely to be named as perpetrators by the SEC. Finally, they also found evidence that facial masculinity was linked to a proxy detecting potential insider trading, and to option backdating¹⁹.

Overall, the results on the 2D:4D are rather mitigated, with half of the studies finding no effect. If for facial masculinity the results appear more conclusive, a number of alternative explanations to brain masculinization could be formulated. For instance, a CEO appearing more “masculine” could be preferred to a less masculine one in the hiring process of riskier firms, or a more masculine CEO could take more risks out of social desirability. Studies trying to disentangle purely biological effects from socially related ones are therefore advisable. Results on these past markers of testosterone exposition thus need to be taken with caution.

2.3. *The impact of genes on risk attitude*

Risk aversion of an individual is often thought as a black box in finance and economics. Its determinants are hard to pinpoint, even though they lead to a significant heterogeneity in portfolio selection for instance. Generally, studies trying to pinpoint the origin of these differences arrive at a R^2 far below 10% (Barnea et al. 2010). Recently, some evidence has underlined the importance of the genetic component in risk-taking.

2.3.1. *Twin studies*

One way to assess the overall genetic component is to make use of twins. Twins can be either genetically identical (monozygotic twins) or genetically different (dizygotic twins). Studies then decompose an outcome variable for an individual as coming from the influence of additive genetic factors, common environmental factors and specific environmental factors for these twins. The idea is to observe the correlation of the outcome variable across each pair of twins – if the correlation is stronger for identical twins, it means a significant share of the variance of the outcome variable is explained by

18. Namely, the F-score whose computation relies on information about accruals quality, performance and market-related incentives.

19. Backdating an option consists of the a-posteriori selection of a favorable grant date of the option that increases the value of the option to the CEO.

genetics. The method is subject to a set of hypotheses, the most stringent one being probably the equal environment hypothesis, stating that monozygotic twins and dizygotic twins share an equivalent environment.

Two studies (Cesarini et al. 2010, Barnea et al. 2010) took advantage of this design and exploited the Swedish database on twins, the largest in the world. Cesarini et al. (2010) exploited this database on twins alongside the asset allocation of Swedish twins in their pension plan. They found that roughly 25% of the variation in portfolio risk was due to genetics, even after controlling for various demographic variables. Another 70% was accounted for by the nonshared environment. They further underlined that the genetic contribution of behaving as an active investor (not taking the default fund) was 40%, while investing in an ethical fund reached 60% and behaving as a return chaser 30%. They hypothesized that genes involved in the regulation of the dopaminergic system might be particularly important in this explanatory power of genetics.

Barnea et al. (2010) confirmed these results by analyzing the same Swedish database on twins. This study however used information on the whole wealth invested in financial assets of the participants, and can therefore be considered more comprehensive. The authors found that the share of investment in equity was explained at around 28% by genetics, whereas preference toward volatility was explained at 37% by genetics. As in the first study, the shared environment was estimated to be close to zero. The largest share of variance was here again explained by the non-shared environment. The genetic and the shared environment parts were having a much stronger effect between the age of 20-30, before sharply declining and staying roughly constant over the rest of the lifetime.

These results are striking, but perhaps not so surprising. In such behavioral genetic studies, it is extremely common for the genetic part to be more important than the shared environment part. In turn, the non-shared environment is generally the most important part, often explaining around 50% of the behavior under consideration²⁰.

2.3.2. *Genotyping studies*

A limitation of these studies is that they do not directly link the part of risk-taking explained to specific genes. One way to do so is to genotype

20. See for instance Turkheimer (2000) "Three Laws of Behavior Genetics and What They Mean".

individuals, in order to measure which genetic variants they possess. Early work only measured a few carefully selected genes, “candidate genes”, on small samples, because of cost consideration. Large scale genome-wide association studies are starting to take place, where the whole genome of a large sample of individuals is assessed. Benjamin et al. (2012) performed such a study, where they measured several economic preferences, including a measure of risk aversion. As their sample is composed of twins they replicated previous studies and show that the heritability of the traits measured is around 30-40%. However, they found no significant relation between specific genetic variants and the preferences measured, including risk, once the correction for multiple hypothesis testing was performed. Benjamin et al. (2012) propose a fourth law of behavioral genetics, presented in greater depth in a later article (Chabris et al., 2015): *“A typical human behavioral trait is associated with very many genetic variants, each of which accounts for a very small percentage of the behavioral variability.”*

For instance, Rietveld et al. (2014) managed to find significant association between three genetic variations and educational attainment, each having an extremely small effect size, $R^2 \approx 0.02\%$. This type of effect size requires a large sample in order to be detected. Accordingly, Benjamin et al. (2012) encourage readers to be cautious toward findings from genotyping studies with samples of only a few hundred individuals at most, even on candidate genes, such as the ones we will present in the following.

Studies on candidate genes involved in the brain’s dopamine and serotonin activity have been performed on small samples of students. Dreber et al. (2009) highlighted that the allele 7R+ in the dopamine receptor D_4 gene compared to the allele 7R- leads to more risk-taking in a risk elicitation task, after controlling for testosterone levels (n=98, males). They estimated that this would account for roughly 20% of the total heritable variation in risk-taking. Zhong et al. (2010) underlined that variations in the Monoamine Oxidase A Gene (MAOA, implicated in the catabolism of dopamine) were associated with attitude toward longshot risk in lotteries and weakly related to hypothetical demand for insurance (n=350). Frydman et al. (2010) also showed that carriers of a specific form of the MAOA genes were more likely to take risks, but they find no significant influence of the various alleles of the D_4 and 5-HTTLPR gene (n=90).

He et al. (2010) underlined that genetic variations coding for serotonin transport (5-HTTLPR gene) were linked to uncertainty and loss aversion in

the lab. Kuhnen and Chiao (2009) found that carriers of the short allele of the D_4 gene and that 7R-carriers of the 5-HTTLPR gene take less risk (n=65). Kuhnen et al. (2013) underlined the potential pathway of expression of these genes. Short allele carriers of the serotonin transporter gene (5-HTTLPR) indeed displayed increased neuroticism and negative affect associated with anxiety, after controlling for a number of demographic factors (n=60). This mediated a decrease in financial risk-taking. Short allele carriers had better credit scores and less credit line, and were less active in managing their financial assets. When asked to allocate a sum of money between different assets, they chose to allocate less in stocks and more in cash.

Sapra et al. (2012) genotyped 60 Wall Street intermediary traders²¹ and compared their share of alleles of specific genes involved in the dopaminergic and serotonergic system to a control group. They found that alleles coding for intermediate levels of dopamine, and therefore promoting milder levels of risk-taking, were more prevalent in the group of traders. A propensity for mild levels of risk taking could be advantageous for intermediary traders. Specific COMT alleles were correlated with the numbers of years working as a trader, a proxy for success in Wall Street in this study. They found no impact of various alleles involved in serotonergic pathways.

Overall, there is evidence pointing to the fact that the share of risk preference explained by genetics is so by different alleles of genes involved in the serotonergic and dopaminergic systems. However, the only large scale genome-wide study on risk taking found no significant results, the only significant results being on a small sample of students on candidate genes, with the caveat depicted in introduction to the chapter. The exact mechanisms by which the gene influences the risk-taking behavior of individuals is therefore still unresolved.

