A literature review on neurofinance

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Abstract

Financial literature has taken to investigating individual investor behaviour. Some of the findings are quite puzzling, seeing as they are not consistent with classical models of rational behaviour. This is a challenge that has been partially solved by new models of investor behaviour in behavioural finance. Neurofinance has emerged as a new field since the late 1990s, seeking to understand the underlying aspects of financial decision-making. Psychology and neuroscience are some of the research fields that are merged in neurofinance to physiologically test finance theories. Our aim in this paper is to review the most prominent topics in neurofinance.

Keywords: neurofinance, emotions, investor sentiment, investor behavior

1. Introduction

For most people, finance is a matter of money, interest rates, savings, taxes, investment strategies, equities, bonds and stock markets. Numerous studies use quantitative data and build models. Assessing investor behaviour (Germain et al., 2014 among others) is one of the key research questions in this domain. Consequently, the psychological processes as well as the neural processes involved in financial decision making must be analysed.

Traditional finance paradigms assume that markets are efficient, and that market participants are rational. According to these theories, any irrationality should disappear in a competitive market (Friedman, 1953; Barberis and Thaler, 2003). However, market events such as bubbles and the latest financial crashes for instance, indicate that investors may not use all the information at their disposal, and that they may not always behave

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in a rational manner. As a result, several authors have dropped the market efficiency hypothesis and the assumption of the rationality of investors (Shiller, 2003). New financial decision settings were investigated (Kahneman and Tversky, 1979; De Bondt and Thaler, 1985; Benartzi and Thaler, 1995 among others), the authors now encompassing findings from psychology and social sciences in their works.

Another field started to expand in the 1980s: experimental finance. Experiments create situations in which the environment is controlled to test a given theory, to observe financial concepts otherwise unattainable, to modify market organisation and to isolate the individual behaviour of financial agents (Pouget, 2001). Neurofinance has been made possible thanks to the improvement of neuroimaging and neuroscience in general, therefore establishing it as a transdisciplinary field which uses neuroscientific techniques. It provides a way to physiologically test a given theory. Therefore, a theory could already be tested empirically and experimentally, and can now be tested physiologically thanks to neurofinance.

The purpose of this review is twofold. First, the aim is to present some of the main findings of neurofinance from the emergence of the field in the 2000s. Second, we intend to show that neurofinance does not make any ex-ante assumptions about agents' rationality. However, the outcome of those experiments supports ex-post behavioural theories, including prospect theory. Indeed, most neurofinancial findings concern the neural basis of financial decisions (and thus also regard traditional financial theories). This study focuses on the neural basis that invalidates classical finance, thereby demonstrating how neurofinance lends further support to several behavioural theories.

There are several reviews in neurofinance already, a first kind being those that focus on a specific aspect investigated thanks to a particular tool. For instance, Wu et al. (2012) provided a meta-analysis about financial risk-taking, an analysis established with magnetic resonance imaging results. These studies highlight the precise brain regions at stake when taking financial decisions. Despite the inherent interest in these studies, there remain several limitations. Indeed, fMRI techniques are complex and prevent field experiments (Lo and Repin, 2002 among others). Other reviews focus mainly on the role played by emotions during financial decision-making (Kalra Sahi, 2012 among others), therefore barring studies on genes, hormones, aging, and anatomy, studies that show the differences in behaviour between individuals.

This paper reviews studies that use all the research materials used in neuroscience to illustrate the neural basis of financial decision-making and the differences in behaviour between individuals: magnetic resonance imaging (MRI), physiological measures (heart rate, heart rate variability, skin conductance), electroencephalography, hormones, genetics and anatomy. We excluded seminal papers that dealt with behavioural concepts or emotions but did not incorporate these materials (Loewenstein et al., 2001; Hsee and Rottenstreich, 2004 among others). In addition, we reviewed papers that only deal with financial decision-making issues. For that reason, we did not take into account studies on neuroeconomic choices (Fehr and Rangel, 2011) and studies on game theories (Sanfey et al., 2003).

The remainder of this paper is organised as follows. The first section revolves around the basics of human decisions. The second section formulates assumptions about investors' characteristics; the brain regions involved in financial decision-making are also presented. The third section shows that the brain areas involved in financial decision-making are also emotion centres, and that feelings have an impact on investors' returns and choices. In the fourth section, we discuss the fact that investors' decisions may vary over time and across individuals, in contradiction with classical financial theories. Section five examines to what extent neurofinancial findings support behavioural theories. Some concluding remarks will be presented at the end of this paper.

2. The brain and decisions

Generally speaking, it was assumed that investors take decisions that maximise their utility function. However, many deviations from this axiom can be observed in the history of financial markets. Therefore, many decisions may appear as sub-optimal. Human beings satisfy rather than maximise (Cohen, 2005). Thus, a biased reasoning may be preferred over an unbiased one. Haselton et al. (2005) explained that an individual systematically chooses to commit the less costly error for him over the costliest one[3].

Human beings essentially act according to two tendencies (Knutson and Greer, 2008): approach and avoidance, respectively associated with positive

3 According to the error management theory, an individual systematically chooses to commit the less costly error for him (type 1) over the costliest one (type 2). This way, even if the error rate increases, as the type 2 error does not, the cost of the error remains stable.

and negative emotional states (reward versus punishment). The brain is divided into three parts, the cortex and the limbic system together form the forebrain, which is the largest part of the human brain. The cortex, associated with thinking and actions, is called the rational part of the brain (Peterson, 2007a, 2007b). The limbic system is involved in feeling processes and is called the emotional part of the brain. A majority of the papers studied in this review refer to the limbic system: the nucleus accumbens (NAcc), the insula and the amygdala. They are known to be linked with financial risk and rewards and positive (NAcc) or negative emotions (amygdala). The second part, the mid-brain, supports movements, along with vision and hearing. The last part, the hind-brain, supports vital processes.

