BRAIN MEASUREMENT AND MANIPULATION METHODS

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1. INTRODUCTION

Biological approaches that enable investigations of the neural foundations of human behavior have recently become the forefront of research in fields of the social sciences closely related to Behavioral Economics, such as Psychology and Social Neuroscience. The subject matter of Behavioral Economics, economic decisions, also carry biological significance as they are concerned with the attainment of monetary and social gains and the avoidance of monetary and social losses, referred to as rewards and punishments by Psychologists and Neuroscientists. The desire to understand the underlying biological mechanisms that guide and constrain economic decisions is reflected in the recent development of the field of Neuroeconomics (Camerer, Loewenstein, and Prelec 2005; Rangel, Camerer, and Montague 2008). Advancements in Neuroceonomics have been enabled by the rapid development of neuroscientific techniques that allow measuring and manipulating the activity of neurons while participants are engaging in economic and social decision-making. A wide range of neuroscientific tools are available to researchers interested in the relationship between human behavior and neural processes, including measurement techniques such as functional Magnetic Resonance Imaging (fMRI), Electro- (EEG) and Magneto-encephalography (MEG), as well as techniques that allow manipulations of neuronal properties, such as transcranial magnetic stimulation (TMS) and transcranial direct current stimulation (tdcs). These techniques are non-invasive and therefore relatively easily implemented with tasks from Behavioral Economics. Moreover, more invasive neuroscientific methods that have a long tradition in Cognitive Neuroscience, such as electrophysiology and lesion studies, have also been applied to questions important for Behavioral Economics (Schultz, Dayan, and Montague 1997; Tobler et al. 2005; De Martino, Camerer, and Adolphs 2010). Given their invasive nature, these experiments are typically conducted with animals, such as rhesus monkeys, and are

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limited to human patients undergoing brain surgery. While each methodology has a set of advantages and limitations, which are outlined in Table 1 and will be discussed in detail below, the converging evidence that can be obtained from multiple neuroscientific approaches can offset the individual limitations associated with each method and lead to greater degrees of certainty about the involvement of particular neural mechanisms in the cognitive and emotional processes that support decision-making. Finally, recent technological developments allow the simultaneous use of multiple methodologies, such as concurrent TMS-fMRI (Ruff, Driver, and Bestmann 2009) and EEG-fMRI (Allen, Josephs, and Turner 2000), providing even more powerful approaches by combining the strengths of multiple neuroscientific measurement techniques in the same subject.

	Single- and multi-unit recordings	EEG	MEG	fMRI	PET	TMS	tdcs
Strengths	- Direct measurement of neuronal electrical activity. - Best spatial and temporal resolution	- Direct measurement of neuronal electrical activity. - High temporal resolution (<1ms) - Possibility to investigate both averaged response and oscillatory activity - Relatively inexpensive portable units available	- Records data from the entire brain simultaneously - High temporal resolution (<1ms) - Improved spatial resolution (relative to EEG) - Provides concurrent insights into timing and location of activity	- Records data from the entire brain simultaneously - High flexibility in experimental designs - Concurrent high spatial resolution and good temporal resolution - Spatio-temporal resolution is continuously improving	- Records data from the entire brain simultaneously - Blood flow measure in absolute terms - Investigation of neurotransmitter binding possible - Good spatial resolution	- Causal approach - Non-invasive - High spatial resolution - Good temporal resolution (ca. 200ms) - Can be used to excite and inhibit neuronal activity - Flexibility: multiple online (single-pulse) and offline (rTMS) sequences available	- Causal approach - Non-invasive - Cheap and easy to apply - Can be used to excite and inhibit neuronal activity - Can be applied to multiple subjects simultaneously - Compared to TMS, no noise and tactile distractions - Portable
Weaknesses	- Focus on neurons in a single brain region limits inferences, especially for complex cognitive process - Invasive nature limits its use to non-human animals and human patients undergoing surgery - Data collection is slow and labor-intensive	- Poor spatial resolution - Focus on well-studied components rather than differentiating the functions of brain regions - Positioning electrodes may require considerable set-up time	- Only a few MEG systems available worldwide - Limits in spatial resolution and identification of exact location of activity remain	- Correlational - Relatively expensive - Relatively noisy signal and dropouts in some regions. - Temporal resolution too low to infer neural dynamics - Participant's head is constrained and needs to remain still.	- Correlational - Relatively invasive (injection of radioactive material) - Costly to produce radio-tracer - Short half-life of radioactive tracer means onsite chemistry lab may be necessary	- Only directly affects neurons close to cortical surface, not within deeper brain areas (e.g., striatum) - Noise and tactile sensations of stimulation can be distracting - For offline studies, duration of TMS time-window uncertain - Ideally used in combination with fMRI to infer network effects of stimulation. - Not portable	- Only affects neurons close to cortical surface, not within deeper brain areas (e.g., striatum) - Low spatial resolution due to diffuse nonlinear stimulation throughout the brain.

Table 1: Strengths and weaknesses of neuroscientific methods

We argue here that these recent developments in neuroscience techniques are relevant for the field of economics, particularly behavioral economics, as they provide insights into the mechanisms underlying economic and social decision-making (Clithero, Tankersley, and Huettel 2008). Importantly, they provide an understanding of how the brain solves common decision problems by giving insight into the computations the brain is capable of performing, but also the limitations imposed on these computations by our cognitive and neural machinery. In this context it is important to note that insights from neuroscience have been incorporated into recent theories of economic and social decision-making that take into account known biological constraints (e.g., (van Winden, Krawczyk, and Hopfensitz 2011; Webb et al. 2016; Camerer and Mobbs 2017). A main goal of this chapter is to provide an introduction to the most important neuroscientific methods that are commonly used in the field of Neuroeconomics. We will highlight recent experiments to illustrate how these methods can be applied to questions that are important for Behavioral Economics and to illustrate the advantages and limitations of neuroscientific techniques that are relevant for Behavioral Economists. We have divided the chapter into three parts, in part one we provide a very brief overview of neuronal communication that neuroscientific techniques capture to enable a looking glass into the brain; in part two we provide an overview of "correlational" methods (e.g., electrophysiology, fMRI) that measure neuronal activity while participants take part in behavioral tasks assessing their economic and social preferences. We focus this part on functional Magnetic Resonance imaging (fMRI) as this is by far the most commonly used neuroscientific method in Neuroeconomics; in the final part we outline manipulation methods (e.g. TMS, tdcs) that allow researchers to disrupt the function of specific brain regions, thereby causing "virtual lesions", to identify a region's contribution to a behavior of interest.

2. OVERVIEW OF NEURONAL COMMUNICATION

According to recent estimates, the adult human brain contains about 86 billion individual neurons (Azevedo et al. 2009). Each neocortical neuron forms about 7 thousand connections with other neurons (Drachman 2005). These connections allow neurons to communicate with each other via

electrochemical signals: chemical signals enable communication between cells, while electrical signals propagate within the cell to allow fast communication to more distant cells (in the case of the sciatic nerve, covering a relatively long distance from the spinal cord to the foot). To better understand how neurons communicate with each other, we need to briefly consider the anatomical make-up of a neuron: neurons consist of a cell body, or the "soma" that appears in anatomical (T1) MRI scans in darker colors and is referred to as "gray matter", as well as axons and dendrites, which appear in lighter colors due to a fatty myelin sheath and are therefore referred to as "white matter" (Figure 1). The cell body contains the cell's organelles including the neuron's nucleus. The nucleus, in turn, contains the cell's DNA and is responsible for generating proteins that are the building blocks of the cell and required for repairing and forming new connections, as well as for producing neurotransmitters. The most common excitatory neurotransmitter is glutamate, while the most common inhibitory neurotransmitter is gamma-aminobutyric acid (GABA). Other important neurotransmitters include the monoamines dopamine (DA), which is involved in reward-motivated behavior (Berridge and Robinson 1998), and serotonin (5-HT), which is involved in the regulation of mood and sleep (Davidson, Putnam, and Larson 2000). When a connecting neuron releases a neurotransmitter into the synaptic cleft between two neurons, some of this neurotransmitter binds to receptors on the dendrites of adjacent neurons. This binding opens ion channels that change the polarization of the cell, converting the chemical signal into an electrical signal. If the joint input from multiple neurons changes the overall charge of the cell, which at rest is -70 mV, beyond a threshold of -55 mV, an action potential is sent down the axon of the neuron. The action potential, in turn, triggers the release of neurotransmitters into the synaptic cleft between the axon of the current neuron and the dendrites of adjacent neurons. The release of neurotransmitters is linked to the rate with which the current neuron fires action potentials. Thus, the frequency of action potentials allows relatively complex communication between neurons (Glimcher 2014).

