Monkey Subjects in Neuroeconomics: A Utilitarian Assessment

Master's Thesis

Thomas MIOTTO

Supervisor: Jack Vromen

Advisor: William Peden

Erasmus Institute for Philosophy and Economics

Erasmus School of Philosophy

Erasmus University Rotterdam 2021-2022

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Introduction

The use of animals in science has always been quite common in the history of scientific research. Economics is no exception to this tradition. The proof being that, in the seventies and eighties, certain researchers such as Kohn Kagel, Raymond Battalio, and Leonard Greene had already become quite popular after having conducted different experiments to study economic behaviour in animals (Kagel & al., 1975, 1981; Battalio & al., 1981, 1985). The results obtained – mainly in rats – were then compiled and published in a book wherein their conformity to and their deviation from popular economic theories was discussed (Kagel & al., 1995). Since their time, this field of inquiry widened to include species as diverse as bees (Shafir, 1994), frogs (Lea & al., 2015), parrots (Krasheninnikova & al., 2018), and even unicellular organisms (Latty & al., 2010). Among all of that, however, it is the study of non-human primates (McGonigle & Chalmers, 1992) which proved particularly relevant to probe the foundations of human rationality and economic behaviour (Chen & al., 2006).

This observation seemingly maintained its validity when a new strand of economic research quickly emerged to push things even further: neuroeconomics. As the name suggests, neuroeconomics is an offshoot of neurosciences. It seeks to explore the neurobiological processes responsible for economic decision-making (Glimcher & Rustichini, 2004). To do so, neuroeconomists heavily rely on neuroscientific tools and methodologies. Such tools and methodologies include the invasive study of the brains of animals *in vivo*. With the coming of neuroeconomics, therefore, the status of non-human primates in economic research changed. It shifted from subjects merely having their behaviour observed to subjects having their brains closely examined and tinkered with. This can raise moral concerns aligning with contemporary preoccupations about the use of animals in laboratories.

One book, in particular, greatly contributed to install the use of animals in labs as a significant moral issue not only for philosophers but for the general public as well. This book is Peter Singer's *Animal Liberation*, first published in 1975. In it, the author opts for a utilitarian perspective to interrogate our relationship with animals. In the second chapter, Singer turns to the issue of animal experimentation and makes the claim that, most of the time, animal subjects have to go through a great deal of pain to obtain a type of knowledge whose relevance is doubtful or simply not worth the suffering induced. In this thesis, I aim to confront the use of monkeys in neuroeconomics to this claim. More particularly, I wish to provide an answer to the following question: Is resorting to non-human primates for neuroeconomic purposes morally warranted from a utilitarian perspective?

Although I am fully aware that it is difficult to establish clear boundaries between all the subdisciplines of neuroscience, I shall attempt to maintain the focus of this thesis by only discussing the type of research conducted on monkeys which (1) provides a study of the brain while (2) making direct references to concepts/situations/phenomena which are of importance for the economic theory of decision-making. That being said, I will structure the present work as follows. Chapter 1 proposes an overview of the type of neuroeconomic research conducted on monkeys and of the reasons evoked to justify the utilization of non-human primates as subjects. Chapter 2 will present the utilitarian framework which will serve as a basis for the ethical assessment of the use of monkeys in neuroeconomics. With the theory introduced, I will then proceed towards the investigation of the harms associated with experimenting on monkeys in Chapter 3, and of the benefits we can possibly expect from this strand of research in Chapter 4. Chapter 5, finally, will put the knowledge derived from the two previous chapters together and reflects on whether or not experimenting on monkeys for neuroeconomic purposes can withstand an ethical assessment based on the utilitarian framework spelled out in the second chapter.

Chapter 1: Neuroeconomics and Monkey Experiments

The very first chapter of this thesis will be devoted to introducing the use of monkeys in neuroeconomics. More accurately, I seek to offer a literature review in order to make two things clear. Firstly, I want to highlight the reasons behind the recourse to monkeys as subjects for neuroeconomic experiments. Secondly, I want to identify the type of experiments monkeys are involved in and the ends they are used to pursue. But before delving into the why and the what of monkey experimentation for neuroeconomic purposes let me first say a little more concerning neuroeconomics as a whole.

1.1. Neuroeconomics: a neuroscientific approach to economics

Neuroeconomics is a very ambitious discipline. It seeks a better – and perhaps even a total – understanding of decision making. It is the convergence of economics, psychology, and neuroscience into "a single, unified discipline with the ultimate aim of providing a single, general theory of human behaviour" (Glimcher & Rustichini, 2004). Neuroeconomists aim at opening the 'black-box' of the brain in a manner similar to organizational economists opening up the black box of the firm. While economics and psychology are already offering rich conceptual tools for modelling and understanding behaviour, neuroscience provides tools to investigate the neuronal connections responsible for it. Neuroeconomics then takes advantage of both worlds by utilizing knowledge obtained from the study of brain mechanisms to inform economic theory. As such, it is to be differentiated from behavioural economics.

Behavioural economics is a subdiscipline of economics incorporating more psychologically realistic assumptions to increase the explanatory and predictive power of economic theory. Neuroeconomics goes further than this. Indeed, it relies on the use of neuroscientific methods to understand the interplay between economic behaviour and neurobiological processes. Those methods include first and foremost psychophysical measurement, brain imaging, single-neuron measurement, and electrical brain stimulation. Brain imaging is by far the most popular. It is rendered possible thanks to Electro-encephalography (EEG), Magnetoencephalography (MEG), Transcranial Magnetic Stimulation (TMS), Positron Emission Topography (PET) and of course functional Magnetic Resonance Imaging (fMRI). Psychophysical measurement is also very common and consists in keeping an eye on certain indicators or bodily reactions. One can think of blood pressure, galvanic skin response (sweating in the palms) or pupil movement and dilatation. As diverse as those methods might be they are employed in a similar fashion. In effect, the point is to study the brain of subjects *in vivo* – and when need be other related bodily functions – while they are performing certain tasks associated with the economic theory of decision-making. A good and concrete example of the this can be found in the early history of the discipline. That is, in the first set of scientific papers that can be associated with neuroeconomic research.