In this paper, we deliberately chose to focus on research papers that use neuroscientific techniques. Some used external physiological measures such as heart rate (frequency of heart contractions), heart rate variability (variation in the beat-to-beat interval) and skin conductance.

Other experiments used techniques to map the brain (Rocha et al., 2013). The most ancient techniques, electroencephalogram (EEG) or magneto-encephalogram (MEG), measure electrical or magnetic fields generated by neurons in a given brain process. New techniques aim to measure the magnetic field variations induced by hydrogen in water molecules that were disturbed by this field. Indeed, this technique can provide a static picture of the brain (structural MRI) or the modification of blood influx in a given activated brain region (functional MRI or fMRI). While the former technique is used to diagnose brain lesions, the latter can detect the areas activated by a particular brain process.

Several papers which have investigated how hormones affect behaviour will now be examined. These studies use the digit ratio (which is the ratio of the lengths of different digits), especially the index finger and the ring finger (respectively 2D and 4D), which are both affected by in utero exposure to different hormones (Apicella et al., 2015).

Despite several limitations[4] (see Barnes et al., 2014 for an extensive review), there are several studies about twins that examine the impact of

4 According to the random mating hypothesis, there are no mating restrictions between individuals. In other words, human beings mate regardless of physical, genetical or sociological preferences. However, several studies have shown violations of this assumption (assortative mating) and mate similarities across several traits such as political affiliations or educational level (Barnes et al., 2014). In addition, according to Caspi (2002), interactions between genes and the individual's environment may exist. For instance, the author explains that genes can moderate violent behaviours in subjects who were mistreated during their childhood.

genes on behaviour. Classical works rely on twins raised in the same family environment. Monozygotic and dizygotic twins are compared (respectively identical and fraternal twins). Research on twins contrasts the similarities between samples of identical twins and samples of fraternal twins. Excess likeliness between identical twins is assumed to have a gene origin rather than an environmental one.

3. Key aspects of the individual investor in classical financial theories

After having first provided a synthetic view of three famous classical financial theories and the hypotheses formed about investors, the brain areas that are at stake in taking financial decisions will be depicted.

The expected utility theory (EUT), initiated by Bernoulli (1738) and von Neumann and Morgenstern (1944), is particularly used in economics and finance. It considers that a rational investor will choose only a risky asset if the utility he can derive from it exceeds the utility he can derive from a riskless asset. Consequently, investors are risk-averse and will prefer only outcomes that are certain over uncertain ones. Regarding risk aversion, the modern portfolio theory (MPT) considers that investors are almost always risk-averse (Markowitz, 1952).

The efficient market hypothesis (EMH), developed by Fama and Samuelson in the 1960s is one of the financial theories most studied by scholars. This theory relies on three assumptions (Barberis and Thaler, 2003; Tseng, 2006). First, investors are rational and assess securities in a perfectly rational manner. Second, even if some of them deviate from rationality, rational investors and arbitrageurs will snap up any opportunity to arbitrage. Third, each investor maximises a well-defined utility function.

The theoretical underlying of the EMH, the subjective expected utility theory (SEU) assumes that uncertainty (risk) and ambiguity[5] are considered in the same way (Savage, 1954). Indeed, as long as an investor can calculate subjective probabilities about an outcome, the expected utility derived is the same under risk or ambiguity. Consequently, the underlying ambiguity of certain games like lotteries is not supposed to influence the gambler's

5 Uncertainty implies that the probability distribution of an outcome is known. On the other hand, under ambiguity, the individual investor does not know the underlying probabilities entirely (Ellsberg, 1961).

decision. The key traits of individual investors according to these theories are the following: first, they are rational and gauge risk efficiently, second, they are able to calculate probabilities and to maximise expected utility functions.

3.1. The investor as seen through neurofinance

A financial investor needs faculties to appraise risks and rewards. However, the theories summarised above were constructed without any physiological, psychological, or even biological aspects for two reasons. On the one hand, they aimed at providing a clear and intelligible outline of investor behaviour. On the other hand, the neuroscientific tools were not as accessible as they are today. As a consequence, the first works in neurofinance investigated how the brain values risks, rewards and probabilities. Wu et al. (2012) clearly showed the differences between traditional economists and psychologists. While the former assign objective statistical properties of financial options, the latter address the subjective and emotional processes of decision makers. More precisely, bridges such as affective neuroscience are required between these two dimensions. Using an fMRI meta-analysis, the authors explained that the brain translates statistical input into affective experience. They found results for three main mathematical tools used in finance: mean, variance and skewness. High versus low mean and high versus low skewness increase ventral striatum activity, a region known to be related with positive arousal, while high versus low variance increases the anterior insula activity, which is linked with negative arousal.

3.2. Risk and reward valuation

Several neurofinancial papers have investigated the brain regions involved in the valuation of risks and rewards. Preuschoff et al. (2006, 2008) highlighted the particular role played by the anterior insula and the ventral striatum (VSt). Using risky simple card gambles and fMRI, they showed that the anterior insula and ventral striatum are involved when valuating risks and rewards. The authors pointed out an activation of the ventral striatum in association with risky choices and an activation of the anterior insula with riskless choices. Therefore, at least one brain region, the limbic system, encodes both risks and rewards, elements that are the core of classical financial theories.

In an fMRI experiment about future rewards, McClure et al. (2004) exhibited that time discounting is under the influence of the limbic system. Specifically, it is activated when a subject faces the possibility of an immediately available reward. However, the prefrontal and parietal regions are involved no matter the length of the delay. Hence, it appears that during a time discounting decision, both regions compete against each other. When the limbic system is more activated, it is more likely that a more immediate reward will be chosen. Conversely, the subjects who choose longer and larger gains exhibit a greater activation of the prefrontal cortex, which is associated with cognitive tasks such as calculation and planning.

