

## Exploring brain activity in neuroeconomics

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Neuroeconomics uses various methodologies to study the neural underpinning of economic decision-making. The goal of the present article is to briefly introduce the most frequently used methods. The main functioning, properties and features, including advantages and limits, of Positron Emission Tomography (PET), functional Magnetic Resonance Imaging (fMRI), Electroencephalography (EEG), Magnetoencephalography (MEG), and Transcranial Stimulation (TMS and tDCS) will be discussed.

**neuroimaging - PET - fMRI - EEG - MEG - TMS - tDCS**

### *Exploration de l'activité cérébrale : en neuroéconomie*

La neuroéconomie utilise un ensemble de techniques pour étudier les processus cérébraux sous-tendant la prise de décision dans un contexte économique. L'objectif de cet article est de présenter celles qui sont le plus couramment employées. Les caractéristiques principales ainsi que les avantages et les limites de la Tomographie par Emission de Positron (TEP), l'Imagerie par Résonance Magnétique fonctionnelle (IRMf), l'Electro-EncéphaloGraphie (EEG), la MagnétoEncéphaloGraphie (MEG) et la stimulation transcrânienne (TMS et tDCS) sont présentées.

**imagerie cérébrale - TEP - IRMf - EEG - MEG - TMS - tDCS**

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## Introduction

One of the most straight forward descriptions of *neuroeconomics* was given by Kenning and Plasmann [2005]: "*The key idea of this approach is to*

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*employ recent neuroscientific methods in order to analyze economically relevant brain processes.*" Neuroeconomics can therefore be considered as a new scientific field that has emerged together with conceptual and technological improvement (Camerer *et al.*, [2005]). Here, we present a brief description of the different techniques used in neuroeconomics to explore the neurobiological correlates of economic decision-making and to help the non-neuroscience reader to better understand results obtained from these methods presented throughout this special issue. Our goal is to provide some basic information regarding the main features, advantages and limitations of each technique with an emphasis on the links between the methodology itself and the experimental design employed.

A study in the field of cognitive neuroscience usually requires certain experimental paradigms to investigate quantitatively the effects of factors of interest on a given behaviour). Different methods can be employed for that purpose. One of them would be the comparison of behavioural measures from patients with altered cerebral functions and structures with that of "healthy" control subjects. Neuropsychology, which can be considered the oldest neuroscientific method, belongs to this group. Newer methods allow for a temporary disruption of brain activity and, to a certain extent, the simulation of brain lesions.

A second common experimental paradigm is to contrast brain activity of the same individual after performing two (or more) different experimental conditions and to relate brain activity (spatially and temporally) to experimental parameters. Such protocols often require the measurement of brain activity or other quantities from which this activity can be deduced or extrapolated. Here, we introduce different techniques developed to (directly or indirectly) estimate brain activity: Positron Emission Tomography (PET) and functional Magnetic Resonance Imaging (fMRI) allow for determining the location of active brain areas with a good spatial resolution. Both are based on the metabolism of brain cells and its correlation with variations in local blood flow inside the brain. Other methods such as Electro- and Magnetocephalography (EEG and MEG, respectively) are direct measures of neural activity with a high temporal resolution and therefore complement the metabolic-based methods. EEG and MEG record variations in the electric potentials and magnetic fields originating from populations of cortical neurons.

## Neuropsychology

Visualization of ongoing brain activity (over time and/or in three-dimensions) is a rather new achievement in neuroscience. Before the advent of such brain imaging techniques often referred to as *neuroimaging*, physicians and researchers had to rely on other methods to study what role a certain brain area would play with respect to a particular behaviour. Being able to correlate (pre- and post-mortem) a given behaviour (or its absence) to a specific damage of the brain of patients allowed for the rise of *neuropsy-*

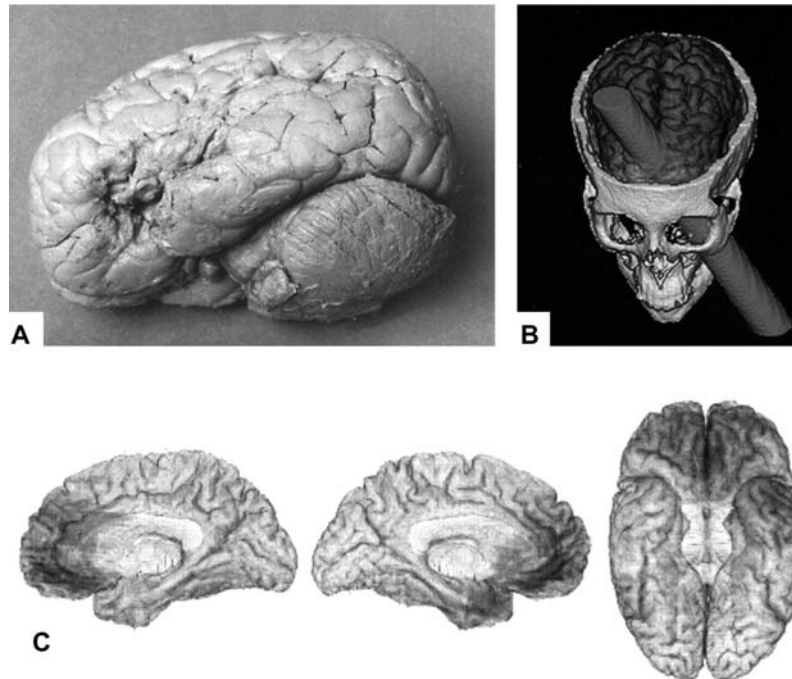
psychology. Individual cases dating back to the 19<sup>th</sup> Century illustrate how physicians and scientists have tried to link a change in behaviour to a brain lesion.

Paul Broca had one patient called Leborgne, who could only make one sound: “tan”. After Leborgne’s death, Broca [1861] autopsied the body and found that a brain region located on the left side of the temporal lobe was impaired (Figure 1A), whereas the rest of the brain seemed unaffected. Broca concluded that the ‘missing’ brain region was involved in the production of spoken words. This region is now referred to as *Broca’s area* and is tightly linked to the brain dynamics of speech production (but see Dronkers *et al.*, [2007] for new insights).

Another case study received a lot of scientific and media attention triggered by Antonio Damasio’s bestseller book *Descartes’ error* (Damasio [1994]) and David Macmillan’s *An odd kind of fame: Stories of Phineas Gage* (Macmillan [2000]). In 1848, Phineas Gage, a railroad worker, suffered an incredible case of brain injury. Following an explosion, an iron bar flew through his head and caused major injuries to the frontal lobe of his brain (Figure 1B). Surprisingly, Gage survived and he was even able to resume his work a year later. However, John Harlow, the physician who originally followed his case, reported that compared to prior to the accident his social behaviour had changed dramatically. Described as a pleasant, polite person and a meticulous employee, he had become asocial, selfish and prone to short temper. In addition, Gage could no longer focus on and plan his actions. This case study was the first that allowed for linking a certain part of the brain (the frontal lobe) to social behaviour. Following those seminal observations, Damasio and colleagues explored the brain of patients with lesions similar to the one suffered by Gage and confirmed Harlow’s original conclusions (Damasio *et al.*, [1994]).