In 1996, Shizgal and Conover published a scientific article entitled "On the neural computation of Utility". In it, the authors sought to describe the neurobiological substrate for choice in rats using a normative economic framework through electrical brain stimulation. With their setting, they identified the role played by lateral hypothalamic stimulation in how the computation of utility is implemented in the brain. A few years later, Paul Glimcher and Michael Platt (1999) experimented on monkeys by making them perform visual gambling tasks. Briefly, monkeys had to choose between different options leading to various ambiguous fruit juice rewards. The authors demonstrated, thanks to single-neuron measurement and eye tracking devices, that the activity of individual neurons in the posterior parietal cortex seemed to be involved in the perception of a reward's magnitude as well as that of its matching probability. Both notions are central for the theory of expected utility.

In the early 2000's, the first neuroeconomic studies in humans appeared. Breiter & al. (2001) set up an experiment to test Kahneman and Tversky's well-known Prospect Theory. In their article, subjects were asked to play a lottery in which the perceived desirability of a particular outcome was manipulated by changing the values of two other possible outcomes. The data gathered with fMRI scans revealed that brain activation in the ventral striatum appeared to match the type of subjective valuations predicted by the theory. The same year, brain imaging was also employed in what is often presented as the first use of game theory in a human neurobiological experiment (McCabe & al., 2001). In that paper, subjects played a trust game either against an anonymous human opponent or against a computer. The neurobiological data revealed that in subjects willing to cooperate the medial prefrontal cortex was more active when they played a human than when they played the computer.

Since its emergence twenty years ago, the neuroeconomic field bloomed. Nowadays, neuroeconomic research is being carried out to investigate every aspect of economic decision-making. Neuroeconomists set sail on a quest to provide biological explanations regarding how the human brain interacts with its environment to produce economic behaviour. Their investigation stretches from individual decision making to collective choices, from the study of compulsive consumption to that of intertemporal planning, and from decisions under risk to situations of uncertainty.

1.2. Why are monkeys privileged subjects in neuroeconomics?

Truth be told, the majority of neuroeconomic experiments was – and still is – being performed in humans with the help of brain imagery techniques. Yet, the recourse to animal subjects upon which the discipline was built did not disappear. Quite the contrary, experimenting on monkeys for neuroeconomic purposes has always been quite common. To be more precise, when neuroscientists of all kinds – including neuroeconomists – talk about experiments involving 'monkeys' they usually refer to one genus of monkeys in particular. Although one can find important studies resorting to marmoset monkeys (Dias & al., 1996, 1997) or more recently capuchin monkeys (Lakshminarayanan & al., 2011, De Petrillo & al., 2017), it is the genus *Macaca*, or macaques in less scientific terms, which is typically used in neurophysiological studies of decision-making. Among this genus one species, the rhesus macaque (*Macaca Mulatta*) as seen in figure 1, represents the most widely used neurophysiological model species.

At this stage, the question of interest for us right now is why? Why is it that such monkeys are privileged subjects for brain experiments? A first answer to that is purely practical. Macaques are the most widely distributed genus of primates on the planet – excluding the genus

Homo of course – and this makes them a very flexible group of species. As a result of their adaptability, macaques are said to live well in captivity compared to other primates. Moreover, their relative abundance makes them more available and affordable to researchers than, say, any of the great apes. But beyond purely practical concerns there is also another set of reasons backing up the use of macaques – and certain other species of non-human primates for all that matter – in neurosciences including neuroeconomics. Those are (1) the similarities between their brains and ours, (2) invasive yet more precise methods can be used on them, and (3) they bring us evolutionary insights.

Figure 1. Mother rhesus macaque with her baby. © Davidvraju.

1.2.1. "Similar" brains

Macaques are our closest biological relatives after the great apes and before the capuchins. Even though they branched off from the human line roughly 25 million years ago, the evolutionary vicinity we share nonetheless granted them with a brain and an overall physiology akin to ours in many ways. Indeed, sharing most of the genetic background, macaques own many distinctive similarities with humans in terms of problem-solving abilities, anatomy, development, social complexity, and cognitive capabilities (Perretta, 2009).

The human brain is, unsurprisingly, highly complex and developed. This level of development can be readily observed when considering its size, neuronal density, as well as the number of its synaptic connexions. Far from being as complex, the macaque brain represents nevertheless a satisfactory proxy. It is indeed fairly developed compared to what can be found in the rest of the animal kingdom and possesses many of the areas present in the human brain, albeit in a more rudimentary form. For instance, although the brain size of a rhesus macaque is approximately 15 times smaller than that of a human being, it is still more than 750 larger than that of a rat, another animal widely used in laboratories for experiments in neuroscience. In addition to that, the macaque brain seems to be structured around many different regions organized in a highly complex way, very much, in fact, like the human brain (Fellerman & al., 1991; Young, 1993; Parvizi & al., 2006).

Non-human primates are notably known to have a central nervous system and a neural circuit organisation that most resemble those of humans. Macaques, of course, are no exception. Actually, similarities between the macaque brain and the human brain can be found in the structure of the cortical mantle (Chiavaras et al., 2000), in the fact that both exhibit a considerable expansion and sub-divisions of the neocortex (Lewis et al., 2000), in similar patterns of neural activities, and, importantly, in an enlarged frontal lobe which is roughly similarly built (Mackey & Petrides, 2010; Sallet & al., 2013; Neubert & al., 2014, 2015). The frontal lobe is an area of great interest for neuroeconomists because this large part of the brain – situated just above and behind the eyes – is known to be largely implicated in executive functions. Yet, executive functions play a decisive role in behaviour including, among other things, decision-making-related abilities such as planning, memory, or the prediction of outcomes. On another note, both species share large forward-facing eyes associated with complex visual behaviour. This translates into comparable specialised areas in the brain devoted to different aspects of vision such as colour (Gegenfurtner, 2003; Conway & al., 2006), motion (Newsome & al., 1986), or focal visual attention (Treue, 2001; Shipp, 2004).

In the end, those findings point towards the same direction. They corroborate the already widely accepted view that macaque brains are good enough estimates for certain human neurobiological processes. In other words, laboratory monkeys can be utilized as satisfactory neurobiological model for human-choice. It is this state of affairs that is mostly invoked to justify the use of macaque in neurosciences, including neuroeconomics, and the generalization of some results from one species to the other.

1.2.2. Subjects of invasive yet more precise methods

In addition to their developed brains, macaques are experimented on because they are eligible to a type of methods whose use would be highly controversial on humans. In particular, monkey studies employ brain measurement technologies that are particularly invasive. Such technologies are referred to as 'single-unit recording' or 'single-neuron measurement techniques'. They permit researchers to have access to highly precise results that would be inaccessible otherwise.

