Brain mechanisms involved in decision making

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Summary. Aim. *To review the studies on brain mechanisms in decision making within the framework of the somatic marker hypothesis, and based on experiments employing the Iowa Gambling Task.* Development. *An overview of the somatic marker hypothesis is presented together with the review of the main results obtained from research in brain damaged patients, and normal subjects with functional neuroimaging studies, that have led to the identification of the neural structures involved in decision making in humans.* Conclusions. *The main region involved in decision making is the ventromedial prefrontal cortex, that integrates sensory, mnesic and emotional information relevant to the task. Other structures intervening in the various relevant processes in decision making are the amygdala (processing and encoding of the emotional signal and its association with contextual stimuli) and the cingulate cortex (process monitoring and response inhibition, especially in situations of uncertainty). The prefrontal dorsolateral cortex would also be involved through the necessary activation of the working memory in the decision making process, especially in the case of complex tasks. [REV NEUROL 2006; 42: 411-8]*
Key words. *Amygdala. Brain damage. Decision making. Emotion. Iowa Gambling Task. Prefrontal cortex. Somatic marker.*

INTRODUCTION

Decision making is a continuous human activity in all walks of life. Choosing from several options may be a very simple task, but on occasions it can become so complex as to be a source of serious preoccupation. A number of cognitive processes come into play in decision making, among them the processing of the stimuli present in the task, the memory of previous experiences and the estimating of the possible outcomes of each option. All these processes require the involvement of the working memory in conjunction with the so called executive functions [1]. Current research is placing more and more weight on decision making's not being merely a rational process of counting or comparing the losses and gains resulting from a specific choice. Rather, it seems that emotional aspects, deriving from the experience of similar situations, be they personal or vicarious, and aspects associated with outcomes or with the context in which the decision occurs, play a decisive role [2].

Emotions guide decision making, they simplify and accelerate the process, they reduce the complexity of the decision and temper potential conflicts between similar options. It is significant that people who do not perform well in experimental tasks of decision making do not show similar emotional changes to those who perform well, and they present serious adaptation problems in their social or interpersonal lives, as occurs with patients with certain frontal cortex lesions and with some groups of subjects suffering drug addiction [3-5].

Accepted after peer-review: 16.03.06.

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This research was partially supported by a grant from the Spanish Ministry of Education and Science, SEJ2004-06062.

We examine here the somatic marker hypothesis as a neurocognitive model of decision making, and its experimental study with the use of the Iowa Gambling Task (IGT).

SOMATIC MARKER HYPOTHESIS

The somatic marker hypothesis, developed by Damasio [2] describes the role emotion might play in decision making and it has served as a guide for research in this field. A somatic marker is a bodily change which reflects an emotional state, be it positive or negative, which may influence decisions made at a given moment. Anticipation of possible consequences of a choice generates somatic responses of an emotional origin which guide the decision making process. Responses which arise from the possible consequences of a choice stem from emotional reactions produced by earlier decisions. The somatic marker facilitates and speeds up decision making, especially in social behaviour, where situations of greater uncertainty may arise.

In this context the emotional response is the subjective and somatic –be it motor or autonomic– reaction of an individual to an event, e.g. the positive or negative outcomes arising from a decision. When this reaction is associated to a situation or to a set of stimuli, it may consciously or subconsciously affect future behaviour, thus becoming a somatic marker. These markers, which are understood at the experimental level as autonomic, muscular, neuroendocrine or neurophysiological changes, can provide unconscious signals which precede, facilitate and contribute to decision making, even before the subjects can explain why they take the decision or can state conceptually or openly the strategy they are using to make the decisions [6,7]. Somatic markers therefore support cognitive processes, they enable appropriate social behaviour, they contribute to making advantageous decisions –by inhibiting the tendency to seek immediate rewards– and they facilitate the representation of future scenarios in the working memory [6].

In contrast, the absence, alteration or weakening of somatic markers leads to unsuitable or disadvantageous decisions. This deficit occurs in patients with ventromedial prefrontal and other prefrontal regions lesions, e.g. the prefrontal dorsolateral and

cingulate cortex, and also in patients with bilateral lesions in the amygdala, in whom there is an incapacity to experiment emotions appropriately or to generate autonomic responses to aversive stimuli.

IOWA GAMBLING TASK

Experimental study of decision making processes is based on a series of tasks, of greater or lesser complexity, in which the subject chooses options trial-by-trial. The most used task has been the IGT [1,2,7-9]. In the IGT the subjects choose from four decks of cards and depending on the deck chosen in each trial, they receive symbolic monetary rewards (winnings or punishments), such that two of the stacks will, over time lead to them losing while the other two will lead to them winning. Moreover, two of the decks are characterised by frequent small losses, while the other two suppose less frequent, but greater losses. Normal subjects begin by choosing the higher risk decks, with greater rewards and losses, and then change, around the 40th assay of the one hundred which make up the test, to the favourable decks, which lead to rewards over the long term.