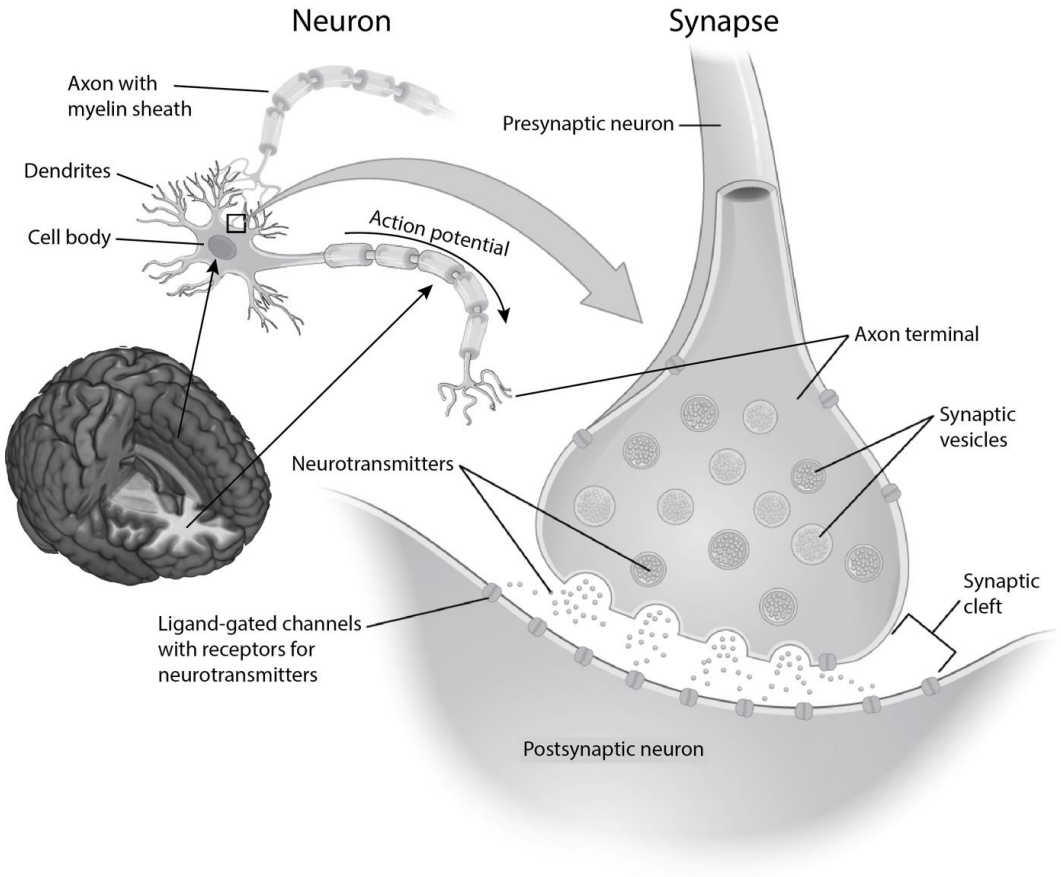

Figure 1: Neurons communicate via Electrochemical signals. Different neuroscientific methods capture specific aspects of neuronal communication: Structural MRI scans depict different components of neurons. Specifically, grey matter, which contains cell bodies, dendrites and glial cells, is reflected in darker colors, while white matter, which contains mainly myelinated axons, is depicted in lighter grey shades. Single- and multi-unit recordings capture the electrical activity triggered by action potentials around a single or multiple neurons, while EEG and MEG capture postsynaptic electrical activity of multiple neurons and resulting distortions in the magnetic field. Like fMRI, PET captures metabolic activity but can also assess neurotransmitter binding at the level of the synapse. Image adapted from OpenStax via Wikimedia Commons.

Modern neuroscientific methods allow experimenters to measure various aspects of this process. Neuronal communication requires energy that is supported by oxygen and glucose. Neuroimaging techniques such as PET and fMRI make use of the energy requirement of neurons by visualizing those parts in the brain that consume relatively more energy. The Blood

Oxygenation Level Dependent (BOLD) response that underlies functional MRI, for instance, reflects the relatively larger amount of oxygen present in a brain region whose neurons are active. Electrophysiological recordings pick up changes in the voltage of electrical signals. They accomplish this either via microelectrodes that are implanted into the brain to reach neurons within regions of interest, or by using electrodes placed on the skull that capture the electrical current from the joint activity of multiple neurons (electroecenphalography, EEG), or by using superconductive quantum interference devices (SQUIDS) that capture magnetic field changes due to dendritic activity in a cluster of cortical neurons (magnetoencephalography, MEG). The causal involvement of brain regions can be investigated via brain stimulation techniques that can up- or down-regulate the neuronal properties of the stimulated brain region and thereby cause changes in behaviors of interest. These manipulation techniques function by sending a strong magnetic field (TMS) or electrical current (tES) that penetrate the skull above the targeted areas to interfere with ongoing neuronal activity. More invasive techniques that involve the insertion of microelectrodes into the brain are typically only performed with animals and in human patients that undergo brain surgery.

3. MEASUREMENT METHODS

3.1 FUNCTIONAL MAGNETIC RESONANCE IMAGING (FMRI)

Magnetic Resonance Imaging (MRI) is a versatile imaging method that enables the visualization of different aspect of the brain's structural and functional neuroanatomy, such as gross anatomical structures via MRI and anatomical connections between different brain regions via diffusion tensor imaging (DTI), but also changes in blood oxygen content over time via the blood oxygenation level dependent (BOLD) contrast using functional MRI (fMRI). A structural MR image, such as the one shown in Figure 2A, allows the differentiation of different tissue types within the brain. Specifically, neuronal cell bodies, or grey matter, can be distinguished from neuronal fibers, or white matter, thus providing a representation of the neuroanatomy of the brain. Structural MRI relies on the heterogeneous magnetic properties of the different tissue types within the brain caused by different quantities of hydrogen atoms. This is captured by (T1-weighted) MRI images, in which water-rich regions, such as neuronal cell bodies, are depicted in darker shades, while fat-rich regions, such as myelinated axons appear in brighter shades.

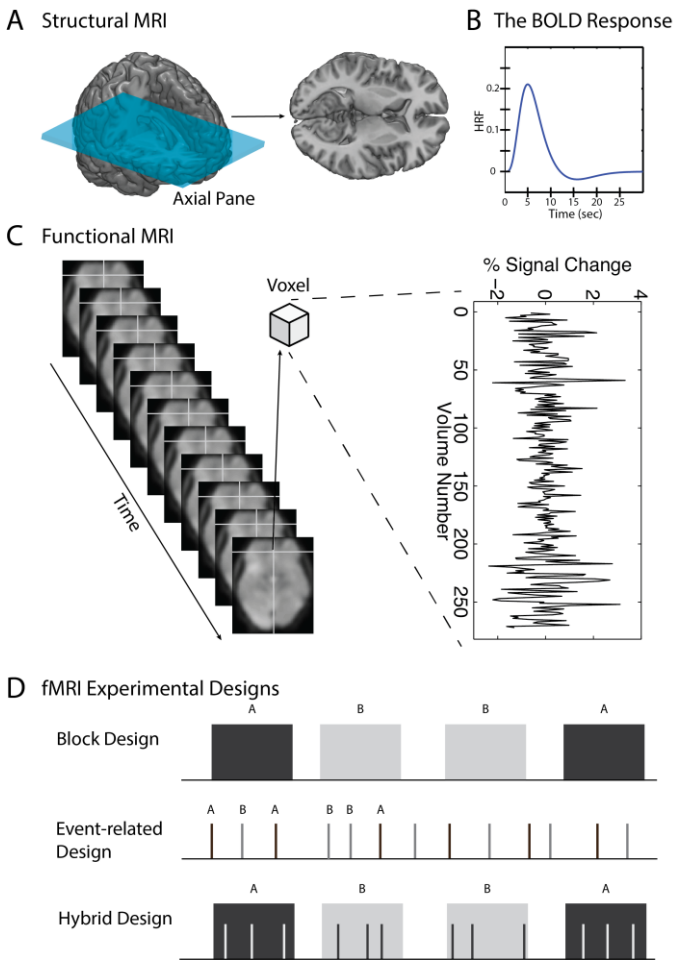

Figure 2: Structural and functional MRI. (A) shows a cut-out of a rendered 3D structural MR image. Making a virtual cut in the axial plane (shown in blue) leads to a 2-dimensional image from the perspective of someone looking at the brain from above. (B) The hemodynamic or BOLD response function. (C) Researchers using functional MRI are interested in signal changes across time as a function of the experimental conditions. To accomplish this, 3-D brain volumes consisting of multiple 2-D brain slices (shown on the left) are recorded repeatedly in an experiment. Each 2-D brain slice consists of a matrix of multiple voxels. The right plot shows an example time series from a single voxel. The general linear model is then used to compare the observed signal changes to the signal that is expected based on the experimental design. (D) fMRI experimental designs include block designs (illustrated via boxcars), event-related designs (illustrated via stick functions) and a combination of the two called hybrid designs. Image in 2B adapted from SPM-wiki via Wikimedia Commons.