In neurosciences, the precision of a method is a two-dimension variable. It is a matter of temporal resolution and of spatial resolution. Temporal resolution refers to the frequency in time with which measurements or manipulations can be made. This time frequency can stretch from milliseconds to hours. Spatial resolution refers to the ability to distinguish, when a measurement is made, adjacent brain regions that differ in functions. Spatial resolution can range from micrometres to the entire brain. Figure 2 plots the repartition of the most common neuroscientific techniques according to both their temporal and spatial resolutions (Ruff & Huettel, 2014). It highlights that single-unit recording possesses a remarkable spatial resolution. It operates at the scale of the neuron itself, between 10 and 100 micrometres. The plot also more largely demonstrates that methods to gather data from human participants tend to operate at relatively coarser spatial scales than those that record from non-human animals.

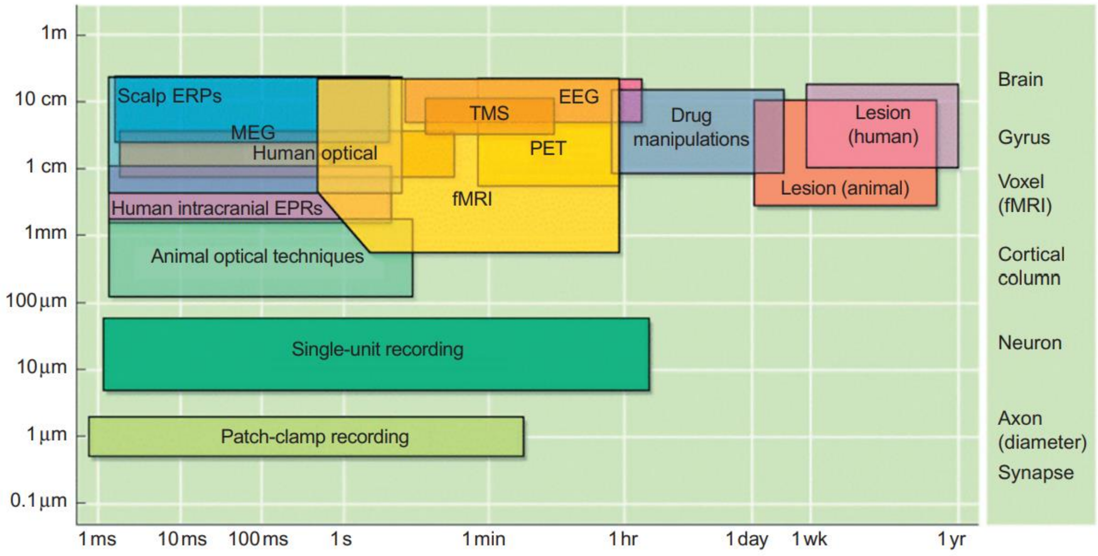

Figure 2. Common techniques in cognitive neuroscience. Vertical axes illustrate spatial resolution in terms of distance (left) and the corresponding brain structures (right). The horizontal axis illustrates temporal resolution.

The main distinction between the methods that can be utilized on human subjects and those that are – exceptional cases put aside – reserved to non-human animals resides, as alluded to earlier, in their invasiveness. A specific recording or measuring technique is considered non-invasive if it can operate without damaging or disrupting the brain. Non-invasive techniques record endogenous brain signals using sensors outside the body. One can think of EEG, MEG, or fMRI. Invasive techniques, conversely, violate this condition. They revolve around the introduction of a chemical or a recording device directly within the brain of the subject. This is precisely what single-unit recording is all about.

Single-unit recording is performed by inserting very fine electrodes – usually composed of a metal wire that is sensitive to relatively high-frequency electrical signals, surrounded by a protective insulating sheath – into the neural tissue immediately adjacent to the neurons of interest. As the manual targeting of precise neurons can be very tedious in non-human primates because of their size and organisation, researchers usually first install high-precision microdrives on the surface of the skull to help them. Once done, they proceed to slowly lower electrodes into a brain region of interest. When the electrodes are properly positioned for the purposes of the researchers, the experiment can begin. In the end, the firing of either single neurons or the activation of several of them in close vicinity will be correlated with whatever task was performed by the subject during the experiment in question. In addition to recording electrical activity from small groups of neurons, the microelectrodes inserted into the brains of non-human primates can also be employed for inducing it. Doing so is commonly referred to as ‘microstimulation’ and involves the transmission of weak electric current to activate neurons in the proximity of the electrodes.

All in all, when standard brain imagery techniques share a similar temporal resolution with single-unit recording, the latter reaches a level of spatial precision almost unrivalled. The use of invasive methods on macaques thereby allows scientists to detect which neurons or small populations of them are activated in response to the experimental setting. From a neuroeconomic perspective, researchers have access to extremely precise data regarding which parts of the brain are involved in economic reasoning. This data would be inaccessible with the standard methods used on human subjects.

1.2.3. Bringers of evolutionary insights

A last reason for the use of monkey subjects in neuroeconomics concerns what it can teach us about human decision-making from an evolutionary perspective. Indeed, one of the main objectives of neuroeconomics is to understand the neural processes underlying the choices that people make. Yet, human decision-making is complex and relies on several mechanisms. Some are rational, some are not. What studies on animals – especially monkeys – can provide is a better understanding of those mechanisms by solving the question of their origin. Where are systematic decision biases and irrational tendencies coming from? Are our irrational decision-making strategies the result of learning over the course of a lifetime of decisions? Do these biased strategies result from specific environmental experiences or contexts? Or could these decision-making strategies be more universal, perhaps resulting from mechanisms that arose over evolution and operate regardless of context or experience?

Santos & Platt (2014) argue that comparative studies with primates such as macaques provide significant tools for answering such questions. It can offer unique insights regarding the origin of human decision-making strategies and help us determine whether our biases are shared by our closest evolutionary relatives. This, in turn, can inform us about how decision-making processes and their flaws arose in the first place. Such knowledge can simply not be accessed by focusing solely on human brains. Macaques and other monkeys do not possess human-like market experience, cultural training, and economic teaching. As a consequence, any cognitive mechanism which is present in both humans and non-human primates is likely to have an evolutionary origin independent of economic or cultural experiences which are unique to human decision-makers. This seems to be the case, for instance, when it comes to framing and context effects which bias the decisions of monkeys and humans alike (Chen & al., 2006; Lakshminaryanan & al., 2008, 2011) or when it comes to exhibiting an eversion towards ambiguous situations (Hayden & al., 2010).