This is a complex task which most normal people (about two thirds) perform with no difficulty. A bad performance in the IGT may be due to different factors [10]:

- Preference towards high risk choices.
- Inability to evaluate the likelihood of reward or punishment associated to each option, or to learn the relationships between the outcomes of the choice and the stimuli associated to the task.
- Hypersensitivity towards the reward.
- Insensitivity towards the punishment.
- Problems in executive functions (e.g. deficient working memory or attentional inflexibility).
- Lack of inhibition or problems in controlling impulses.

Thus, given the complexity of the task, other tasks have been designed and used to isolate the components and allow separate study of aspects such as working memory, attentional flexibility or change, impulsiveness or lack of motor inhibition, or the effect of earlier learning or the subject's preference of risk. Examples include the Cambridge Gamble Task and the Risk Task, of Rogers et al [11,12], and the Guessing Task of Elliott et al [13].

The changes in electrodermal activity (skin conductance levels and responses) caused by the decision making situation are the somatic markers which have been studied most. These changes are the result of the sympathetic activity caused by the situation, the mental effort and emotional activity, including the anticipation of the consequences of a decision taken and the memory of the emotional reaction which occurred previously in response to the consequences of the same choice. Two types of electrodermal responses occur in the IGT: those which follow a reward or punishment, and anticipatory ones which precede a choice. Studies by Bechara et al [6,7,14] indicate that normal subjects show skin conductance responses provoked by the consequences of their choices –winnings or losses– and these are greater the higher the intensity of the reward or the punishment. The main finding by this research group is, however, the presence of anticipatory electrodermal responses, i.e. those that appear immediately prior to the subjects' making their choice. At the beginning of the task, cards are taken from disadvantageous decks, but as the task progresses, those subjects who switch to choosing cards from the advantageous tasks show greater conductance responses prior to choosing disadvantageous decks. These responses have been interpreted as somatic markers, which are associated to choices made by the subject which derive from experience of the outcomes of the choices in earlier trials. The greater magnitude of responses prior to choosing a disadvantageous deck represents the accumulated somatic signal, which biases or guides the subjects away from that deck. Inexistent or low intensity anticipatory conductance responses are associated to a higher choice of unfavourable cards and, hence, worse results. This occurs in subjects suffering prefrontal lesions, especially in the ventromedial sector [6,7,14].

These data have been partially replicated by other researchers. Crone et al [15] found that the losses, compared to the gains, led to increases in the levels of skin conductance together with a deceleration in the heart rate. These autonomic changes correlated with the magnitude of the loss. Subjects who performed well in the IGT were those who showed the most pronounced heart rate deceleration, especially following losses, and an increase in the levels of skin conductance prior to unfavourable choices. In contrast, those subjects who performed badly in the task showed no differences in anticipatory autonomic activity for advantageous and disadvantageous choices. The deceleration in heart rate, which was higher in subjects who performed the task well, was interpreted by the researchers as an anticipation of the punishment, and it could thus be considered a somatic marker which exerts an influence on decision making, like the changes in skin conductance.

Elsewhere, Tomb et al [16] have found that the greater or lesser amplitude in the skin conductance responses to the advantageous decks may be due more to the size of the rewards and the punishments than to net outcomes, be they positive or negative, of the choices. Likewise, Suzuki et al [17] reported higher conductance responses as a consequence of the choice of advantageous decks, especially when the result is a loss. Thus, these responses have an emotional character, since they occur in accordance to the magnitude of the result and the consequence, especially when the latter is negative.

The presence of weak somatic markers, or their absence, leads to inappropriate or disadvantageous decisions. Suzuki et al [17] found a negative correlation between the amplitude of the conductance response at the beginning of the IGT and the choice of advantageous decks. However, these researchers reported no relation between the anticipatory conductance responses and the results of the subjects in the task. Anticipatory conductance responses to the disadvantageous decks either do not exist or are of lower intensity in subjects who perform badly in the task [15]. This reduced level of autonomic response leads subjects to disadvantageous decisions and a bad task performance. Thus, just as the somatic marker hypothesis proposes, there exists a subgroup of normal subjects who show reduced physiological responses during the IGT, as well as performing badly –a situation which resembles that of patients with lesions in the ventromedial sector of the prefrontal cortex.

Indirect proof of the need for somatic markers in decision making comes from a series of experiments by Hinson et al [18] in which the working memory overload leads to diminished conductance responses and a worse performance of the task.

However, in that experiment the higher conductance responses did not appear for disadvantageous decisions but for advantageous ones. Hinson et al [18] point to a certain cognitive resource competence or interdependence between the working memory and affective markers. Hence, the increase in the working memory load hinders decision making, leads to there not being an affective response and decreases the conductance response.

Authors who are critical of the somatic marker theory, e.g. Maia et al [19], do not discard there existing emotional mechanisms or unconscious processes which guide decision making, although they insist that to date there is no proof of the existence of a somatic marker. The appearance of skin conductance responses associated to the choices is not necessarily indicative of any emotional activity which guides such a decision. Nevertheless, experimental evidence does, at least in part, support the somatic marker theory.