In order to detect the distribution of atoms and visualize the anatomy of the brain, the MR scanner makes use of three main ingredients: a strong and static magnetic field to which the hydrogen atoms align, a radiofrequency pulse that causes spin excitation in some hydrogen atoms, and radiofrequency coils that receive the signal from excited hydrogen atoms to generate MR images. (1) **The Magnetic field**. The human brain is composed of more than 73% of water (Mitchell et al. 1945). Water contains 1 oxygen atom and 2 hydrogen atoms, the latter of which have magnetic properties that the MRI scanner utilizes to create images of biological tissue. In their natural state, hydrogen protons spin about themselves in random directions. This has two consequences: (1) The spin creates a magnetic moment that causes a magnetic force (torque) when the hydrogen proton is placed within a magnetic field; (2) in their natural state, the random orientations of all magnetic moments of the hydrogen protons cancel each other out, leading to a net magnetization approaching zero. When a strong magnetic field is applied to the hydrogen protons, however, their spin moments align to the magnetic field, thereby inducing a positive net magnetization. To accomplish this, modern MRI scanners use superconducting electromagnets to create a homogenous and strong magnetic field with typical strengths ranging between 1.5 and 9 Tesla (T). To give an intuition about the strength of this magnetic field, a 7 Tesla scanner's magnetic field is around 140,000 times stronger than the earth's. The strong magnetic field distinguishes between high- and low-energy hydrogen protons. Specifically, spins line up either parallel (i.e. low-energy state) or antiparallel (i.e. high-energy state) to the magnetic field. The protons in the low-energy state are crucial for MR images because they can absorb external energy and briefly enter a high-energy state that can be measured. (2) **The Radiofrequency Pulse.** The MR scanner delivers a radiofrequency pulse at the same frequency as the spin precession of the hydrogen protons. This excites the spins of some of the protons in the low energy state. When the pulse ends, the hydrogen protons release the energy they absorbed in the process of returning to their preferred equilibrium state. The release of this energy can be detected by the MR scanner. (3) **Imaging.** The MR scanner records (via radiofrequency coils) the amount of energy emitted by hydrogen protons when they return to their equilibrium state and stores these signals in a greyscale image that reflects the energy distribution within a single slice of the brain within a two-dimensional matrix. A brain slice can be pictured as a two-dimensional image of the brain when looking at the brain from the top (axial view, Figure 2 A). A three-dimensional image of the brain can be generated by repeatedly sampling multiple slices in descending order from the top to the

bottom of the brain (or vice versa). The basic unit of the MR image is the **voxel**, which can be pictured as a three-dimensional cube (Figure 2B). If a voxel contains more water than fat, which is the case when the brain tissue within a given voxel is comprised mostly of cell bodies, a stronger signal will be generated because of the larger amount of hydrogen atoms. These signals will be collected by the scanner with a specific duration after the excitatory pulse was sent (for a more detailed discussion of the underlying physical basis of MRI see Huettel, Song, and McCarthy 2014).

Of interest to Neuroeconomics is the recent development of voxel-based morphometry (VBM), which provides estimates of the grey matter density of brain regions, a quantitative measure that reflects the neuronal density in brain regions of interest (Ashburner and Friston 2000). Individual differences in the structural composition of brain regions of interest can then be correlated with economic preferences. Using this method, it was recently shown that grey matter density in the temporoparietal junction, a region important for understanding and predicting other people's actions (Saxe and Kanwisher 2003), is associated with social preferences (Morishima et al. 2012).

3.2 FUNCTIONAL MRI AND THE BLOOD OXYGENATION-LEVEL DEPENDENT (BOLD) SIGNAL

As opposed to structural MRI, the goal of functional MRI is to record changes in the BOLD response of the brain when subjects perform an experimental task. As outlined above, the BOLD response captures an increase in the metabolic demands of active neurons. As such, it does not measure neuronal activity per se, but correlates with the summed electrical signal from populations of neurons, called local field potentials (LFP) (Logothetis 2002; Logothetis 2008). More specifically, when neurons actively contribute to a behavior of interest, they consume increased levels of oxygen. Oxygen is transported to the brain via hemoglobin, which is an iron-containing protein found in red blood cells. Interestingly, hemoglobin has different magnetic properties depending on whether it is bound to oxygen or not: deoxygenated hemoglobin, which is paramagnetic, has significantly more magnetic susceptibility than oxygenated hemoglobin, which is diamagnetic. Ogawa and colleagues (Ogawa et al. 1990) discovered that the MR scanner can detect the difference between deoxygenated and oxygenated hemoglobin. Their experiment demonstrated that T2* weighted MR images (a specific MR contrast that is sensitive to changes in

the BOLD response) depict the presence of signal loss in blood vessels of rat brains when the animals breathed normal air, an effect that was absent when the animals breathed pure oxygen. This finding comprises the basis of the BOLD response: a greater ratio of oxygenated relative to deoxygenated hemoglobin therefore causes localized increases in the MR signal.

There is, however, one caveat in simply translating Ogawa et al.'s results to fMRI. An intuitive prediction is to assume that greater oxygen consumption due to increased neural activity should lead to greater amounts of deoxygenated relative to oxygenated hemoglobin in active brain regions, and consequently a decrease in MR signal when neurons are active. When inspecting the hemodynamic response function (HRF) that reflects the canonical BOLD response shown in Figure 2B, it is apparent that this is only the case for a short period of time within the first second. After that, an increase in the BOLD signal is observed, which is due to an over-compensatory increase in regional cerebral blood flow to active brain regions (Fox and Raichle 1986). This leads to a greater amount of oxygenated hemoglobin that displaces the deoxygenated hemoglobin and consequently causes an MR signal increase. From Figure 2B, it is also apparent that this signal is quite sluggish, taking about 4-6 seconds to peak and another 10 seconds to return back to baseline, which constitutes a limitation on the temporal resolution of fMRI (Table 1).

3.3 HOW IS THE BOLD SIGNAL RECORDED AND INTERPRETED?

While structural brain images require only one recording of the entire brain, functional brain images are created by repeatedly sampling the whole brain in a relatively short period of time that ranges between 1 and 3 seconds in a typical experiment. The time it takes the MR scanner to record the multiple slices that together compose a brain volume (a predefined area that typically covers the whole brain) is referred to as the repetition time (TR). As illustrated in Figure 2C, the final data set typically contains hundreds of brain volumes that were recorded sequentially throughout the experiment. A general linear model is then constructed based on the experimental design that reflects the predicted BOLD response at specific time points (based on the HRF shown in Figure 2B) and this model is fit repeatedly to the observed response within each voxel (Fox and Raichle 1986; Friston et al. 1995). Using this approach, a statistical parametric map (SPM) is generated for each subject that reflects the spatial distribution of the beta estimates (regression coefficients) from the statistical model across all the voxels in the brain. Group-level statistical inferences about which brain regions correlate with the behavior of interest can then be generated by summarizing

the statistical parametric maps from each subject's first-level statistical model in a random-effects second-level model that includes a random subjects factor. Of note, due to the fact that a statistical test is performed for each voxel in the brain and the resulting large number of statistical tests (at a resolution of 2mm isotropic voxels functional brain images contain about 254,000 voxels), it is important to correct for multiple comparisons. This is typically accomplished via the application of Gaussian Random Field Theory that takes into account the spatial structure of activation clusters (Friston et al. 1995; Chumbley and Friston 2009), as well as nonparametric permutation tests (Eklund et al. 2014). For a detailed outline of fMRI analysis methods see Chapter II.3 by Lebreton and Preuschoff in this volume.

THE PROBLEM OF NOISE

When using fMRI to investigate economic decision-making, experimenters measure relatively small changes in the MR signal in the order of 1-5% that is due to the experimental treatment (relative to a well-matched control condition) in an environment that is inherently noisy (Purdon and Weisskoff 1998; Amaro and Barker 2006). Noise in the context of fMRI is understood as changes in the BOLD response due to influences that are not related to neuronal activity. Sources of noise are manifold and include participant-related noise, such as head motion and physiological noise due to the subject's cardiac and breathing cycles that cause changes in blood and CSF flow, as well as blood oxygen content (Krüger and Glover 2001; Murphy, Birn, and Bandettini 2013). Physiological noise is particularly worrisome if it covaries with the experimental condition. One example from the field of neuroeconomics is the commonly observed increase in physiological arousal during high risk decisions compared to low risk decisions (Bechara et al. 1996; Tranel 2000; Critchley, Mathias, and Dolan 2001; Crone et al. 2004; Figner and Murphy 2011). Moreover, noise can be caused by the MR scanner system in the form of thermal noise, as well as instabilities in gradient and magnetic fields that are commonly observed as a slow drift in signal strength over time. A number of measures to counteract such noise have been developed: head motion can be reduced ex ante by stabilizing the subject's head, and estimated ex post via specialized algorithms that use rigid-body transformations to align all brain volumes recorded during an experiment to a reference. Motion-based regressors, as well as global signal regressors, can also be added to first-level statistical models to remove the variance associated with motion (Power et al. 2014). The influences of physiological noise on the BOLD response can be reduced by recording

physiological responses, such as breathing, heart rate and galvanic skin conductance responses, and including these as nuisance regressors in fMRI models (Kasper et al. 2017). In the absence of physiological data, data driven methods using for instance independent component analysis (ICA) to estimate physiological noise from functional MR data offer an alternative (Tong and Frederick 2014; Salimi-Khorshidi et al. 2014). Multiple software solutions exist to account for scanner drift and spikes in standard fMRI analysis packages.