For Kalenscher & Van Wingerden (2011) this type of knowledge is requisite for a complete understanding of human decision-making. For them, neither pure theoretical reasoning nor exclusive experimentation with human subjects will be sufficient to obtain a comprehensive picture of how humans make choices; a picture including situations where human beings abide by the principles of rationality but also where and why they violate them. The authors claim, in line with Santos & Platt (2014), that in order to understand not only how we make decisions but also to investigate why our decisions are what they are, it is imperative to know the reserve constraints, evolutionary pressures, and adaptive benefits that moulded the choice behaviour in the first place. As they write themselves: “the prime way to obtain access to the evolutionary pressures shaping our decision mechanisms and to identify common denominators in choice behaviour is to study animal behaviour and its neural mechanisms” (Kalenscher & Van Wingerden, 2011, p.7).

1.3. To what ends are monkeys used in neuroeconomics?

Now that I have reviewed the reasons why monkeys are privileged subjects in neuroeconomics, it is time to turn to what they are used for exactly. As I mentioned earlier, the neuroeconomic research agenda quickly expanded to every dimension of economic decision-making. This appears to be the case for monkey experimentation as well. Indeed, monkeys were used to pursue investigations pertaining to any dimension of neuroeconomics. As it would be impossible to cover everything in detail, I will just focus on the three main domains that can be distinguished in neuroeconomics (Loewenstein & al., 2008). They are (1) decision-making under risk and uncertainty, (2) Valuation and intertemporal choice, and (3) game theory and social decision-making. In what follows I will mention, for each of those domains, a few research articles based on the use of non-human primates in order to give the reader a good idea of the type of results we can derive from experimenting on them.

1.3.1. Decision-making under risk and uncertainty

The extensive economic research on decision making under risk or uncertainty leaves unanswered the question of which brain mechanisms underlie these behavioural phenomena. A first piece of evidence regarding what such mechanisms might be was, it seems, provided by Fiorillo & al. (2003). The authors conditioned two monkeys with distinct visual stimuli indicating the probability of a liquid reward being delivered. They then proceeded to record the activity of groups of dopamine neurons in ventral midbrain areas while the subjects were choosing between different visual targets. The researchers observed that, although dopamine neurons showed little or no response to fully predicted reward, they displayed typical activations when reward was delivered in an uncertain manner. What is more, the magnitude of the reward responses increased as the probability decreased. This result, as the authors concluded, appears to support the claim that dopamine neurons have a possible role in the coding of uncertainty within the brain. A similar methodology based on saccadic eye movements and bar-like visual cues was employed by Hayden & al. (2011). The twist of the experiment, however, resides the introduction of surprise. From time to time, the reward obtained would differ – it would either be surprisingly large or surprisingly small – compared to what the visual cue suggested. Hayden & al. found that neuronal responses in dorsal anterior cingulate cortex (dACC) were enhanced whenever the outcome was surprising. This finding suggests the possible implication of dACC in the perception of uncertainty. On another note, more recent studies provided evidence that the coding of uncertain rewards was also partly operated in deeper areas of the brain such as the septal area (Monosov & Hikosaka, 2013) and the striatum (White & Monosov, 2016).

In a well-known experiment, McCoy & Platt (2005) studied subjective risk preferences using two adult male rhesus macaques. The monkeys were once again presented two visual targets among which they were able to choose by shifting their gaze. Staring at the “certain” target led to a constant juice reward while staring at the “uncertain” target led to two potential outcomes with a 50/50 chance. McCoy & Platt showed that, overall, both monkeys preferred the risky targets. What is more, the frequency of choosing them increased systematically with the degree of risk. Examining the monkeys' brains with single-unit recording methods, the authors observed that neuronal activity in posterior cingulate cortex (CGp) increased with the making of risky choices and was scaled with the degree of risk. This result suggests that neuronal activity in CGp reflects subjective risk preferences and demonstrates a direct relationship between subjective preferences for uncertain rewards, or the opportunity to harvest a relatively large reward, and the activity of neurons thought to participate in the allocation of attention. O'Neill & Schultz (2010) pursued the investigation of risk-taking in macaques in an experiment where the visual cues presented to the animals were bars whose positions on the screen reflected the magnitude of the juice reward to be obtained as well as the level of risk associated with it. While the monkeys were choosing, the activity of single orbitofrontal neurons was recorded. Remarkably, and in consistence with results obtained previously, the authors observed that monkeys preferred risky options over safe ones. Their main finding, however, was that a group of orbitofrontal neurons coded information about reward risk and that a minority of such risk-sensitive neurons also seemed to encode reward value.

1.3.2. Valuation and intertemporal choice

Theoretically, decision-makers are said to integrate the various dimensions of an option into a unique measure of subjective value before choosing the option that is most valuable to them. In fact, comparisons between different kinds of options are systematically said to rely on this abstract measure of subjective value, a kind of "common currency" for choice, and important results were obtained in monkeys giving us a better understanding of how a common scale for subjective value might be encoded in the brain (Kable & Glimcher, 2009).

A first set of studies, in particular, has documented the role of neurons in the orbitofrontal cortex (OFC) in encoding the subjective economic values of different rewards. In a widely-cited study, Padoa-Schioppa & Assad (2006) recorded neuronal activity in the OFC while macaque monkeys had to choose between pairs of juices. Based on the actual choices of each monkey, the authors calculated a subjective value for each juice reward which could explain these choices in a common value scale. With this setting, they found three dominant patterns of neuronal responses: *offer value neurons* whose firing is correlated with the subjective value of one of the rewards, *chosen value neurons* which tracked the subjective value of the chosen reward independently of the type of juice, and *taste neurons* that showed a categorical response when a particular juice was chosen. According to the researchers, offer value signals could be very much analogous to "utilities" in economic terms. That is, they resemble the kind of value representation posited by most decision theories. Such results were consolidated by the authors themselves in a follow-up study (Padoa-Schioppa & Assad, 2008), and the role that the orbitofrontal cortex seems to play in valuation more generally is still being stressed nowadays on monkey subjects (Yamada & al., 2018; Setogawa & al., 2019).

Beside the orbitofrontal cortex, a second set of studies revealed that the striatum is another area which plays a role in the representation of the subjective value of choice options. Recording from physically active striatal neurons, Lau & Glimcher (2008) found three kinds of task-related neuronal responses closely related to the orbitofrontal signals of Padoa-Schioppa and Assad (2006). Indeed, the authors were able to similarly discriminate between offer value neurons, chosen value neurons, and taste neurons. Those results were consistent with what had been found three years earlier by Samejima & al. (2005) in an experiment wherein monkey were trained to perform a manual choice task. They had to turn a lever leftward or rightward to obtain rewards. Recording from the putamen, the researchers found that one-third of all modulated neurons tracked action value. Similar to OFC, the implication of the striatum in encoding subjective valuation appears to be robust as it was observed times and times again (Seo & al., 2012; Burton & al., 2015; Kang & al., 2021).