3. How may neurofinance better explain discounting and credit related decisions?

A large part of the financial theory deals with intertemporal decision-making, allowing the comparison of various outcomes at different points in time in order to produce an optimal allocation of the resources.

21. Traders who buy and sell financial assets on behalf of clients rather than for their firm.

The intertemporal choice that resides at the center of discounting seems to be closely related to the choices under risk, as both correspond to comparing and choosing between two alternatives. One of these alternatives is outside of the immediate perception, either because it could or could not eventually manifest itself (risk decision) or because it will only manifest itself later (intertemporal choice). One might easily argue that something that is going to happen in the future is, by the most common experience, risky. Many researchers have indeed argued that the behavioral impact of time distance in intertemporal choice is the same as the impact of probability in the risk decision. That connection has been made for humans and animals alike (see for example Kagel et al., 1986; Prelec and Loewenstein, 1991; Kacelnik and Bateson, 1996; Green and Myerson, 1996, 2004; Sozou, 1998; Frederick et al., 2002; Yi et al., 2006). The neurological mechanisms seem however different and justify treating discounting separately from risk. For example, behavioral studies dissociating these can be seen in Rachlin et al. (1986) Snyderman (1987) or Mazur (1989) and evidences from lesions seem to concur (Cardinal and Howes, 2005).

The classical financial approach, originally put forth by Samuelson (1937) contains a number of axioms for “Discounted Utility Theory” (monotonicity of time preference, completeness of time preference, intertemporal transitivity, continuity of time preference, intertemporal independence, stationarity). This setting of discounting, however, has been criticized and challenged. Many behavioral studies, both with humans and animals, have exposed many systematic violations of this theory of intertemporal decision, implying that the neurological mechanisms at play may not follow the tenets of traditional exponential discounting.

For example the stationarity axiom predicts that the order of preference between multiple timed items should remain identical when they are shifted by a constant period. Empirical evidence shows that often there is a reversal of preferences when the two alternatives are further in the future, despite an identical interval between them (Green and Myerson, 1996). When immediacy is involved, that phenomenon is increased to the point where discontinuities of preferences may happen (Thaler, 1981).

The neuroscience research that can shed light on the topic needs to understand two elements, the concept of “delay” or time distance, and the concept of “gratification magnitude” or possibly “displeasure magnitude” (which may not be treated in a similar way) and how the treatment of such

elements interacts in the brain. Moreover, the neural representation of the “subjective value” of our choices, may or may not be a “common currency” (Montague and Berns, 2002) and could instead be distributed and specific to the decision domains. One key element is to understand how the impact of time may be non-constant, supporting hyperbolic discounting against the standard exponential.

We are going to depict in the following the neurofinancial studies that deal with discounting and credit related matters. As for financial risk, we are going to tackle first neuroimaging studies, that underlined the impact of emotions on these decisions. We are then going to move on to the impact of hormones and genetics.

3.1. The role of emotions with respect to time and default – brain imaging

3.1.1. Time and reward neural representation

In order to make an intertemporal decision, in other words, to discount, two elements are present and their representation has to correspond to some brain mechanisms. These two elements are the magnitude of the reward or subjective value of the cash flow considered and the distance separating the decision-maker from said reward.

The activation of various brain areas corresponds to the information needed to represent the actual or expected magnitude of a reward. The activity of single units of the brain is modulated by the magnitude of an expected reward: the dorsolateral prefrontal cortex (DLPFC) has been pointed by some, like Leon and Shadlen (1999) or Wallis and Miller (2003). The orbitofrontal cortex (OFC) activity is also a function of the magnitude of the gratification, as shown by Wallis and Miller (2003), Roesch and Olson (2004) or Van Duuren et al. (2007), and the post-arcuate premotor cortex (Roesch and Olson, 2004) of rats and monkeys, and in the avian equivalent of the prefrontal cortex (Kalenscher et al., 2005) is also related to that reward size. The activation of these areas takes place either during the presentation of a reward-predicting cue, or during the delay between the cue and the delivery of the reward, hence before the actual reward is delivered.

These elements are considered an indication that frontal structures play a central role in assessing the value of a reward both when it is current and

when it is delayed and expected to happen in the future as indicated by Schoenbaum et al. (1998), Montague and Berns (2002), Winstanley et al., (2004) or Van Duuren et al. (2007). In terms of single units involved in the evaluation of a reward, we also find the striatum, in particular in the ventral striatum, including the nucleus accumbens (NAc) (see for example Cromwell and Schultz, 2003), as already pointed out in the risk part. Different zones of the OFC, DLPFC or the basolateral amygdala (BLA) as mentioned in Schoenbaum et al. (1998) discriminate between anticipated rewards according to quality and type as well as simple quantity. One might note that the amygdala controls reactions of fear and anxiety. Again, we might note here that if the DLPFC is rather related to higher cognitive function such as planning or emotion regulation, the other structures are again related to emotions.

Just like the reward magnitude, time or delay in gratification correlates with activity in multiple brain areas. Several distributed zones have been shown to be involved in the evaluation of time intervals, including thalamus, cerebellum, striatum and various parts of the cortex (see Buhusi and Meck, 2005 for a review). The evaluation of delays in the brain might come from a climbing or ramping activity, that is, a progressive (possibly in a linear fashion) increase in neural discharge rate during a given delay (see for instance Komura et al., 2001).

In using a temporally distributed discounted task, Ballard and Knutson (2009) have managed, using fMRI, to observe simultaneously reward magnitude correlates (nucleus accumbens, mesial prefrontal cortical and posterior cingulate cortical activation) and temporal delay negative correlates (dorsolateral prefrontal cortical and posterior parietal cortical activation). This allows to better understand the combined effect of both elements central to rewards discounting.

3.1.2. Neuroanatomy of Delayed Reward Discounting

Discounting, also known to neurologists as “delayed reward discounting”, is the element that allows the comparison and ultimately the choice between a small immediate reward and a larger one that will be obtained in the future, based on how much things lose value by virtue of being shifted into the future. As this is a very complex and involved mechanism, it is mostly studied via anomalous behaviors (Bickel and Marsch, 2001; Madden and Bickel, 2009). These studies are also frequently performed on animals since

Delayed Reward Discounting seems to be an evolutionary ancient function (Hodges and Wolf, 1981).

Indeed, steep discounting, or strong preference for immediate rewards, is involved in a number of behaviors connected with impulsivity, such as credit card debt (Meier and Sprenger, 2010), frequency of health screenings (Bradford, 2010) or even with pathologies such as substance addiction, gambling disorders, and attention deficit hyperactivity disorder (Reynolds, 2006; MacKillop et al., 2011; Amlung et al., 2017; Jackson and MacKillop, 2016).

Two meta-analyses of fMRI studies (Carter et al., 2010; Wesley and Bickel, 2014) seem to indicate that when making temporal decisions, the areas of the brain that are activated relate to valuation of reward (mostly the ventral striatum, orbitofrontal cortex, insula, ventral tegmental area), to self-reflective and future-oriented thought (e.g., medial prefrontal cortex, posterior cingulate, temporoparietal junction, lateral and medial temporal lobe) and to cognitive control (like the dorsolateral prefrontal cortex). In contrast to the large number of fMRI studies of intertemporal decision, there have been surprisingly few studies trying to relate brain structures with DRD (Delayed Reward Discounting). Cho et al. (2013) in a study on a rather small cohort (34 young healthy subjects) find that DRD was associated with grey matter volume in the ventromedial prefrontal cortex, the anterior cingulate, and the ventral striatum. A later study by Tschernegg et al. (2015) also found a relation between ventral striatum grey matter volume and DRD, when only looking at subcortical regions. However, two other studies found associations with the lateral prefrontal cortex, but not the medial prefrontal cortex (Mohammadi et al., 2015).