Peters and Büchel (2010) proved that patience about future rewards increases if these rewards are linked with events considered as important by the agent, who perceives the future more prominently.

Similarly, Hershfield et al. (2011) provided results about individuals' future choices. This study used virtual reality to expose subjects to their own future, by being shown pictures of their future selves. Manipulating this visual exposure enhances the subjects' ability to allocate resources to their future. Participants are then more likely to accept later monetary rewards rather than immediate ones.

3.3. Neural processes of risk versus ambiguity

Classical financial theories assume that investors deal equally with risk and ambiguity (Savage, 1954). This section points out the contribution of neurofinance in testing the robustness of theoretical models.

Ambiguity refers to situations where all probabilities are not completely known (Ellsberg, 1961). An fMRI study (Hsu et al., 2005) investigated the neural process of risk with two different treatments. In the first condition, subjects knew the probabilities of the possible outcomes (risk) and in the other condition they were not fully aware of the probability distribution (ambiguity). They found that the orbito-frontal cortex (OFC) and the amygdala are the most active regions during ambiguity. The OFC supports cognition processes and emotion integration while the amygdala is involved when reacting to emotional cues. The authors note that none of these regions is involved in the risk setup. Therefore, there are specific brain areas linked with ambiguity.

In a subsequent paper, Huettel et al. (2006) showed using fMRI that ambiguity and risk share common neural regions like the insula. However, the identified areas in the prefrontal cortex (insula) and dorsolateral cortex regions are overall associated with individual ambiguity preferences. On the other hand, the posterior parietal cortex is associated with risk preferences.

Levy et al. (2010) investigated the Ellsberg paradox during an fMRI experiment. In this study, participants were asked to bet on drawing red or blue chips from an urn while the colours of some chips were unknown. The results of their experiment followed that of Hsu et al. (2005), who demonstrated that ambiguity activates the OFC. They also pointed out that participants with OFC damage are less sensitive to risk and ambiguity.

We are all usually ambiguity averse. Payzan-LeNestour and Bossaerts (2011) proved the sensitivity to ambiguity by showing in their experiment that participants' tendency to explore in a six-arm bandit task decreases with ambiguity.

To summarise, the amygdala and orbitofrontal cortex are associated with ambiguity while the anterior insula and ventral striatum are involved in risk coding.

3.4. Expected utility calculation in the brain

Different brain regions are at stake regarding expected utility. Two studies have shown an increased activation of the NAcc during gain anticipation only. The first study showed the role of three different subcortical regions with fMRI imaging in the expectation of monetary rewards (Knutson et al., 2001b). They found that while subjects anticipated a reward, the ventral striatum (including the NAcc) was activated and that while they received said reward, the ventromedial frontal cortex was activated.

In a second study, Knutson et al. (2001a) investigated rewards and punishment. The authors found that anticipation of increasing rewards leads to a rise of the self-reported happiness, and to NAcc activation and medial caudate activation, while anticipation of punishment activates neither. However, only the NAcc is correlated with self-reported happiness.

In a latter fMRI experiment, the anticipation of a positive monetary reward was shown to activate the NAcc whereas it stops being active during its realisation (Knutson et al., 2003). Indeed, the medial prefrontal cortex (mPFC) is involved during the assessment of a realised outcome.

Early neurofinancial works pointed out the brain areas at stake to evaluate the expected utility of gains. Later on, several studies focused on some of the main statistics widely used in finance such as mean, variance and skewness. The following subsections will focus on mean and variance, neural results about skewness will then be presented along with the preference individual investors have for it.

3.5. Mean and variance calculation in the brain

A meta-analysis of studies about financial risk-taking (Wu et al., 2012) identified the neural responses for several financial measures. The paper showed that neural responses to high versus low means have the highest probabilities to activate the ventral striatum (including the NAcc), followed by the anterior cingulate cortex and finally the bilateral anterior insula. Regarding variance, the same study reported the highest probabilities to neural response to high versus low variance in the anterior insula and left ventral striatum. However, we can state that mean and variance both activate the same brain sections: the ventral striatum and the anterior insula.

3.6. Skewness calculation

Skewness has been widely studied in order to explore financial preferences and decision-making (Brunnermeier et al., 2007; Goetzmann and Kumar, 2008), as it involves large asymmetric and unlikely payoffs like lotteries. Its neural basis has recently been investigated as well.

In an fMRI meta-analysis, Wu et al. (2012) showed that high versus low skewness activates the ventral striatum. However, their study reports few works which highlight only the comparison between low and high skewness. In an fMRI experiment, Wu et al. (2011) found that positive and negative skewness impacts the brain differently. Indeed, the anterior insula is linked with negatively skewed gambles when the ventral striatum is correlated with positively skewed gambles. In addition, in terms of affect, positively skewed gambles elicit more positive arousal. Conversely, negatively skewed gambles produce more negative arousal. Furthermore, subjects prefer positively and symmetrically skewed gambles to gambles with negative skewness, even if the expected value is equal. The preference for skewness is indicated as a result of NAcc activation, which is considered to be the pleasure centre of the brain.

We can summarise these results as follows (Kuhnen and Knutson, 2005): investing in riskier assets relies on a greater activity of the ventral striatum, while a higher activity of the anterior insula is associated with investing in safer assets. In addition, these findings are consistent with the existing literature on the respective roles of the ventral striatum and the anterior insula on emotions (pleasure versus pain and uncertainty) (Knutson and Huettel, 2015).