BRAIN MECHANISMS

A number of studies with patients suffering brain damage, together with others using functional neuroimaging techniques, indicate the prefrontal cortex, especially the ventromedial orbitofrontal portion, as the key region in decision making in humans. Lesions in this region may cause disorders in the decision-making process. Neither is there a shortage of studies pointing to the intervention of other structures, such as the anterior cingulate cortex. Hence, the study by Ernst et al [20] using positron emission tomography (PET) extends the regions activated during the IGT to the orbitofrontal, dorsolateral prefrontal, ventral prefrontal, anterior cingulate, insular and parietal cortices, and cerebellum. Elliott et al [13] found with functional magnetic resonance that the Guessing Task activates the dorsolateral prefrontal cortex, the right orbitofrontal cortex, the anterior cingulate cortex, the bilateral inferior parietal cortex and the right thalamus. When the task becomes more complicated and there is an increase in uncertainty, however, the preference is for activation of the medial orbitofrontal cortex and the left lateral orbitofrontal cortex.

Ventromedial prefrontal cortex

The hypothesis put forward by Damasio and colleagues [7, 14,21] points to the ventromedial region of the prefrontal cortex integrating the different sources of activity involved in decision making. The ventromedial prefrontal cortex refers to the medial ventral region of the prefrontal cortex and to the medial sector of the orbitofrontal cortex, and it includes the Brodmann areas 25, the inferior portion of areas 24 and 32, and the medial sector of areas 10, 11 and 12. This region is in charge of integrating the somatic states with the information present and provided by the decision making situation, thus providing the substratum for the integration of the relations learnt between the complex situations and the internal states, including those emotional ones associated to such situations in previous experiences. The activation of this region may be somatic and direct, caused by the information which reaches the somatic sensorial cortex, but also indirect, such that it is possible that a cortical activation is produced with no somatic changes. In this case, we would be talking about a mnesic reactivation of somatic sensations, caused by context stimuli which evoke similar somatic markers to those previously experienced. Thus, when a decision is going to be taken, those emotional states which appeared as an outcome of decisions made before in similar circumstances are 'relived' or updated in the ventromedial prefrontal cortex. The somatic state provoked by the situation is thus recovered, and this guides the decision to be taken.

Somatic states, sensory information and previous experiences are integrated in the ventromedial prefrontal cortex with information coming from the amygdala, the hypothalamus and other nuclei of the brain stem [14]. The ventromedial prefrontal cortex exerts its influence on the autonomic and motor activity through circuits which are directed towards the amygdala, the hypothalamus and the striatum, and from there to the brain stem nuclei. In conclusion, this region of the brain intervenes in the estimation of the long term outcomes of decisions taken due to the integration of the somatic states and key information coming from the situation itself or that stored in memory.

Lesions

The main source of data on the implication of the ventromedial prefrontal cortex in decision making comes from the study of patients with lesions in this region. These patients usually show alterations in their social behaviour, decision making and emotional processing. Although they have difficulties in learning from their errors, their intellectual capacities, their intelligence and their memory, along with the other cognitive functions are preserved at normal levels [22]. However, in their social, work and economic lives they are prone to taking decisions and to adopting conducts which lead to negative outcomes. They lose behavioural flexibility and they present problems in adapting to the changes produced in tasks. They show difficulties in planning their daily and future activities, in choosing friends, partners and activities. They are insensitive to long term future outcomes, be they positive or negative, and they are guided rather by immediate outcomes [3, 9,21,23,24] Apparently, they have lost the capacity to use emotions and feelings to guide their behaviour. The most plausible hypothesis to explain their behaviour is that they do not have access to somatic indicators which signal the various alternatives and their possible outcomes [1,25]. Proof of this is that patients with ventromedial prefrontal lesion do not perform well in the IGT and do not develop anticipatory electrodermal responses in the disadvantageous choices [26]. In contrast, these patients experience somatic reactions to the consequences of the decisions they take, i.e. to losses or winnings, just like the normal subjects, although their responses are of lower intensity. Their lesions prevent or interfere in the use of somatic signals triggered off by the amygdala, the hypothalamus and the brain stem nuclei which are to be used into future decisions and which are necessary for suitable decisions to be made. The impression is that the patients with ventromedial lesion, and with no memory problems, do not take into account previous experience in their decisions and when the new decision making situation comes, they do not show anticipatory somatic reactions, which leads to disadvantageous choices.

Different alterations have been found as a function of the lesion location in this region. Anterior lesions to the ventromedial cortex cause bad performance in the IGT decision making task, but a good realisation of working memory tasks. Posterior lesions to the same region, however, lead to bad realisation of

both. Since the dorsolateral prefrontal cortex is directly involved in working memory, Bechara et al [26] propose that the posterior ventromedial prefrontal cortex carries out parallel functions to dorsolateral prefrontal cortex, since its lesion also worsens the working memory, in particular the capacity to store information which will be used later. However, the task employed in this experiment (delayed non-matching to sample) involves two processes both of which are parts of working memory: one is a memory process (remembering what the stimulus was over a delay period), and another is an inhibition process (inhibiting the response to the matching stimulus and selecting the non-matching one). Poor performance can be the result of interference with either process. If the subjects are dis-inhibited it is not necessarily because they forget.