ADDRESSING NOISE CONCERNS VIA EXPERIMENTAL DESIGN

Due to the relatively small signal changes that are due to differences in BOLD response during the experimental task compared to the control condition and the relatively large number of potential sources for noise, it is crucial to apply measures to reduce noise wherever possible to implement a successful fMRI experiment. This can in part be accomplished by careful experimental design. One approach in fMRI experimental design that differentiates it from typical experiments in Behavioral Economics is to present identical trials within the same experimental condition repeatedly to subjects to allow signal averaging (Anders M Dale and Buckner 1997). The idea behind **signal averaging** is relatively simple: given little variation in the fMRI signal triggered by identical events over multiple repetitions in combination with random noise, noise should influence the individual time points of the HRF differentially across repetitions (note, however, that not all sources of noise are random). It is therefore possible to obtain a better estimate of the HRF with increased repetitions, thereby improving the ratio of signal to noise (SNR) (Huettel and McCarthy 2001). Signal averaging improves both estimation and detection power: (1) by decreasing the noise associated with the estimate of the hemodynamic response to a given trial by a factor equal to the square root of the number of repetitions of a given trial type (Huettel and McCarthy 2001); and (2) by increasing the spatial extent of activation clusters via increased SNR in near-threshold voxels at activation cluster borders (Huettel and McCarthy 2001).

OPTIMIZATION

Repeating identical trials multiple times throughout the experiment implies that the sequence and timing of the experimental design can be optimized to improve the **efficiency** of the experiment to estimate the hemodynamic response function (HRF) associated with individual task events (Ander M Dale 1999; Birn, Cox, and Bandettini 2002; Wager and Nichols 2003; Liu 2004). **Event-related designs** constitute by far the most common fMRI experimental design today (Figure 2D). To

illustrate event-related fMRI designs, suppose that we are interested in detecting the neural correlates reflecting the cognitive and emotional processes that underlie social decision-making. To address this, we could design a simple experiment in which we ask our subjects to make decisions in two conditions: condition A involves outcomes for other participants (such as in trust or ultimatum games), while condition B involves decisions that are equivalent to decisions in condition A (e.g., the same amounts of money can be transferred, the same buttons are pressed to communicate the decision, choice options are represented using the same visual display) except that they do not lead to outcomes for others (Sanfey et al. 2003; Baumgartner et al. 2008; Krueger et al. 2007). In event-related designs trials from the different conditions are typically presented in (pseudo-) random order and assumed to trigger relatively short and discrete neural events that are time-locked to the onset of a trial (Figure 2D). Importantly, trials are separated by a relatively brief delay, called the intertrial interval (ITI) that typically varies between 2 to 10 seconds. Given the relatively sluggish HRF response discussed above, such short delays lead to the hemodynamic responses associated with condition A to overlap with those associated with event B making it difficult to estimate the HRF for individual events. One solution to this is the introduction of temporal "**jitter**" of the trial onset relative to the onset of the starting point of recording a brain volume (TR). This can be accomplished by introducing intertrial intervals of varying length that differ after every trial. Jitter improves the efficiency of estimating the shape of the HRF for each trial type (Ander M Dale 1999; Liu 2004), as the overlap between two repeated events falls on different points of the HRF after every trial. Additional psychological advantages are reduced anticipatory responses and temporal expectations. Optimization of event-related fMRI experimental design involves finding the ideal (pseudo-) random sequence and timing (including the distribution of jittered intertrial intervals) of events that maximize the statistical power of the design (Ander M Dale 1999; Liu et al. 2001; Birn, Cox, and Bandettini 2002; Wager and Nichols 2003).

Event-related fMRI designs permit the identification of the neural correlates of specific psychological events, such as an individual decision (Wager and Nichols 2003). This is one major advantage over block designs outlined below, which have greater statistical power to detect an activation due to an experimental treatment, but only allow identification of the neural correlates of classes of events (Liu et al. 2001). This implies that event-related fMRI designs are the method of choice for neuroeconomics, where researchers have a specific interest in measuring the neural

responses to relatively small changes in economic variables, such as gain and loss amounts (Tom et al. 2007; Engelmann et al. 2015), or the risk levels of choice options (Preuschoff, Bossaerts, and Quartz 2006; Engelmann and Tamir 2009). A common approach to model how the level of a choice-relevant variable influences the BOLD response is parametric modulation (Cohen 1997). A parametric modulator is a regressor in the fMRI statistical model that makes specific predictions about the magnitude of the BOLD response. For instance, we might predict that a linear relationship between subjective values of choice options and BOLD responses exists, such that trials that offer choice options with increasing subjective values are associated with increasing BOLD response in relevant brain regions that track subjective value (Büchel et al. 1996). Indeed, recent experiments have shown that the BOLD signal in vmPFC and striatum tracks subjective value on a trial-by-trial basis, showing linear increases in BOLD signal with increases in subjective value (Kable and Glimcher 2007a; Tom et al. 2007; Plassmann, O'Doherty, and Rangel 2007; Bartra, McGuire, and Kable 2013; Engelmann et al. 2015), and related variables including monetary amounts (Knutson et al. 2003), gain and loss amounts (Tom et al. 2007; Engelmann et al. 2015), pleasantness ratings of rewarding stimuli (Kringelbach et al. 2003) and goal values (Hare, Camerer, and Rangel 2009). Moreover, this approach can be combined with computational models, such as reinforcement learning models. In **model-based fMRI**, a computational model is first fit to the behavioral data to extract model parameters of interest that are then subsequently used as regressors in the fMRI statistical model. Model-based analysis has become one of the hallmarks of neuroeconomic research (Gläscher and O'Doherty 2010) because it enables testing of mechanistic predictions about the relationship between neural activity and behavior (O'Doherty, Hampton, and Kim 2007; Palminteri et al. 2015).

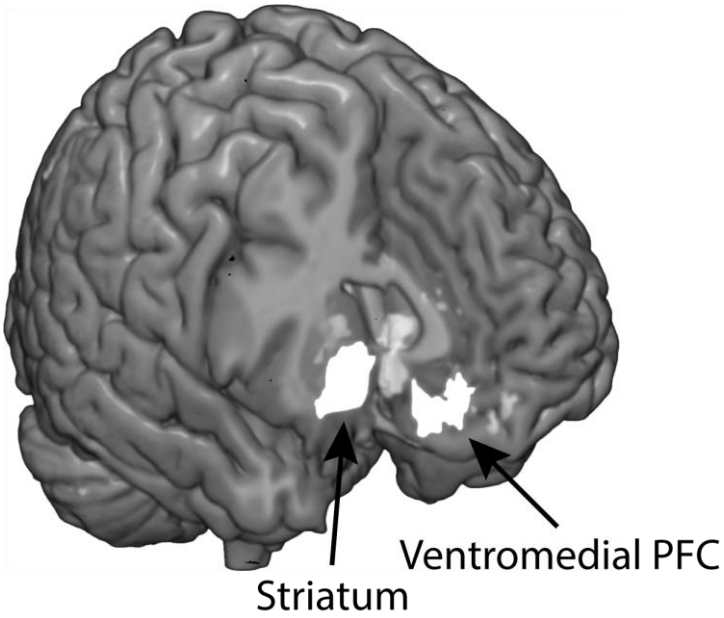

Figure 3: The valuation system. Regions that consistently show correlations with subjective value are highlighted in white and include the ventral striatum and ventromedial prefrontal cortex. Activations were extracted from the neurosynth reverse inference map created by performing a meta-analysis of 344 fMRI studies on the topic of "value".

Two alternative designs include blocked and hybrid fMRI experimental designs (Figure 2D). In **blocked designs**, trials from the same condition are presented sequentially after one another in the context of blocks that last up to 60 seconds. We could implement the event-related design outlined above in the context of a blocked design by asking our subjects to make 8 sequential decisions in condition A (the social condition), followed by a brief pause, which is followed again by 8 sequential decisions in condition B (the non-social condition). Contrasting the BOLD response during the social block to that during the control block reveals activations that are specific to making decisions when other participants can be affected. This approach holds only under the assumption that the cognitive and emotional processes of interest are constant for the duration of the block and that decisions during the control block involve all the same cognitive and emotional processes, except the process of interest. Blocked designs were almost exclusively used in the beginning stages of fMRI due to their favorable **detection power** (Birn, Cox, and Bandettini 2002; Friston et al. 1999) because the prolonged cognitive states triggered by repeated

task performance produce large BOLD signal changes due to the experimental manipulation. However, it can easily be seen that such an experimental design might not be optimal for experiments in the field of neuroeconomics: asking subjects to make the same decision repeatedly in a brief period of time likely changes the strategy with which such decisions are made in the absence of introducing other variables. Consider for instance a binary one-shot trust game in which subjects are asked to either invest 10 Euros or to opt out and are paired with a new anonymous opponent on every trial. If the decision is made repeatedly, the subject could easily adopt a strategy at the beginning of the block and then, for all other trials in the block, simply give the same answer that was memorized during the first trial but without engaging any of the cognitive and emotional processes involved in an actual decision. The likelihood of such perseverative responding is significantly reduced in event-related fMRI experimental designs, in which conditions A and B alternate on each trial in a manner that is unpredictable to the subject. This is particularly the case when other variables vary on each trial, such as the potential monetary amounts that could be gained or lost (see for instance Tom et al. 2007; Kable and Glimcher 2007a; Engelmann et al. 2015).