4. Emotions inside the brain

4.1. The brain areas involved in financial decisions are also emotion centres

The previous section was focused on the different brain sections involved when investors take financial decisions and deal with economic mathematical tools. Two regions are involved in financial decision-making: the ventral striatum, including the NAcc, and the anterior insula. The first brain area is involved in valuating risks and rewards, anticipated rewards, but also mean and variance and positive skewness. The second one is sensitive to mean, variance and negative skewness. Pointing out these particular areas goes hand in hand with stating the behavioural consequences.

An activation of the NAcc produces an emission of two neurotransmitters, dopamine and serotonin. While the first neurotransmitter is associated with pleasure and desire, the second one is associated with inhibition (Peterson, 2007a, 2007b). When someone anticipates making risky choices, or anticipates experiencing feelings of pain, anger, happiness, aversive stimuli or fear, the anterior insula is activated. Conversely, when someone anticipates positive monetary outcomes, the NAcc is activated. In a seminal paper with event-related fMRI, Kuhnen and Knutson (2005) exposed the systematic deviations made by investors when they take financial decisions. More precisely, they defined two deviations from the optimal investment strategy of a risk neutral agent: risk-seeking mistakes (the subject picks up the risky asset when the safe security was the actual optimal choice) and risk aversion mistakes (the participant chooses the safe security when the risky asset was the actual optimal choice). The authors explained that NAcc activation precedes risky choices as well as risk-seeking mistakes, while anterior insula activation precedes riskless choices as well as risk aversion mistakes. Hence, activating one of these two regions with external stimuli, such as pictures or sounds, can lead to a switch of the agent's risk preferences for respectively risky or riskless choices.

4.2. Implications of emotions and beliefs

In the previous subsection, we pointed out that the NAcc and the anterior insula are involved when an investor takes financial decisions. Several works have demonstrated the effects of an activation of the loss avoidance system on stress, anxiety or panic among other symptoms (Bechara et al., 2000). It is therefore necessary to investigate how positive and negative emotions can affect an investor's returns and choices along with their consequences.

Emotions on the trading floor

Several studies have investigated the physiological responses to market events and the role played by emotions for financial professionals. For instance, Lo et al. (2005) showed that professional traders exhibit emotional reactions to monetary gains and losses. Using professional traders in their own environment as the subjects of studies is a tricky task that limits the research materials to physiological measures such as heart rate and heart rate variability (HRV). For that purpose, Lo and Repin (2002) analysed the emotional decision-making process on ten professional traders, taking biofeedback measures such as heart rate, skin conductance and blood pressure as proxies for these emotions. They indicated that traders exhibit greater emotional arousal around important events such as volatility peaks. Furthermore, experienced traders feel these emotional arousals to a lesser extent than less experienced ones. The authors argued that making quick decisions based on their emotional arousal is a necessary condition in traders' decision-making.

This research highlights the emotional responses of traders with respect to market events and explains that experienced traders are less sensitive to emotional cues. However, this paper does not examine how professional traders learn to regulate their emotions in the span of their careers (i.e. emotion regulation is part of their expertise). Several papers have shown the usability of HRV as a good proxy for intentional emotion regulation (León et al., 2009; Denson et al., 2011).

A physiological research with investment bank traders examined emotion regulation and traders' experiences using HRV (Fenton-O'Creevy et al., 2012). The results showed that volatile market events are correlated with lower HRV while greater experience is correlated with higher HRV. Hence, the authors evidenced traders can hardly control their emotions during volatile market conditions and thus the importance of emotion regulation in traders' expertise.

Stress and financial decisions

The previous subsection examined how a stressful environment, such as the trading pit, and stressful decisions, such as market events, can generate emotions (Lo and Repin, 2002; Fenton-O'Creevy et al., 2012). The effects of stress on financial decision-making can now be tackled.

Porcelli and Delgado (2009) studied the effects of acute stress on financial decision-making. In their experiment, stress is induced in subjects by immersion of one hand in cold water for several minutes. Non-stressed control subjects follow a similar procedure with hot water. The patients engaged in a gambling game where they faced two alternatives either presented as a gain or as a loss. During the task, skin conductance was measured. The results showed a significant increase in skin conductance levels in the stress condition. Stressed participants made riskier choices. Furthermore, participants under stress made riskier choices in the loss domain compared with non-stressed participants, and less risky choices than non-stressed participants in the win domain. The authors therefore argued that acute stress alters financial decision-making. They tend to use a somewhat automated risk bias. The authors concluded that stress may disrupt resources used by the executive functions of the brain, which may lead to an excess reliance on low level automated systems.

Regret

In this review, we have underlined the fact that investors are far from behaving in a rational manner. On the contrary, they are driven by emotions. Indeed, investors try to limit or avoid possible future regrets by taking suboptimal decisions, even when they possess specific financial knowledge. Coricelli et al. (2007) observed that people with lesions in the orbitofrontal cortex (OFC) do not anticipate the negative consequences of their choices and decide according to actual situations only. Hence, they do not feel regret.

In a stock market experiment using fMRI, Frydman and Camerer (2016) proposed a test of the implications of regrets. They showed that participants who observe a positive return on a particular stock they do not hold experience regrets. In addition, they highlighted the impossibility for participants to repurchase stocks that had increased in value even if it could be optimal for them, which can be referred to as the repurchasing mistake.

Positive anticipated emotions

Knutson and Greer (2008) defined anticipatory affect as the emotional state people experience when anticipating significant outcomes. They reviewed the consequences of an anticipatory affect and its consequences over individual choices, and showed changes in brain circuits activation when subjects anticipate monetary incentives. On the one hand, NAcc activation increases when gains are anticipated. On the other hand, the anterior insula activation increases when both losses and gains are anticipated. Moreover, NAcc anticipatory activation is correlated with a self-reported positive arousal, a preference for risky gambles, and precedes the purchase of desirable goods. Conversely, the anterior insula is correlated with both positive and negative arousal, the desire for non-overpriced items and the choice for non-risky gambles.

