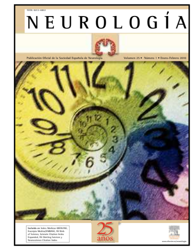
Neurología. 2011;**26(3)**:173-181

NEUROLOGÍA

www.elsevier.es/neurologia



REVIEW ARTICLE

Neuroanatomy of financial decisions

P.E. Bermejo,[a,*] R. Dorado,[b] M.A. Zea-Sevilla,[c] V. Sánchez Menéndez[d]

[a] *Servicio de Neurología, Hospital Universitario Puerta de Hierro, Majadahonda, Madrid, Spain*
[b] *Fundación Instituto San José. Servicio de Neurología, Madrid, Spain*
[c] *Servicio de Neurología, Hospital del Henares, Coslada, Madrid, Spain*
[d] *Servicio de Neurología, Hospital Universitario Reina Sofía, Córdoba, Spain*

Received on 19th March 2010; accepted on 18th September 2010

KEYWORDS
Neuroeconomics;
Nucleus accumbens;
Reward system;
Medial prefrontal córtex;
Amygdala;
Insula;
Orbito-frontal cortex

Abstract
Introduction: Neuroeconomics is a new science that studies the brain processes involved in taking decisions, particularly related to economy and it has experienced an important advance in recent years due to the development of new neuroimaging techniques, basically functional magnetic resonance imaging. The aim of this paper it to carry out a review of the literature on the different neurological mechanisms involved in taking financial decisions, the concerned brain structures and the diseases that can affect them.
Sources: We made a non systematic review of the literature in primary (PubMed) and secondary (Tripdatabase and Cochrane Library) bibliographic databases. We also used bibliography given by the Asociación Española de Neuroeconomía.
Development: Brain reward and loss aversion systems suppose a balance that makes us take one or another decision. Dopamine plays an important role on it and several brain structures have been involved in this balance such as the amygdala, the insula, the medial prefrontal cortex, the anterior and posterior cingulated cortex, the nucleus accumbens and the ventral tegmental area. The alteration of this balance may produce inappropriate financial behaviours that may occur in common diseases including depression, mania, alcoholism, gambling and several impulse control disorders.
Conclusions: Neurologists should define our role in this interdisciplinary field due to the privileged position of our specialty to study how the brain works and due to the potential growing of this science in the near future.

*Corresponding author.
E-mail: pedro.bermejo.v@gmail.com (P.E. Bermejo).

PALABRAS CLAVE
Neuroeconomía;
Núcleo accumbens;
Sistema de recompensa cerebral;
Área prefrontal medial;
Amígdala;
Ínsula;
Corteza orbitofrontal

Neuroanatomía de las decisiones financieras

Resumen
Introducción: La neuroeconomía es una nueva disciplina que estudia los procesos cerebrales de toma de decisiones, fundamentalmente económicas y que ha adquirido un importante avance en los últimos años con el desarrollo de las modernas técnicas de neuroimagen, como la resonancia magnética cerebral funcional. Este artículo realiza una revisión de la bibliografía sobre los diferentes mecanismos neurológicos implicados en la toma de decisiones financieras, las estructuras cerebrales involucradas y las enfermedades que pueden afectarlos.
Fuentes: Realizamos una revisión no sistemática de la literatura, tanto en fuentes de información primaria (PubMed) como de información secundaria (Tripdatabase y Cochrane Library). También se utilizó bibliografía cedida por la Asociación Española de Neuroeconomía.
Desarrollo: Los sistemas de recompensa cerebral y de aversión a la pérdida suponen un equilibrio que hará que optemos por una u otra decisión. En este equilibrio en el que la dopamina desempeña un papel primordial, se han visto involucradas varias estructuras cerebrales como la amígdala, la ínsula, la corteza prefrontal medial, las cortezas cinguladas anterior y posterior, el núcleo accumbens y el área tegmental ventral. Su alteración supone la producción de conductas financieras inapropiadas como tienen lugar en enfermedades tan frecuentes como la depresión, la manía, el alcoholismo, la ludopatía o diversos trastornos del control de impulsos.
Conclusiones: Los neurólogos deberíamos definir nuestro papel en esta ciencia pluridisciplinar, dada la posición de privilegio de nuestra especialidad para estudiar el funcionamiento cerebral, y al más que posible crecimiento que se espera que la neuroeconomía adquiera en un futuro cercano.

Introduction

Neuroeconomics is a new discipline that has come into being in recent years and deals with applying what we know about how the human brain works to economics, above all as regards making financial decisions. Throughout history, numerous books have been written about economics and all explain it as an exact and rational science that can be explained by classical mathematics. According to this traditional prism, prices would be determined by the balance between supply and demand in an efficiently running market. The current crisis and all the other crises that have existed and have since been forgotten call the efficiency of this market into question and demand that the striking differences between theoretical economy and the real economy be taken on board.[1] For several years now, a new current of thought known as *behavioural economics* considers that our financial decisions are less rational and more emotional that originally thought.[2] However, the development of modern neuroimaging techniques, such as functional magnetic resonance, that enable us to study the brain structures involved in economic decision-making, is what has caused the emergence of neuroeconomics.[3]

As neurologists, we should define our role in this new science that is coming into being and that is winning over more and more advocates. Recently created associations (Society for Neuroeconomics, Association for Neuropsychoeconomics or the *Asociacion Española de Neuroeconomía* [ASOCENE]) and the development of more and more powerful brain imaging techniques foretell greater growth of this discipline in the coming years.