## Application

In spite of serving as the basis of knowledge on brain functioning for more than a century and a half, it must be noted that neuropsychology also has its limitations, as the way in which lesions, even when located in similar regions of the brain, influence behaviour differs from patient to patient (e.g. Koenigs and Tranel, [2007]; Figure 1C). Nevertheless, this approach still plays an important role in cognitive (neuro)science. Data from patients’ behavioural deficits are still strong arguments to support a specific neuroscientific model and/or the interpretation regarding an involvement of certain brain regions in specific functions. For instance, a major part of our current knowledge about how the brain works is more or less inspired by neuropsychological observations. This is particularly the case for Damasio’s *somatic marker hypothesis* regarding the role of emotions in decision-making processes, a topic of particular interest in microeconomics that is at the core of neuroeconomics (Bechara *et al.* [2000]; Damasio [1994]). Damasio and colleagues compared the behaviour of healthy subjects with behaviour of patients suffering from orbitofrontal lesions when confronted with a card



**Figure 1. A. Picture of the brain of Broca's first patient, Leborgne. The external lesion is clearly visible in the left inferior frontal lobe [adapted from Dronkers *et al.*, 2007, Figure 3, p. 1436. B. Computer reconstruction of the trajectory of the iron bar through Phineas Gage's head. The damaged brain area is the left prefrontal cortex. [adapted from Damasio *et al.*, 1994, Figure 5, p. 1104. C. Lesions of seven VMPC patients displayed in ventral and sagittal views. VMPC refers to the area of maximal lesion overlap (darkest region ; Brodmann areas 10, 11, 25) [adapted from Koenigs and Tranel, 2007, Figure 1, p. 952.**

game called the *Iowa Gambling Task* (Bechara *et al.*, [2005]; see also Schmidt, this issue, for a detailed treatment). The somatic marker hypothesis is the first model that linked decision-making to emotions at the brain level. It has, however, received a lot of criticism regarding both the task itself and the conclusions drawn by the authors (e.g. Dunn *et al.*, [2006]; Maia and McClelland [2004]).

As illustrated by Damasio and colleagues, the neuropsychological approach consists of comparing the behaviour between patients and control subjects in a given task. It turns out that such an approach can also be useful in studies in neuroeconomics as illustrated by recent findings on the neural correlates of regret (Ambrosino and Coricelli, this issue; Camille *et al.* [2004]) or fairness (Koenigs *et al.* [2007]). In these experiments patients with orbito-frontal and ventromedial lesions (see Figure 1C), were asked to play eco-

nomical games in an attempt to determine whether the impaired brain area of interest is *used* by the subject to perform a certain task in a given context. However, one should bear in mind that there is no direct correspondence between a certain brain region and a complex behaviour, be it decision-making or another complex task (Kelso [1995]; Oullier *et al.* [2006]). Hence, when studying how a specific behaviour is affected (or cannot be performed) because of a lesion in a given brain region, one must be careful not to conclude that this particular brain area is *necessary* to perform the task. Given the plasticity of the brain, i.e. the ability for certain brain regions to “do the job” for others, a task may still be achieved even when the part of the brain that usually does it is damaged. Questions can also remain regarding whether the impaired area is only playing a kind of relay or connective function between other areas. Hence, imaging tools that enable to (directly or indirectly) measure brain activity are necessary for further exploration and a better understanding of local brain dynamics and how different brain areas interact.

## Transcranial Magnetic Stimulation (TMS) and Transcranial Direct Current Stimulation (tDCS)

Transcranial Magnetic Stimulation (TMS) and Transcranial Direct Current Stimulation (tDCS), two techniques based on the fact that neurons communicate with each other via electric signals, have become more and more popular in neuroeconomics as they allow for stimulating specific brain areas. They both are not neuroimaging techniques *per se*, which reminds us that neuroeconomics is not solely based on creating fancy images of brain activity when economic decisions are made. The stimulation methods can, however, be considered as related to neuropsychology, their principle being to elicit an artificial, local, and reversible perturbation of brain activity, in short, a temporary lesion (see Kobayashi *et al.* [2003]; Pascual-Leone *et al.* [2000] for reviews). When such a lesion is simulated in a specific brain region, as for neuropsychology, its effects on behavioural performance can be studied. The advantage of these techniques is that the experimenter (more or less) controls the location and duration of the perturbation. Both techniques rely on electric current generated locally in a subject’s cortex that disrupts the functioning of and communication between neurons<sup>7</sup> (Allen *et al.* [2007] ; Bestmann [2008] ; Fregni *et al.* [2007]).

7. The synaptic transmission on the dendrite of a neuron generates a local exchange of ions between the two sides of the membrane of the cell. The consequence is a variation of the polarization of the membrane and the transmission of primary intracellular electric currents. The integration of polarizations caused by input from the dendrites in the body of the cell might generate (or *fire*) a depolarization, the *action potential* (also called *spike*), which then propagates along the axon and serves as input for other neurons (for more details on neuron biology and electrophysiology see Preusschoff, *et al.*, this issue).

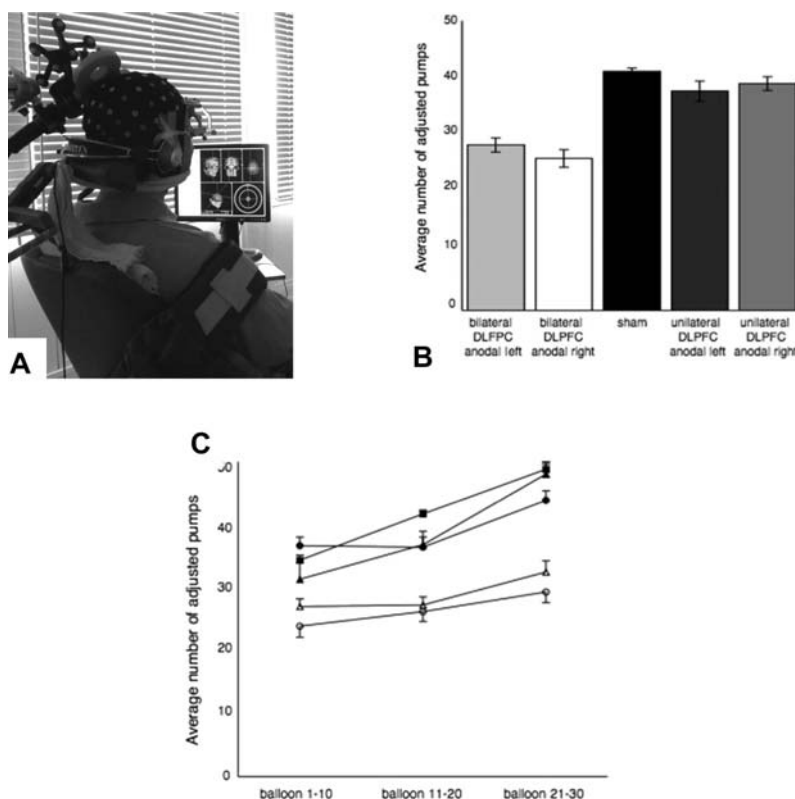
TMS, first introduced in the mid 1980's, was originally used for therapeutic treatments. A TMS device is made of a small coil which is placed on the scalp of the subject (Figure 2A) and induces electric currents in predetermined brain area through a magnetic pulse (Walsh et Cowey [2000]). The effect of TMS usually lasts only as long as the stimulation is applied, but trains of repeated stimulations induce effects that can last from minutes to hours (see Knoch *et al.* [2006]; van't Wout *et al.* [2005] for neuroeconomics studies using rTMS).

tDCS was invented in the 1970's, and was reintroduced in the field of cognitive neuroscience in the 2000's. In this technique, an electric current is directly applied between two electrodes placed on the subject's head. Both TMS and tDCS can facilitate or inhibit the emission of electric signals by a neuron depending on the intensity and frequency of the magnetic stimulation for TMS, or the polarity of the stimulation in the case of tDCS. TMS has a good spatial specificity of few millimeters, which is slightly better than the specificity of tDCS. Although it was not the case originally, nowadays before stimulations are applied, subjects undergo an anatomical MRI scan of their head. This scan is then uploaded into a software that controls a three-dimensional navigation system. Thus, it is possible to choose a brain area of interest for the study and to stimulate this region with high spatial accuracy (Figure 2A). However, a major limitation persists: stimulation depth. Transcranial stimulation only allows for perturbation of superficial parts of the cortex.

The experimental paradigms used for TMS and tDCS are similar to those in neurophysiology: contrasting a group of subjects who underwent an actual transcranial stimulation with a group whose stimulation was only simulated (a so-called *sham* stimulation, one can also consider a sort of placebo stimulation). Moreover, depending on the protocol, TMS and tDCS can allow for a single subject to be her own control. Transcranial stimulation studies are important because they can show that a brain area plays a crucial role in a given process. As for neuropsychology, TMS and tDCS studies should be interpreted carefully: when behavioural effects of disruption in a certain area are found this does not necessarily mean that this area is the only one involved in the process studied, neither that its role in the process is by any means understood.