Knutson et al. (2008) investigated the effect of a positive anticipatory exciting environmental signal (anticipatory affect) on risk-taking behaviour in financial markets. They conducted an fMRI experiment on young student males. Before trials, they were shown suggestive female pictures. The authors found that risk-taking was increased after an activation of the subject's NAcc via this prior picture. Therefore, the subjects were more likely to participate in lower expected value gambles and to make riskier choices.

In addition, Wu et al. (2014) showed the affective traits of incentive anticipation of gains and losses using fMRI. The subjects played a monetary incentive delay task. During each trial, the participants began by seeing a cue indicating potential gains or losses of different amounts. They then watched a cross and waited for different intervals and responded with a button to a target appearing for varying time spans to see the outcome. The results established NAcc activation during positive arousal and anticipation of large gains, while the anterior insula was activated during negative arousal and anticipation of large losses.

Andrade et al. (2016) tested the relationship between excitement and bubbles. Their experiment followed the experimental design of Smith et al. (1988). Before the experiment starts, the experimenter shows participants a video tape to introduce emotions. The emotional states that can be introduced are fear, calm and excitement. The authors noted that bubbles are much larger in the excitement state than the others. The bubble amplitude in the first round, meaning the difference between the average trading price of the asset and its fundamental value, is larger than in the calm and fear treatments. The results suggest that the excitement generated by increasing prices in real stock markets actually fuels bubbles.

Most studies investigate the relation of emotions and "suboptimal" choices, leading to bad decisions. However, positive emotions can also induce altruism. Indeed, one of the persistent assumptions about human beings is that they are self-interested only. However, sometimes we may share things with people whom we do not know. Genevsky and Knutson (2015) showed that affective mechanisms can influence the success of microloans. Positive affective features of photographs increase the success of those requests in an internet microloans database request. With a small sample and fMRI imaging, the authors demonstrated that NAcc activation and self-reported positive arousal predicted the success of loan requests on the internet.

Positive beliefs

The brain regions involved in processing risk and rewards are also in charge of processing emotions, thus we can wonder whether emotions affect financial choices and beliefs.

Emotions play a role in the belief formation process of investors. Brunnermeier and Parker (2005) established that agents forming optimistic beliefs about their future outcomes are happier. This belief has an immediate impact on their subjective well-being via anticipatory emotions and encourages them to prefer skewed assets. In a physiological experiment, Baechler et al. (2018) use two equal lotteries except for their skewness. The first lottery has a positive skewness and the second one has a null skewness. The authors point out that subjects participating in the non-skewed lottery exhibit greater self-regulation than other subjects. Hence, they are less prone to optimism. Furthermore, they confirm that all participants feel positive anticipatory emotions during the waiting interval between the revelation of the lottery and the draw.

Another paper (Kuhnen and Knutson, 2011) proved the emotional impact of both risk-taking behaviour and beliefs formation in individuals, using an experimental design where subjects need to update their beliefs about the distribution of a risky asset. The authors found that events associated with positive arousal led to riskier choices while those associated with negative arousal led to risk-averse choices. They also showed that affect transforms the participants' belief formation process. Positive affects increase subjects' confidence in their capacities to assess risky choices. Beliefs are updated in a way that preserve a positive state of mind, leading subjects to incorporate only news that does not interfere with their previous choices. Thus, they form incorrect beliefs.

5. Stability of behaviours over time and across individuals

5.1. Stability of behaviours over time: the example of aging

In the previous subsections, we pointed out why investors deviate from the classical financial paradigms and do not behave as wise and rational investors, due to emotions actually shaping their decisions. Another axiom of classical theories is that investors are always rational and risk-averse, characteristics that are supposed to be persistent over time. Therefore, using the example of aging, we will examine the consistency of human behaviour.

Li et al. (2013, 2015) investigated the interaction between aging and financial performance. The authors pointed out that older people show "crystallised intelligence" (general and domain specific knowledge). They use their own expertise to enhance their financial decisions, in accordance with the behavioural evidence that aged people are more patient than younger ones. The ventral striatum neural activity, known to encode various anticipated and monetary rewards (Liljeholm and O'Doherty, 2012), decreases less in older people. This means that they similarly encode delayed and early rewards (Samanez-Larkin et al., 2011).

However, another study (Samanez-Larkin et al., 2010) indicated that older adults make poorer investment choices compared to younger persons. They make more frequent investment errors. The authors explained this result as a difference in the interpretation of expected gains made by older adults. Indeed, NAcc activity decreases the value prediction accuracy made by older adults, generating financial mistakes.

Similarly, Kovalchik et al. (2005) compared decision-making in neurologically healthy elderly individuals (82 years old) and young individuals (20 years old on average). They concluded that older subjects behave similarly to younger ones, and are even less biased.

5.2. Stability of behaviour across individuals

We have shown that behaviours may change through life. However, we also need to investigate whether they vary across individuals. Several empirical papers have investigated the differences between men and women as financial decision makers (Barber and Odean, 2001). These results were checked with an electroencephalographic study which explained that men and women use different sets of neurons to take financial decisions (Rocha et al., 2015). It is therefore highly likely that other differences exist across individuals.

Genetic differences

Making investment choices is an individual task and may vary across individuals. Some agents are more willing to gamble (Grinblatt and Keloharju, 2009) or to invest in short-term assets. Therefore, under equal conditions, successful financial decisions strongly depend on investors themselves, with very few of them able to "beat the market". Several studies have investigated the role played by financial knowledge (van Rooij et al., 2012), endowment (Agnew and Szykman, 2005), age (Li et al., 2013) and gender (Barber and Odean, 2001). However, these factors only partially explain risk-taking behaviours. Other factors such as genes may play a role.