Finally, experimenters interested in investigating the effects of prolonged contextual manipulations on decision-making can employ **hybrid fMRI designs** (also referred to as mixed block/event-related) that combine block with event-related components (Visscher et al. 2003). In the field of neuroeconomics, hybrid experimental designs are useful for manipulating the context within which decisions are made via the blocked condition, such as the level of incentive motivation (Engelmann, Damaraju, et al. 2009), or the emotional state of the subject (Engelmann et al. 2015). This approach enables investigations of the impact of relatively prolonged contexts on the neural correlates of decision-making and, at the same time, can increase the ecological validity of the experiment by investigating contextual effects on decision processes. Moreover, hybrid designs allow for separate estimation of longer-lasting sustained BOLD signals related to the blocked condition, and event-related transient signal related to the decisions made on each trial (Visscher et al. 2003; Yarkoni et al. 2005).

A TYPICAL EXPERIMENTAL SETUP FOR FMRI

Differences exist between the typical experimental setup in Behavioral Economics and Neuroeconomics. First of all, because participants are tested individually in a separate

magnetically-shielded room that houses the scanner, the experimental setup allows only limited interaction between the subject and the experimenter, or other participants. Interaction is possible mainly via visual information that is presented to the subject, and by communicating over the intercom with the subject. The noise of a working MRI scanner entails that the subject is relatively isolated inside the scanner room during an experimental run. This does not, however, stand in the way of implementing social games in an imaging context (Sanfey et al. 2003; Baumgartner et al. 2008). While early studies have made use of deception to implement social games in fMRI, the use of pre-recorded (strategy) decisions from earlier experiments that participants are matched with on every trial does not deem deception necessary (Engelmann et al. 2017). Moreover, recent experiments in social neuroscience that investigated the neural correlates of empathy have created sophisticated experimental designs in which interaction partners stay with the subject inside the scanner room during an experimental run (Hein et al. 2010; Hein et al. 2015).

Due to the costs involved in using MRI scanners (upwards of $300 per hour), a typical fMRI study has between 20 and 40 subjects, which is relatively small compared to studies in Behavioral Economics (the average sample size of 18 recently replicated Behavioral Economics experiments published in Top 5 economics journals between 2013 and 2014 was 122 and ranged between 42 and 288, (Camerer et al. 2016). Note, however, that many fMRI experiments vary the levels of important treatment variables within-subject, thereby increasing power. There is no good rule of thumb about how many subjects constitute a well-powered fMRI study (Desmond and Glover 2002; Yarkoni 2009; Friston 2012), so, given that automated power analysis tools are available, the number of subjects required to reach reasonable detection power should be considered individually for each study (Mumford 2012). The relatively low number of subjects in fMRI studies is furthermore offset by the relatively large number of trials per treatment level required to improve BOLD signal estimates (Anders M Dale and Buckner 1997). Repeating trials also leads to an increase in the length of the experiment, which is typically between 1 and 2 hours long and subdivided into multiple runs that last about 5-15 minutes. Each run is followed by a short break that serves as a rest period to prevent fatigue and allows the experimenter to communicate with the subject and vice versa.

A typical fMRI experiment in the field of Neuroeconomics follows the following setup: First, to ensure the safety of the subjects the experimenter needs to confirm that the subject (and

any object) that enters the magnetic field of the scanner is free of ferromagnetic metal parts. The participant is then placed in a supine position on the scanner bed and her head is fixated via foam pads within the head coil, in order to minimize head movements during scanning that are detrimental to data quality. A mirror is mounted on top of the head coil that allows the subject to view visual stimuli projected onto a screen, while an MR-compatible response box is placed in the subject's hand to allow the subject to communicate her decisions. It is also possible to deliver other types of stimuli, including drinks (McClure et al. 2007; Plassmann et al. 2008), smells (Sommer et al. 2012) and electrical shocks (Engelmann et al. 2015; Engelmann et al. 2017), and thereby mimic real-life decisions and create emotional contexts. It is good practice to reduce the duration of a scanning session to about one hour, since longer periods of time could result in discomfort and might affect data quality via loss of attention, tiredness and associated increases in head movement. Sessions usually begin or end with an anatomical (T1-weighted) scan that enables the alignment of each subject's functional dataset to a template brain during initial processing of the fMRI data. This is followed by multiple runs that present the experimental conditions as outlined in detail above.

APPLICATIONS RELEVANT FOR BEHAVIORAL ECONOMICS

The biological concept of reward is intimately related to the economic concept of value (Shizgal 1999; Montague and Berns 2002; Schultz 2004). Rewards are defined as stimuli that motivate appetitive (approach) behavior (Montague and Berns 2002; Berridge and Kringelbach 2008) as animals have been shown to invest energy in the form of physical and mental effort to obtain rewards (Salamone et al. 2003). Starting with the demonstration of Olds and Milner (1954) that rats readily work for electrical stimulation to specific areas of the brain, such as the medial forebrain bundle (MFB), a plethora of animal studies has used multiple neuroscientific techniques to investigate the brain's putative reward circuit (for review see Haber and Knutson 2010). Cognitive neuroimaging studies have confirmed the presence of overlapping reward-related neural circuitry in the human brain (O'Doherty et al. 2002; Knutson et al. 2003; Delgado et al. 2005). This research has laid some of the foundations for neuroeconomics, which pursues the goal of identifying the cognitive and emotional mechanisms underlying economic and social decision-making and associated neural circuitry. One important advancement that the field of neuroeconomics has made is the identification of a neural network consisting of ventral striatum,

ventromedial prefrontal cortex and anterior insula, which consistently tracks the subjective value of choice options (Bartra, McGuire, and Kable 2013).

Kable and Glimcher (2007b) offer an illustration of how the neural correlates of subjective value can be investigated using fMRI. While undergoing fMRI, participants in this study made repeated intertemporal decisions between an immediate reward that offered a relatively small monetary amount (fixed at $20) and a delayed one that offered a larger amount. The delays and monetary amounts were varied on each trial and subjects made multiple decisions to enable estimations of hyperbolic discount functions for individual subjects. Using individual discount functions, objective values were transferred to subjective values and entered as a parametric modulator in the fMRI statistical model. This approach probes for brain regions that track subjective value on a trial-by-trial basis and thereby creates a strong link between behavior and its neural correlate. Regions that were identified to correlate with subjective value include ventral striatum, ventromedial prefrontal cortex and posterior cingulate cortex. The authors then fit hyperbolic discount functions to the fMRI data extracted from these regions and demonstrated the presence of a close match between the behavioral and neural discount rates.

The neural correlates of subjective value in other domains of decisions-making, such as risky decision making have been investigated using similar approaches (Levy et al. 2010). More recent experiments have investigated how context effects influence subjective value coding in the brain, including framing effects (De Martino et al. 2006), advice about decision strategies (Engelmann, Capra, et al. 2009; Biele et al. 2011; Engelmann et al. 2012) and emotional contexts (Knutson et al. 2008; Engelmann et al. 2015), thus providing richer experimental approaches that simulate situations and emotional states commonly found in real life scenarios.

POSITRON EMISSION TOMOGRAPHY (PET)

Positron emission tomography (PET) visualizes the distribution of positron-emitting radioactive isotopes in the brain, or any other tissue in the human body (Raichle 1998). It has some overlap with fMRI in that it can be used to record metabolic activity, but has wider applications as it allows investigations of neurotransmitter binding, such as dopamine (Hakyemez et al. 2008). PET experiments involve multiple steps: due to the relatively short half-life at which radioactive isotopes decay, a positron-emitting radiopharmaceutical needs to be synthesized using a cyclotron (a particle accelerator) that is positioned relatively close to the PET scanner. Using a cyclotron,

the radioactive isotope is attached to a molecule that is utilized by neurons, such as glucose, oxygen or neurotransmitters. The radioactive isotope is then injected into the bloodstream of the participant and travels to the brain where it distributes based on the ongoing metabolism. For instance, a commonly used tracer, radioactive glucose (11C-labeled glucose, Raichle et al. 1978), will be more prominently present in areas containing neurons with increased glucose metabolism, which is tightly linked to ongoing neuronal activity (Sokoloff 1999; Mergenthaler et al. 2013). Because of its unstable nucleus, the radioactive isotope decays by emitting positrons, which, when they collide with an electron, emit two photons (gamma rays) that travel in approximately opposite directions (Raichle 1998). These gamma-rays can be detected by radiation detectors (scintillator crystals) that form the core of the PET scanner. When two such events occur simultaneously in opposite detectors, these are assumed to occur due to the decay of the radioactive tracer (and not background radiation) (Raichle 1998). Such events are recorded and used to construct 3D statistical images of the distribution of radioactivity in the brain.