The aim of this article is to review the current status of knowledge about the brain structures involved in economic decision-making on which the development of neuroeconomics is being built.

The brain reward system and the loss-aversion system

From the times of Aristotle in Ancient Greece, philosophers and scientists have hypothesized about the presence of two brain structures that define almost all human behaviour: the brain reward system and loss-aversion system (or risk-aversion)[4]. When a potential benefit is perceived in the atmosphere, the brain reward system becomes activated, and when a potential risk is perceived, the brain risk-aversion system becomes activated. The resulting balance between both systems will influence behaviour and decision-making.

Brain reward system

This system consists of a series of dopaminergic pathways that connect the midbrain, the limbic system and the

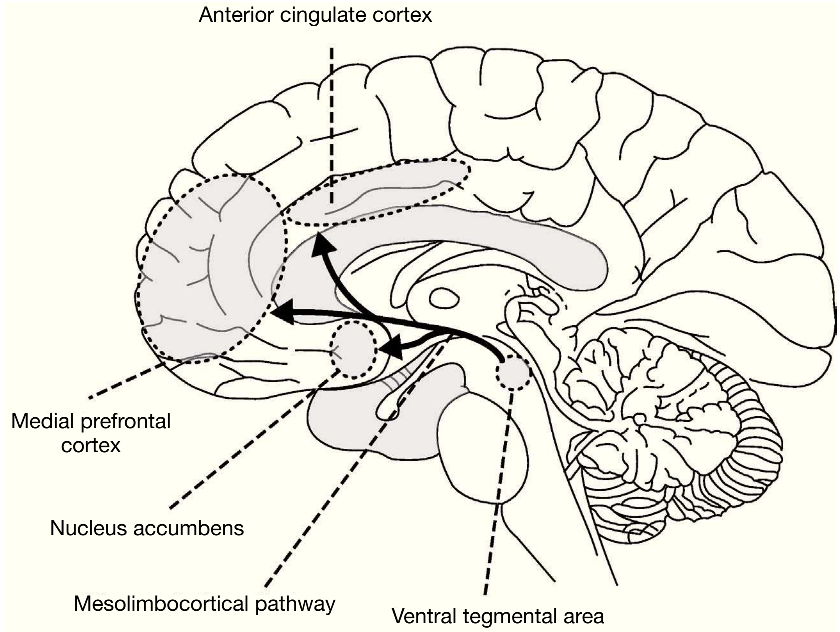


Figure 1 Dopaminergic brain reward system.

neocortex. In fact, dopamine has come to be known as the pleasure substance, due precisely to its involvement in the brain reward system. Furthermore, this system can be activated by certain illicit drugs, which have come to be known colloquially as "dope", a term derived from dopamine.

These pathways include the mesolimbic pathway that runs from the ventral tegmental area through the nucleus accumbens of the limbic system to the frontal lobes, such as the medial prefrontal cortex and the anterior cingulate cortex (fig. 1).[5,6] Each of these structures will become activated when faced with a different situation. On the one hand, the nucleus accumbens will become activated more when economic benefits are greater, whereas the prefrontal cortex, involved in calculation and in a great many cognitive functions,[7] will become activated when there are greater possibilities of such benefits occurring.[8-10]

It has been suggested that the orbito-frontal cortex integrates emotions in economic decisions.[11] Its activation correlates with the subjective emotional experience and the affective stimuli related with a certain monetary decision.[12] Lesions of the prefrontal cortex, including the orbito-frontal cortex, interfere with the processing of emotions while sparing the most fundamental cognitive functions. These lesions produce alterations in decision-making mechanisms that compromise the economic decisions of everyday life to a large extent.[13]

Greater activation of the brain reward system will lead to decisions aimed at obtaining this gratification, which may be not only monetary, but also decisions of a very different nature, such as beverage, food, smoking or sexual relations, among others.