It is clear that the neuro-sources of discounting are at the same time rich and a key to understanding a lot of our behavior, particularly when it becomes “pathological”. However, a large part of the mechanisms involved are very complex and therefore, still not perfectly understood.

3.1.3. What can we learn from neurofinancial brain-imaging on real estate and mortgage default?

An extensive use of brain imaging techniques to unveil the reasons behind practical issues related to discounting was performed by Seiler et al. who studied the real estate domain. In particular, in the wake of the subprime crisis, these authors conducted a systematic and thorough investigation of

the reasons behind Strategic Mortgage Defaults²² through three papers. An interesting point of these studies was that they used as a sample middle-aged people who actually owned a house, making these studies more ecologically relevant than if a student sample had been used. As they underline, the use of fMRI enabled them to “see behind the curtain and truly observe the underlying thought processes that motivate people to behave the way they do” (Seiler and Walden, 2015).

In a first study, Seiler and Walden (2014) test two theories behind strategic mortgage default: sunk cost fallacy and cognitive dissonance. They present to homeowners 36 hypothetical mortgage scenarios, in which the purchase price of the home, its current price, the loan balance, down payment and equity position varied. The authors do not find support for sunk cost fallacy, as subjects in their experiment behaviorally give priority to the (negative) equity position. However, they find support for cognitive dissonance. Through fMRI, they found that having a large negative equity was associated with a peak of activity in the anterior cingulate cortex, an area that was linked in previous work with cognitive dissonance (Van Veen et al. 2009).²³ They also found that the decision to strategically default was associated with an increased activity in the lingual gyrus and motor cortex, which are areas activated when people engaged in autobiographical thinking. It therefore appears that homeowners experience significant cognitive dissonance when being confronted to negative equity situations, and thus engage in some form of autobiographical justification when making the decision to strategically default.

In a second study, Seiler and Walden (2014) studied whether the reputation of the lender (conservative versus “egregious”), its implementation and relation with the borrower (local v. online) and the number of foreclosures in the area of the homeowner affect the decision of strategically defaulting. They also varied whether the bank granted a loan modification to the borrower. Behaviorally, it appeared that being granted a modification of the loan, borrowing from a local bank, a conservative one, and being in a region where defaults are rare all had the effect of reducing the willingness to default. The neural circuitry involved when dealing with a lender having morally reprehensible lending practices was coherent with an attempt at inhibiting a retaliation action. In situations where defaults are rare, the

22. A situation where an individual can afford the monthly loan payment but still chooses to default.

23. As noted earlier, the cingulate cortex is overall heavily involved in emotion regulation.

neural circuitry involved pointed toward increases in a disgust feeling, as if people were thinking about breaking a social norm. When the bank refused a loan modification, the neural circuitry involved was coherent with retribution-seeking thoughts. Overall, the neural circuitry activated was composed of numerous brain structures involved in emotional processing.

In their third and last study on strategic default, Seiler and Walden (2015) studied informational and social factors. Subjects were again presented with an array of situations where their equity balance on their home was negative. However, in this experiment the authors presented subjects with opinions, both from a real estate expert and other homeowners. Behaviorally speaking, it appears that subjects tended to follow more the opinions that promoted strategic defaulting than the opinions that promoted no defaulting. Behavioral brain imaging data underlined that both when receiving advice from a peer home-owner and advice from a real estate expert, areas in the visual cortex (occipital pole, lateral occipital complex and occipital fusiform gyrus bilaterally) known to be related to stimuli associated with human beings were more activated than when no advice was given. There was thus a social dimension to these pieces of advice. In addition, when receiving advice from peers, the precuneus cortex was also significantly activated, which is congruent with the mental representation of self. The authors concluded that there is therefore a form of social awareness to peer advice, where subjects feel freer to take their own decisions, whereas they think more like followers when presented with expert advice.

A final study on the topic of real estate investment – not dealing with strategic default – was performed by Gibson et al. (2016). In a rigged fMRI experiment, they study how subjects make decisions over prospects, sometimes exhibiting negative skewness (which is the case of Real Estate Investment Trusts, REIT). They also ask knowledge questions to their subjects in between trading periods, to assess whether performance on the market affects efforts in other areas of life. Their first interesting finding is that subjects focus more on “local” (recent) gains and losses than on the global ones, a finding in line with mental accounting (Thaler, 1980). Second, they show that after a gain subjects are more willing to choose negatively skewed prospects (large probability of moderate gain and small probability of a large loss). In addition, such a decision activated significantly less all the brain regions of their subjects, as if there was not much thought granted to the question. They interpreted this finding as pointing to the fact that

people might be more willing to hold on previously gaining REIT during times of crisis. Finally, they found that after losing during a trading period, subjects devoted more cognitive effort on knowledge questions, without it resulting in better performance. They interpreted it as a sign of potential contagion effects between different life domains.

The use of fMRI in these studies therefore enabled to unveil what was felt by the subjects during the decision process. The three papers on strategic default provide a unique insight into the neurological process involved in taking the decision, from the individual to the social aspect on the highly relevant and current topic of strategic default. Again, as in the part concerning risk, we might note how the brain structures activated are massively from the emotional system.

3.2. The endocrine system and discounting

We noted in the introduction to this part on discounting the similitude existing between discounting and risk. As for risk, some papers have investigated the link between circulating level of testosterone, a marker of past exposure to testosterone, cortisol and discounting. Another avenue of research concerning discounting has been to investigate the relation between alpha-amylase, a digestive enzyme²⁴ present in saliva, and discounting. Alpha-amylase levels are indeed thought to increase as a response to stress. However, the research is less extensive than for risk, and generally used small samples of young students.

3.2.1. Circulating level of hormones/enzymes and their link with discounting

Takahashi et al. (2006) investigated the link between endogenous testosterone levels and the discounting of delayed gains and losses in 75 male students. They do not find any link between testosterone and discounting in the loss domain, but find an inverted U-shape link between testosterone and discounting in the gain domain. Their findings are rather in line with Doi et al. (2015). While Doi et al. (2015) found a positive correlation between discount rate and testosterone for the female part of the sample (n=30), they find a negative one for the male participants (n=27). Since males have higher testosterone levels on average, when analyzing male and

24. Alpha-amylase is therefore not a hormone, and is not part of the endocrine system. It is thought to reflect the activity of the adrenergic system. We however included it in the endocrine system part, as its method of measurement also involves saliva sampling, and similarly to hormone levels a correlation is then sought with the dependent variable of interest.

female together, the overall pattern is again an inverted U-shape. However, and similarly to what was observed for risk, it appears that the exogenous administration of testosterone compared to a placebo had no effect on the discounting rate (Ortner et al., 2013). Again, it could either be because there is no actual causality between testosterone levels and behavior, or because the effect of exogenously administered testosterone differs from that endogenously present in the body.