The data obtained from patients with ventromedial frontal lesions have been confirmed by almost all researchers in the case of general lesions which take in the orbital prefrontal cortex. Rogers et al [11] also report an increase in deliberation time, which is probably widespread in this type of lesions. Elsewhere, Manes et al [27] report that patients with extensive, diffuse frontal lesions resemble patients with restricted lesions to the ventromedial prefrontal cortex: bad performance in the IGT, with a clear preference towards high risk options and a tendency to bet higher stakes in the search for higher rewards.

Patients with focal lesions do not present as many problems. Focal orbitofrontal lesions do not produce a significant deterioration in the realisation of the IGT, with patients showing a level which is near to that of the normal controls, although they do take longer to respond [27]. When patients are grouped applying a criterion similar to that of Bechara and collaborators, those presenting a lesion in the orbitofrontal region whose damage extends to other areas are those who have the greatest problems in decision making. There may be, therefore, confounding effects resulting from the location and extension of the lesion.

The data provided by functional neuroimaging also shows the involvement of this prefrontal region in decision making. Rogers et al [12] reported a selective activation of three regions of the right inferior orbital prefrontal cortex: The anterior part of the middle prefrontal gyrus, corresponding to Brodmann area 10, the orbital gyrus, corresponding to area 11, and the anterior sector of the inferior frontal gyrus, corresponding to area 47. Other studies have also found an activation of the middle frontal gyrus during realisation of the IGT. There thus appears a positive correlation between the activation of the medial prefrontal cortex and the scores obtained in the decision making tasks [28]. Other studies with neuroimaging highlight the role of the orbital prefrontal cortex in decision making and report a greater activation in the processing of rewards and also when short and long term response trends are in competition [13,20,29]. Altogether, these data support in general the hypothesis of Damasio et al.

Lateralisation

The right hemisphere is more involved in emotional functions, in awareness and in the 'map' or subjective reference of the corporal states, and in understanding somatic information at the neurocognitive level. Lesions here alter visual processing of faces or social scenes, emotional experience and expression, as well as imagination of emotions. Likewise, emotional autonomic responses, e.g. skin conductance, are weakened or disappear [30]. The right prefrontal cortex seems to be more involved in avoidance behaviors and in the processing of negative emotions. A lesion in this region may lead to insensitivity to the negative outcomes of actions and hypersensitivity to positive outcomes [25].

The data obtained from functional neuroimaging show that the right orbitofrontal cortex is activated in the Risk Task [12]. Other data indicate that the right prefrontal region is activated more as a reaction to punishment and during defense and withdrawal responses, while the left region is activated more in response to reward and the approach to the stimulus [10,30]. Elsewhere, Ernst et al [20] associate right lateralisation to affective processing, but also to inhibitory processes.

A ventromedial lesion in the right hemisphere leads to worse decision making than does a left side ventromedial lesion [30]. In patients with frontal lesions whose damage is limited to the orbital prefrontal cortex, those who present right side lesions show a preference for risky choices [10]. An effect of the size of the lesion also appears, to the extent that the further it extends to areas beyond the ventromedial prefrontal cortex, the greater the tendency to make disadvantageous choices and the worse the performance in the IGT. A more detailed analysis relates the bad results of these patients in the IGT to lesions in the right middle and upper frontal giry and in the right medial prefrontal cortex. Clark et al [10], however, found no lateralisation effects in IGT derived tasks, which is not surprising in the Gambling Task, since the working memory is not required here, nor in the Risk Task, which evaluates risk propensity. Patients with left frontal lesions performed rather worse in the IGT than normal subjects, due possibly to attention problems or to a general effect of the psychomotor slowing, common to the left superior frontal gyrus lesion.

To summarise, the right ventromedial prefrontal cortex is more involved than the left one in social behaviour, emotions and decision making. It does not appear to be activated in tasks requiring working memory, except when the uncertainty demands an additional effort, and its possible function is related to the evaluation of the affective consequences or the behavioural significance of the choice [13].

Dorsomedial and dorsolateral prefrontal cortex

The dorsolateral prefrontal cortex performs an essential role in working memory and in other executive and attentional functions. Working memory is closely related to decision making, although they are different processes. In normal circumstances, the working memory contributes to decision making and to the use of somatic markers in the process [26]. Unicellular studies in monkeys and functional magnetic resonance studies in humans show that this region is involved in attentional control and integrates sensory data from various sources of information. The more information there exists to process a given task, the more this region is activated [23,24,31-33].

Lesions

A lesion to the dorsolateral prefrontal cortex affects decision making, information retention and working memory, although the deterioration is greater in tasks which require the latter functions. Patients with lesions in this region perform badly some tests related to executive functions and they show plan-

ning disorders. Patients with dorsomedial prefrontal damage make more disadvantageous choices in the IGT, although not in simpler derived tasks. Thus, they perform well the Gambling Task, which does not require working memory, and the Risk Task, which evaluates the tendency to take risks [27]. Other authors report that patients with dorsolateral prefrontal lesion show a normal, or slightly lower, level of performance in the IGT, and that only those patients with widespread diffuse lesions showed a bad performance in the IGT, with a preference for risky decisions [10]. As we saw above, dorsal or posterior ventromedial lesions disrupt working memory and affect decision making [26]. Bechara et al [6] highlight that patients with dorsolateral prefrontal lesion show problems in decision making, but these are secondary and are mainly due to problems in executive functions, especially working memory, and this effect is more pronounced in lesions of the right hemisphere. Thus, the general idea is that these lesions indirectly alter decision making, since they have an adverse effect on working memory [14].