A point which is also important to mention while discussing valuation is the importance of time. Indeed, instant rewards are usually given a subjective value differing from that of rewards with the same magnitude obtained later on. This state of affairs is commonly referred to as 'time-discounting'. Time-discounting has been widely explored behaviourally in non-human primates (Hayden & Platt, 2007; Pearson & al., 2010; Hwang & al., 2009; Hayden, 2016) but there also exists a handful of studies linking neuronal activity to the value of future rewards in monkeys. Roesch & Olson (2005), for instance, recorded the firing of neurons in the orbitofrontal cortex of two rhesus macaques performing a visual task. Cues presented before each trial predicted whether the delay before the animal could respond and receive a reward of fixed size would be short or long. In the end, the authors found that a cue predicting a short delay was commonly associated with a stronger neuronal response. Moreover, neurons activating more strongly in response to a short-delay cue also tended to fire more strongly in response to a cue affiliated with a big reward. Those results seem to highlight the role of OFC in discounting future rewards which had been intuited a few years prior (Hikosaka & Watanabe, 2000). Kobayashi & Schultz (2008), on their own, showed that reward delay influenced both intertemporal choice behaviour and the responses of dopamine neurons. Firstly, behavioural measures showed that the kind of discounting the monkeys resorted to was hyperbolic. Secondly, the responses of dopamine neurons to the conditioned stimuli decreased with longer delays at a rate similar to behavioural discounting. In contrast, the dopamine response to the reward itself increased with longer delays. For the authors, these results suggest that neuronal dopamine responses reflect the subjective reward value discounted by delays and thus may provide useful inputs to neural mechanisms involved in intertemporal choices. Similar findings were obtained by Fiorillo & al., (2008) who also observed high sensitivity of dopamine neurons to the duration of a stimulus-reward interval.

1.3.3. Game theory and social decision-making

Decision-making is not limited to how isolated individuals make choices. On numerous occasions, individuals need to interact with one another and take the behaviour of other individuals into account while acting. From an economic perspective, the study of social-decision making is usually effectuated in the context of game theory. Over the past two decades, the development of neuroeconomics led researchers to develop a growing interest regarding the neurophysiological processes involved in social interactions.

A good example of this lies in the participation of monkeys in simple and zero-sum games such as matching pennies (Lee & al., 2004). In the matching pennies game, two players are individually asked to choose between two alternatives. One of the players, the "matcher", wins if the choices of the two players match and loses otherwise. In Barraclough & al. (2004), monkeys played this game against a computer by having to choose between two visual targets:

one on the right and one on the left. Recording brain activity, the authors noticed that neurons in the dorsolateral prefrontal cortex and anterior cingulate cortex fired at critical times suggesting an encoding of the animal's past decisions and payoffs, as well as the conjunction between the two. They, therefore, concluded that those areas might have a key role in encoding and optimizing decision-making strategies. This was consolidated in later years (Seo & Lee 2007). In a similar vein, Thevarajah & al. (2009, 2010) revealed that neuronal activity in the superior colliculus – a part of the midbrain – was also important for strategic behaviour as it appears to be shaped by both previous and upcoming choices and rewards.

Along with matching pennies games, rock-paper-scissors games are another typical example of simple experimental setting used in game theory with monkeys (Lee & al., 2005). Abe & Lee (2011), for instance, trained three macaques to perform a computer-simulated rock-paper-scissors game task. Juice rewards were scaled on how well the chosen option fared against the one picked by the computer and, after each game, the animal received visual information regarding the outcome of his choice as well as concerning the hypothetical outcomes that he could have received from the other two unchosen targets. This setting allowed the researchers to show that across multiple trials the monkeys adjusted their choice behaviour according to both actual and hypothetical outcomes from their chosen and unchosen actions. The recording of brain activity demonstrated that, once again, neurons in dorsolateral prefrontal cortex and orbitofrontal cortex are important in the coding of strategic choices as they were seemingly responsible for this adaptation. Indeed, they activated immediately after the signals related to actual and hypothetical outcomes were revealed to the animal.

Another type of game performed by monkeys in the neuroeconomic literature which is worth mentioning is the inspection game. Briefly, the experimental subject has to choose between a certain and a risky option while the opponent selects between 'inspect' and 'not inspect' with a given cost associated to the former. For the subject, the certain target leads to the same payoff irrespective of what the opponent does. The risky target, however, delivers a reward twice as big as the certain target if the opponent does not inspect but nothing if they do. Dorris & Glimcher (2004) examined the activity of neurons in the posterior parietal cortex of monkeys playing the inspection game against a computer. The authors found neurons that carried a signal behaving like relative expected utility. In fact, neuronal activity in posterior parietal cortex was correlated with the relative subjective desirability of an action. That is, the way monkeys subjectively perceived both the certain and the risky target. In other words, Dorris & Glimcher identified a neurobiological process responsible for the valuation of options in a strategic context. In a situation where the payoffs obtained by different courses of action are intertwined with and dependent on what another person – here mimicked by a computer – seeks to do.

1.4. Conclusion of Chapter 1

Experiments on monkeys – rhesus macaques first and foremost – are far from being uncommon in neuroeconomics. Although the use of brain imagery in humans remains the standard procedure, monkeys are often experimented on to obtain results that would have been inaccessible otherwise. On the one hand, they permit researchers to utilize recording techniques possessing an unmatched precision to measure the activity of single neurons. On the other hand, they give us insights regarding the evolutionary roots of human decision-making and economic behaviour. Those two advantages combined contributed to making the macaque brain a popular neurophysiological model species for the study of economic decision-making. This explains why it is used in a wide array of neuroeconomic studies including decision-making under risk and uncertainty, valuation and intertemporal choice, and even game theory. Yet, this widespread use of monkeys in neuroeconomic experiments can raise moral considerations. In the end, invasive neuronal recording methods are employed on highly sentient and social beings. Chapter 2 of this thesis, to which we now turn, seeks to present an ethical framework to evaluate the morality of monkey experimentations in neuroeconomics from a utilitarian standpoint.