Loss-aversion system

The loss-aversion system is less well-defined than the brain reward system, although it is taken for granted that certain structures such as the amygdala, the insula, *locus ceruleus* or the hypothalamus are involved in it. One of the most interesting studies to address the risk-aversion system is that published by Baba Shiv in 2005.[14] In that paper, controls were compared with patients who had different types of lesions in brain areas related to loss-aversion, largely the amygdala and the insula. Each of the participants was given 20 dollars and had 20 investment possibilities on which to gamble one dollar. If the patients decided not to invest, they got to keep the dollar and waited for the following round. If, on the contrary, they decided to invest, the dollar was taken away and a coin was tossed in the air. If it was heads, the players lost the money, but if it was tails, they won 2.5 dollars. Statistically, those players who never invested would have 20 dollars at the end of the study, whereas the ones who always bet, supposing that they won 50% of the times, would have 25 dollars. Therefore, the expected benefit per round was one dollar for those who didn't bet and 1.25 dollars for those who did (the mean of 0 and 2.5 dollars). Hence, since the benefit is greater if the subject always bets, the most logical choice would be to bet in every round. However, there were clear differences between the controls and the patients with lesions in the loss-aversion system. The control subjects invested 57.6% of the times, whereas up to 83.7% of those who had lesions did so. Furthermore, after a failed investment (the loss of one dollar) only 40.7% of the controls and up to 85.2% of the subjects with lesions invested in the following round, which also demonstrated much greater (and illogical) risk-

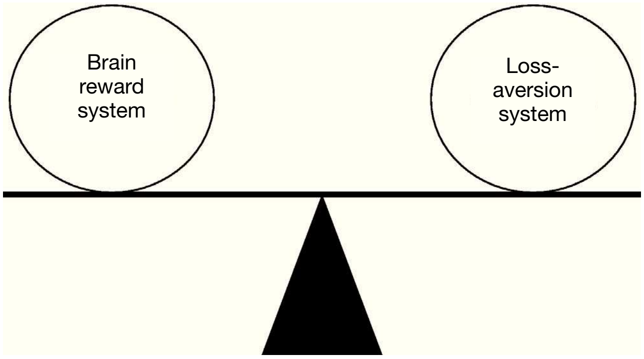


Figure 2 Balance between the brain reward system and the loss-aversion system.

aversion in control subjects. These differences were particularly noticeable in those patients with lesions in the insula, who invested up to 91.3% of the times and up to 96.8% in the rounds after losing. The fact that the patients with lesions in the insula had a greater tendency to risk their money and obtain more money overall suggests that this structure in particular and the loss-aversion system in general may be an impediment for rational economic decision-making. Various later studies[15-19] corroborate the participation of these structures in making decisions that involve risk.

Several examples reveal the presence of clear loss-aversion in economic decisions that sometimes lead to taking the more mathematically illogical option:

In one study,[20] participants were asked to choose between safely winning 3,000 dollars and a game in which there was an 80% chance of winning 4,000 dollars and a 20% chance of losing it all. Despite the fact that the mathematically most valuable option would be risky (0.80 x 4000 = 3,200 versus 3,000 dollars), most of the people chose to play it safe. However, if the choice was to invest and the participants could choose between losing 3,000 dollars for sure and a game with an 80% chance of losing 4,000 dollars and a 20% chance of not loosing anything, most of the people (92%) chose the risky option when the mathematically safe option would involve losing less money.

Another of the most interesting studies was carried out at Yale University.[21] The researchers trained five capuchin monkeys to trade with metal coins and to be able to get fruit in return.[22] Two humans were in charge of trading with the monkeys. When the monkeys traded with the first human, they received one piece of fruit for each coin and a 50% chance of being given another one later on. When they traded with the second human, they obtained two pieces of fruit and a 50% chance of having one of them taken away later on. The monkeys repeated the experiment enough times as to know that, statistically speaking, they would receive the same number of pieces of fruit (1.5 on average) with each of the two humans. However, the monkeys preferred to deal with the first human 71% of the times. The authors concluded that the monkeys chose to avoid possible loss over possibly achieving a gain, displaying clear loss aversion, which appears to have a clear impact on decision-making. Moreover, it has been suggested that this behavioural characteristic is present since the first common ancestors before the branches of the capuchin monkeys and humans diverged, indicating a possible role in the survival as a species.

Although the previously mentioned studies are among the most representative of loss-aversion, this behaviour has been related to many experimental scenarios,[23] as real as the property market,[24] consumer preferences[25] or job choice.[26,27]

Balance between the two systems

The decision to make a given investment or not will depend on the resultant balance between the brain reward system and the loss-aversion system (fig. 2). When a decision is presented as potential gain, the brain activates the reward system. When the decision is presented as potential loss, the loss-aversion system is activated. The very way in which the same investment is presented will cause us to have a different opinion. A "golden opportunity" and a "risky, speculative investment" may possibly be the same investment, merely presented in a different way. The different activation of both brain systems will impact how we perceive the investment and our subsequent behaviour.[28]

In a recent study,[29] functional magnetic resonance was used to determine the areas of the brain that were activated when the subjects made economic decisions in positive or negative economic contexts. These responses indicated relative specialization depending on the economic context. When the economic context was positive, activation was seen predominantly in structures involved in the brain reward system, such as the nucleus accumbens and the orbito-frontal cortex, whereas when the economic context was negative, greater activation was seen in the insula and the amygdala, which are related to the loss-aversion system. The results of this study point to the presence of different pro and con brain localizations in decision-making that may be affected by contextual factors.