Takahashi et al. (2010) is the only²⁵ study to our knowledge to study the link between stress hormonal and enzymatic levels (cortisol, cortisone and alpha amylase) and the discount rate of 42 males and 45 females. They found alpha-amylase to be negatively related to discount rate in subjects who never smoked. Cortisol and cortisone were negatively related to discount rate in non-smoker men and positively related to it in non-smoker female. No significant relation was found for smokers.²⁶

Finally, we must note the study of Kimura et al. (2013). Instead of administering cortisol exogenously, they induced a stress for their subjects through the Trier Social Stress Test. This test consists in requiring subjects to perform a speech in front of an audience for 10 minutes, followed by the performance of arithmetic calculations in front of the same audience. Subjects' discount rates were elicited prior and after this task. The authors indeed find an acute stress response in their subjects due to the task, with an elevation in perceived stress, heart rate and cortisol. They proceed to show that the 30% of subjects presenting the greatest elevation in cortisol levels were also seeing a sharp increase in their discount rate. Here again, the sample was rather small (39 subjects), limiting the scope of the results.

3.2.2. Testosterone at critical stages of development and discounting

Lucas and Koff (2010) is the only study to have investigated the link between 2D:4D and the discount rate. They find no link between the ratio and discount rate in males, but found lower 2D:4D ratio to be linked with higher delayed discounting in females. Similar to the part of risk, we reiterate our word of caution concerning the 2D:4D ratio, and suggest

25. Not including Takahashi et al. (2004) who found that low cortisol levels are associated with larger discount rate and Takahashi et al. (2007) who found that low levels of alpha amylase are also associated with larger discount rate, as these two studies each have a sample size of 18 subjects and are therefore rather exploratory.

26. Since discounting has been reported to be related to a variety of non-healthy behaviors including drug abuse and smoking, the lack of relation for smokers might make sense. But a significant limitation of this study is the fact that 38 subjects were smokers in the study, therefore limiting the number of subjects for whom a relation was found to 49.

the corresponding results should be taken with a grain of salt until further evidence is gathered.

3.3. The impact of genes on decisions involving discounting

3.3.1. Twin studies

In the previous part on risk, we cited two studies using the Swedish twin database and crossing the data either with the pension system data (Cesarini et al., 2010) or with data from the 1.5% wealth tax from the Swedish tax agency (Barnea et al. 2010). The second method appeared more robust, as it enabled a better view of the total wealth position of the individuals in the study. Two of the authors of this latter study (Cronqvist and Siegel, 2015) used the same database to decompose this time saving behavior as coming from the influence of additive genetic factors, common environmental factors and specific environmental factors. The findings are again striking: roughly 33% of the variation in savings propensities is explained by genetics, the remaining being explained by the non-shared environment. It appears that the common environment was having little to no effect. The findings were robust to various measures of savings.

In another twin study, Cronqvist et al. (2016) again used their database from the Swedish twin registry, to assess genetic and environmental explanatory power in various decisions regarding home-ownership. One of the decisions they investigate is of direct interest for finance and is linked to discount rate: renting versus buying. Without accounting for socioeconomic factors, they found the proportion of variance explained by genetics to be around 50%. When accounting for socioeconomic variables which explained 55% of the variation in the tenure decision, the proportion drops to 21%. The proportion of variation explained by the common environment is negligible again.

Overall, as for risk, it seems that financial decisions linked to the discount rate have a significant genetic component, which seems to be around 20-30%.

3.3.2. Genotyping studies

As underlined in the risk part, a limitation of these twin studies is that they do not pinpoint directly the genes responsible for the behavior observed. It however appears that the genotyping efforts have been more limited regarding attitude toward time.

Seiler and Walden (2016) carried out a genotyping study comparing eight borrowers who chose to strategically default on their loan versus nine who chose not to default. The author studied the dopamine receptor D_4 gene, the 5-HTTLPR gene and the COMT gene that produces an enzyme regulating dopamine level in the brain. The reader might note that such genes have already received attention in the risk part. While the author finds no specific association for the D_4 and the 5-HTTLPR gene, he finds that individuals having 1 or 2 of the “A” alleles on the COMT gene were more likely to be a strategic defaulter. As the author recognizes, his study is mostly exploratory due to the small sample size, but we must again note the ecological validity, as the sample consists of home-owners that actually defaulted.

To our knowledge, only two other papers on genotyping studies have been published, both on a sample of 91 subjects. Kawamura et al. (2013a) studied the Dopamine Receptor gene DRD2 and find that subjects having more minor alleles (T) on the SNP C957T had a higher discount rate, while Kawamura et al. (2013b) investigated the FKBP5 gene, whose overexpression results in a higher cortisol level. The results underline that subjects with more minor alleles (T) displayed less impulsivity.

The genotyping research is therefore still nascent concerning the discount rate, saving and defaulting decisions. Overall, research in the area confirms the importance of genes linked to the dopaminergic circuitry in the brain, which is already a point of focus of research on risk aversion.

4. How may neurofinance better explain stock market reaction to information?

The last century has been characterized by the development of financial theories which allowed one to analyze and explain how information may influence investors when trading, and what is the impact on prices and market equilibrium. On one side, this has been very fruitful because some papers managed to develop theories on how the investors use information and how it is incorporated into financial markets. Some fundamental papers like Fama (1970) developed the efficient market hypothesis (EMH) and made more understandable how information is integrated into prices. Other papers like Grossman (1976) and Grossman and Stiglitz (1980) or Akerlof (1970) built models on how the uninformed infer information signals from the informed on financial markets. On the other side, the theory of market

efficiency seems unsatisfactory for at least three reasons. The theory relies on such stringent constraints that it is hard to find it realistic (perfect markets, free access to information, investors' rationality, etc.). Second, anomalies have put into question the foundations of the financial theory. The major and primary works, which have put forward market anomalies, are those written by Thaler and Shiller on market inefficiencies. DeBondt and Thaler (1985, 1987, 1990) have proved empirically the existence of investor and analyst overreaction, illustrating the representativity bias. According to Shiller, stock returns are predictable over the long term, and dividends yields and Earnings-to-price ratio are significant predictors of future stock returns.

Last, we do not know really which mechanisms are used to infer information from prices and trades. Thus, neurofinance is a cornerstone to better understand which neural circuits and biological drivers are at work to make financial decisions on the basis of information in situations of risk or uncertainty, and to analyse more deeply which regions of the brain are activated when the investors try to infer information from the markets. This part is devoted to explaining how neurosciences may help better understand the financial mechanisms when the investors learn or infer information and how they react to public information when trading.

4.1. Information process and trading decision: how is the efficient market hypothesis put into question?

The EMH, which stipulates that stock prices fully reflect all available information, relies on very strict hypotheses, like perfect markets, atomicity of the financial markets and investor rationality. The major ambiguity to EMH is linked to the fact that we do not really know how the investors take into account information into their trades. The EMH assumes that every investor revises his/her own expectations by following the Bayes rule. The EMH depends on this assumption, but it is not easy to detect which brain mechanisms are used when people observe information or observe prices on the financial markets. In these conditions, neurofinance may be a good tool to examine how the investors really infer information signals on the market. This is the main contribution of neurofinance to financial decision-making.