Chapter 2: The Utilitarian Framework

The present chapter will be dedicated to building the theoretical backbone of this thesis. More accurately, I will detail the theoretical framework I deem appropriate to investigate the morality of resorting to monkey subjects for neuroeconomic experiments. Once done, I then wish to discuss two of its important implications. As the utilitarian perspective is the one I shall embrace I want to start, however, by briefly mentioning the intuition shared by forefathers of this line of thought regarding non-human animals. Their insights will logically lead us to the description of the utilitarian framework to be used.

2.1. Early utilitarians and animals

Utilitarianism is a type of moral philosophy pioneered by Jeremy Bentham in the early nineteenth century. After his passing, it was notably endorsed and refined by two famous thinkers who would also leave an important mark on western philosophy i.e., John Stuart Mill and Henry Sidgwick. Utilitarianism, as a moral theory, is consequentialist. Contrary to deontologism it does not hold that the morality of an action resides in its conformity to a universal rule. Rather, it states that the morality of an action stems from its consequences. More particularly, what sets utilitarianism apart from other consequentialist theories is its emphasis on happiness and pain. This is prominent in Bentham's work. In his first substantial publication, dating back to 1776, he brings forth what he described as a 'fundamental axiom'. For him, "it is the greatest happiness of the greatest number that is the measure of right and wrong" ([1776] 1977, p.393). Paraphrasing Bentham's view, an action is thus considered morally acceptable if it maximizes happiness overall or, at least, minimizes the pain caused. This is usually a common ground for utilitarians and both Mill and Sidgwick shared this conception of the good.

With that in mind, it was probably just a matter of time before Bentham would consider including into the utilitarian calculus not solely human beings but other sentient organisms as well. For if what matters for right and wrong is happiness and suffering then the mere ability to subjectively feel one or the other should suffice for a being's interests to be taken into consideration. For Bentham, the leap was quite timidly taken in what is probably one of his most influential texts. In a footnote to *An Introduction to the Principles of Morals and Legislation* full of common sense and perspicacity, one can find an already much-quoted line. Pondering upon our relationship with animals he writes: "The French have already discovered that the blackness of the skin is no reason why a human being should be abandoned without redress to the caprice of a tormentor. It may come one day to be recognized, that the number of the legs, the villosity of the skin, or the termination of the *os sacrum*, are reasons equally insufficient for abandoning a sensitive being to the same fate […] the question is not, can they reason? nor, can they talk? but, can they suffer?" (Bentham, 1823, p.245).

Following the Benthamian tradition, similar concerns for animals can be found in the writings of John Stuart Mill and Henry Sidgwick. The former, for instance, claimed that "the reasons for legal intervention in favour of children, apply not less strongly to the case of those unfortunate slaves and victims of the most brutal part of mankind, the lower animals" ([1848] 1965, p.952). And reflecting on the utilitarian creed as "an existence exempt as far as possible from pain and as rich as possible in enjoyments," he made explicit that such an existence should be "secured to all mankind, and not to them only, but, so far as the nature of things admits, to the whole sentient creation" (1863, p.17). This statement was also very much conceded by Sidgwick, albeit in different terms. Indeed, in *The Methods of Ethics*, "the great nineteenth century systematiser of utilitarianism", as Bass (2012) calls him, wrote that "it seems arbitrary and unreasonable to exclude from the [utilitarian end] any pleasure of any sentient being" (Sidgwick, [1907] 1981, p.414). This completes another point made by the author earlier in the text very well. As he put it "I think that common sense agrees with Bentham that the pain of animals is in itself to be avoided" (p.237).

Truth be told, there exists differences between the versions of utilitarianism defended by each of the above-cited philosophers. Discussing such technicalities, however, is far beyond the scope of what we are concerned with here. Besides, those distinctions are irrelevant for the main takeaway I want us to draw from this brief discussion of early utilitarianism. Indeed, the point I wish to stress by quoting those authors is this: they all seem to have realized that, if utilitarianism is to be embraced, there is *a priori* no reasons to focus solely on the happiness and pain of human beings. They all embraced the Benthamian idea that morality is defined by the greatest happiness of the greatest number. From this, they logically intuited that this should probably be the case for all sentient beings.

As time passed, the utilitarian framework was further developed on both theoretical and empirical grounds. Consequently, and with the work of following generations of philosophers, new strands emerged. The intuition that the sentient world as a whole should perhaps be incorporated, however, never quite disappeared. As of this day, many utilitarians are deeply convinced that caring for what non-human animals feel is logically derived from utilitarianism's core principles. A perfect example of this is Peter Singer who made this point very explicitly. For him, "if a being suffers there can be no moral justification for refusing to take that suffering into consideration. No matter what the nature of the being, the principle of equality requires that its suffering be counted equally with the like suffering of any other being." (Singer, [1975] 2015, p.38).

2.2. The utilitarian framework

There are countless human activities that have consequences – be they good or bad – on animal lives. Using non-human animals as tools for research is one of them. Each day, in laboratories, a substantial number of animals are held captive in usually very stressful environments and forced to serve as subjects in experiments for various purposes. All of this, including the use of monkeys in neuroeconomics, represents a considerable source of suffering for sentient beings. Yet, if we accept the idea that the principles of utilitarianism encourage us to include animals in the utilitarian calculus, the recourse to the utilitarian framework to question the morality of any type of animal experimentation becomes completely relevant.

The problem with utilitarianism, however, is that it is a very flexible framework; it can be interpreted in many different ways. Generally – and following Bentham's axiom – everyone agrees that happiness is to be faced and balanced with unhappiness or suffering. There are, however, dissents regarding what happiness and unhappiness truly consist of. The same can be said about which approach to adopt when aggregating happiness and unhappiness and how to compare or weigh them. On this note, one can for instance distinguish between preference utilitarianism and hedonistic utilitarianism. Proponents of the former conceive of happiness and unhappiness as states of preference satisfaction/dissatisfaction (Rabinowicz & Osterberg, 1996). Such authors would usually employ the terms 'welfare' or 'wellbeing' and conceive of X as happier than Y if and only if X's preferences are more fully satisfied than Y's. Proponents of the latter – starting with Bentham himself – conceive of happiness and unhappiness in more general and abstract terms, as subjective emotional states of pleasure and displeasure (Conee, 2001). As this work is not meant to be a discussion of the diverse types of utilitarianism, I will not venture into details here. I will simply focus my attention on being clear about what I mean when using utilitarian concepts. For, if anything, the fact that utilitarianism can be understood in several yet distinct ways calls for caution and precision when specifying the framework one wishes to utilize.