One study carried out by Knutson in 2007[8,30] presented the participants with several products that they could purchase while cerebral magnetic resonance was used to study the brain regions that were activated. Each of the three brain regions studied, the nucleus accumbens, prefrontal cortex, and amygdala, had a different meaning: the nucleus accumbens was associated with the preference for an object and its activation predicted that the participant was interested in the object and would probably buy it. The medial prefrontal cortex was activated when prices were very low and predicted that the participants would buy. The insula was activated when risky decisions were made and when mistakes due to risk-aversion were made.

Alteration of the balance between the reward system and the risk-aversion system

The balance between these systems will define our behaviour in light of a given economic action and, as occurs in the rest of the body, pathologies can arise in one of them that can cause the balance to tilt to one side or the other. Among the disorders that have been involved in these systems, the following stand out:

1. Depression and mania: decreased function of the brain reward system may be behind the anhedonia and lack of motivation associated with depression. This hypothesis is founded on the evidence of reduced dopaminergic transmission in depression and decreased response of the reward system.[31] This imbalance between both systems will foster a predominance of loss-aversion with a reduced appetite for risk in these individuals. In manic patients, on the other hand, a different pattern of activation of the nucleus accumbens has been found, with less activation of this nucleus after obtaining the desired object, which may underlie the disinhibition typically seen in this disorder.[32]
2. Alcoholism: alcohol, like many other drugs, activates the mesolimbic dopaminergic pathway and, with chronic use, produces alterations in the brain reward system, leading to atrophy of the structures comprised in it.[33] Specifically, ethanol appears to act by means of the glycinergic receptors of the nucleus accumbens and through the nicotinic receptors of the ventral tegmental area.[34] Manipulation of these two receptor systems could modulate ethanol use and represent a treatment for alcoholism.
3. Gambling and other impulse control disorders: compulsive gambling is the oldest economic disorder ever described and was already known since Classical Greece. It has an estimated prevalence rate of 0.5% in women and 1% among males, whereas mild gambling problems have a prevalence rate of 3.6% among females and 6.9% in men.[35] Compulsive gambling is included within a group of disorders known as impulse control disorders and is characterized by a lack of sensitivity to risk, increased impulsivity, and lack of self-control. Furthermore, compulsive gamblers display emotional disorders such as depression, anxiety, and toxic substance use, above all, alcohol. A decrease in the number of dopamine receptors has been observed in the structures comprised in this system, making it less sensitive to the novelties and interests that appear daily. These subjects have been proven to present a smaller increase in anticipatory heart rate when facing an economic loss or gain in comparison to normal subjects. They neither fear loss nor do they become as excited after winning as non-gamblers. This has also been proven through studies conducted with functional magnetic resonance where their brain reward system has been shown to be less activated than in normal subjects. This diminished activity of the dopaminergic brain reward system causes these subjects to need to self-stimulate through games of chance and thereby momentarily increase their levels of dopamine and re-establish the balance with the loss-aversion system (fig. 3). Curiously, compulsive gamblers also have decreased activity in the prefrontal lobe in areas of planning, estimation of time, calculation, reasoning, and impulse.

   Disorders of the brain reward system have also been involved in other impulsive behaviours, such as substance abuse,[36-38] hypersexuality,[39] and even in obesity.[40,41] In fact, the term *reward deficiency syndrome* has been suggested to refer to the greater tendency toward addictions, obsessive-compulsive disorders (addiction to sex, gambling, eating behaviour disorders), and toward high-risk behaviours in subjects suffering from it. Subjects with this disease tend to seek non-natural rewards to stimulate the intrinsic deficiency of rewards and release dopamine to compensate dopaminergic hypoactivity of the nucleus accumbens.[42,43]
4. Alzheimer's disease and other neurodegenerative diseases: the loss of abilities in various neurodegenerative diseases can associate a disorder in financial abilities that, for the most part, is under-diagnosed given that other symptoms predominate in these illnesses. For instance, altered numerical and financial abilities are known to be present in Alzheimer's disease from the very earliest stages of the disease and should be evaluated.[44,45] With respect to Parkinson's disease, there is a growing body of evidence of the existence of various impulse control disorders, including altered financial decision-making. They are related with being male, younger, early onset of the disease, and taking dopaminergic agonists[46] and should be evaluated in all patients with Parkinson's disease.[47]

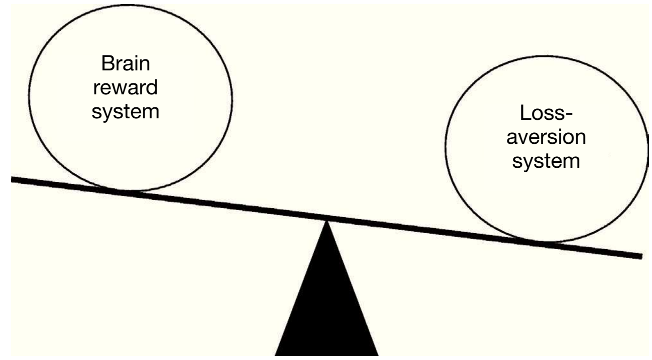


Figure 3 The alteration of the brain reward system in gamblers will produce the need for greater involvement of this system; consequently, the balance between this system and the loss-aversion system will decompensate and foster increased risk in financial investments.