The efficient market hypothesis (EMH) assumes that all investors, especially the uninformed, have rational expectations and make up their minds

in a uniform manner. However, by analyzing deeper the way that investors build their strategies, we can suspect that brain activity may depend on market conditions, the direction of trades and losses and gains. By using EEG²⁷ (Electroencephalography) to map the brain, Vieito, Da Rocha and Rocha (2015) prove that the investors do not show the same neural circuits when buying, selling or holding their positions. Moreover, it seems that bear and bull markets may have a different influence on the way that the investors make up their minds in financial decision-making. Gehring and Willoughby (2002) also used the electroencephalogram (EEG) to analyze brain activity associated with financial decision-making and found that a negative-polarity event-related brain potential was greater in amplitude in the case of losses than in the case of gains. We may deduce that brain activity is probably different when strategies result in losses and gains.

In the same way, neurofinance has been helpful to show that gender may have an effect in financial decision-making. Vieito et al. (2013) are the first to investigate if men and women show different brain activity when making up their minds. They chose to examine decisions made by men and women on financial markets when these markets were growing or very volatile. The results, originating from the use of the EEG proved that men use the same region of brain when buying, selling or holding their positions, whereas women were using different neural circuits during the three types of decisions.

The EMH also makes the assumption that uninformed traders are perfectly able to infer information from trades. In the extreme, Grossman and Stiglitz (1980) show us that through this specific mechanism the uninformed could be able to infer the same signals as those received by the informed traders. In this context, the financial markets could ultimately disappear because no one would have any incentive to pay for information which could be easily observed by others without paying and taking risk. However, the financial markets continue to function, because there is some noise in the system which prevents the uninformed from observing

27. EEG is a physiological method to record all of the electrical activity generated by the brain from electrodes placed on the scalp surface. It provides excellent time resolution, but poor spatial resolution. As the electrodes measure electrical activity at the surface of the brain, it is difficult to know where the signal comes from exactly, either from the cortex or from another region of the brain. Thus fMRI, which is a complex imaging methodology, is complementary to EEG, because fMRI provides a precise map of the brain, by describing how it looks at a set moment in time. However, the drawback with fMRI is the temporal resolution. As it takes several seconds for the blood flow to change, and the actual recording is limited by computational factors, the data collection is slowed down. See table A-1 in appendix for more details about the tools used in neurofinance.

the same information (transaction costs, Grossman and Stiglitz, 1980; exogenous demand, Hellwig, 1982; relaxing the price-taking assumption, Jackson, 1991).

However, the assumption according to which the uninformed can perfectly infer information from prices has not been examined up to now. This is the goal of papers such as Bruguier et al. (2010) who analyse trader intuition. Instead of relying on mathematical or logical foundations, biological mechanisms, issued from Theory of Mind, are at the origin of the information process by the uninformed. Theory of Mind contributes in the analysis of mental states, such as beliefs, intentions, desires or knowledge from others. The authors report that skill in forecasting price changes in markets with insiders is correlated with Theory of Mind, the ability to detect intentionality in the strategic environment. The activity of some brain regions suggests that Theory of Mind is at work instead of mathematical or logical mechanisms.

Standard asset-pricing theory assumes that investors are price-takers instead of having strategic behaviour. In other words, they cannot influence prices by their trades and have no intention other than trading. Considering this hypothesis, we do not really understand why financial markets can lead to bubbles and if we are conscious that stock prices may derive from the fundamental value, bubbles are hard to predict when starting and exploding. By observing this phenomenon, De Martino and Camerer (2013) succeed in proving that neural mechanisms may explain the formation of bubbles on the basis of Theory of Mind. They prove that investors are naturally inclined to forecast others' intentions when they anticipate the future value of stocks and consider the market being strategic. They do not rely only on the observation of stock prices and trades. More precisely, De Martino and Camerer (2013) led an experiment using functional magnetic resonance imaging (fMRI) and discovered that a specific region of the brain (the ventromedial prefrontal cortex, vmPFC) is highly solicited when the subjects build their expectations of future values or prices. In the case of bubbles, the increase of prices provokes a representation of inflated trading values, which incites the subjects to buy. This representation comes from another region of the prefrontal cortex, the dorsal prefrontal cortex (dmPFC), used to represent the mental state of other individuals. This region of the brain, which is linked with Theory of Mind, is highly activated in revising prices

in the vmPFC. The subjects integrate the intentions of others when they anticipate prices.

Palan (2013) has made a large survey on bubbles and crashes in experimental asset markets. On the basis of the famous article written by Smith et al. (1988), they compile the work done in around 60 papers which replicate the initial structure of Smith et al. (1988) with variations, which may explain the formation of bubbles and crashes. Despite the quality of these results in the survey, no research had been conducted on the link between neural mechanisms and the formation of bubbles until the paper written by Smith et al. (2014). These authors have used a multisubject fMRI in order to measure neural activity in participants in experimental asset markets leading to endogenous price bubbles. In their paper, they show that neural activity in the nucleus accumbens drives prices towards the formation of the bubble. Conversely, the market crash seems to be associated with a high propensity to sell among high earners who receive a signal in the anterior insula cortex.

Neural mechanisms at the origin of the formation of bubbles can also be reinforced by a biological driver such as testosterone. As we have seen in the previous part, the association between testosterone (both endogenous and exogenous) and risk taking was significantly positive. Testosterone has a significant influence on human behaviour. In terms of financial decision-making, it pushes people toward higher risk-taking. Nadler et al. (2018) built an experiment on a continuous-double auction market, where a subsample of men were administered testosterone or a placebo. The administration of testosterone shifted investment towards riskier assets compared to a placebo. By controlling the subjects' level of testosterone, Nadler et al. (2018) proved that higher-testosterone traders tend to bid up at higher prices, despite the fact that they perfectly know the fundamental value, thus leading to the development of bubbles.

The formation of bubbles could result not only from the consequence of a higher level of hormones such as testosterone, but also from emotions such as excitement. In their paper, Andrade et al. (2016) prove that excitement induced by video clips just before trading induces bubbles with higher amplitude and magnitude contrary to a treatment of the same valence with lower intensity such as calm or a treatment of the same intensity with opposite valence such as fear.

4.2. *Trading and reaction to information: The role of emotions*

Since the work of Fama (1970) on market efficiency, a large body of empirical literature has shown that public announcements of information lead to stock price variations and change in trading volume on the financial markets when there is new information content in the messages. Market price variations reflect the average change in traders' expectations or beliefs due to the announcement of new information, while trades reflect the dispersion of initial beliefs and jumbling of beliefs from one investor to another. As a consequence, traders' belief revisions are a crucial intermediate between information and prices (Chen, Cheng, and Lo, 2014), and investors are supposed to follow the Bayes rule when they revise their expectations conditionally to the new information. However, these revisions are difficult to observe in real time, and database as well as laboratory experiments have failed to dissect mechanisms behind investors' belief revisions following the announcement of information. Beyond mathematical or logical mechanisms, investors may be influenced by other factors, e.g. biological or psychological. The efficient market hypothesis (EMH) in its semi-strong form largely ignores the influence of emotions on financial decision-making.