## Applications

Studies using TMS strongly suggest a critical role of a brain area called the dorsolateral prefrontal cortex (DLPFC) when making decisions in a risky context. For instance, Fecteau and co-worker [2007a] revealed that disrupting this area resulted in risk-taking behaviours. In a related study, they investigated the opposite effect, *i.e.* whether an artificial activation of the DLPFC with tDCS could induce risk adverse behaviours (Fecteau *et al.* [2007b]). The former study is important with respect to experimental design in neuroeconomics: it starts with bilateral stimulation of the DLPFC which is pretty rare (*i.e.* the stimulation is applied concomitantly to both the right and



**Figure 2.** A. TMS equipment coupled with a navigation system to localize the target area in the subject’s brain. The TMS coil is held by an articulated arm (top left corner). Here the TMS is also coupled with an EEG system [courtesy of Mireille Bonnard]. B. Diagram of the average number of adjusted puffs (*i.e.* total puffs minus the ones that made the balloon explode) for each group of subjects. The total number of puffs for subjects under bilateral stimulation is significantly lower than for the other groups [adapted from Fecteau *et al.*, 2007b, Figure 2, p. 6215 – C. Average number of adjusted puffs for each group and time period (the first 10 balloons, second 10 balloons, and last 10 balloons). Open bars, bilateral DLPFC stimulation ; filled bars, unilateral and sham stimulations.

the left DLPFC). DLPFC is actually a good target for transcranial stimulation since it is located on the surface of the cortex, just under the skull. This is not the case, for deeper areas known for participating in risk evaluation, such as the medial orbitofrontal cortex (e.g. Tobler *et al.* [2006]). As a consequence, even if this study would bolster the role of DLPFC in decision-making it addresses only one aspect of the brain processing of risk.

The experimental paradigm in Fecteau *et al.*'s [2007b] study using tDCS is a group comparison of behavioural results for a risk-increasing task: subjects accumulate money while gradually inflating a balloon and lose all the money if the balloon explodes. The amount of balloons is limited and they can set aside accumulated money if they take a new balloon. The performances on this *Balloon Analog Risk Task* (BART) has been previously correlated with indicators of real-life risky behaviours (Hunt *et al.* [2005]). A total of 47 subjects played the BART on a computer. The authors conducted a first experiment on 35 subjects divided into four groups. Group 1 received an active tDCS on both the right and the left target. Group 2 received an active tDCS with the current direction reversed compared to group 1. Group 3 received a sham tDCS that is a control for stimulation conditions (subjects had electrodes placed on their scalp but no real stimulation was delivered) and group 4 had no stimulation at all. Fecteau and colleagues [2007b] showed that subjects who received a real stimulation inflated their balloons less than the ones who received a fake stimulation (Figure 2B). The experiment also revealed that inflating remained constant for the subjects who received a real stimulation but increased towards the end of the experiment for those who received sham stimulation (Figure 2C). The authors tested other effects such as gender and the direction of the current but both showed no significant effect on the results.

This study (Fecteau *et al.* [2007b]) confirmed the hypothesis that a facilitation induced by tDCS on bilateral DLPFC induced a risk-averse behaviour in an increasing-risk context<sup>8</sup>. The authors performed a control experiment with 12 subjects to test whether unilateral tDCS was sufficient to elicit the risk-averse behaviour. The results of this second experiment are similar to the first. The overall interpretation of Fecteau and colleagues is that bilateral and unilateral DLPFC facilitation favors risk-averse behaviour (Fecteau *et al.* [2007b]).

## Positron Emission Tomography (PET)

After briefly reviewing methods that allow to explore the effects of brain lesions (neuropsychology), disruption (TMS) or stimulation of brain activity (tDCS), we are now going to explore brain imaging methods that allow for an estimation of neural activity.

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8. An alternate interpretation of a perturbation of brain mechanisms responsible for cognitive inhibition could be raised, namely, subjects could be more prone to inhibit the response with the higher frequency, *i.e.* to inflate the balloon rather than setting it aside. A *Stroop task* was therefore performed by the subjects with and without transcranial stimulation to control for this alternate hypothesis. The Stroop task is a classical cognitive task supposed to measure a person's susceptibility to interference effects in various mental functions (Stroop [1935]; see also Jensen et Rohwer [1966] for a review). It consists in colored words with congruent naming (the word "red" written in red) or incongruent naming ("blue" written in yellow). The response time in a simple decision task about the color of the ink is greater in the case of incongruent stimulus. In the study by Fecteau and colleagues [2007b], as subjects did not show any significant effect of stimulation on response time, the alternate explanation was discarded.



Brain activity results, in part, from the dynamics of cells called neurons, which interact through highly interconnected and complex networks of various size and density. Neurons have the ability to process and transmit information in form of small electric discharges (see Preuschoff *et al.*, this issue). Several conditions have to be met for the recording of brain activity in humans. First, the technique employed has to be as little invasive as possible. Second, one has to find a phenomenon that generates a recordable signal somehow representative of brain activity.

Those conditions are met by Positron Emission Tomography (PET), the first metabolism-based imaging technique to allow the measurement of a signal correlated with local brain activity. PET is carried out by injecting a radioactive tracer in the blood of a subject before the beginning of an experiment and to measure the local concentration of this marker in the brain. When a brain area is active, more blood is required to carry energy (oxygen) to the area where the active cells are located. The injected tracer emits a positron that in tissue immediately collides with his anti-particle, an electron, leading to a pair of photons of high energy that fly away in opposite directions and are detected by the PET scanner (Figures 3A-B). The link between this signal and brain activity varies depending on the radioactive tracer used.

The first radioactive tracer used in PET was a molecule of glucose marked by a fluorine isotope: [ $^{18}\text{F}$ ] also known as fluoro-deoxy-glucose (FDG). When a neuron discharges, the "refill" requires energy brought by the metabolism of the cell which consumed glucose. Thus, the more a neuron is active, the more it consumes glucose. When marked glucose is present in the blood, the radioactive tracer will be found in greater quantity in the active cells hence indicating where increased activity is located in the brain. This radiotracer has been very useful in the early stages of PET but its long half-life<sup>9</sup> (110 minutes) limits the kind of study in which it can be used.

Today, the most common PET radiotracer is [ $^{15}\text{O}$ ]  $\text{H}_2\text{O}$ , *i.e.* water with a positron generating oxygen atom<sup>10</sup>. The principle is a little different from PET with FDG but also relies on the metabolism of neurons. In short, the energy production necessary to refill the neuron consumes oxygen carried by blood. Thus, when neurons are more active, the blood flow in the vicinity of these neurons increases. As water is a component of blood, by injecting marked water it becomes possible to trace the variations of blood flow in certain regions of the brain and therefore to indirectly measure neural activity (Figure 3C). Another way to use PET is to specifically focus on a neurotransmitter. For example [ $^{11}\text{C}$ ] raclopride is an analogue of dopamine (see Preuschoff *et al.* [2008] for a description of the *dopamine* system). Thus [ $^{11}\text{C}$ ] raclopride is bound by the dopamine receptors of neurons. Therefore, a

9. The half-life of a radioactive tracer is the amount of time to decay to half of its initial radiation value.

10. Positron is the antimatter counterpart of electron that is spontaneously generated by nuclei with an excess of protons. Such nuclei are unstable and emit a positron when one proton becomes a neutron. This positron combines with a nearby electron to generate a pair of specific gamma photons with high energy. The PET measuring system is a cylinder of photon detectors placed around the subject's head. From the coincident detection of the pair of photons, it is possible to reconstruct an image of the radiotracer distribution in the brain.

measure of its local concentration shows where dopamine is used during a brain process.

PET suffers several limitations. First, the data collection itself might be an issue when a protocol requires measurements in different conditions on the same subject. The half-life of radioactive elements used in PET needs to be very short (2 minutes for [ $^{15}\text{O}$ ]). Thus experimenters need a direct access to a cyclotron where positron-generating nuclei are produced to inject them without any delay and start the PET session.