Manes et al [27], however, report a bad IGT performance for patients with dorsomedial prefrontal lesion and conclude that the activity of the ventromedial and dorsomedial prefrontal cortices in decision making cannot be separated. Elsewhere, Rogers et al [12], using functional neuroimaging, found no activation of the dorsomedial prefrontal cortex, and, therefore, working memory would not be necessary to perform the Risk Task.

Lateralisation

The right prefrontal cortex seems to play a crucial role in decision making [27]. Compared to normal subjects and patients with lesions in the left hemisphere, patients with right dorsomedial frontal lesions show a bad performance in delayed tasks, which points to a deficit in working memory, and a deficient performance in decision making tasks, which likens them to patients with ventromedial lesions [10]. Bechara et al [26], however, report that these patients perform well the IGT, but with a low normal score.

In contrast, patients with dorsolateral frontal lesions in the left hemisphere perform similarly to normal subjects after several trials, which shows a learning effect [10]. Bechara et al [26] report that such patients perform well in both decision making and delay tasks.

According to Clark et al [10], it is highly likely that the effects of lateralisation and the extension of the lesion are confused in their patients. Under equal conditions of extension, the right side disrupts decision making more, and the degree of alteration correlates with the volume of the lesion. This happens even when the lesion affects the dorsolateral prefrontal cortex but does not reach the ventromedial cortex. A contrasting piece of data can be found in the study by Elliott et al [13], who report a greater activation of the left dorsolateral prefrontal cortex in the Guessing Task, which requires the intervention of the working memory. These authors interpret this as a result of the activation of the regions involved in verbal categorising, memory or practice, as occurs when naming or categorising cards according to face, suits or colours. In conclusion, the right dorsolateral frontal lesion resembles the ventromedial lesion in its effects on the decision making task, apparently due to disturbance of the working memory.

Amygdala

The amygdala takes part in the acquisition of fear conditioned to signals which anticipate a danger or a threat. Within this structure takes place the convergence of sensory information proceeding from the conditioned stimulus and that from the aversive unconditioned stimulus, and in a way that the motivational and emotional meaning of the stimuli is reflected in the autonomic responses [34]. Associations or previous connections between stimuli and their aversive consequences are produced in the amygdala, which are then used in decision making in similar situations. This structure processes the emotional content of unfavourable choices and promotes autonomic responses, and thus it is possible that the cognitive appraisal of the situation is made on the basis of the earlier emotional appraisal [35].

Research attributes an important role to the amygdala in the triggering of emotional responses and is decisive in recognition, learning and response to affective stimuli [36-39]. The importance of the amygdala in processing emotional stimuli with a negative affective load has also been highlighted in studies using functional neuroimaging [40-42]. Ernst et al [20] place the role of the amygdala in the initial stages of the decision making task, even before the subject has developed a defined strategy.

Lesions

Patients with amygdala lesion do not present electrodermal responses in reaction to rewards or punishments, nor fear-conditioned autonomic responses [36,37,43]. However, there is an explicit conscious appraisal of the situation [35]. Lesions in the central nucleus of the amygdala disrupt the conditioning and manifestation of fear and hinder recognition of the facial expression of fear [14,44]. These patients do not show anticipatory conductance responses to disadvantageous choices. Lesions in the amygdala give rise to similar outcomes to those in patients with ventromedial frontal lesion when performing the IGT, i.e. they perform worse than the normal control subjects and they do not develop anticipatory autonomic responses to disadvantageous choices. Nevertheless, the nature of the difficulties differs between the two groups of patients, so these structures –amygdala an ventromedial prefrontal cortex– may carry out different functions in decision making [14,44]. In patients with amygdala damage there is an incapacity to experiment sufficiently the emotional aspects of situations with an affective load, which impedes the appearance of the somatic state which facilitates deliberation or judgment about the outcomes of an event. Patients with ventromedial lesion do show autonomic responses as a result of winnings or losses in the IGT, while the problems of those patients with lesion in the amygdala lie in connecting affective aspects to the stimuli. Hence, the ventromedial prefrontal cortex would integrate the somatic states with the subject's previous experience, including those emotions processed in the amygdala.

The hypothesis proposed by Bechara [25] is that the mental activity triggered by the decision making reaches the ventromedial prefrontal cortex which, in turn, activates the amygdala. This then leads to reactivation or 'remembering' of a somatic state which integrates the likely probabilities of a reward or punishment following a choice, based on previous experience. The final somatic state, indicated by autonomic responses

such as skin conductance, influences the decision that will be taken.

Anterior cingulate cortex

The anterior cingulate cortex is a paralimbic region closely related to the striatum and associated with the anticipation of the outcomes of a choice. This region appears to be more active when negative outcomes are expected, especially in the right hemisphere [45,46]. Studies using functional neuroimaging relate the anterior cingulate cortex to a control or monitoring process of the behaviour itself which includes the evaluating and the response inhibition processes, in which the lateral orbitofrontal cortex is also involved [47]. It is most activated in circumstances like incongruence or the conflict between options common to decision making or to the Stroop task [20,33]. Electrophysiological data place in the cingulate cortex the origin of error-related negativity which appears when making errors [48-50].