Evidence from psychophysiology (Damasio, 1994) shows that the involvement of emotions is not only crucial for accurate decision-making but that advantageous (economic) decision-making is not possible without emotions (Bechara *et al.*, 1997). Damasio 1994 defines emotions as the "collection of changes in body and brain states which are triggered by a dedicated brain system that responds to specific contents of one's perceptions, actual or recalled, relative to a particular object or event". So, human emotions serve the function of unconsciously focusing and prioritizing one's attention on significant events such as in the announcement of new information. To this extent, emotions may play a great role in explaining investors' reactions. Neurofinance may help investigate cognitive and emotional factors affecting the financial decision-making processes of individuals, groups, and organizations (Howard, 2012). Gajewski *et al.* (2017) have used skin conductance response (SCR) to observe the emotions underlying traders' belief revisions. In psychophysiology, SCR is regularly used to measure emotional arousal and to address how we attribute value to the choices we make (Naqvi and Bechara, 2006). Gajewski *et al.* (2017) have built a multi-trial within subject experiment on a simple but representative financial decision-making process

where a subject-trader first forecasts a firm's current EPS, based on historical EPS and financial analysts' consensus forecasts. Then, the subject is asked to take either a long or short position in that firm's stock. The emotional response of the participant is then measured twice: first, when the actual EPS reported by the firm in an earnings press release is announced to the participant; and second, when the participant is informed of the contemporaneous change in the firm's stock price and of the resulting gain or loss from his investment decision. The authors found that, after the earnings announcement, investors emotionally respond when they are informed of their gains or losses which convey information akin to rewards and punishment (Carver and White, 1994). According to prospect theory (Kahneman and Tversky, 1979; Tversky and Kahneman, 1992), they found that a loss is likely to lead to a stronger emotional response than a gain. They also found that emotions moderate the rational relationship between earnings surprise and excess stock returns.

Barton et al. (2014) have used fMRI in order to analyze how investors react to earnings announcements. As the level of earnings can be compared with the analyst consensus, they are processed by investors as rewards or sanctions. In the human brain, it is the ventral striatum, an area rich in dopamin neurons which encode prediction errors. Brain activation is measured by blood-oxygen-level-dependent (BOLD) signals, which capture metabolic changes around neurons processing. Barton et al. (2014) conducted an experiment where 35 adult investors forecast the earnings per share of 60 firms traded on the NYSE or NASDAQ exchange and take a position in the firms' stocks. fMRI allows scanning at the same time when investors read the earnings level and react to the earnings surprise. Barton et al. (2014) observe an increase in BOLD signals when there is a good surprise, and a decrease when there is a bad surprise. There is no effect when the level of earnings meets the consensus.

As for explaining stock market reaction, Barton et al. (2014) made regressions of stock market reaction on earnings surprise and BOLD response. They showed that the BOLD response explains 25 to 41 percent of the variance in stock returns around the earnings announcement.

These results prove the contribution of neurofinance to better explaining the relation between information, such as accounting numbers, and stock market reaction.

In the same way, when the investors receive external information in the form of advice from an expert, choices under uncertainty are affected through neural and biological mechanisms. By using fMRI, Engelmann et al. (2009) show that an expert's advice may change the probability weighting function in the direction of the expert's advice. These results support the hypothesis that one effect of expert advice is to "offload" calculations of the value of alternative behavioral options that underlie decision-making from the individual's brain.

Finally, the evolution of the financial markets or realized gains and losses may lead to investors' emotions. Lo and Repin (2002) tested the importance of emotions on a small sample of 10 professional foreign exchange traders. They measured various physiological responses linked to emotional responses, such as skin conductance responses, heartbeat, blood volume pressure, temperature changes, respiration rates and respiration amplitude. They connected these physiological responses to simultaneous market changes really lived by the traders. They notably found a relation between a heightened volatility and cardiovascular variables. Similarly, they found a relation between market events such as price or return deviation from the mean and skin conductance response. Body temperature changes also proved significant for certain types of events for less experienced traders. What is most interesting is that these features proved significant both before and after the event compared to a baseline level. The emotion was therefore not just an outcome of the events, as classic theory might have postulated. A limitation of this study, besides the size of the sample, is that the authors did not have access to the P&L of the traders due to confidentiality issues (Lo et al., 2005).

This is not to say however that being overemotional is a good thing in the financial markets. The authors of the previous study completed another paper on the topics, where this time they were granted access to the P&L of the traders. These 80 traders, with a median account size of 35,000\$ were individuals participating in an on-line training course on trading. Through an on-line questionnaire at the end of each day, the authors show that subjects who exhibited higher emotional reactions to their daily profits and loss tended to be less successful.

This importance of emotions regulation in trading was confirmed by two studies by Fenton-O'Creedy. In a first qualitative study (Fenton-O'Creedy et al., 2011), the detrimental role of non-relevant emotions emerged as one

of the main themes of the interviews with 118 traders and 10 managers. In turn, it appeared that this called for a form of emotion regulation in these traders. This emotion regulation was different amongst low experience and high experience traders. Low experience traders had apparently more difficulty in talking about emotions. They were in addition less tolerant toward negative emotions experienced after a fall in the value of their portfolio than experienced traders. Here again, there was also apparently a good side to emotions for these traders, particularly for experienced ones, as they were also related to intuitions.

Fenton-O’Creevy et al. (2012) have studied the emotional regulation of traders more deeply. They carried out a field experiment on 28 traders, measuring their heart rate variability at high frequency. Heart rate variability is the variability between two heartbeats and it is – counter-intuitively – a marker of health: the greater the variability, the better the adaptive capacity of the heart. It generally decreases with age. Crucially for this study, it is also linked to emotional regulation. Fenton-O’Creevy et al. (2012) show that there was a positive link between traders’ number of years of experience and heart rate variability, which would indicate a greater capacity for emotion regulation. However, during times of high volatility and uncertainty as measured by the VIX index, this heart beat variability tended to decrease for all traders, showing the emotional impact associated with an increase in risk. Sokhol and Hessner (2009) already underlined that experimental traders were showing greater arousal when faced with loss compared to gains. When engaging in conscious emotional regulation, by trying to take a bigger perspective, the traders were showing a reduced loss aversion, in terms of both arousal and affective behavior.

Concerning trader’s intuition, which appeared as important in the qualitative study of Fenton-O’Creevy et al. (2011), Bruguier et al. (2010) explored the topic on markets with insiders. As a first step, they showed a replay of trade that occurred in such a market to subjects who did not take part in the trading. They asked them to predict price movement. At the same time, they carried out an fMRI on these subjects. They realized that the brain regions activated were the ones corresponding to what is known as Theory of Mind, the ability to recognize malevolent or benevolent patterns in one’s environment. In a second step, the participants in the experiment took standardized tests to assess their skills in Theory of Mind. The authors then underline that this skill is significantly correlated with their ability to

predict price movements, whereas math skills were not correlated with this ability. This first neurofinance study of Bruguier et al. (2010) on the topic of intuition sparked interest in the literature. We can cite two working paper related to the topic. Corgnet et al. (2015) underline that Theory of Mind is non-significant in explaining experimental trader performance, once one takes into account the capacity to resist common behavioral biases. On the other hand, Hefti et al. (2016) highlight that there may in fact be an interaction between quantitative skills and Theory of Mind capability: traders who performed the best in their experimental markets were the ones who scored high on both dimensions. It therefore seems that there is indeed room for trader intuition, a concept strongly related to emotional capacity.

Kandasamy et al. (2016) conducted an experiment on the London trading floor. According to their experimental results on the basis of heart rate, Kandasamy et al. (2016) observed that traders are better able to perceive their own heartbeats than non-traders. Moreover, this ability is correlated with their relative performance and their survival in the financial markets. It seems that they can infer signals from their bodies easily, which helps them to perform.