Second, the reconstruction of the tracer's local concentration from coincident detection is a quite complicated process. Therefore, in order to extract results from raw data, sophisticated statistical analyses are required (Friston *et al.* [1991, 1993]).

Third, the temporal resolution of PET is much lower than the time scale on which neuronal events occur. For instance, reconstruction requires an integration of events detected over periods on the magnitude of 40 seconds while synaptic transmission takes around 10 milliseconds. Finally, the spatial accuracy of [ $^{15}\text{O}$ ]  $\text{H}_2\text{O}$  PET is around 8 mm with a low signal-to-noise ratio.

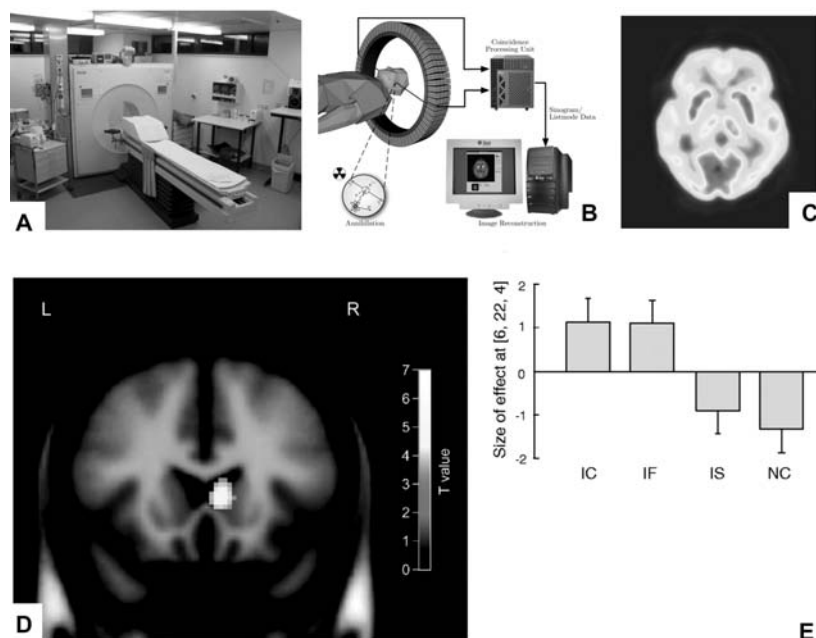
However, PET is the only technique allowing for tracking of chemical changes in the brain when used with a radioactive neurotransmitter analogue.

## Applications

In neuroeconomics, PET has been used to investigate the relationship between reward processing and dopamine transmission previously established with electrophysiology in monkeys (Zald *et al.* [2004]). A good illustration of the use of PET in neuroeconomics is an experiment by de Quervain and colleagues [2004]. This research group used PET on a well designed set of conditions to study altruistic punishment<sup>11</sup> through a one-shot adapted *trust game* (see Schmidt, this issue, for a detailed treatment of the trust game).. The experiment was designed such that Player A (*the investor*) was confronted with Player B's (*the trustee*) defection and had the opportunity to actually punish him. Each one-shot trust game phase was followed by a one minute long punishment phase where brain imaging was performed using PET.

At the beginning of the punishing phase, A and B were given 20 monetary units (MU). The experiment was based on the comparison between four kinds of punishment: (1) *Intentional and Costly* (IC): A could inflict B a punishment knowing that a 2 MU reduction of B's money would cost him 1 MU. (2) *Intentional and Free* (IF): Reducing B's endowment had no cost for A. (3) *Intentional and Symbolic* (IS): control condition, punishment is symbolic,

11. Urs Fischbacher [2004] defined altruistic punishment as "*a readiness to incur costs to punish others for norm violations in the absence of any individual economic benefits for the punishing individual*", and test the hypothesis that this process involves neural features related to reward processing (see also Fehr and Gächter, [2002]).



**Figure 3.** A. Picture of a PET scanner. B. Overview of the processing chain in a PET study, from the emission of a positron by the radioactive marker to the reconstruction of brain activity. C. Typical reconstruction with color scale of the local concentration of a radioactive marker in the brain. Note the low spatial resolution [courtesy of Jens Langner]. D. Activation of the right caudate nucleus in the contrast between the conditions in which the subjects actually punished (IC and IF) and the conditions where almost no punishment occurred (IS and NC) overlaid on an normalized anatomical scan (anatomical scans for each subject are acquired independently and normalized on a template) to localize the activity. Statistical threshold is at 0.05 corrected for multiple comparisons. E. Level of activity in the caudate nucleus for each condition relative to mean brain activation. The diagram shows a higher activation when the subject actually does punish and a deactivation in the conditions without punishment, [adapted from de Quervain *et al.*, 2004, Figure 2, p. 1256 – *Permission required*].

there was no loss of money neither for A nor B. (4) *Non-intentional and Costly* (NC): another control condition, B's decision was randomly determined so that there is no intention behind it. A should pay 1 MU to reduce B's payoff by 2 MU. The experimenters asked the subjects to fill out a questionnaire between each trial in order to assess the relevance of these four different conditions. Subjects had to scale how B's unfairness was per-

ceived and their desire to punish him. Behavioural effects are consistent with this choice of conditions<sup>12</sup>.

De Quervain and colleagues [2004] used a standard experimental paradigm: first they investigated A's brain activity by contrasting conditions and then, they correlated these activities with behavioural parameters. As for contrasts, they compared the PET signals between the conditions where B was inflicted a monetary loss by A (IF) to conditions with no monetary loss. They found that among the regions whose activity variation significantly contributed to the measured signal difference, only one, a subcortical structure called the *caudate nucleus* appeared in each contrast (Figure 3D). This brain region is known to participate to the reward circuitry, error prediction and feedback processing. Typically, the caudate nucleus is involved in tasks such as adaptive learning or spatial navigation (which can be quite far from economic-decisions depending on the context).

Comparing the level of activation of the caudate nucleus in each condition to the average brain activation leads to another result: there is a significant activation in the IC and IF conditions and a deactivation in the IS and NC conditions (Figure 3E). The most interesting result is the similarity of the activation in both the IC and IF condition where the consequences of the decision of A's payoff are different. The authors conclude that activity in the caudate nucleus is related to the processing of another kind of reward, i.e. not the actual payoff. They interpret this reward as the satisfaction to punish.

The authors also analyzed the correlation between the amount of money the subjects paid to punish and the level of caudate activation in the IC condition. The positive and significant correlation they found strengthened their claim.

When looked at in detail the results reveal that in the IF condition, where punishment is not costly, the level of caudate nucleus activation differed for subjects who punished at the maximum level. This allowed the authors to look at the correlation between the amount these subjects paid in the IC condition and their caudate activation in the IF condition. The correlation was also positive and significant, supporting the interpretation that in this situation caudate activation reflects individual differences in anticipation of rewards derived from punishment. Hence, the higher the caudate activation, the more the subject is willing to pay to be satisfied when punishment has a cost. Thus activity in the caudate nucleus might reflect expected satisfaction (de Quervain *et al.* [2004]).

## Functional Magnetic Resonance Imaging (fMRI)

Performing an experiment using PET requires quite an effort. As already mentioned, a cyclotron is required. Besides, the fact that radioactive sub-

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12. Perceived unfairness and desire to punish were almost null in the NC condition. The reduction of money was significantly lower in NC than in IC and IF conditions and in IC condition compared to IF condition.

strates are injected in the body limits the number of PET scans that subjects can undergo each year. These are the main reasons why functional Magnetic Resonance Imaging (fMRI) has become a more popular technique than PET in cognitive neuroscience, unless investigations focus on biochemical exchanges, which remains PET's prerogative (for comparisons, see Connelly *et al.* [1996]; Friston *et al.* [1996]). Developed in the early 1990's, fMRI has some similarities with PET and, as another metabolic-based technique, also a poor temporal resolution. Depending on the scanner and the protocol one to several seconds are necessary to scan the full brain with fMRI technology. The spatial accuracy is slightly better: on the order of a few millimeter (see Houdé *et al.* [2002] for details).