Several papers have studied the link between risk-taking behaviour and genetic components. Using a large sample of twins from Sweden, Cesarini et al. (2010) confirmed that around 25% of variation in portfolio risk is due to genetic components as well as the decision to invest in socially responsible assets.

Barnea et al. (2010) studied a dataset on identical twins completing financial portfolio decisions. They found a genetic component explaining around 30% of the variation in stock market participation and asset allocation. The authors highlight the non-permanent effect of the family environment. It has a measurable effect on young individuals' behaviour but does not last as the individuals gain experience. They argue that twins who grow up in similar environments as well as twins growing up in different environments exhibit the same investment behaviour beyond a common genetic component.

These papers show the role played by genetic components in risk-taking behaviours. However, they fail to explain the specific genes at stake. Other research has focused on the specific gene configurations that affect risk-taking by modulating dopaminergic and serotonergic circuitries involved in decision-making processes. All these systems are known to modulate decision-making such as pathological gambling (Ibanez et al., 2003). Two genes in particular are involved in financial risk-taking: the dopamine receptor D4 gene (DRD4) and the serotonin transporter polymorphism (5-HTTLPR), which have previously been linked with emotional behaviour, anxiety and addiction (Kuhnen and Chiao, 2009).

Kuhnen et al. (2013) also investigated neuroticism through the polymorphism in the promoter region of the serotonin transporter gene (5-HTTLPR). They found that carriers of short alleles invest less in equities, make less active financial decisions and have fewer credit lines. In addition, short allele carriers perceive stocks as riskier and tend to feel more negative emotions when faced with risky investment choices, the authors attribute this to neuroticism.

Kuhnen and Chiao (2009) found that carriers of the DRD4 7-repeat allele take 25% more risks than non-carriers. On the other hand, Sapra et al. (2012) disclosed the role of dopamine in risk-taking by examining 60 professional traders. They showed that successful traders are carriers of COMT (catecholamine-O-methyltransferase) and DRD4P (dopamine receptor 4 promoter), gene alleles that moderate dopamine and hence they take more appropriate risks. Inversely, carriers of short 5-HTTLPR allele genes (which modulate serotonergic activity) take 28% less risks than others (Kuhnen and Chiao, 2009).

Frydman et al. (2011) tested the effects of several genes on financial risk-taking behaviour with a simple gambling game. They spotted that people with the MAOA-L gene are more likely to take financial risks compared to MAOA-H carriers but only when they perceive it as advantageous. MAOA-L carriers exhibit higher connectivity between the prefrontal cortex and the amygdala and the gene is known to contribute to aggressive and impulsive behaviour. Hence, they are more willing to take risks.

In a seminal paper, Cronqvist and Siegel (2014) studied the genetic foundation of several investment biases such as lack of diversification, home bias, turnover, the disposition effect, chasing for performance and the preference for skewness. They found higher correlation for the biases under their scope for identical twins compared with fraternal twins: the correlation for identical twins is about twice the correlation between fraternal ones. For the latter, correlations are higher for same sex fraternal twins. The authors also pointed out that some moderators exist to investment biases such as having work experience and knowledge in finance.

Hormone differences

Several studies have established the role played by hormones in financial decision-making, especially testosterone[6] and cortisol[7]. Coates and Herbert

6 Testosterone is produced by the Leydig cells and the adrenal cortex. It has been found to play a role in winning and losing. For instance, testosterone levels rise for an athlete preparing for a run and even more if he wins (and falls if he loses).

7 Cortisol is produced by the adrenal cortex and is related to situations of uncertainty and uncontrollability and plays a role in response to physiological stressors.

(2008) analysed the “winning effect” of testosterone with seventeen professional traders in London, taking measures for testosterone and cortisol in the morning and the afternoon. On days when morning testosterone levels were high, traders experienced afternoon profits higher than on days when these levels were lower. Moreover, they showed that cortisol levels increase with portfolio variances and market volatility. This result is consistent with previous knowledge. Indeed, cortisol is known to influence brain regions linked with irrational financial decisions. Therefore, it fluctuates with risks and returns, and it may alter a trader’s ability to make optimal decisions.

In experimental asset markets with induced testosterone, Nadler et al. (2017) showed that testosterone has an effect on both trading behaviour and price bubbles. It generates high bids and the slow incorporation of the asset fundamental value, causing longer lasting bubbles. These results are in line with Eckel and Füllbrunn (2015) among others, who analysed gender differences in price bubbles. They found that women generate less bubbles than men, and overall trade less than men (Barber and Odean, 2001).

In another study, Cueva et al. (2015) explored the links between financial risk-taking, testosterone and cortisol using the experimental market design of Smith et al. (1988). They found that higher cortisol levels in aggregate and in individuals predict risk-taking and price volatility. In addition, testosterone increases optimism about changes in future prices. The authors then administered cortisol or testosterone to male subjects participating in an experimental game. In this experiment, subjects were shown plots about past prices of two stocks. Then, participants were asked to choose between two stocks either with high or low variance of returns. Subjects who were administered cortisol or testosterone were either way more likely to take the riskier choice, demonstrating that both hormones increase risk-taking and price destabilisation with market bubbles followed by a crash. Furthermore, testosterone administration resulted in increased optimism regarding future stock prices.

Anatomic differences

The results about the second-to-fourth digit ratio are mixed. Apicella et al. (2015) pointed out that the field, which appeared ten years ago, is still emerging, despite the non-invasive character of this proxy to hormones measurement. However, several studies have provided positive results about risk-taking and 2D:4D. Coates et al. (2009) used 2D:4D as a predictor of future financial success among traders, and 2D:4D has been proved as a good predictor of future success in highly competitive sports already. The authors mentioned 2D:4D as a sign of long-term profitability and the number of years traders will remain in the business.