Hormonal influences in financial decision-making

There are clear differences in decision-making between men and women, in which an important role might be played by sex hormones. Whereas females have greater risk-aversion, males, particularly young men, suffer from a greater excess of confidence. A recent study carried out in 17 male stockbrokers in London[48] came to the conclusion that when the subjects had elevated levels of testosterone in the morning, they recorded greater profits, which was related to the fact that testosterone is capable of increasing confidence and the taste for risk. Another study[49] reveals that greater concentrations of testosterone in women's saliva were related with a greater taste for risk and with the choice of riskier careers in the field of finances.

Another of the conclusions from these studies is that cortisol concentrations increase with the prospect of obtaining a benefit[48] and that the high levels of this hormone have the opposite effect of testosterone and cause investors to assume fewer risks and to be more cautious.

The herding effect, the amygdala, serotonin, and mirror neurons

Ideas, like yawns, are contagious. The herding effect is the tendency of certain species of animals to replicate the behaviour of their kind, which has been related with a role in the safety of species. The fact of living and reproducing the herd's activities can increase the chance of the individual's survival and this, which might have been useful for Neolithic man, may have been passed down to our days and account for the multitude of current behaviour patterns, from different fashions to investor and stock market behaviour.[50,51] Although the brain mechanisms involved in these social behaviours are not clear, several possibilities have been postulated:

1. The amygdala has been related to social decision-making.[52,53] When an individual has an independent vision that differs from that of their group, the amygdala is highly activated, which might represent a negative emotional charge, since the amygdala is associated with pain when it differs from the herd's ideology.
2. Serotonin appears to regulate the acquisition of social behaviour. This substance is derived from an amino acid that is present in the diet, tryptophan, and when tryptophan is eliminated from the diet, serotonin levels in the brain fall. A more antisocial behaviour and increased personal interests over group interests have been found in subjects with diets that are poor in tryptophan.[54,55] There is a decrease in the activation of the anterior cingulate sulcus and of the orbito-frontal cortex, which suggests that people with low levels of serotonin are less influenced by the herding effect.
3. Mirror neurons become activated when an animal observes a certain activity in another individual, generally that of their own species, as well as when carrying out a given activity being observed in another. These have been identified in several animal species, particularly in primates and, of course, in human beings. It has been supposed that these neurons play an important role in cognitive abilities linked to learning and to social life.[56,57] They also appear to be related with empathy, imitation, and social behaviours.[58]

Tendency to prediction and the price of surprise

Pavlov's dogs are a classical example of the brain's ability to predict. Pavlov associated a stimulus to the dogs' food. After several days of carrying out the same operation, he proved that the dogs salivated with only the sound of the bell and without being given any food.[59] The brain's tendency to make predictions is also related to dopamine and the brain reward system. After performing a given action for which we have received a benefit, whether economic or not, our dopaminergic reward system will be activated. This, on the one hand, will foster learning and on the other hand, will reinforce the patterns of behaviour that have led to the circumstances through which we have obtained the benefit.[60]

The capacity to be surprised appears to be a trait that is quite specific to human beings and sets them apart from other animals. Humans and the large apes are among the few animals that have a special kind of neuron called spindle cells that are found in a brain region known as the anterior cingulate cortex. These neurons are in charge of encoding the feeling of surprise when an event does not take place in the expected way. Although this region is the most widely studied, others, such as the right inferior orbito-frontal cortex, the supplementary premotor area, and the posterior cingulate cortex also exhibit different activation patterns.[61]

The spindle cells of the anterior cingulate cortex process and integrate huge amounts of information in a very short period of time and make it possible to respond very quickly. Thus, it is an intuitive system, the peculiarity of which is the speed of response. According to the studies conducted by Allman,[62] this system does not seek an ideal response, but simply survival. When homo sapiens were taking their first steps, it was more important to recognize mistakes as quickly as possible than to recognize successes, and distinguishing one small error might be the difference between surviving or not.

A clear asymmetry has been seen in the responses to monetary surprises. When the news consists of money having been lost, these neurons activate much more in terms of both number and intensity than when the surprise is positive and more money was won than initially foreseen, once again reinforcing the notion that what mattered to the Palaeolithic brain was the identification of negative surprises with the aim of staying alive.[63-65] This asymmetry in money management has a clear application in financial investments. Our brain will be more predisposed to reacting quickly, intensely, and irrationally to a negative piece of news than to a positive piece of news.