Lesions to the anterior cingulate cortex produce disorders in behavioural control and in the capacity to evaluate risks or effort involved in the search for rewards. This region, together with the orbital cortex, seems to be more active during the performance of decision making tasks involving risk or uncertainty [51,52]. According to the data provided by these authors and in the body of the research, while the frontal orbital cortex is related to the associations between the stimuli and the reward, the anterior cingulate cortex would participate in the control and selection of the most suitable conducts, error detection and the calculation of the likelihood of a reward.

CONCLUSIONS

The somatic marker hypothesis of Damasio [2], along with the use of the IGT in patients with brain lesion and in normal subjects with functional neuroimaging techniques, have shed light on those brain structures and systems which may be activated in decision making. The following cortical and subcortical regions have been identified as intervening in the various relevant processes in decision making: integration of sensory, mnesic and emotional information (ventromedial prefrontal cortex); processing and encoding of the emotional signal and its association to contextual stimuli (amygdala); monitoring of the response inhibition process, especially in situations of uncertainty (cingulate cortex). Although there is not unanimity, the participation of the dorsolateral prefrontal cortex would be involved by the necessary activation of the working memory in the decision making process, especially if the task is complex.

Bechara [53] proposes two systems that would intervene in decision making, which interact between themselves, and which are seen to be altered in those patients with the lesions referred to here and in drug addicts:

- An impulsive system, that pertains to the amygdala, which indicates pleasure or pain as an immediate outcome of the possible options.
- A reflexive system based in the ventromedial prefrontal cortex, which is sensitive to future consequences set in motion by those same options.

The first system responds to what is present at the moment of the choice and it provides fast motor or visceral responses. The second system responds to future outcomes and is based more in memory and in anticipation to elicit emotional reactions, which guide decisions. The critical region is the ventromedial prefrontal cortex, which requires three subsystems:

- One made up by the insula and the somatosensory cortex, especially that of the right hemisphere, which would contribute to represent bodily patterns of affective and motivational states.
- A second subsystem made up by the dorsolateral prefrontal cortex and the hippocampus, which are critical for the executive functions and memory, which are in turn necessary in decision making.
- A third subsystem would be in charge of behavioural inhibition, and would involve the anterior cingulate region and the anterior basal brain.