One reason why only relatively few PET studies have been conducted recently in the field of Neuroeconomics (de Quervain et al. 2004; Hakyemez et al. 2008) is because this method is more intrusive than fMRI, as it involves the injection of a radioactive isotope into the bloodstream of the participant. Moreover, PET suffers from a lower spatial (1cm vs. 3mm) and temporal (60s vs. 2s) resolution compared to fMRI (Table 1). Particularly the temporal resolution limits the applicability of PET experiments that focus on metabolic activity to Neuroeconomics, as event-related designs are often not feasible at time scales of >1 minute (Kable 2011). One application of PET that is of great interest to Neuroeconomics is the ability to directly measure aspects of neurotransmission during decision-making. For instance, Treadway et al. (2012) showed that differences in striatal and prefrontal responsivity to a dopaminergic agonist (d-amphetamine) correlated positively with individual's willingness to invest more effort to obtain larger valued rewards, while the opposite relationship was found in the anterior insula (Treadway et al. 2012).

ELECTROENCEPHALOGRAPHY (EEG)

Electroencephalography (EEG) is the first non-invasive method developed to detect neuronal activity in human subjects (Berger 1929; Adrian and Yamagiwa 1935; Jasper and Carmichael 1935; Jasper, Bridgman, and Carmichael 1937). EEG detects oscillations of electrical potentials

of neuronal ensembles via multiple electrodes (between 2 and 256) that are attached to the scalp of participants. The source of the signal that is detected by EEG is believed to be the electrical potentials generated by the postsynaptic activity of a large number of cortical neurons (in the order of 10^7; (Cooper et al. 1965) that need to be simultaneously active (Logothetis et al. 2001; Nunez and Srinivasan 2006; for review Woodman 2010; Luck 2005). The EEG signal is likely generated mainly by the activity of pyramidal neurons, which are a specific type of neuron that is characterized by a single axon, multiple dendrites and a conic shaped cell body, given their favorable orientation and location within cerebral cortex (Woodman 2010).

EEG data exhibits characteristic wave patterns that differ in their oscillation frequency (or band) and electrode location (György and Draguhn 2004). Different frequency bands have been associated with different cognitive states (Lansbergen, Schutter, and Kenemans 2007; Wang 2010; HajiHosseini and Holroyd 2015). For instance, alpha band power, with oscillation frequencies that typically fall between 9-12Hz, have been associated with the speed of cognitive performance (Surwillo 1961; Klimesch et al. 1996), while theta band power (4-8Hz) is associated with sleep deprivation (Borbély et al. 1981). Other commonly investigated EEG frequency bands include the beta-band (20-30Hz), that has been associated with impulsive behaviors (Lansbergen, Schutter, and Kenemans 2007), and the gamma-band (30-80Hz), that has been associated with visual perception (Rodriguez et al. 1999).

As outlined for fMRI in the previous section, the application of EEG data to research questions investigating the neural underpinnings of cognitive and emotional processes during decision-making is achieved by averaging the signal that is triggered in response to an experimental event (Van Veen et al. 1998; Delorme and Makeig 2004). This method generates event related potentials (ERP), which are waveforms reflecting the electrical activity of neurons engaged in cognitive processes that occur within a given time window after some experimental event. Waveforms are classified and distinguished by assessing their amplitude and latency (Polich 2007). Specifically, the amplitude (measured in μV) of an ERP component reflects the difference between the positive or negative peak of an ERP response relative to a baseline response (typically the mean of the ERP response before the experimental event). Latency (measured in ms) reflects the time point at which this peak occurs relative to the onset of the experimental event (typically within about 500ms). Commonly observed ERP components include the P1 and N1, which can

occur together and reflect an initial positive ERP response at about 100ms, followed by a negative ERP response just before 200 ms. This pattern of ERP responses is modulated, for instance, during tasks that require attention to visual stimuli (Gonzalez et al. 1994; Hillyard, Vogel, and Luck 1998; Hopfinger and Mangun 1998). Another waveform, the P300, refers to a positive potential about 300ms after event onset (for review see Polich 2007). Interestingly, this signal has been shown to be sensitive to the reward magnitude (Yeung, Sanfey, Alan 2004) and the frequency with which experimental events are presented to participants (Polich and Margala 1997).

While EEG is an older neuroscientific method, it has not been rendered obsolete by modern neuroimaging techniques for multiple reasons. Primary among those are that EEG directly measures neuronal electrical activity in the form of postsynaptic potentials, while other neuroimaging methods such as fMRI and PET rely on indirect approaches related to blood flow. Moreover, EEG enjoys very high temporal resolution in the order of milliseconds (<1ms), compared to the relatively sluggish BOLD response (2-6s). This allows for detecting subtle changes in neuronal processing at the very brief time scales utilized by cognitive and emotional processes. Important limitations of EEG include its relatively poor spatial resolution (ca. 10 cm) and imprecise spatial localization of the source of the EEG signal in the brain (Pascual-Marqui 1999; Grech et al. 2008). Limitations related to spatial localization are based on the "inverse problem", which reflects the fact that EEG measurements of electrical potentials above the scalp could be caused by an infinite number of underlying electrical current distributions, thus preventing a unique mathematical solution (Nunez and Srinivasan 2007; Barnes, Hillebrand, and Hirata 2010).

A TYPICAL EXPERIMENTAL SETUP FOR EEG

First, the subject is seated in front of a computer screen that displays the choice options and is provided with a response box or keyboard to communicate her decisions. The electrodes are then attached to the scalp of the subjects, and may include the application of gel to improve conductance. Modern EEG equipment uses flexible caps that contain between 32 and 256 electrodes. This has two advantages: (1) the use of a cap allows faster and more accurate placement of the electrodes using standard EEG lead placement systems, such as the 10-20 system that uses the distance from the nasion (the intersection between the frontal bone of the skull with nasal bones) to the inion (the occipital bone at the base of the skull) (Herwig, Satrapi, and Schonfeldt-Lecuona 2003) and (2)

the spatial resolution of the EEG data is improved with a larger number of electrodes (Gevins et al. 1994). An amplifier samples the electrical signals from the electrodes at relatively high frequencies between 250 and 1000 Hz to allow inferences about signal changes at very rapid time scales. Since EEG is highly sensitive to signal from internal and external sources that is not related to ongoing cognitive and emotional processes, hardware- and software-based de-noising and artifact reduction of the incoming signal is crucial (see also Ruff and Huettel 2014). The first measure to counteract external electromagnetic noise is to conduct EEG recordings in a shielded room. Hardware-based solutions to account for eye movements and blinks require the placement of additional electrodes to record muscle activity around the eyes (electrooculography, EOG). EOG data is then commonly used to estimate the impact of ocular artifacts on EEG data, which is then removed from further analysis (Hoffmann and Falkenstein 2008). Multiple software-based solutions exist that use statistical approaches to capture noise components of the EEG signal, such as independent component analysis (Delorme, Sejnowski, and Makeig 2007).

APPLICATIONS RELEVANT FOR BEHAVIORAL ECONOMICS

ERP components that are sensitive to monetary outcomes as a result of decisions made in the context of gambling tasks have been identified as far back as 40 years ago (Sutton et al. 1978; Johnston 1979). There are two components that are of particular importance: (1) the feedback-related negativity (FRN), which shows a negative peak at about 250ms and whose amplitude increases in response to negative performance feedback (Nieuwenhuis et al. 2002) and monetary loss (Gehring and Willoughby 2002; Yeung, Sanfey, Alan 2004; Hajcak et al. 2006); and (2) the P300, which has a positive peak at about 300ms and whose amplitude has been shown to scale with the amount of money received (Yeung, Sanfey, Alan 2004).

Yeung and Sanfey (2004) dissociated the roles of the P300 component from the feedback negativity component in the context of a choice task that could lead to monetary gains and losses (Yeung, Sanfey, Alan 2004). Participants in this study selected between two colored cards that could lead to financial gains and losses that differed in their magnitude and were unpredictable to participants. ERPs in response to the chosen outcome showed both a P300 and a FRN component, albeit at different preferred locations above the scalp. Importantly, independently varying the valence (gains vs. losses) and magnitude of the outcome allowed the authors to functionally dissociate these two components. Specifically, the P300 amplitude showed sensitivity to reward

magnitude but not to gains compared to losses (increased P300 amplitude for large relative to small outcomes irrespective of valence), while the FRN amplitude was greater after losses relative to gains, but insensitive to the magnitude of outcomes. These findings indicate that the valence and magnitude of gains and losses are represented in different spatial locations and by different underlying ERP components, suggesting distinguishable brain mechanisms for these economic variables that need to be integrated during decision making.