Excessive confidence

Another bias that continually occurs in financial decision-making is the excess of confidence and the illusion of knowledge. In an experiment carried out in Seattle, two psychiatrists[66] asked a group of drivers about their ability behind the wheel the last time they drove their car. Most of them rated it as "good" or "very good". The odd thing about the study is that the group of drivers had been selected from a hospital and all of them had been admitted for causes related to a motor vehicle accident. Moreover, according to the Seattle police, 68% of those drivers had been directly responsible for their accidents; 58% had traffic fines, and 44% had a criminal record. In general, human beings believe that they are above average. According to another study, between 65 and 80% of the drivers thought they were above average.[67]

A recent study showed that the medial prefrontal cortex, the area where the dopaminergic pathways of the reward system converge, is involved in learning while making decisions.[12] When this area becomes activated, it is a signal that the individual is headed in the right direction to achieve his or her goals and it strengthens the means by which this activation has occurred. This means we pay less and less attention to the potential dangers of our decisions.

The medial prefrontal cortex is activated by many ways other than money. Any product that we like (coffee, beer, smoking, or an attractive person) is capable of activating the prefrontal cortex, which is why its activation only indicates satisfaction with the product. Some drugs, such as cocaine or amphetamines, activate this brain region, bringing about a false feeling of pleasure.

The brain is going to generate signals to favour the behaviour that leads to rewards. When a reward is attained, the dopaminergic neurons fostering the behaviour that has brought about this reward are activated. These dopaminergic neurons act on the medial prefrontal cortex.[68] When these behaviours no longer lead to a reward, noradrenalin is released, a substance that stimulates the search for new opportunities.

When investors have achieved good results for one or two years, they become confident and believe that they are going to continue to obtain the same results. Their dopaminergic system has created a series of changes that foster the behaviours that led to success (to the reward).[69] However, these professionals have serious difficulties in maintaining their attention to risk. This combination of neurotransmitters (activation of the dopaminergic system and decrease of the noradrenergic system) make the investors careless when facing certain events such as economic bubbles with disastrous outcomes.[70]

Conclusions

New neuroimaging techniques have made it possible to determine which brain structures are in charge of economic decision-making, which has led to the birth of neuroeconomics.

The structures involved to a greater degree in financial decision-making are the amygdala, the insula, the medial prefrontal cortex, the anterior and posterior cingulate cortices, the nucleus accumbens, and the ventral tegmental area. These structures and others that have yet to be related to decision-making will be studied in great depth in the years to come, given the important practical applications of this new science.

As neurologists, we should define our role in this interdisciplinary science, given the privileged position of our specialty to study brain functioning and the more than likely growth neuroeconomics is predicted to undergo in the near future.

Conflict of interest

The authors state that there is no conflict of interest.

Acknowledgements

The authors would like to thank the Spanish Association of Neuroeconomics (ASOCENE in its Spanish acronym) for providing bibliographic material.

References

1. Bermejo PE, Izquierdo RJ. Cerebro rico, cerebro pobre. Una introducción a la neuroeconomía. Madrid: DCT21; 2010.
2. Camerer C. Behavioral economics: reunifying psychology and economics. Proc Natl Acad Sci U S A. 1999;96:10575-7.
3. Glimcher PW, Camerer CF, Fehr E, Poldrack RA. Neuroeconomics. Decision making and the brain. Londres: Elsevier; 2009.
4. Spencer H. Principles of Psychology. New York: Appleton Press; 1880.
5. Bozarth MA. Pleasure systems in the brain. In: Warburton D.M., editors. Pleasure: The Politics and The Reality. New York: John Wiley & Sons; 1994. 5-14.
6. Manes F, Sahakian B, Clark L, Rogers R, Antoun N, Aitken M, et al. Decision-making processes following damage to the prefrontal cortex. Brain. 2002;125:624-39.
7. Bermejo PE, Castillo-Moreno L. Acalculia: clasificación, etiología y tratamiento clínico. Rev Neurol. 2006;43: 223-7.
8. Knutson B, Adams CS, Fong GW, Hommer D. Anticipation of increasing monetary reward selectively recruits nucleus accumbens. J Neurosci. 2001;21:159.
9. Knutson B, Fong GW, Bennett SM, Adams CM, Hommer D. A region of mesial prefrontal cortex tracks monetarily rewarding outcomes: characterization with rapid event-related fMRI. NeuroImage. 2003;18:263-72.
10. Christopoulos GI, Tobler PN, Bossaerts P, Dolan RJ, Schultz W. Neural correlates of value, risk, and risk aversion contributing to decision making under risk. J Neurosci. 2009;29: 12574-83.
11. Bechara A, Damasio H, Damasio AR. Emotion, decision making and the orbitofrontal cortex. Cereb Cortex. 2000;10: 295-307.
12. Rolls ET, Grabenhorst F. The orbitofrontal cortex and beyond: from affect to decision-making. Prog Neurobiol. 2008;86: 216-44.
13. Bechara A. The role of emotion in decision-making: evidence from neurological patients with orbitofrontal damage. Brain Cogn. 2004;55:30-40.
14. Shiv B, Loewenstein G, Bechara A, Damasio H, Damasio AR. Investment behavior and the negative side of emotion. Psychol Sci. 2005;16:435-9.
15. Weller JA, Levin IP, Shiv B, Bechara A. The effects of insula damage on decision-making for risky gains and losses. Soc Neurosci. 2009;4:347-58.
16. Xue G, Lu Z, Levin IP, Bechara A. The impact of prior risk experiences on subsequent risky decision-making: the role of the insula. Neuroimage. 2010;50:709-16.
17. Clark L, Bechara A, Damasio H, Aitken MR, Sahakian BJ, Robbins TW. Differential effects of insular and ventromedial prefrontal cortex lesions on risky decision-making. Brain. 2008;131: 1311-22.
18. Polezzi D, Sartori G, Rumiati R, Vidotto G, Daum I. Brain correlates of risky decision-making. Neuroimage. 2010;49: 1886-94.
19. Bechara A, Damasio H, Damasio AR. Role of the amygdala in decision-making. Ann N Y Acad Sci. 2003;985:356-69.
20. Zweig J. Your money and your brain. New York: Simon and Schuster paperbacks; 2007.