A functional MRI scanner (Figure 4A) applies a strong magnetic field to the subject and records the variations of the magnetic field induced by a local increase in blood flow in the brain. This indirect measure of brain activity is known as the Blood Oxygenation Level Dependent (BOLD) signal. The change in this signal between an area that is active compared to the same area when it is not recruited is quite small and ranges between 1 and 3%. MRI is based on nuclear magnetic resonance, a technique also used in chemistry and physics. In an MRI scanner, the subject is placed in a strong magnetic field that aligns the protons in his body the same way as the earth's magnetic field leads a compass to point to the north<sup>13</sup>. Whereas in PET one has to inject a radioactive tracer, the contrast agent for fMRI is already present in the subjects' bodies: the hemoglobin molecule that carries the oxygen in the blood. After leaving the lungs this molecule comes in a form called oxy-hemoglobin; after the oxygen is released to a cell it changes to deoxy-hemoglobin<sup>14</sup>.

Essential from the viewpoint of imaging is the fact that the two forms have different magnetic properties: oxy-hemoglobin is diamagnetic and interacts only weakly with magnetic moments of the protons in the brain, whereas deoxy-hemoglobin is paramagnetic and has a stronger interaction which perturbs the alignment of protons with the external magnetic field. The change from oxy- to deoxy-hemoglobin happens mainly in brain regions where oxygen is consumed because cells are active, and the scanner is capable of localizing these regions (Figure 4B). How this is done in details, let alone how to reconstruct a three-dimensional image is beyond the scope of this article.

The main goal of fMRI is to detect the local variation of the BOLD signal in the brain and its potential correlation with a given task or action. Functional MRI allows more flexibility than PET for the design of a protocol because its temporal specificity is slightly better. For example, with a larger number of trials per experiment one can cross more factors, build a parametric study, or just increase statistical power with the number of repetitions for one

13. The magnetic field used in an MRI scanner is 10,000 to 30,000 times stronger than earth's. Therefore, no metallic objects are allowed in the room where the scanner is located.

14. Hemoglobin is the molecule that carries oxygen in the blood and gives it the red color. When the blood is highly charged with oxy-hemoglobin, its color is scarlet red. Dark red blood indicates a low level of oxygen, hence a high concentration of deoxy-hemoglobin.

condition. Moreover, fMRI is more suited than PET to study phasic activations with a protocol that alternates conditions on a trial-per-trial basis.

The trade-off between the time it takes to scan the whole brain and the size of the minimum three-dimensional unit recorded (called a *voxel*) usually leads to a spatial accuracy of the order of 3 mm and a latency of 3 seconds between two consecutive scans of the entire brain. Actually, the bottleneck for the temporal resolution lies not really in the technology but is defined by the metabolic response which determines the dynamics of the BOLD signal: there is a delay of about 6 seconds before a neural event leads to a variation of the blood flow called the *hemodynamic response*. In addition, the rise and the decrease of the BOLD signal spread over 10-15 seconds. Even though it is common to apply a deconvolution to the signal, the temporal resolution for fMRI is some orders of magnitude higher than the time it takes for a typical neural event.

Some experimental restrictions for fMRI experiments originate from the strong magnetic field: subjects must not have any metal in their body which would be simply torn out by the magnetic field, and the same rule applies to all the materials used inside the scanner room. Subjects bearing surgery clips or pacemakers cannot have an MRI exam. Moreover, the fMRI scanner is a narrow tube and subjects have to lay for 30-60 minutes in a confined space that may cause claustrophobia. As with all other brain imaging techniques, head movement has to be minimized, thus the protocol should not require more than hand movements and it is not unusual to immobilize the head of the subject.

Data analysis requires sophisticated statistical processing (Cox, 1996). As in PET imaging, fMRI emphasizes the localization of brain area showing the metabolic activity relative to a specific experimental design. However, experimenters have to keep in mind that brain activity is only one aspect of brain coding and that stronger activity could wipe out smaller but relevant effects.

However, fMRI is not limited to the search for active brain areas: the question of timing could be studied through the time course of activity (i.e. the variation of activity over time) in selected regions and specific methods have been recently developed to study both the functional connectivity between brain areas involved in a specific task with *Psycho-Physiological Interactions*<sup>15</sup> (Friston [1997]; Friston *et al.* [1997]), *Dynamic Causal Modelling*<sup>16</sup> (Friston, *et al.* [2003]) and the anatomical connectivity through the

15. *Psycho-Physiological Interactions* (PPI) is a statistical method that applies on one region only and looks for voxels in the brain that exhibit a correlation with this region modulated by a psychological parameter, i.e. a function of the conditions in the experimental protocol.

16. *Dynamic Causal Modelling* (DCM) is based on a model built by the experimenters of interactions between different regions as a linear dynamical system. Then Bayesian estimation gives the parameters such that the BOLD signal that would be generated by the regions under the constraint that the model fits the measured BOLD signal. Compared to PPI, DCM is model-dependent but allows to extract the interaction between activities from several regions while performing a given task.

tracking of axons<sup>17</sup>, *i.e.* the fibers that physically connect one region to others and carry information as electric signals (DaSilva *et al.* [2003]; Le Bihan *et al.* [2001]).

## Applications

To illustrate how an fMRI study is well designed and conducted in neuroeconomics we present an experiment by Delgado and colleagues [2005] where the effects of previous belief based on moral information on someone's learning mechanism through a trust game is investigated<sup>18</sup>. They made precise hypothesis about the cerebral mechanisms involved. The protocol and analysis were done to specifically address this level of understanding. Delgado and colleagues [2005] investigated on the role of the caudate nucleus in the trust game (de Quervain *et al.* [2004]; King-Casas *et al.* [2005]). Considering that during a trust game, one player is able to anticipate the other player's decision patterns, and that the caudate nucleus seems to have an important role in this adaptive learning process<sup>19</sup>, Delgado and co-workers proposed three hypotheses for the effect of moral information on learning processes. (1) No effect. (2) Moral information generates predictions which are compared to outcomes through a learning process. (3) Moral information interferes with the learning process itself through modulation of feedback. The authors' goal was to discriminate between these hypotheses.

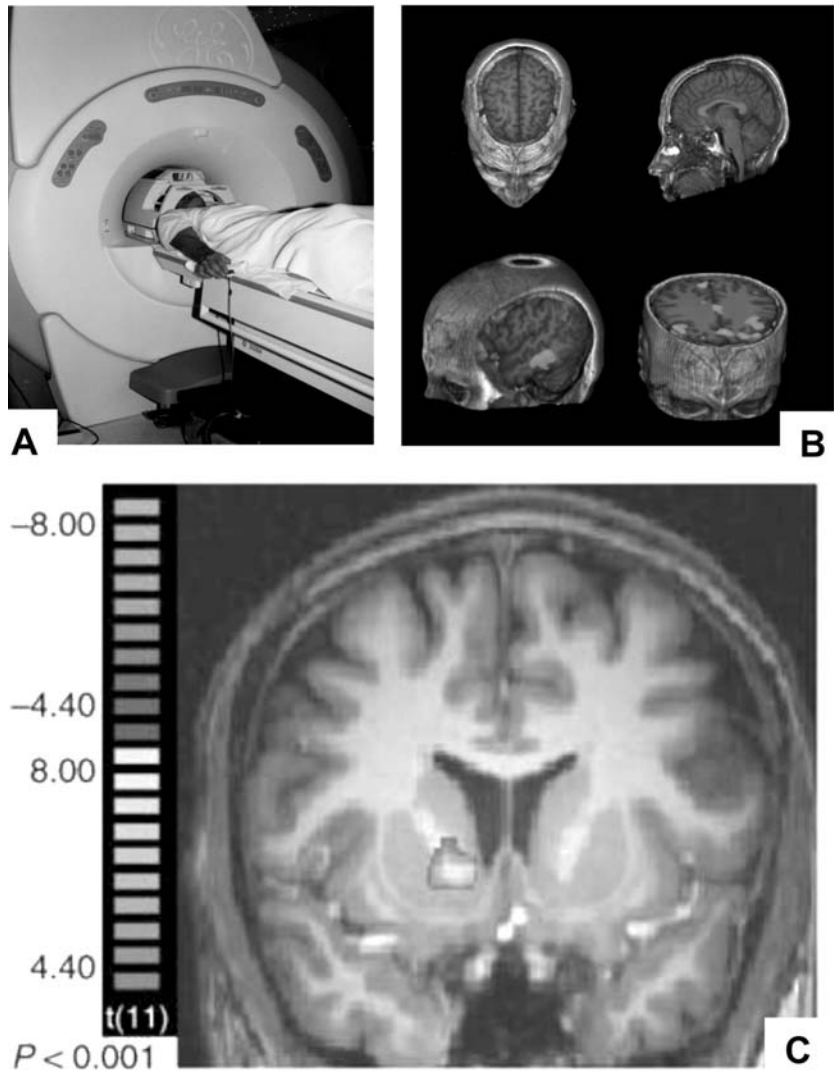
Fourteen subjects played a repeated trust game, always in the role of player A (*the investor*) versus different (fictional) B players (*the trustees*). One of the parameters manipulated was the moral reputation of B. The experimenters presented subjects with a short biography with the intention to induce an *a priori* bias regarding the personality of B. Three different trustees (B) were proposed: the good, the bad and the neutral/control<sup>20</sup>. fMRI data was collected while subjects played twenty four trust game