5. Conclusion

This literature review examined the contribution of neuroeconomics to finance. The main conclusion is that neurofinance, through its unique set of methods, can help resolve some previously unresolved patterns in finance.

First, neurofinance allows the opportunity to cast light on the explanations behind some puzzling behaviors in the financial markets, including the multiple “biases” unveiled by behavioral finance. Behavioral finance often provides several potential explanatory theories for a given phenomenon, a fact often considered a weakness by its detractors (see Barberis and Thaler, 2003). The unique capabilities offered by neurofinance can provide the opportunity to pinpoint the most likely explanation. Neurofinance indeed enables to observe theoretical entities that were previously invisible, such as emotions or intuition (see for instance the disposition effect which appears to be explained by realization utility, Frydman et al., 2014). Second, in the same way that behavioral finance started pointing some decades ago to the impact of emotions on financial decision-making, neurofinance points to the impact of our very biological fabric on our decisions. We can only hope

that neurofinance will enable to complete the picture offered by behavioral finance, in order to obtain a holistic view of financial decision-making. Some progress has been already made in this direction, with insight from neuropsychology being used in behavioral finance papers to highlight new biases (see for example the paper on number processing recently written by Roger et al., 2018).

Finally, neurofinance has provided the opportunity to tackle novel questions that were largely philosophical in the past, such as the debate about nature v. nurture. While it might be too early to declare neurofinance “the new behavioral finance”, there is little doubt that the new methods this field provides grants finance scholars a far deeper understanding of behavior in the realm of finance. Some methods (see Table 1 in the appendix for more details and discussion) appeared particularly amenable for research in neurofinance. Concerning behavioral brain-imaging, the methods of choice are the Electroencephalography (EEG) and the fMRI. EEG will be preferred in situations where timing is more important for its better temporal resolution, and it is also more affordable.²⁸ Hormonal sampling appears a particularly useful tool for future research. The data gathered are simple to analyze, and this tool is extremely amenable for a variety of experiments, including in the field ones.

Concerning genetics, we encourage finance researcher to use twin databases, within the framework of quantitative genetic. They appear to be the tool of choice for teasing apart the contribution of the environment and additive genetic factor toward complex behavior in finance. While some papers have been published on the subject, numerous questions can still be tackled with this methodology. Clear directions for future research emerge from this literature review. While numerous studies have been carried on market finance, the research on corporate neurofinance remains scarce. We therefore strongly encourage research in this domain. In addition, the majority of studies have so far been carried out on small student samples in the lab so field experiments could provide greater ecological validity. Additionally, numerous other currently relevant biases could be investigated, such as the confirmation bias (see Pouget et al, 2017 for a recent study) or even the neural processes behind mental accounting (Thaler, 1980).

28. The fMRI is more expensive, has a worse temporal resolution but enable to see smaller details.

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Appendix

A1. Methodological aspects

Neurofinance uses neuroimaging methods, as well as methods from behavioral endocrinology and behavioral genetics. We give a necessary brief overview of these methods in Table 1, depicting their main advantages and disadvantages. This table is based mainly on the textbooks of Carter and Shieh (2015) for the neuroimaging part, Plomin et al. (2012) for the behavioral genetics part and Nelson (2011) for the behavioral endocrinology part.²⁹ Tools that we consider particularly amenable for research in neurofinance are in bold.

A few points have to be made here. Neuroimaging techniques generally require a tradeoff between *spatial resolution* (capacity to visualize small details), *temporal resolution* (time needed for data acquisition) and cost. The most common methods are the Electroencephalography (EEG) and Functional Magnetic Resonance Imaging (fMRI). The EEG presents excellent temporal resolution (milliseconds) at the detriment of a poor spatial resolution (1cm). The opposite holds true for fMRI, with a temporal resolution of several seconds but a spatial resolution of less than 1mm. Magnetoencephalography (MEG) would present a middle ground between the two solutions, with good spatial and temporal resolution. However, it is extremely costly and needs an insulated room. Positron Emission Tomography (PET) is seldom used, because of both poor spatial and poor temporal resolution, high cost and the necessity to inject radioactive products into subjects. Its only advantage resides in the possibility to use radioactive isotopes that bind to specific receptors in the brain, thus tagging them for the neuroscientist, making it a very specialized solution. Finally, lesion patients have been the traditional way of studying behavioral patterns, with the caveat that patients presenting perfectly focal lesions are rare. In addition, such lesions can become compensated by brain plasticity.

Concerning tools borrowed from neuroendocrinology, the simplest method consists in simply sampling given hormones in a group of subjects and establishing correlation with a variable of interest. A number of hormones are indeed thought of having direct or developmental effect on the brain and

29. We also would like to point the reader to two excellent on-line courses: "Introduction to Neuroeconomics" by V. Klucharev and "Introduction to Human Behavioral Genetics" by M. McGue.

thus on behavior. Salivary sampling is generally preferred, as it is completely non-invasive. For most hormones, it simply involves a subject passively drooling in a vial. It is possible with a number of hormones (notably testosterone and cortisol). As most hormones have a diurnal cycle, the sampling needs to be done at a similar time of the day – preferably at the time where the hormonal levels presents less variability – for all subjects. While this method present numerous advantages, its main downside is that it can only provide correlational evidences. An obvious solution to this problem could therefore be to directly manipulate the level or action of the hormones by exogenously administering an active compound to a test group of subjects and comparing them to a control group. While such a method presents the advantage of clearly establishing a causality, it creates a risk of side effects depending on the hormone and doses administered. In addition, exogenous substances might have different effects compared to endogenous ones.

Concerning genetics, a number of tools can be used, falling in the general categories of quantitative genetics and molecular genetics, two subfields that today tend to converge. Two of the main tools of quantitative genetics are twin studies and adoption studies. In these types of studies, individuals differing in their degree of genetic relatedness are compared to assess the part of a complex trait or behavior – whose genetic source comes from multiple genes – that comes from Additive genetic factors (A), Common environment (C), and specific environmental factors (E). Both methods are subject to a number of hypotheses quite often violated, but have tended to show over the year that a significant amount of behavior variability was explained by genetic factors. On the other hand, molecular genetics has historically been concerned mainly with simple binary traits, that could be explained by a single genetic polymorphism. However, it is now converging toward quantitative genetics, by analyzing the correlation between the presence of genetic variants and complex traits or behavior.

Some other useful measures, which can capture biological states, include Skin Conductance Response (associated to sweating), Heart Rate and its variability, and temperature. They have been used with success in a number of studies (see for instance Lo and Repin, 2002) to measure general arousal. These measures generally do not discriminate between different sources of emotions. On the other hand, Facial Recognition Software are now able to discriminate between different sources of arousal. The emotions recognized are generally the basic ones: happiness, surprise, fear, anger, disgust,

sadness (see for instance Breaban et al. 2016). Eye tracking glasses provide a means to track the focal point of attentions of subjects. Finally, while we presented these methods in isolation, some of them might be combined on the same group of subjects.