21. Chen MK, Lakshminarayanan V, Santos LR. How basic are behavioral biases? J Political Econ. 2006;114:517-37.
22. Westegaard GC, Liv C, Chavanne TJ, Suomi SJ. Token mediated tool-use by a tufted capuchin monkey [Cebus apella]. Animal Cogn. 1998;1:101-6.
23. Tversky A, Kahneman D. Rational choice and the framing of decisions. J Business. 1986;59:251-78.
24. Odean T. Are investors reluctant to realize their losses? J Finance. 1998;5:1775-98.
25. Hardie BGS, Johnson EJ, Fader PS. Modeling loss aversion and reference dependence effects on brand choice. Marketing Sci. 1993;12:378-94.
26. Krueger AB, Summers LH. Efficiency wages and the inter-industry wage structure. Econometrica. 1988;56:259-93.
27. Akerlof GA, Yellen JL. The fair wage-effort hypothesis and unemployment. Q J Economics. 1990;105:255-83.
28. Peterson RL. The neuroscience of investing: fMRI of the reward system. Brain Res Bull. 2005;67:391-7.
29. Hardin MG, Pine DS, Ernst M. The influence of context valence in the neural coding of monetary outcomes. Neuroimage. 2009;48:249-57.
30. Knutson B, Rick S, Wimmer GE, Prelec D, Loewenstein G. Neural predictors of purchases. Neuron. 2007;53:147-56.
31. Martin-Soelch C. Is depression associated with dysfunction of the central reward system? Biochem Soc Trans. 2009;37:313-7.
32. Abler B, Greenhouse I, Ongur D, Walter H, Heckers S. Abnormal reward system activation in mania. Neuropsychopharmacology. 2008;33:2217-27.
33. Makris N, Oscar-Berman M, Jaffin SK, Hodge SM, Kennedy DN, Caviness VS, et al. Decreased volume of the brain reward system in alcoholism. Biol Psychiatry. 2008;64:192-202.
34. Söderpalm B, Löf E, Ericson M. Mechanistic studies of ethanol's interaction with the mesolimbic dopamine reward system. Pharmacopsychiatry. 2009;42:87-94.
35. Laplante DA, Nelson SE, Labrie RA, Shaffer HJ. Disordered gambling, type of gambling and gambling involvement in the British Gambling Prevalence Survey 2007. Eur J Public Health. In press.
36. Di Chiara G, Bassareo V. Reward system and addiction: what dopamine does and doesn't do. Curr Opin Pharmacol. 2007;7:69-76.
37. Gil-Verona JA, Pastor JF, de Paz F, Barbosa M, Macias-Fernández JA, Maniega MA, et al. Neurobiología de la adicción a las drogas de abuso. Rev Neurol. 2003;36:361-5.
38. Nolley EP, Kelley BM. Adolescent reward system perseveration due to nicotine: studies with methylphenidate. Neurotoxicol Teratol. 2007;29:47-56.
39. Moncho-Bogani J, Martínez-García F, Novejarque A, Lanuza E. Attraction to sexual pheromones and associated odorants in female mice involves activation of the reward system and basolateral amygdala. Eur J Neurosci. 2005;21: 2186-98.
40. Castellanos EH, Charboneau E, Dietrich MS, Park S, Bradley BP, Mogg K, et al. Obese adults have visual attention bias for food cue images: evidence for altered reward system function. Int J Obes (Lond). 2009;33:1063-73.
41. Stoeckel LE, Weller RE, Cook EW, Twieg DB, Knowlton RC, Cox JE. Widespread reward-system activation in obese women in response to pictures of high-calorie foods. Neuroimage. 2008;41:636-47.
42. Linazaroso G, van Blercom N, Lasa A. Hipótesis: enfermedad de Parkinson, síndrome de deficiencia de recompensa y efectos adictivos de la levodopa. Neurologia. 2004;19:117-27.
43. Comings DE, Blum K. Reward deficiency syndrome: genetic aspects of behavioral disorders. Prog Brain Res. 2000;126: 325-41.
44. Weintraub D. Impulse control disorders in Parkinson's disease: prevalence and possible risk factors. Parkinsonism Relat Disord. 2009;15:110-3.
45. Weintraub D, Hoops S, Shea JA, Lyons KE, Pahwa R, Driver-Dunckley ED, et al. Validation of the questionnaire for impulsive-compulsive disorders in Parkinson's disease. Mov Disord. 2009;24:1461-7.