REFERENCES

1. Tranel D, Damasio AR. Neuropsychology and behavioral neurology. In Cacioppo JT, Tassinary LG, Berntson GG, eds. Handbook of psychophysiology. 2 ed. New York: Cambridge University Press; 2000. p. 119-41.
2. Damasio AR. El error de Descartes. Barcelona: Crítica; 1998.
3. Bechara A. Risky business: emotion, decision-making, and addiction. J Gambl Stud 2003; 19: 23-51.
4. Bechara A, Dolan S, Denburg N, Hindes A, Anderson SW, Nathan PE. Decision-making deficits, linked to a dysfunctional ventromedial prefrontal cortex, revealed in alcohol and stimulant abusers. Neuropsychologia 2001; 39: 376-89.
5. Verdejo A, Aguilar de Arcos F, Pérez-García M. Alteraciones de los procesos de toma de decisiones vinculados al córtex prefrontal ventromedial en pacientes drogodependientes. Rev Neurol 2004; 38: 601-6.
6. Bechara A, Damasio H, Tranel D, Damasio AR. The Iowa Gambling Task and the somatic marker hypothesis: some questions and answers. Trends Cogn Sci 2005; 9: 159-62.
7. Bechara A, Damasio H. Deciding advantageously before knowing the advantageous strategy. Science 1997; 275: 1293-5.
8. Bechara A, Damasio AR, Damasio H, Anderson SW. Insensitivity to future consequences following damage to human prefrontal cortex. Cognition 1994; 50: 7-15.
9. Bechara A, Damasio H, Damasio AR. Emotion, decision making and the orbitofrontal cortex. Cereb Cortex 2000; 10: 295-307.
10. Clark L, Manes F, Antoun N, Sahakian BJ, Robbins TW. The contributions of lesion laterality and lesion volume to decision-making within the human prefrontal cortex. Neuropsychologia 2003; 41: 1474-83.
11. Rogers RD, Everith BJ, Baldacchino A, Blackshaw AJ, Swainson R, Wynne K, et al. Dissociable deficits in the decision-making cognition of chronic amphetamine abusers, opiate abusers, patients with focal damage to prefrontal cortex, and tryptophan-depleted normal volunteers: evidence for monoaminergic mechanisms. Neuropsychopharmacology 1999; 20: 322-39.
12. Rogers RD, Owen AM, Middleton HC, Williams EJ, Pickard JD, Sahakian BJ, et al. Choosing between small, likely rewards and large, unlikely rewards activates inferior and orbital prefrontal cortex. J Neurosci 1999; 20: 9029-38.
13. Elliott R, Rees G, Dolan RJ. Ventromedial prefrontal cortex mediates guessing. Neuropsychologia 1999; 37: 403-11.
14. Bechara A, Damasio H, Damasio AR, Lee SW. Different contributions of the human amygdala and ventromedial prefrontal cortex to decision making. J Neurosci 1999; 19: 5473-81.
15. Crone EA, Somsen RJM, Van Beek B, Van der Molen MW. Heart rate and skin conductance analysis of antecedents and consequences of decision making. Psychophysiology 2004; 41: 531-40.
16. Tomb J, Hauser M, Deldin P, Caramazza A. Do somatic markers mediate decisions on the gambling task? Nat Neurosci 2002; 5: 1103-4.
17. Suzuki A, Hirota A, Takasawa N, Shigemasu K. Application of the somatic marker hypothesis to individual differences in decision making. Biol Psychol 2003; 65: 81-8.
18. Hinson JM, Jameson TL, Whitney P. Somatic markers, working memory and decision making. Cogn Affect Behav Neurosci 2002; 2: 341-53.
19. Maia T, McClelland JL. A reexamination of the evidence for the somatic marker hypothesis: what participants really know in the Iowa Gambling Task. Proc Natl Acad Sci U S A 2004; 101: 16075-80.
20. Ernst M, Bolla K, Mouratidis M, Contoreggi C, Matochik JA, Kurian VS, et al. Decision-making in a risk-taking task: a PET study. Neuropsychopharmacology 2002; 26: 682-91.
21. Bechara A, Tranel D, Damasio H. Characterization of the decision-making deficit of patients with ventromedial prefrontal cortex lesions. Brain 2000; 123: 2189-202.
22. Bechara A, Van der Linden M. Decision-making and impulse control after frontal lobe injuries. Curr Opin Neurol 2005; 18: 734-9.
23. Allegri RF, Harris P. La corteza prefrontal en los mecanismos atencionales y de memoria. Rev Neurol 2001; 32: 449-53.
24. Jódar-Vicente M. Funciones cognitivas del lóbulo frontal. Rev Neurol 2004; 39: 178-82.
25. Bechara A. The role of emotion in decision-making: evidence from neurological patients with orbitofrontal damage. Brain Cogn 2004; 55: 30-40.
26. Bechara A, Damasio H, Tranel D, Anderson SW. Dissociation of working memory from decision making within the human prefrontal cortex. J Neurosci 1998; 18: 428-37.
27. 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.
28. Fukui H, Murai T, Fukuyama H, Hayashi T, Hanakawa T. Functional activity related to risk anticipation during performance of the Iowa Gambling Task. Neuroimage 2005; 24: 253-9.
29. 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.
30. Tranel D, Bechara A, Denburg NL. Asymmetric functional roles of right and left ventromedial prefrontal cortices in social conduct, decision-making, and emotional processing. Cortex 2002; 38: 589-612.
31. Goldman-Rakic PS. Working memory and the mind. Sci Am 1992; 267: 111-7.
32. Mac Donald AW, Cohen JD, Stenger VA, Carter CS. Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. Science 2000; 288: 1835-8.
33. Rorie AE, Newsome WT. A general mechanism for decision-making in the human brain? Trends Cogn Sci 2005; 9: 41-3.
34. LeDoux JE. Cognitive-emotional interactions. In Lane RD, Nadel L, eds. Cognitive neuroscience of emotion. New York: Oxford University Press; 2000. p. 129-55.
35. Aguado L. Procesos cognitivos y sistemas cerebrales de la emoción. Rev Neurol 2002; 34: 1161-70.
36. Aggleton, JP, Young AW. The enigma of the amygdala: on its contribution to human emotion. In Lane RD, Nadel L, eds. Cognitive neuroscience of emotion. New York: Oxford University Press; 2000. p. 106-28.
37. Davis M. The neurophysiological basis of acoustic startle modulation: research on fear, motivation, and sensory gating. In Lang PJ, Simons RF, Balaban M, eds. Attention and orienting: sensory and motivational processes. Mahwah, NJ: Lawrence Erlbaum; 1997. p. 69-96.
38. Emery NJ, Amaral DG. The role of the amygdala in primate social cognition. In Lane RD, Nadel L, eds. Cognitive neuroscience of emotion. New York: Oxford University Press; 2000. p. 156-91.
39. Sánchez-Navarro JP, Martínez-Selva JM, Román F. Emotional response in patients with frontal brain damage: effects of affective valence and information content. Behav Neurosci 2005; 119: 87-97.
40. Critchley HD, Rotshtein P, Nagai Y, O'Doherty J, Mathias CJ, Dolan RJ. Activity in the human brain predicting differential heart rate responses to emotional facial expressions. Neuroimage 2005; 24: 751-62.
41. Kuniecki M, Urbanik A, Sobiecka B, Kozub J, Binder M. Central control of heart rate changes during visual affective processing as revealed by fMRI. Acta Neurobiol Exp 2003; 63: 39-48.
42. Sabatinelli D, Bradley MM, Fitzsimmons JR Lang PJ. Parallel amygdala and inferotemporal activation reflect emotional intensity and fear relevance. Neuroimage 2005; 24: 1265-70.
43. Davis M. Differential role of the amygdala and bed nucleus of the stria terminalis in conditioned fear and startle enhanced by corticotrophin-releasing hormone. In Ono T, McNaughton BL, Molotchnikoff S, Rolls ET, Nishijo H, eds. Perception, memory and emotion: frontiers in neur oscience. Oxford: Elsevier; 1996. p. 525-48.
44. Tranel D. Electrodermal activity in cognitive neuroscience: neuroanatomical and physiological correlates. In Lane RD, Nadel L, eds. Cognitive neuroscience of emotion. New York: Oxford University Press; 2000. p. 192-224.
45. Gehring WJ, Willoughby AR. The medial frontal cortex and the rapid processing of monetary gains and losses. Science 2002; 295: 2279-82.
46. Knutson B, Westdorp A, Kaiser E, Hommer D. fMRI visualization of brain activity during a monetary incentive delay task. Neuroimage 2000; 12: 20-7.
47. Volkow ND, Fowler JS, Wang GJ. The addicted human brain viewed in the light of imaging studies: brain circuits and treatment strategies. Neuropharmacology 2004; 47: 3-13.
48. Hajcak G, Holroyd CB, Moser JS, Simons RF. Brain potentials associated with expected and unexpected good and bad outcomes. Psychophysiology 2005; 42: 161-70.
49. Periáñez JA, Barceló F. Electrofisiología de las funciones ejecutivas. Rev Neurol 2004; 38: 359-65.
50. Yeung N, Holroyd CB, Cohen JD. ERP correlates of feedback and reward processing in the presence and absence of response choice. Cereb Cortex 2005; 15: 535-44.
51. Cohen MX, Heller AS, Ranganath, C. Functional connectivity with anterior cingulate and orbitofrontal cortices during decision-making. Brain Res Cogn Brain Res 2005; 23: 61-70.
52. Milham MP, Banich MT, Claus ED, Cohen NJ. Practice-related effects demonstrate complementary roles of anterior cingulate and prefrontal cortices in attentional control. Neuroimage 2003; 18: 483-93.
53. Bechara A. Decision making, impulse control and loss of willpower to resist drugs: a neurocognitive perspective. Nat Neurosci 2005; 8: 1458-63.