Stenstrom et al. (2011) tested the impact of testosterone on risk-taking. They used the second-to-fourth-digit-ratio (2D:4D) and the length of the second finger relative to the sum of the lengths of all four fingers (rel2) as a proxy of prenatal exposure to testosterone across five topics: financial, recreational, social, ethical and health-related risk-taking behaviours. They found that lower rel2 is predictive of greater risk-taking in the financial, social and recreational domains and lower 2D:4D is predictive of greater risk-taking in the social and recreational domains.

Cronqvist et al. (2016) examined the link between several prenatal environmental differences and the heterogeneity of financial decisions one may take later in life. In this purpose, they investigated birth weight and prenatal exposure to testosterone. For prenatal testosterone, the authors compared twins of opposite sex pairs with twins of the same sex pair. For women who grew up with a male twin, they noticed an increase in prenatal testosterone exposure which leads to a "masculinisation" of financial behaviour, meaning a high risk-taking and trading in adulthood. In addition, the study mentions that a higher birth weight is related to a higher participation in stock markets, while a lower birth weight is correlated with the tendency to prefer skewed assets and to choose portfolios with higher volatility.

Are all investors risk-averse?

The neural basis of risk aversion was sparsely known until the rise of neuroimaging. Some studies using structural MRI show the relation between the grey matter (central tissue of the nervous system) volume of different brain areas managing risk-taking and investor differences in risk-taking decisions. In two voxel-based morphometry studies, subjects exhibiting greater risk aversion had altered grey matter volume (Nasiriavanaki et al., 2015), a lower grey matter volume in the posterior parietal cortex, a lower grey matter volume in the anterior insula (Gilaie-Dotan et al., 2014) compared with risk-seeking participants.

Furthermore, risk-averse subjects have different brain activation during each stage of their financial decisions, anticipation of risks and rewards, choosing between different risky options and processing the outcome of a risky choice. During the anticipation phase, risk-averse subjects appear to overestimate risks. They exhibit a higher activation of the ventral striatum and the anterior insula (Rudorf et al., 2012), which are regions involved in risk processing (Preuschoff et al., 2006, 2008). While the NAcc is directly connected with the insula, this connection appears to be distorted in investors having a preference for skewed assets and gambles (Leong et al., 2016).

According to Rudorf et al.(2012), risk-averse people still overestimate risks. They are unable to assess their expectation of risk whereas the results of the gamble are known to be less risky than they would have expected: a reduced risk prediction error (the tuning of the estimated risk of a hazardous choice when the outcome is known) is altered in their insular cortex.

Participation in financial bubbles

Some studies suggest that some investors may trigger financial bubbles by trying to infer the investment intentions of other market participants. In an fMRI experiment De Martino et al. (2013) pointed out an increase in prefrontal cortex activity in subjects exhibiting a tendency to participate in bubbles (region involved in inferring intentions of others): they "ride bubbles", taking into account the intentions of other players.

Smith et al. (2014) found a positive correlation between aggregate NAcc activity and changes in prices during bubbles. In this experimental market, prices were entirely determined by twenty participants trading between each other while two subjects were scanned. The experiment was based on one risky asset (a stock) and a non-risky one (numeraire). One of the main findings of this study is that the evolution of the risky stock price follows the same patterns as the NAcc activation in all participants. Also, the peak of the bubble corresponds exactly to the peak in NAcc activity. Thus, NAcc activity represents risk streaks and the erroneous idea that prices will keep rising. "Smart traders"[8] however, exhibit greater anterior insula activation, a brain area known to be related with uncertainty (in this case the uncertainty about the continuous increase in prices). Traders with a superior anterior insula activation sell a few moments before the peak of the bubble, when traders with greater NAcc activation continue to buy. Hence, according to

8 In a behavioural perspective, three types of traders can be detected in this experiment. Fundamental traders sell their stocks at the beginning of each trial at the fundamental value and then wait until the end. Momentum traders buy stocks at the beginning of the bubble and keep buying after it bursts. Smart traders buy when prices start to rise and sell before the peak. Obviously, the last type of traders gets the highest returns at the expense of momentum traders.

the authors, when they start selling stocks, smart traders use their intuition[9] rather than statistical signals.

In an experiment, Efremidze et al. (2017) showed the role played by reinforcement learning in financial bubbles. For this purpose, the authors administered a drug known to inhibit learning to several participants. Compared with the control group, asset prices were 60% higher in the drugged participants.

6. Neurofinancial tests of behavioural theories

This review has previously shown why individual investors do not behave according to classical financial theories, even when they are able to compute classical financial statistics, valuating risks and rewards and calculating expected utilities. These decision centres are also areas of human emotions that shape investors' decisions. Neuroscientists have tested other financial theories that can fit in the non-rational behaviour, with Kahneman and Tversky (1979) proposing a theory where heuristic and behavioural biases are the core of financial decision-making.

6.1. Test of the prospect theory

In the prospect theory, an investor values an outcome relative to his own reference point. He is less sensitive to subjective gains than he is to subjective losses (risk-averse in the domain of gains and risk-seeker in the domain of losses). The latter is viewed as a negative deviation from the investor's own reference point. In addition, he values shifts from this reference point in a decreasing way. This explains the concavity of their utility function in the gain region and the convexity in the loss region.

6.2. Probabilities valuation and reference point

De Martino et al. (2009) ran an experiment where participants act as buyers and sellers of lottery tickets with fMRI acquisition. Their results show activity in the orbitofrontal cortex that tracks the expected value of the lottery, indicating absolute value computation (reference-independent)

9 Bruguier et al. (2010) tested the "trader's intuition", using an experimental trading market with insiders and fMRI acquisition. They showed that participants with higher dorsomedial prefrontal cortex activation were the most able to infer others' intentions and made more money.

when the activity in the ventral striatum indexed the degree to which stated prices were altered as for a reference point.