17. The tracking of fibers in the brain by Diffusion Tensor Imaging (DTI) is another magnetic resonance imaging technique. DTI is a measurement of the anisotropy in the diffusion of water molecules in brain tissue. Since the fibers bundles facilitate the diffusion along their direction, it is possible to image the structural connectivity between brain regions. DTI does not reveal information on brain activity however recent technical development (Le Bihan *et al.* [2006]) have shown that diffusion could target biological events directly related to synaptic transmission, which leads to exciting perspectives for the improvement or the temporal specificity in MRI.

18. Basically the idea is that if someone is told that he is playing the trust game with a person who is supposed to be a thief or a crook, he would be less inclined to entrust money to her. On the other hand, when playing with someone who seems to have high moral values with respect to social norms, more money will be placed in the trust game.

19. An earlier study by King-Casas *et al.* [2005] using fMRI to record brain activity of players in a ten round trust game revealed that the caudate nucleus is involved in player B's (*the trustee*) decision to return some money (or not) after player A (*the investor*) proposed him a share of his own money. In addition, the use of two-fMRI that simultaneously recorded metabolic changes in the brains of both players, revealed for the first time that B learned to anticipate his partner's choice. In the early rounds, activity in the caudate nucleus peaked after player A's offer was revealed, but in the late rounds, this peak appeared 14 seconds earlier, *i.e.* before player A's choice was known.

20. The authors verified that the perception of the moral character was well established with questionnaires prior to the experiments.



**Figure 4.** A. Picture of a subject before he enters in the fMRI scanner. The device around his head is the radio-frequency coil for recording the signals. B. Typical 3D images produced after MRI data collection. Top row : anatomical MRI. Bottom row : functional MRI mapped onto anatomical MRI (B, courtesy of [www.neuroeconomie.fr](http://www.neuroeconomie.fr)). C. Activation of the caudate nucleus when contrasting the positive versus negative feedback in all conditions, mapped onto an anatomical MRI scan to localize the peak of activity [adapted from de Delgado *et al.*, 2005, Figure 2, p. 1613].



rounds with each kind of player B and twenty four simple lottery trials as control task for feedback processing ; decision phase and feedback processing phases were separated throughout the protocol.

Behavioural results showed that subjects invested twice as much with a player B with a good moral reputation compared to players B presented as individuals with low moral standards. The first imaging result comes from the contrast between positive versus negative feedback. It activated a set of regions that belong to the classic reward network (McClure and Montague [2004]). The biggest cluster among these activations was located in the caudate nucleus, corroborating the authors' hypothesis on how players are learning (Figure 4C). Then, the study focused on caudate activity to discriminate between the three proposed interaction mechanisms between a priori information about the moral reputation and learning. As for caudate activation during the feedback phase, Delgado and colleagues showed that there was a significant interaction between perceived morality of player B (moral vs. neutral) and feedback (player B kept all or shared). Then interactions were calculated for good and bad reputations separately, and the interaction between morality and feedback turned out to be significant only for the case of neutral versus good partners. To go even further with feedback processing, the time courses, i.e. the dynamics of caudate nucleus activation, for good and bad feedbacks were compared for each morality condition and for the case of the lottery feedback phase.

The results lead to the interpretation that the processing of feedback by the caudate nucleus in the neutral condition and to a lesser extent in the bad condition is coherent with a learning signal. However, the lack of a difference with the good condition could be interpreted as a disruption of a learning signal triggered by the difference between good and bad feedback in the case of contradicting prior belief.

The analysis of the decision phase led to two results. First, although no significant activation was found in the caudate nucleus, activity in the ventral striatum showed significant increase. The study of ventral striatum activation across moral conditions (and decisions to keep or share the money) revealed a significant difference for the 'bad' partner but did not allow for a clear interpretation regarding the role of prior moral information on decision since no significant interaction was found between B's perceived morality and the decision to keep or share. Second, the analysis of incongruent decision trials (i.e., share with a bad partner) and keep with a good partner replicated classic results about cognitive conflict and ambiguity (Botvinick *et al.* [2004]; Krain *et al.* [2006]).

Overall, this study favours the third hypothesis, namely that moral information interferes with the learning process itself through the modulation of feedback. This result is really interesting because it shows that a brain imaging study with clear neural hypotheses can shed new light on how a basic mechanism such as learning could be influenced by an external parameter (moral reputation in this case) in a decision-making process.

## ElectroEncephaloGraphy (EEG) and MagnetoEncephaloGraphy (MEG)

Information regarding the activity of a single neuron can be recorded using microelectrodes directly inserted in the body of the cell. These electrodes measure the electric current that mediates information exchange between neurons. This technique, known as *neurophysiology*, constitutes the first method to directly measure brain activity and allows for a recording of action *potentials* (also called spikes) generated by the neuron. The problem with electrophysiology is that such a technique is much too invasive to be used in research on healthy humans. Electrophysiology is however very useful in studying and treating pathologies such as Parkinson's disease or epilepsy. Nevertheless, neurophysiology can be relevant for neuroeconomics. As surprising as it may sound to economists, most of our early knowledge on the neural basis of decision-making comes from electrophysiological investigations performed on primates (see Schultz [2000] and Sugrue *et al.* [2005] for reviews). For instance, in what is considered one of the seminal studies on the neural underpinning of preference mechanisms, Tremblay and Schultz [1999] showed that relative preferences are coded in neurons located in the orbito-frontal cortex of primates.

The electrical properties of neurons lead to another kind of recording technique. The post-synaptic intracellular current that appears during a few milliseconds after the synapse transmission generates an electric field<sup>21</sup>. The sum of the contribution of many such neurons can be measured outside of the brain. Actually, this signal reflects the coherent electric activity of neurons that have to meet certain criteria<sup>22</sup> with respect to spatial organization and temporal synchronization in order to be detected outside the brain.

Two non-invasive techniques can measure the components of this electromagnetic field, namely, ElectroEncephaloGraphy (EEG) and MagnetoEncephaloGraphy (MEG).

EEG measures the difference of potentials between electrodes on the scalp of subjects. EEG was used for the first time at the end of the 1920's. A set of electrodes is usually inserted in a soft cap that is placed on the subject's head. Electrodes are positioned following an international standard and a system that allows for localizing them in three dimensions with respect to

21. Considered from the distance of the measuring captor, the distribution of local electric charges along the neuron membrane generated by the post-synaptic currents could be seen as a dipole.