46. Martini L, Domahs F, Benke T, Delazer M. Everyday numerical abilities in Alzheimer's disease. J Int Neuropsychol Soc. 2003;9:871-8.
47. Sinz H, Zamarian L, Benke T, Wenning GK, Delazer M. Impact of ambiguity and risk on decision making in mild Alzheimer's disease. Neuropsychologia. 2008;46:2043-55.
48. Coates JM, Herbert J. Endogenous steroids and financial risk taking on a London trading floor. Proc Natl Acad Sci U S A. 2008;105:6167-72.
49. Sapienza P, Zingales L, Maestripieri D. Gender differences in financial risk aversion and career choices are affected by testosterone. Proc Natl Acad Sci U S A. 2009;106:15268-73.
50. Baddeley M. Herding, social influence and economic decision-making: socio-psychological and neuroscientific analyses. Philos Trans R Soc Lond B Biol Sci. 2010;365:281-90.
51. Raafat RM, Chater N, Frith C. Herding in humans. Trends Cogn Sci. 2009;13:420-8.
52. Amaral DG. The primate amygdala and the neurobiology of social behavior: implications for understanding social anxiety. Biol Psychiatry. 2002;51:11-7.
53. Amaral DG. The amygdala, social behavior, and danger detection. Ann N Y Acad Sci. 2003;1000:337-47.
54. Tiihonen J, Virkkunen M, Räsänen P, Pennanen S, Sainio EL, Callaway J, et al. Free L-tryptophan plasma levels in antisocial violent offenders. Psychopharmacology (Berl). 2001;157:395-400.
55. Virkkunen M, Ebeling H, Moilanen I, Tani P, Pennanen S, Liesivuori J, et al. Total plasma l-tryptophan, free l-tryptophan and competing amino acid levels in a homicidal male adolescent with conduct disorder. Acta Psychiatr Scand. 2003;108:244-6.
56. Rizzolatti G, Fabbri-Destro M. The mirror system and its role in social cognition. Curr Opin Neurobiol. 2008;18:179-84.
57. Noordzij ML, Newman-Norlund SE, de Ruiter JP, Hagoort P, Levinson SC, Toni I. Brain mechanisms underlying human communication. Front Hum Neurosci. 2009;3:14.
58. Oberman LM, Pineda JA, Ramachandran VS. The human mirror neuron system: A link between action observation and social skills. Soc Cogn Affect Neurosci. 2007;2:62-6.
59. Pavlov IP. Conditioned reflexes: an investigation of the physiological activity of the cerebral cortex. Londres: Oxford University Press; 1927.
60. Kheirbek MA, Beeler JA, Ishikawa Y, Zhuang X. A cAMP pathway underlying reward prediction in associative learning. J Neurosci. 2008;28:11401-8.
61. Chandrasekhar PV, Capra CM, Moore S, Noussair C, Berns GS. Neurobiological regret and rejoice functions for aversive outcomes. Neuroimage. 2008;39:1472-84.
62. Allman JM, Hakeem A, Erwin JM, Nimchinsky E, Hof P. The anterior cingulate cortex. The evolution of an interface between emotion and cognition. Ann N Y Acad Sci. 2001;935:107-17.
63. Williams ZM, Bush G, Rauch SL, Cosgrove GR, Eskandar EN. Human anterior cingulate neurons and the integration of monetary reward with motor responses. Nat Neurosci. 2004;7:1370-5.
64. Bush G, Vogt BA, Holmes J, Dale AM, Greve D, Jenike MA, et al. Dorsal anterior cingulate cortex: a role in reward-based decision making. Proc Natl Acad Sci U S A. 2002;99: 523-8.

65. Gehring WJ, Willoughby AR. The medial frontal cortex and the rapid processing of monetary gains and losses. Science. 2002;295:2279-82.
66. Preston CE, Harris S. Psychology of drivers in traffic accidents. J. Appl Psychol. 1965;49:284-8.
67. Svenson O. Are we all less risky and more skillful than our fellow drivers? Acta Psychologica. 1981;47:143-8.
68. Weber B, Rangel A, Wibral M, Falk A. The medial prefrontal cortex exhibits money illusion. Proc Natl Acad Sci U S A. 2009;106:5025-8.
69. Matsumoto K, Tanaka K. The role of the medial prefrontal cortex in achieving goals. Curr Opin Neurobiol. 2004;14:178-85.
70. Presson P, Benassi V. Illusion of control: a metaanalytic review. J Social Behavior Personality. 1996;3:493-510.