In my case, I shall opt for a utilitarian approach revolving around two key features. Those features are very much present in the literature and usually invoked when addressing the issue of animal experimentation. They are (1) a strong emphasis on maximisation over alternatives and (2) resorting to sentience when deciding what is morally relevant to consider for an ethical assessment. The second characteristic is very much in the vein of the early utilitarian intuition and perfectly embodied by Singer in *Animal Liberation* ([1975] 2015). The first one, on the other hand, turns the framework into something a bit more demanding. Yet, such exigence, I believe, is not overdue to prevent unnecessary and suboptimal suffering. Let us now turn to an examination of what I mean by (1) and (2) starting with the latter.

2.2.1. Resorting to sentience

In the literature, there is a constant debate regarding the moral status of animals (Gruen, 2003). Some argue, for instance, that human beings possess distinct capacities setting them apart from the rest of the sentient creation, monkeys included. It is on the basis of those capacities that humans are said to have a moral status – or at least a higher one – compared to animals. Fortunately enough, nowadays almost no proponent of such a view goes as far as Descartes by claiming that animals can be used freely and without concern because there are mere 'anima without sensations'. Most of them acknowledge that humans have obligations towards animals but maintain that those obligations are of a lower moral order, they are not as morally binding as what is due to fellow humans.

Along such lines, Carl Cohen (1986, 1997) points out that only humans are capable of moral reasoning by formulating moral claims and acknowledging the power of moral restriction on their will. Christine Korsgaard (1996, 2009), on her side, stresses the unique ability humans possess to situate themselves in a mental space; to be aware of their emotions, impulses, perceptions, desires, and question them as valid reason for action[1]. From the perspective of

[1] Here, caution is needed. Indeed, Christine Korsgaard is famous for being a fervent advocate of the moral consideration of animals on Kantian grounds (Korsgaard, 2018). I do not wish to deny this fact. But it is clear that

human exceptionalism, animal experimentation can be perceived as morally warranted because animals lack certain abilities compared to the human community which, in turn, makes them less subject to – but not completely devoid of – moral consideration.

A significant issue with human exceptionalism, however, is what is referred to as *the problem of marginal cases* (Dombrowski, 1997; Norcross, 2004). Briefly, it is exceedingly difficult to find a morally relevant difference between humans and non-human animals. This is so because for any feature one might choose to distinguish both categories of beings, one will be faced with instances where either some animals possess the feature or some humans do not. Concretely, we gladly attribute rights and higher moral significance to certain human beings that do not exhibit advanced cognitive abilities such as the possibility for moral reflection or introspection. Think about infants, mentally-disabled individuals, or people in comas.

In general, it seems right to assume that no human being with a sane mind would consider it morally acceptable to experiment on such marginal humans just like scientific research is commonly conducted on animals. No one would claim – hopefully – that we can tinker with the brains of infants or mentally-disabled people using very invasive techniques the way neuroeconomic research is being conducted on monkeys[2]. But the question is, why? If both categories of beings lack the same feature that we deem morally relevant, what reasons do we have to treat them any differently? Doing so can be seen as inconsistent or even completely arbitrary because we would find ourselves in a situation where we would attribute higher moral significance to beings on the sole grounds that they belong to our own species. The same can be said about arguing that marginal humans deserve a moral status different from that of marginal animals because it would be in the very nature of every human being to exhibit cognitive abilities conducive to moral reasoning and introspection. Indeed, one might advance that we would have reasons to doubt that such capacities could truly be said to be 'in the nature' of, say, a severely mentally-disabled human, if the individual in question was born that way and their condition such that it can never be improved, therefore constraining them to possess the same cognitive limitations until their passing.

The arbitrariness that can result from a moral consideration biased in favour of members of our species was fully acknowledged by Singer ([1975] 2015, p.47-50) – who referred to such attitudes as *speciesism* – but also notably by Regan (1983). The latter drew from this inconsistency – among other things – the necessity to confer animals, just like humans, rights that cannot be violated irrespective of the consequences. Singer, although at one with Regan in his attempts to eliminate the atrocities inflicted on animals, never embraced the right-based view. He judged it "too inflexible to respond to the various, real, and imaginary circumstances in which we want to make moral judgments" (Singer, 1987, p.13). This inflexibleness is manifest in the case of animal experimentation for which granting inviolable rights to the

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earlier in her career she wrote things which, although it might not have been her intention, can be used to support – and probably reflect – the ideology of human exceptionalists. In *The Sources of Normativity (1996)*, she was for instance writing that: "A lower animal's attention is fixed on the world. Its perceptions are its beliefs and its desires are its will. It is engaged in conscious activities, but it is not conscious *of* them. That is, they are not the objects of its attention. But we human animals turn our attention on to our perceptions and desires themselves, on to our own mental activities, and we are conscious *of* them. That is why we can think *about* them…And this sets us a problem that no other animal has. It is the problem of the normative. The reflective mind cannot settle for perception and desire, not just as such. It needs a reason." (p.93). It is to this targeted part of her work I am referring to.

[2] See chapter 3 for the details.

subjects means forbidding such experiments irrespective of what can be expected from them. In particular, it is tantamount to always disregarding the tremendous benefits we can sometimes – perhaps very rarely but still – obtain from such experiments, to consider them morally irrelevant. This is contentious and something for which a utilitarian, it seems, would be more flexible by favouring a case by case analysis based on consequences.

For Singer, what is truly important for moral consideration are not the differences between humans and non-human animals but the similarities. More accurately, what counts is *sentience,* the ability to suffer and feel enjoyment. In his words: “if a being is not capable of suffering, or of experiencing enjoyment or happiness, there is nothing to be taken into account. So the limit of sentience is the only defensible boundary of concern for the interests of others.” (Singer, *ibid*, p.38). Sentience is thus particularly important here because it is used to draw the line between what is relevant for the moral assessment of a deed and what is not.

Reverting to Bentham’s axiom, resorting to sentience allows us to be more specific about what we mean when we say: “the greatest happiness for the greatest number”. It asks us to include in “the greatest number” all beings that exhibit the capacity to feel, something which animals have demonstrated times and times again. This is true for their ability to feel enjoyment and, more importantly, to suffer. This ability is obvious to anyone who either has or has had a pet or that lived in the vicinity of animals. As a result, it becomes obvious that we would have no valid reasons not to include them in our conception of the greatest number.