MAGNETOENCEPHALOGRAPHY (MEG)

Similar to EEG, Magnetoencephalography (MEG) detects changes in the electrical activity generated by neuronal ensembles. The electric currents generated by neuronal activity also give rise to magnetic fields that pass through the skull and scalp with relative ease, but are nonetheless relatively weak (about 100 femto Tesla). MEG detects changes in these weak magnetic fields via specialized sensors called SQUIDs, which stands for superconductive quantum interference devices, that are highly sensitive to magnetic field changes. Because of the high sensitivity of SQUIDS (they can detect the presence of a car at 2km distance, (Barnes, Hillebrand, and Hirata 2010), MEG systems are housed in magnetically shielded rooms to reduce such sources of noise. Modern MEG systems contain between 100 to 300 SQUIDS that simultaneously record changes in the magnetic field while subjects perform experimental tasks. Given that similar neuronal processes give rise to the MEG and EEG signal, MEG has a temporal resolution that is equivalent to modern EEG systems (< 1ms) and is analyzed in much the same way as EEG as either oscillatory activity or changes in activity that are time-locked to experimental events (ERPs) (Ruff and Huettel 2014). One main advantage of MEG is the superior spatial resolution that allows for enhanced localization of the source of the neuronal signal, as magnetic fields are not impeded by the local conductance of skull and scalp and thus pass through tissue and bone more uniformly (Okada, Lahteenmäki, and Xu 1999; Flemming et al. 2005). This feature allows scientists to localize the sources of signals and dynamically capture the process of economic information, such as reward magnitude and reward variability (Bach et al. 2017). Nonetheless, MEG still suffers from the inverse problem outlined for EEG above that prevents an unambiguous identification of the neuronal source that generated the observed signal (Barnes, Hillebrand, and Hirata 2010) .

The experimental setup using MEG is also similar to that of EEG, with the exception that the participant is seated under the helmet-like MEG system. Sources of noise are based on head

movements and magnetic fields generated by eye movement, both of which can be monitored throughout the experiment using hardware-based solutions (such as reference sensors that record noise only, (Vrba et al. 1995) and removed using software-based solutions (Taulu, Simola, and Kajola 2004)

BRAIN STIMULATION TECHNIQUES

TRANSCRANIAL MAGNETIC STIMULATION (TMS)

Transcranial magnetic stimulation (TMS) is a noninvasive method that uses a magnetic field to focally stimulate regions of the brain. To apply TMS, a stimulator coil, typically in the shape of an eight, is placed against the head above the brain area of interest. An electric current in the coil produces a magnetic field, which induces an electric current (neural activity) in the underlying neurons (Wassermann, Epstein, and Ziemann 2008). The TMS pulse is considered very precise due to its spatial resolution of a few millimeters and a temporal resolution of less than 1 millisecond, although the duration of the pulse effect can last longer (Walsh and Cowey 2000). Depending on the intensity of the TMS pulse (or the stimulator output), the stimulation can penetrate the brain up to a depth of 3 centimeters. In typical experiments an intensity just below (about 90%) the motor threshold (MT) is used (Sandrini, Umiltà, and Rusconi 2011). The motor threshold is the pulse intensity that successfully elicits a motor evoked potential (MEP), or visible twist of the fingers, on half of the testing trials when applied to the hand area of the brain. Although TMS is considered a noninvasive method, side effects due to contraction of the muscles, such as transient headache, local pain at the stimulated site and neck pain have been reported by a minority of subjects (Rossi et al. 2009).

Because of its spatial limitations, TMS research focuses on investigating functional processing of cortical areas that can be reached by the TMS pulse (Table 1). If a stimulated site is critical for a certain functional process, then TMS should influence performance on the task that is used to measure this process, which can vary from facilitating effects on performance to interference of performance, depending on the timing, type and frequency of stimulation.

The most frequently used types of stimulation protocols are single pulse TMS and repetitive TMS. Single-pulse TMS is commonly used to investigate the temporal dynamics of cognitive processing in a certain brain area, such as vision or attention. In this set-up, TMS is

applied “on-line”, which means that one pulse is delivered on each trial during the task at different stimulus onset synchronies (SOA’s) between the TMS pulse and the target to which participants have to respond. For example, in a seminal study by Amassian et al. (1989), single pulse TMS was applied to early visual cortex (V1) at different SOA’s after a briefly presented letter at fixation which participants had to identify (Amassian et al. 1989). Their study demonstrated visual suppression when the pulse was applied at 80ms and at 100ms after stimulus onset, but not at shorter or longer SOAs, clearly showing the time window in which V1 is essential for conscious visual processing.

Repetitive TMS (rTMS) is used to investigate if a certain brain area is involved in a cognitive process, such as memory or decision making. With rTMS, a train of repetitive pulses is applied to a brain region of interest to modulate the cortical excitability of that brain area. Typically, low frequency rTMS results in a decrease of cortical excitability, whereas high frequency rTMS can lead to both a decrease or an increase of cortical excitability depending on the protocol (see for reviews Kobayashi and Pascual-Leone 2003; Chung et al. 2016). Because the change in cortical excitability can last for 20 minutes, most often rTMS is applied “off-line”, which means that participants perform the task immediately after rTMS is administered. In order to decrease cortical excitability, two different rTMS protocols exist. The first protocol is low frequency stimulation, in which a brain area is stimulated at 1 Hz for 10 to 20 minutes. For example, in a study by Knoch et al. (2006), low frequency rTMS (1 Hz) was applied for 15 minutes to right or left dorsolateral prefrontal cortex (dlPFC) before participants performed a gambling task that measures decision making under risk (Knoch et al. 2006). The results showed that participants displayed increased risk taking after rTMS to right than to left dlPFC, suggesting the involvement of right dlPFC in inhibitory control of impulsive decision making.

The second protocol to decrease cortical excitability is continuous theta burst stimulation (cTBS), in which a brain area is stimulated with trains of 3 pulses at 50 Hz (20ms between each pulse) at a frequency of 5 Hz (i.e. trains repeated every 200 ms) for 40 seconds (200 bursts; see for review on cTBS by Chung et al. 2016). The application of cTBS has a clear advantage over rTMS: it is clearly faster (40 sec vs 10 to 20 min) than 1Hz rTMS stimulation, while delivering similar inhibitory effects (Nyffeler et al. 2006) and being considered just as safe as other rTMS protocols (Oberman et al. 2011). cTBS should therefore be the method of choice for future

neuroeconomic studies interested in investigating the causal role of cortical brain regions in the cognitive and emotional processes that support economic and social decision making.

A TYPICAL EXPERIMENTAL SETUP FOR TMS

In a basic set-up of a TMS experiment, a magnetic stimulator and a coil suffices. The stimulators vary in their capability of producing different types of waveforms (e.g., monophasic, biphasic and biphasic burst) and the speed of generating trains of multiple TMS pulses within a short time-window. There are two types of coils, a figure eight coil (butterfly coil) and a circular coil. The figure eight coil is most often used in cognitive neuroscience and allows for focal stimulation, but the penetration of the electric field is less than with a circular coil (see for specifics on stimulators and coils, (Wassermann, Epstein, and Ziemann 2008). One problem that arises in TMS studies is how to localize the area of interest on the scalp of the subject to which the TMS pulse is to be applied. Several methods have been developed that vary in their accuracy of targeting the underlying brain region. Regions can be identified: 1) based on overt behavioral changes (only applicable to motor or occipital cortex), 2) with the use of the EEG 10-20 system fabric cap (roughly indicating underlying brain areas), 3) with individual fMRI-guided TMS neuronavigation or, 4) with individual MRI-guided TMS neuronavigation. In the latter two cases, an additional neuronavigation system is required that utilizes an anatomical MRI scan of the subject's brain to visualize the location and direction of the TMS pulse (see for a comparison between methods 2-4 by Sack et al. 2009).

In order to establish whether the targeted brain area is indeed involved in the cognitive process that is measured, several control conditions can be added to the experimental condition. In single pulse experiments, different SOA's are used as control (Amassian et al. 1989), but most often a non-TMS or a sham TMS condition is added to the experimental condition. Sham TMS can be applied with a so-called sham coil or with the orientation of the coil tilted 90° to the head to the same brain area as in the experimental condition (to still produce an audible click without the neural effects). A non-TMS condition is sometimes replaced by stimulating the vertex, to control for unspecific TMS effects (sound, physical sensation, etc). In rTMS protocols, the control condition consists of stimulating a different site with the same TMS parameters as the site of interest, for example to investigate lateralization (Knoch et al. 2006).