MECANISMOS CEREBRALES DE LA TOMA DE DECISIONES

Resumen. Objetivo. *Revisar los estudios sobre los mecanismos cerebrales de la toma de decisiones en el marco de la hipótesis del marcador somático y basados experimentalmente en el empleo de la tarea de apuestas de Iowa (*Iowa Gambling Task*).* Desarrollo. *Se presenta la teoría del marcador somático y las características de la citada tarea de toma de decisiones y otras relacionadas. A continuación, se revisan los principales estudios llevados a cabo en personas con lesión cerebral y los procedentes de sujetos normales, con el empleo de neuroimagen funcional, que han hecho posible la identificación de las estructuras neurales implicadas en la toma de decisiones en humanos.* Conclusiones. *La principal región implicada es la corteza prefrontal ventromedial, donde se produce la integración de la información sensorial, mnésica y emocional necesaria para la tarea. Otras estructuras que intervienen en diferentes procesos relevantes para la toma de decisiones serían la amígdala (procesamiento y codificación de la señal emocional y su asociación con estímulos contextuales) y la corteza cingulada (monitorización del proceso e inhibición de respuesta, especialmente en situaciones de incertidumbre). La corteza prefrontal dorsolateral también participaría en este proceso debido a la necesaria activación de la memoria de trabajo en la toma de decisiones, en especial cuando la tarea es compleja. [REV NEUROL 2006; 42: 411-8]*

Palabras clave. *Amígdala. Corteza prefrontal. Emoción.* Iowa Gambling *Task. Lesión cerebral. Marcador somático. Toma de decisiones.*

MECANISMOS CEREBRAIS DA TOMADA DE DECISÕES

Resumo. Objectivo. *Rever os estudos sobre os mecanismos cerebrais da tomada de decisões no quadro da hipótese do marcador somático e baseados experimentalmente na utilização da tarefa de apostas do Iowa (*Iowa Gambling Task*).* Desenvolvimento. *Apresenta-se a teoria do marcador somático e as características da referida tarefa de tomada de decisões e outras relacionadas. A seguir, procede-se à revisão dos estudos principais levados a cabo em indivíduos com lesão cerebral e os provenientes de sujeitos normais, com o emprego da neuroimagem funcional, que tornou possível a identificação das estruturas neurais implicadas na tomada de decisões no seres humanos.* Conclusões. *A principal região implicada é o córtex pré-frontal ventromedial, no qual se produz a integração da informação sensorial, mnésica e emocional necessária para a execução da tarefa. Outras estruturas que intervêm em diferentes processos relevantes para a tomada de decisões seriam a amígdala (processamento e codificação do sinal emocional e a sua associação a estímulos contextuais) e o córtex cingulado (monitorização do processo e inibição de resposta, especialmente em situações de incerteza). O córtex pré-frontal dorsolateral também participaria neste processo devido à necessária activação da memória de trabalho na tomada de decisões, em especial quando a tarefa é complexa. [REV NEUROL 2006; 42: 411-8]*

Palavras chave. *Amígdala. Córtex pré-frontal. Emoção.* Iowa Gambling Task. *Lesão cerebral. Marcador somático. Tomada de decisões.*