22. The quadrupole structure of action potentials generates a field decreasing with  $1/\text{distance}^3$  ( $1/\text{distance}^2$  for a dipole) thus only dipole contributes to a signal measured some centimetres away from the source. The dipole generates a field with an intensity of the order of only  $2 \cdot 10^{-14}$  Am, this is why a temporal and spatial synchrony of many thousand of neurons is needed to provide a measurable signal. The primary post-synaptic currents and the secondary extra-cellular currents long last enough (10 ms or more) to allow for temporal integration. Moreover synchronization of neural activity is required. The spatial organization of dendrites of neurons in macro-cortical columns allows an additive integration of electromagnetic fields in contrast to dendrites in sub-cortical structures, which have a star-shaped organization.

anatomical landmarks on the skull for a better localization of the source (Figure 5A). EEG is sensitive to so-called secondary currents generated in superficial layers of the cortex<sup>23</sup>, and, therefore, does not provide information about sub-cortical activity in the brain. Another limitation of EEG lies in the quality of the signal that is blurred by the cerebrospinal fluid and the skull and can also be affected by artifacts originating from eye or head movements. Nowadays there are ways to remove the latter artifacts (within a certain range) from the signal in the pre-processing phase prior to data analysis.

MEG was first used in the 1970's when superconducting materials made it possible to measure the extremely low intensity magnetic fields ( $10^{-13}$  Tesla) produced by the currents inside the brain. MEG detects the tiny magnetic fields using small coils called *Superconducting Quantum Interference Devices* (SQUID), which need to be maintained at low temperature inside a dewar filled with liquid helium. Up to several hundreds of SQUIDs can be placed inside a solid helmet where subjects put their head (Figure 6A). Such a measurement can only be performed in a magnetically shielded room and, if additional experimental equipment is required for the experiment, it must not have magnetic properties that potentially interfere with the MEG signal. Similar to fMRI, the MEG device and its maintenance are expensive. In contrast to EEG, MEG measures the contribution of primary post-synaptic currents and only from the cortical regions where the cell columns are arranged tangentially to the skull. MEG is even more sensitive to artifacts originating from eye or muscular movement, heartbeat, breathing and also dental fillings than EEG.

EEG and MEG also pick up background activity that is unrelated to the task, thus when studying a specific brain process, it has to be isolated from the spontaneous brain signals. A simple but powerful technique used to extract the response related to a given event such as a stimulus is to use a protocol with a large amount of repetitions of the event under investigation. Then the signal is averaged across repetitions. Typically, the response related to a given event is a succession of components (or waves) reflecting the succession of neural activations induced by stimulus processing with a high temporal resolution (of the time scale of milliseconds). Early responses to a stimulus are called *evoked responses* and come from the automatic first stage of sensory information processing. Later responses are related to more cognitive processing.

As for the spatial resolution, since the measured signal is an aggregate of unknown source contributions, localization of the sources is an inverse problem whose solution is not unique. In some specific cases or when strong hypotheses constrain the model, it is possible to obtain a spatial resolution almost as good as fMRI. Different methods have been developed to extract sources from MEG and rely on specific algorithms (see Fuchs, [2007]).

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23. In early studies about brain structures, cell coloration techniques resulted in the distinction of 6 layers in the human cortex ; each layer differed by cell organization and typology (Brodmann [1909]).

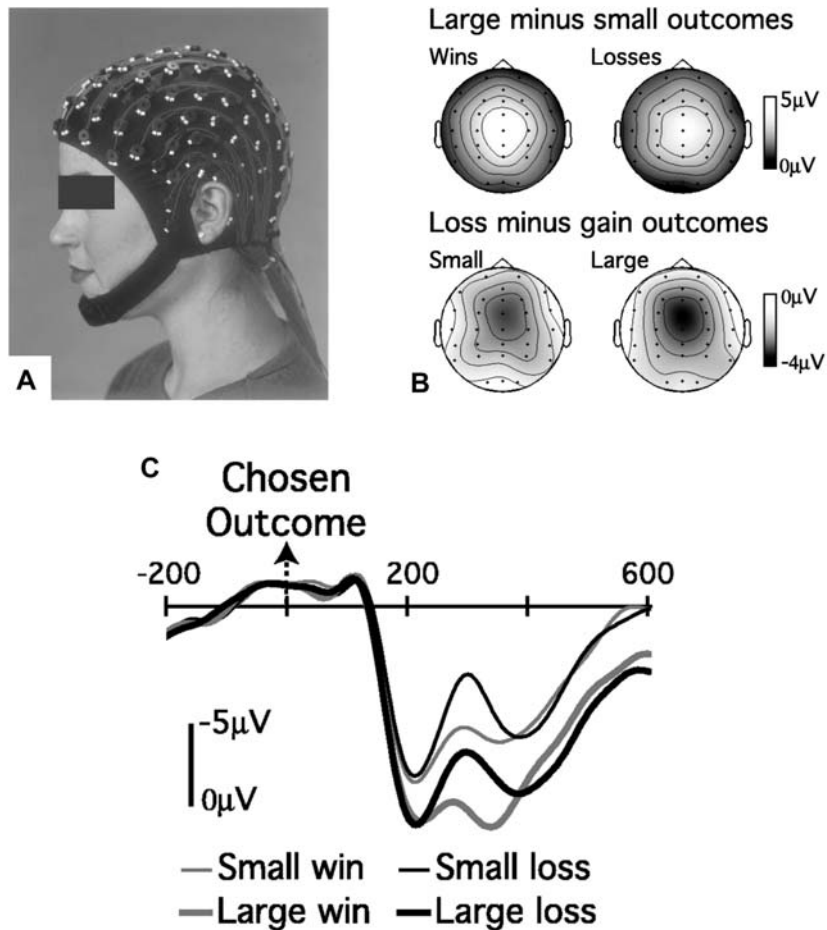
## Applications

Yeung and Sanfey [2004] published an interesting study where they used EEG to investigate the coding of reward magnitude and valence in the human brain. They proposed a protocol to study two well known event-related potentials showing a relationship with reward processing: the *P300* and the *Feedback Negativity*. The *P300* wave has first been described as related to the detection of an unexpected stimulus; it appears 300ms after the stimulus and its amplitude decreases with habituation (Sutton *et al.* [1967]). The *Feedback Negativity* is elicited by a negative outcome and shows a latency range between 250 and 350 ms after feedback. Previous studies reported that in a monetary gamble task, both *P300* and *Feedback Negativity* were elicited by feedback and were related to reward processing but their roles had still to be clarified (Holroyd and Coles [2002]; Sutton *et al.* [1978]).

The paradigm used by Yeung and Sanfey [2004] consists of a gambling game. In each trial, the subject is presented with two lotteries (2 colored rectangles on the screen), he has to select one of them. After a 500 ms delay, the outcome of the chosen lottery is displayed on the screen for 1000 ms. Then a 500 ms delay occurs before the outcome of the other lottery (the one that was not chosen) is revealed for another 1000 ms. In the study, there were two kinds of lotteries, each associated with one of the two colors. One lottery led to high positive or negative outcomes (32 to 40 cents) and the other to low positive or negative outcomes (6 to 11 cents). Sixteen subjects took part in the experiment. The EEG signal was recorded during both outcome periods (chosen lottery and non chosen one) from a set of cranial electrodes positioned along the standardized 10-20 system. Data pre-processing included baseline correction and removal of eye movement artifacts. Then the authors extracted the amplitude of the *P300* and *Feedback Negativity* peaks from the signal and conducted an analysis of variance (ANOVA) with reward magnitude, reward valence and two electrode locations as factors.

The main result of this study is that *P300* and *Feedback Negativity* showed a double dissociation with respect to the chosen lottery outcome. The main effect of reward magnitude on EEG signal amplitude was significant for the *P300* but not for *Feedback Negativity*. The main effect for reward valence was significant for *Feedback Negativity* but not for the *P300* (Figures 5B-C). The *P300* effect could not be related to an increase in attention in case of higher reward because such an effect should have induced a difference for *Feedback Negativity* as well. The authors also ruled out the interpretation of difference in frequency of high and low outcomes because the subjects mainly chose the lottery leading to the higher gain. The authors conclude that magnitude and valence of reward are processed by two distinct brain mechanisms.