Table A1. Methodologies in neurofinance

Type	Description	Advantage	Disadvantage	
Physiological measures of arousal	Skin conductance response	Measures the increase of secretion of electrolyte solution by eccrine sweat glands in the palm of the hand at the onset of a stimulus	Non-invasive Moderate cost Excellent temporal resolution Correlates with different brain regions linked to arousal (vnPFC, insula, amygdala)	Difficult to identify the precise emotion A detailed review by Kreibitz (2010) underlines that this response might be somewhat emotion-specific, even though there is to the best of our knowledge still no consensus on the questions
	Heart rate variability	Measures the heart rate	Non-invasive Moderate cost Correlates with SCR	Difficult to identify the precise emotion
	Eye-tracking	Measures the eye-activity	Non-invasive Moderate cost Excellent spatial resolution	Does not measure neurophysiological changes
Behavioral Brain imaging related techniques	Electro-encephalography (EEG)	Records the electrical activity along the scalp, produced by neurons firing	Excellent temporal resolution (1 milliseconds recording) Non-invasive Moderate cost Relatively unobtrusive material	Poor spatial resolution (around 1 cm)
	Magneto-encephalography (MEG)	Records magnetic fields produced by brain electrical activity	Excellent temporal resolution (1 milliseconds recording) Good spatial resolution (around 1 mm) Non-invasive	Very expensive Requires a room that can obstruct magnetic fields from outside sources

Type	Description	Advantage	Disadvantage
Functional Magnetic resonance Imaging (fMRI)	Measures the activation of brain regions by detecting increase in oxygen levels (Blood Oxygen Level-Dependent, BOLD, responses)	Excellent spatial resolution (< 1 mm) Non-invasive	Poor temporal resolution (2-8 seconds) Expensive Indirect (measure BOLD responses) Noisy and cannot be performed on some participants
Positron Emission Tomography (PET)	Measures the activation of brain regions by injecting a radioactive isotope and assessing its point of decay in the brain	Possibility to use isotopes that bind to specific receptors in the brain	Poor temporal resolution (1 min) Rather poor spatial resolution (4 mm) Very expensive Radioactive injection
Behavioral Brain imaging related techniques	A magnetic field generator delivers pulses, in order to inhibit or shut down the activity in some regions of the brain	Can bring unique causal insights on the role of some brain regions	Numerous adverse effects: produces muscle contractions, risk of syncope and seizure Difficulty to stimulate deeper brain structures
Patients with lesions	Compares a group of patients having suffered lesions in a specific region of the brain to another group of healthy individuals	Can bring unique causal insights on the role of some brain regions Non-invasive alternative to direct stimulation or single/multi-unit recording (implementing a device to measure activity of a group of neurons), these other methods being rather used on animals	Often rare, and generally multiple brain structures present lesions (not focal) The effect of the lesion can be compensated by brain plasticity

Type	Description	Advantage	Disadvantage
Measure of endogenous levels of hormones	Measures hormones naturally present in the subject, through salivary (preferred) or blood sample	Salivary sample is non-invasive Generally cheap, does not require investment Data obtained is simple to analyze	Does not enable to establish causality, merely correlation Blood sample is slightly invasive – in general and when possible, a salivary sample is preferred
Administration of exogenous hormones or some agonist/antagonist related techniques	Administers hormones, or any agonist (mimics) or antagonist (blocks) molecule to subjects of a test group and compares them to a control group	Enable to establish causality (with the caveat that exogenous substances might have a different effect than endogenous hormones) Generally cheap, does not require investment Data obtained is simple to analyze	Potential mild side effect depending on the substance administered
Patients with dysfunctional endocrine organs	Compares a group of patients with absent, diseased or dysfunctional endocrine organs with another group of healthy individuals	Can bring causal insight A substitute for humans of the traditional “ablation and replacement” technique used on animals	Rare Multiple organs might be affected
Twin studies	Compare identical (monozygotic) versus fraternal (dizygotic) twins	Enables to assess the share of variation in a trait attributable to genetic, shared and specific environment Numerous large databases of twins exist: Sweden (170 000 twins), Denmark (88 000 twins), Norway, Finland, Australia, Sri Lanka (14 000 twins), and the United Kingdom	Numerous assumptions, the most stringent one being that monozygotic twins and dizygotic twins share equivalent environment Twins might not be representative of the population
Behavioral genetics related techniques			

Type	Description	Advantage	Disadvantage
Adoption studies	<p>Two main designs (1) The adoptee's method compares similarities between an adoptee and foster relatives versus biological relatives (2) The familial method compares non-biological siblings raised in the same household</p>	<p>Enables to assess the share of variation in a trait attributable to genetic, shared and specific environment</p>	<p>Can raise numerous ethical problems Data might be hard to obtain Numerous assumptions, very often violated (adoptant often a family member, might treat adopted children differently, adoption agency generally selects foster families similar to biological one...) Adoptee might not be representative of the population</p>
Behavioral genetics related techniques	<p>Determines the genetic variant an individual possesses</p>	<p>While sequencing the whole DNA of an individual is prohibitively expensive, genotyping studies on candidate genes are affordable</p>	<p>Requires to have a candidate gene to genotype, i.e. a prior hypothesis Numerous caveat: behaviors are probably the product of multiple genes that may interact, genotype environment interaction may exist, advent of epigenetic considerations (heritable change in gene expression not linked to DNA) Individual genes probably have small individual effects, leading to the need for extremely large samples. In genome wide association studies in particular, a correction need to be performed for multiple hypothesis testing</p>

A2. Brain structure and systems of interests

Figure 1. Triune brain theory of MacLean, structure and systems of interest

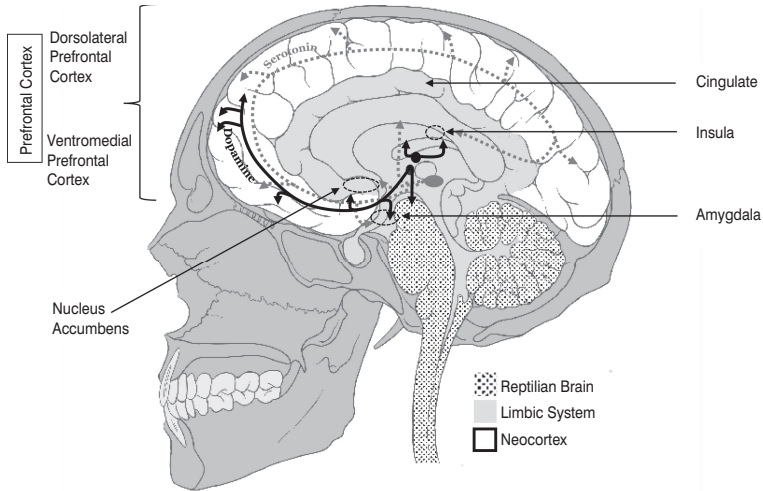


Table A2. Main functions of some brain structures of interest

System	Area	Function
Neocortex	Dorsolateral prefrontal cortex (DLPFC)	Planning and emotional regulation
	Ventromedial prefrontal cortex (VmPFC) – Including the Orbitofrontal Cortex (OFC)	Plays a role in the inhibition of emotional responses, and in the process of decision-making and self-control. Processing of the integrated values of a prospect
Limbic	Left and right ventral striatum (VSt), and particularly the nucleus accumbens (Nacc)	Reward, motivation and learning
	Insula	Involved in various emotions, awareness of body states
	Amygdala	Emotions treatment, conditioned learning, in particular for fear and anxiety
	Cingulate	Emotional processing, learning, memory

Table A.2 and Figure 1, result from the aggregation and summary of information from several sources, drawing in particular from Glimcher and Fehr (2009) and Patestas and Gardner (2015).