The concavity in the gain region and the convexity in losses has been investigated in an fMRI study (Hsu et al., 2009). In this experiment, most participants overweight low probabilities and underweight mid and high probabilities, with an activation of the ventral striatum, illustrating the non-linearity of their probability function, which is consistent with the prospect theory.

6.3. Myopic loss aversion

Shiv et al. (2005) proposed a test of myopic loss aversion. The authors investigated if investors with emotional disorders are sensitive to myopic loss aversion. To that extent, they compared the outcomes achieved by different samples of participants. In the normal group participants do not exhibit any brain damage. In the target group, patients display brain damage in regions involved in emotion processing (the amygdala or the orbitofrontal cortex). In the control group, subjects possess brain lesions not involved in emotion processing. All participants play a lottery game where, for each round, they can decide whether to invest or not. The results show that patients in the target group are more willing to take risks, investing more frequently. On average they also earned higher outcomes from the game. Furthermore, target patients do not disclose increasing risk aversion when facing previous losses compared with other groups. They continue to invest whether they have won or lost while other participants show greater risk aversion when facing previous losses. This result shows that when fear is involved in the neural process it alters judgment, and "the negative side of emotions" inhibits the capacity one may have to think clearly.

Other studies based on fMRI imaging have also investigated the neural basis for loss aversion. For instance, De Martino et al. (2010) tested the influence of the amygdala in loss aversion. For this purpose, they used two women with symmetrical and bilateral damage to their amygdala due to the Urbach-Wiethe disease. The subjects have two tasks to perform, a loss aversion task consisting of accepting or rejecting a series of gambles with equal probabilities and a double or nothing task where participants need to choose between a safe option or playing a gambling game (i.e. flipping a coin to double the safe option or getting nothing). Both participants showed unaltered abilities to code risks and values, and exhibited a total absence of loss aversion. This is explained by the function of the amygdala which regulates fear and anxiety.

Loss aversion is commonly linked with monetary choices. It is experimentally measured with monetary stimuli rather than pictures or other objects. Lee et al. (2015) studied two different loss aversion games with different stimuli (monetary and non-monetary), measures of behaviour (ratings and keypress) and modes of loss aversion (global and local loss aversion). They found that individuals had similar loss aversion patterns despite the differences between the games.

On the other hand, Canessa et al. (2013) pointed out that participants who exhibit higher loss aversion have a greater grey matter volume of their amygdala-thalamus-striatum network (structural MRI result). In fMRI studies, loss averse investors can be identified by a specific layout of neural activation: an increase of the anterior insula activity (Paulus et al., 2003) and a higher NAcc activation (Matthews et al., 2004) with an increased harm avoidance.

Finally, loss aversion does not appear to vanish with age. It has even been noticed that children exhibit loss aversion, and cannot enunciate risky gambles in terms of expected value (Harbaugh et al., 2003).

6.4. Framing

De Martino et al. (2006) tested framing with fMRI imaging. In their experiment, subjects have to choose between options framed differently. The "sure" option is expressed as a gain ("you keep…") or as a loss ("you lose…"). The gambling option is presented similarly with a pie chart expressing the probabilities. The results show that subjects are very sensitive to framing. They are risk-averse when frames are expressed as gains, preferring the sure option over the gamble one. On the other hand, when frames are expressed as losses, participants are risk seekers. These results are in line with the prospect theory. The authors also found that the amygdala seems to mediate framing. It is activated with gain frames for both sure and gamble conditions. Furthermore, they show an activation of the orbital and medial prefrontal cortex, which are regions associated with reasoning, in subjects less sensitive to framing.

6.5. Disposition effect

The repurchase effect is the tendency an investor may have to buy stocks he or she owned previously that have declined in value and to avoid buying stocks they previously owned that have increased in value.

On the selling side, Frydman et al. (2014) proposed a neural test of the disposition effect, where subjects traded a stock inside an fMRI unit. The authors found a higher activity in the ventral striatum when participants sell a winning stock. In addition, they demonstrated that activity in the ventromedial prefrontal cortex, the region which encodes decision values, is correlated with capital gains. In another paper, Frydman and Camerer (2016) documented a regret signal in the ventral striatum containing the NAcc that drives the repurchase effect. It acts as a factor of inertia. Indeed, traders do not buy previously owned stocks that have increased in value because of the "regret inertia". Traders with a strong regret signal are thus the most prone to the repurchase effect.

7. Conclusion

This review endeavoured to guide the reader through some of the most prominent findings in neurofinance. The neural basis of human decisions has been explained, and the key aspects of individual investors according to traditional financial theories were outlined. We highlighted the neural basis used for several financial measures and the brain processes used to assess risk, reward and ambiguity. The brain areas involved in financial decision-making are also involved in emotional processes and we discussed the reason why these brain areas also shape decisions. Then, we showed the financial consequences of this emotionally driven behaviour. We reviewed why investor behaviour may vary across time and across individuals. For the reasons aforementioned, classical financial theories cannot be supported. In consequence, turning to behavioural theories and examining them through the scope of neurofinance was necessary and enabled us to grant said theories our support.

Neurofinance upholds behavioural theories. However, most of the research in neuroscience as well as most of the studies discussed in this paper are conducted within the scope of laboratory experiments. These findings were obtained in a static and isolated environment while real financial decisions are taken in a dynamic and more often than not stressful environment. Further research must be done to confirm the relevance of these experimental results. Few papers investigate emotions or trading behaviour in an everyday life environment. The tools used are obviously limited because of the inherent constraints of such studies. In addition, most experiments are made with subjects from occidental and well-developed countries. Further research is needed to check whether financial behaviour is country dependent.

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