Additional results are related to the alternative, i.e. the non-chosen outcome. The *P300* is sensitive to the magnitude of feedback related to the alternative outcome. The *P300* also exhibited an effect of valence with larger amplitude when the alternate outcome was a gain compared to a loss. There was no effect on *Feedback Negativity*. These results revealed that reward



**Figure 5.** A. A typical EEG cap (courtesy of Electrical Geodesies). B. Topological plots of the electric potential recorded from all the electrodes 300 ms after feedback. The magnitude contrast reveals the central P300 while the valence one shows the fronto-central Feedback Negativity. C. Average waves recorded by the fronto-central electrode as a function of time in each of the four conditions. The P300 appears between 200 and 400 ms after feedback presentation and is modulated by a narrow feedback negativity at 300ms [B & C, adapted from Yeung *et al.*, 2004, Figures 2 et 3, respectively, p. 6260].

processing related to the P300 component could be interpreted as an objective coding of the reward magnitude. Yeung and Sanfey [2004] discuss the fact that the magnitude effect for the alternative outcome and the effect of valence on the P300 could be related to other mechanisms such as an

evaluation of emotional stake when the alternative lottery reveals its outcome (see Ambrosino and Coricelli, this issue, for a similar experimental context addressing regret).

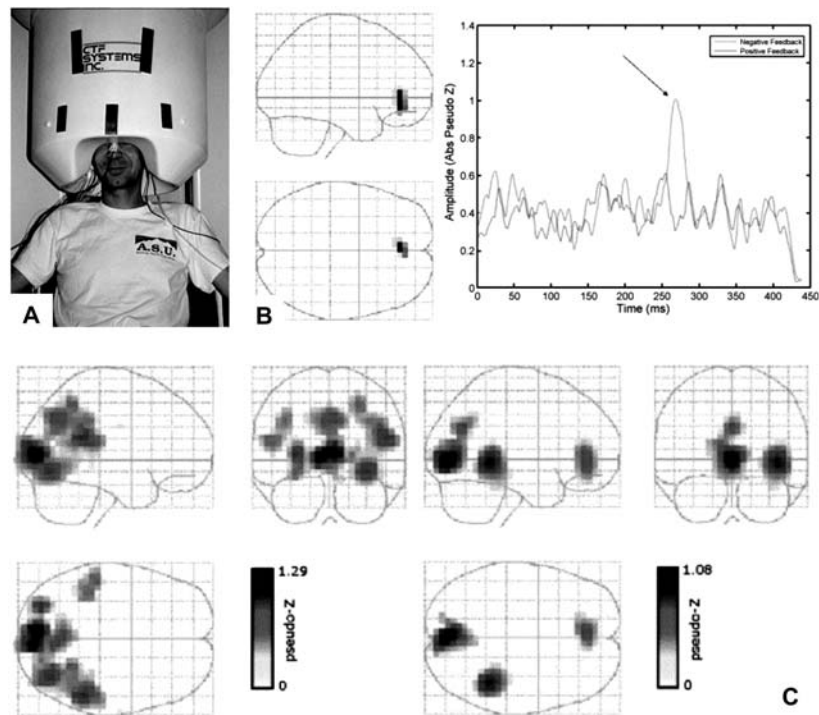
The last result is related to a behavioural pattern observed from the subjects' responses: after a loss, they are more likely to choose a high-outcome lottery. In a split-group analysis, subjects who were more likely to exhibit this behaviour showed a greater Feedback Negativity. This result and the lack of effect of reward magnitude contradicted the usual interpretations of Feedback Negativity as related to associative learning and expected value. Since the anterior cingulate cortex is considered to be the source of Feedback Negativity (Gehring et Willoughby [2002]), this study contributes to the debate over the functions associated with this brain area (Rushworth *et al.* [2007], see also Schmidt, this issue).

To illustrate the use of MEG, we have chosen a study that shows the exciting perspectives of source localization from MEG recordings in relation with experiments previously depicted in this article. Spatiotemporal analysis of feedback processing during a card sorting task using spatially filtered MEG by Bayless and colleagues (Bayless *et al.* [2006]) provides a measurement of neural activity related to feedback processing with good spatial and temporal resolution. Feedback and especially negative feedback is a relevant signal in adaptive learning. In addition, it happens to be related to a specific event-related component: the Feedback Negativity (cf. previous section).

The authors used MEG and a special source localization method (the so-called beamforming) based on spatial filtering, which is referred to as *Synthetic Aperture Magnetometry* (SAM). In contrast to dipole localization procedures where one or a few sources are assumed to be active in the brain, the beamforming methods allow for an estimate of neural activity in every voxel. They allow to identify active regions as does fMRI but also the time course of the neural activation on a time scale of milliseconds. Their spatial accuracy is not as good as fMRI.

Twelve subjects were presented with the following matching decision task. They were told to use their index, middle and ring fingers to answer, each finger being associated with a colored shape (the "references"). The stimulus consisted of a reference mapping on the upper part of a screen and a colored shape (the "target") on the lower part. The task was to respond with the finger whose reference corresponded to either the color or the form of the target. The mapping between the three response fingers and the three references changed randomly every 4 to 6 trials. 1000 ms after the presentation of a cue, a right or false feedback appeared on the screen for 500ms.

During task performance the MEG signal was recorded and an anatomical MRI scan was taken from each subject in order to apply the spatial filtering algorithm. Data processing focused on two types of events: correct feedback prior to a mapping change and false feedback after a mapping change. The authors analyzed the event-related response for both types, each of which showed two components, the first around 100-150ms and the second around 200-300 ms after the feedback (Figure 6B). Then they applied the SAM spatial filtering to extract sources for both types of events. In order to identify the sources related to negative feedback processing, Bayless and co-workers [2006] contrasted the sources for the two types of events using



**Figure 6.** Subject in an MEG helmet, surrounded by the magnetic captors and under the tank of liquid helium that maintains the extremely low temperature required for superconductivity. **B.** Activation of the anterior cingulate cortex isolated from a contrast between the sources for negative and positive feedbacks ; group averaged signal recorded from the isolated region showing a peak around 360ms after negative feedback only. The time series reveals group averaged and rectified time courses of ACC activation. **C.** Sources reconstructed for each subject using a beamforming method from the MEG signal at 260ms after feedback and then normalized and averaged. Two conditions were separated : sources for signals recorded after positive feedback (left) and negative feedbacks (right) [adapted from Bayless *et al.* 2004, Figures 4 et 3, respectively, p. 34].

an analysis procedure similar to the contrast methods in fMRI and PET. One region met the statistical threshold: the rostral anterior cingulated cortex (rACC; (Figures 6B-C)). The MEG signal allows to extract the time course of source activity which showed a peak at 260ms after feedback. Among other results, this study confirmed that the Feedback Negativity found in EEG originates in ACC and confirmed the role of this cortical region in feedback processing as has also been found in studies using fMRI (Elliott *et al.* [2000]).

## Conclusions

Various techniques allowing for the investigation of brain dynamics are used in studies in neuroeconomics, each of which as we have seen has its advantages and disadvantages. Moreover, there are other techniques that we have not reviewed in this article such as *Near Infrared Spectroscopy* (NIRS) or the increasing use of neuropeptides, such as oxytocin delivered by nasal spray, to alter economical behaviour in trust, dictator and ultimatum games (Kosfeld et al [2005]; Zak *et al.* [2007]).

In this review, each technique has been presented independently but some of them can be combined for instance fMRI with either EEG or MEG. Such requires a carefully designed protocol but it combines the spatial resolution of fMRI and reliable information about source location with the temporal resolution of the electrophysiological techniques that provide the time course of neural activation. There exists experimental equipment that allows for the simultaneous recording of fMRI and EEG, whereas MEG and fMRI have to be recorded separately. Another combination is the simultaneous recording of EEG and MEG to have a measure of both, the signals generated by tangential and radial sources (Grabowski *et al.* [1996]). A recent development is the simultaneous recording of two interacting subjects called dual-EEG (Tognoli *et al.* [2007]; see also Oullier *et al.* this issue) and hyperscan-fMRI (King-Casas *et al.* [2005]), which allows for studying the brain activity of different individuals while they are interacting with each other.

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