APPLICATIONS RELEVANT FOR BEHAVIORAL ECONOMICS

To establish a causal role for a certain brain area in a behavioral process, converging evidence from a combination of TMS and other techniques is preferred. For example, in a recent sophisticated TMS study that investigated the causal role of the right temporal parietal junction (rTPJ) in strategic social behavior, a combination of computational modeling, fMRI and inhibitory cTBS was implemented (Hill et al. 2017). Half of the participants first received cTBS to rTPJ, the other half cTBS to the vertex. Subsequently, participants played the inspection game (Hampton, Bossaerts, and O'Doherty 2008) in the scanner while brain activity was measured. Behavioral results showed a difference in behavior between the two groups that was confirmed with the computational model. The control group showed behavior that demonstrated mentalizing about the strategy of the opponent, whereas the experimental group showed a lack of social insight in the opponent's behavior and how their own actions would influence the opponent's behavior. Moreover, with fMRI, Hill and colleagues were able to show that selectively disrupting neural processing in rTPJ causally affected neural processing in other parts of the brain associated with mentalizing, such as dorsomedial and ventromedial prefrontal cortex.

TRANSCRANIAL ELECTRONIC STIMULATION (TES)

Transcranial electric stimulation (tES) is used as a term for non-invasive brain stimulation techniques comprising transcranial direct current (tDCS), alternating current (tACS), and random noise (tRNS) stimulation (Paulus 2011). Unlike TMS, which uses a magnetic field to induce an electric current in the brain, tES utilizes a weak current directly flowing between two electrodes to impact neural processing. Typically, stimulation duration is between 5 and 30 minutes and experimental tasks are performed during stimulation "online", or after stimulation "offline", as the induced neural changes outlast the stimulation (up to 90 minutes; Paulus 2011). With tDCS, a constant stable current is flowing from one electrode to the other. Neural excitability of the targeted area is decreased with cathodal stimulation (V-) and increased with anodal stimulation (V+) (Nitsche and Paulus 2001; Hsu, Juan, and Tseng 2016). With tACS, an oscillating current within a specific frequency band is flowing between the electrodes to induce neural synchrony in oscillations (entrainment) between two areas (Thut and Miniussi 2009; Feurra 2012). Consequently, brain oscillations of a specific frequency can be causally linked to a specific cognitive process. With tRNS, an alternating current at random frequencies (from 0.1 Hz to 640 Hz) is applied to increase cortical excitability. The latter technique is fairly new and has been

applied relatively little to date, but several studies show effects specifically on learning, for example perceptual or motor learning (Kuo and Nitsche 2012).

A TYPICAL EXPERIMENTAL SETUP FOR TES

The basic set-up of studies using tES to manipulate brain function consists of a portable battery-driven stimulator with a maximum output in the milliampere range. The technique safely delivers electric current to the scalp via two electrodes. The electrodes consist of either metal or conductive-rubber electrodes in a perforated sponge pocket which is saturated with electrolytes or conductive gel. In order to localize the area of interest, the EEG 10/20 system is commonly used as outlined for EEG and TMS above. A rubber band is used to fixate the electrodes above a brain region of interest on the scalp of the subject. Almost all stimulators include a feature to automatically ramp current on and off, which is advised for the comfort of participants. Moreover, the ramping on of the current is often used as a control (sham) condition, in which the stimulation is switched off after about 30 seconds. Common control conditions in tDCS include, in addition to a sham condition, the stimulation of other brain areas, unilateral versus bilateral stimulation, or stimulation using the opposite polarity, while in tACS an additional frequency or phase that differs from the experimental frequency is preferentially used as a control.

APPLICATIONS RELEVANT FOR BEHAVIORAL ECONOMICS

To establish the causal role of the dlPFC in risk taking behavior, Fecteau et al. (2007) compared the behavioral effects of bilateral tDCS stimulation, with cathodal stimulation over the right and anodal stimulation over left dlPFC (and vice versa), relative to sham, as well as unilateral stimulation over the right or left dlPFC (Fecteau et al. 2007). After 5 minutes of stimulation (which continued during the task) participants were asked to perform the Balloon Analog Risk Task (BART) as a measure of risk taking behavior. The results showed that increasing cortical excitability of either the left or right dlPFC induced a risk averse response style (see also Fecteau et al. 2007; Ye et al. 2015). Using the related methodology of alternating current stimulation, two recent studies demonstrate the importance of oscillatory activity between different brain regions. (Sela, Kilim, and Lavidor 2012) demonstrated a differential effect of left compared to right alternating current stimulation of dlPFC on risky decision making. Specifically, while performing the BART task participants received theta-band tACS to either the left or the right dlPFC. The results showed that AC stimulation of the left dlPFC increased risky choice behavior relative to

right and sham stimulation, demonstrating that the theta-band oscillatory balance between left and right hemispheres is causally involved in risky decision making. Besides inducing neural synchrony in oscillations, tACS can also be used to induce desynchronization. Polanía et al. (Polanía et al. 2015) applied anti-phase tACS to desynchronize oscillation within the fronto-parietal circuit in the gamma band, which is known to be correlated with value-based decision making (Polanía et al. 2014). During stimulation, participants made perceptual or value-based choices between two food stimuli. Results showed that desynchronizing gamma band activity between frontopolar and parietal cortex resulted in inaccurate decisions concerning the value of food items, while leaving matched perceptual decisions unaffected. Moreover, computational modeling revealed that desynchronization caused inconsistent preferences on a trial-by trial basis, while the average preference across trials remained stable. The authors concluded that accurate value-based decisions critically involve synchronized activity in the gamma band between frontal and parietal brain areas.

CONCLUSION

Neuroeconomists have a large number of neuroscientific tools at their disposal with which to measure and manipulate neural activity. Due to space limitations, the above discussion of research methods was far from exhaustive and did not include important, but more intrusive research methods that are more commonly employed with animals making economic choices. Such methods include microstimulation, as well as single- and multi-cell recordings (Schultz, Dayan, and Montague 1997; Kalenscher et al. 2005). These studies have yielded important insights about brain-behavior relationships by demonstrating the presence of evidence accumulation mechanisms in higher-order visual regions (Britten et al. 1996) and the firing patterns of dopamine-rich neurons that support learning (Schultz, Dayan, and Montague 1997; Tobler et al. 2005). Moreover, lesion studies in human participants have yielded important insights about the causal role of the prefrontal cortex in economic decision-making (Bechara and Damasio 2005; Krajbich et al. 2009), and findings from pharmacological studies stress the important role of neuromodulators in social decision-making (Crockett et al. 2008; De Dreu et al. 2010). Recent advances in neuroscience methods, such as optogenetics (Deisseroth 2011), show that ongoing developments of novel neuroscientific techniques open potential avenues for future ways to measure and manipulate brain

activity in the context of experimental tasks that are relevant for neuroeconomics (Zalocusky et al. 2016).

While each of the methods outlined above suffer from limitations (Table 1), the converging evidence acquired by multiple methods can strengthen conclusions about the neural mechanisms involved in the underlying cognitions and emotions that support economic decision-making (see also Kable 2011). One promising avenue is to combine multiple methods with complementary strengths and weaknesses in the same subject. Two methods that have been gaining prominence in the recent past are simultaneous EEG-fMRI (Huster et al. 2012) and concurrent TMS-fMRI (Bestmann et al. 2008; Ruff, Driver, and Bestmann 2009). How such approaches can counteract the limitations of each method can easily be demonstrated via the example of joint EEG-fMRI: with its limited temporal resolution, fMRI cannot identify the order within which neural activations occur (Logothetis 2008), while, as outlined above, the inverse problem prevents accurate source localization in EEG. Integrating simultaneously recorded EEG-fMRI improves both spatial and temporal resolution and has the potential for insights above and beyond those garnered from separate recordings (Huster et al. 2012). Similar arguments have been made for concurrent TMS-fMRI (Bestmann et al. 2008; Ruff, Driver, and Bestmann 2009).

Finally, as briefly discussed above, most recent neuroeconomic studies rely on model-based fMRI (O'Doherty, Hampton, and Kim 2007; Gläscher and O'Doherty 2010). This approach combines the strength of fMRI with computational modeling, whose parameters provide specific estimates of subjective value on a trial-by-trial basis. Model parameters can then be employed to make systematic predictions about the magnitude of the BOLD response to identify regions that correlate with model parameters of interest. This method has proven particularly fruitful in the domain of reinforcement learning, which offers a class of computational models that update subjective value based on comparisons between the expected and actual value on a trial-by-trial basis (Gläscher and O'Doherty 2010).

Economic decisions are fundamentally linked to our biology and have the function to improve our health and wellbeing (Montague and Berns 2002; R. P. Montague, Hyman, and Cohen 2004). It is therefore essential to understand and investigate the biological mechanisms underlying economic decision-making. Using the methodologies outlined above, neuroeconomics can continue to develop new hypotheses that are relevant for economics (e.g. Clithero, Tankersley, and

Huettel 2008), with the ultimate goal to provide mechanistic explanations about how neural processes give rise to the cognitive and emotional mechanisms that support economic decision-making. This, in turn, will pave the way for neurobiologically plausible economic theories of human decision-making that take into account the state of current neuroscientific knowledge.

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