Moreover, taking into consideration the interests of every being that can feel also stresses a hedonistic understanding of the words “happiness” and “unhappiness”. It invites us to understand them as subjective emotional states and not as states of preference satisfaction; to perceive happiness as a general term designating a wide array of positive feelings including joy, excitement, calmness, or pleasure. And, on the opposite, unhappiness as a general term for the range of negative feelings that can be experienced. One can think of fear, pain, suffering, discomfort, or stress. Overall, and quite simply, a sentient being will be said to be hedonistically happier in state X than in state Y if they subjectively feel better in X. That is, if the number and intensity of positive feelings experienced in state X is superior to those felt in Y or if the number of negative feelings induced by both states is inferior in X.

In the end, although animals are unable to communicate with us how they subjectively feel using words, they can do so throughout modifications in their behaviour. This is especially the case for negative feelings, those we wish to avoid or minimize as utilitarians. A monkey kept in a cage and used for research purposes can – and usually does – manifest his discomfort, pain, or stress by grunting, shaking, or refusing to eat for instance. Those external signs are manifestations of a subjective state of unhappiness. This unhappiness can be manifested before, after, or while the experiment is being conducted. But what matters is that the ability the monkey has to feel good or bad, its sentience, leads us to consider its interests as morally significant when assessing the ethics of it being experimented on.

2.2.2. Maximising over available alternatives

On par with the importance of taking into consideration the feelings of all sentient beings involved, the utilitarian framework I will rely on has a second key feature. This feature is, as said earlier, the need for a maximization over available alternatives. Once again, recalling

Bentham's axiom: "the greatest happiness of the greatest number" one can very well perceive the importance of maximization for utilitarianism. When it is made clear what one means by happiness, utilitarian ethics demands that it be maximized.

This emphasis on maximization needs to be reminded. Indeed, utilitarianism is often conceived as a weighting rather than a maximizing moral philosophy, as holding that an action is morally justified if its benefits (the happiness it creates) outweigh its costs (the suffering involved). Yet, as Norcross (2012) perfectly puts it: "It is important to note that a utilitarian demands of an action or institution not that it results in a greater amount of happiness than unhappiness, but that it results in a greater balance of happiness than available alternatives" (p.70). The author then proceeds to illustrate this crucial point with the case of slavery. Imagine a society, Norcross writes, with a small number of slaves and a larger number of free citizens. Now, even if the slaves are extremely unhappy and the unhappiness of each slave many times greater than the happiness of each free citizen, there would still be a point where there are enough free citizens to outweigh the suffering of the slaves. Critics could then point out – and actually did – that utilitarianism is defective because it can be used to justify slavery. This criticism is short-sighted. Obtaining a positive balance of happiness over unhappiness is not sufficient for utilitarians to morally justify an act or an institution. What is needed is to obtain the greatest, the maximum, balance that can be reached with the alternatives at hand. Reverting to slavery, one would have to show that the balance of happiness over unhappiness is greater in the society with slavery than in a free society. This, of course, need not always be the case.

What was just said perfectly applies to experimenting on animals. Demonstrating that the benefits to be drawn from a given experiment outweigh the suffering and discomfort felt by the subjects is not enough. Hypothetically, this might be a first hint that the experiment is morally acceptable. But making this certain requires an additional step. It necessitates sound reasons to believe that what is being done offers the greatest balance of happiness over unhappiness compared to what could have also been achieved. Unfortunately, this point is often overlooked. As Norcross concludes: "this detail is important, though sometimes ignored in discussions of the justifiability of animal experimentation" (p.70). No doubts, however, this maximizing feature of utilitarianism is particularly relevant to assess the morality of animal experimentation. This relevance stems from the need to avoid unnecessary suffering or to make the most out of it and of the resources employed. Let us assume that a researcher is given two monkeys to serve as subjects and that she has two alternatives. Alternative 1: using highly invasive and pain-inducing experimental techniques on the monkeys for purposes X. Alternative 2: using the very same techniques and subjects but with the hope of achieving Y instead. Let us further assume that both alternatives have a positive balance of happiness overall but that the one of alternative 1 is greater. The researcher, because she finds Y more attractive than X, has a strong preference for implementing alternative 2. What should she do? If all that truly matters is happiness outweighing suffering then both alternatives can be justified on moral grounds. Nothing, *per se*, could prevent the researcher to follow her preference and pursue alternative 2. From a maximizing point of view, however, alternative 1 should be prioritized.

Both alternatives generate, by construction, the same amount of suffering. Yet, only alternative 1 guarantees that this suffering brings about the highest obtainable benefits. The ratio of happiness over pain that is, the amount of enjoyment per 'unit' of suffering, is clearly in favour of alternative 1. This is a good reason to distinguish it from alternative 2 and label it as morally warranted compared to the latter. This 'maximizing condition' of utilitarianism, as we can call it, is more demanding than mere outweighing. Yet, it appears necessary to limit the creation of pain and suffering, which are terrible feelings for any sentient being, to ends that can make the most out of them to ensure that nothing is 'wasted' in the process by being employed for suboptimal purposes.

2.3. Utilitarianism and its implications

Putting the pieces together, namely considering what was developed in the previous two sections, we can say the following. From a utilitarian standpoint, the use of animals for given scientific purposes, such as using monkeys in neuroeconomics, is morally justified if and only if (1) it results in a greater balance of happiness over unhappiness than available alternatives and (2) happiness and unhappiness are understood as subjective emotional states that can be experienced by all sentient beings involved. This ethical principle, however, has two main implications. First, resorting to sentience asks us to specify how the aggregation of happiness and unhappiness across species ought to be carried out. Second, embracing the utilitarian perspective leads to the conclusion that the only type of knowledge worth gaining when experimenting on animals is the one which contributes to minimize pain or to maximize happiness. Let me address those points in turn.

2.3.1. Happiness and unhappiness across species

The utilitarian perspective specified here regards happiness and unhappiness as morally significant whatever the species. At this point, however, one can point out that considering the feelings – good and bad – of different sentient beings leads to an aggregation problem. Should aggregating happiness and suffering across species be carried out equally? Or should what is felt by certain categories of sentient creatures count less than whatever is experienced by others? Singer clearly argues in favour of equal consideration. As already quoted earlier, "No matter what the nature of the being, the principle of equality requires that its suffering be counted equally with the like suffering of any other being." (Singer, ibid, p.38). Proponents of the second stance, on their side, respond that animal suffering should count less than human suffering and that, in the same manner, human enjoyment should count more than animal enjoyment (Kagan, 2019). Advocates of such a view do not deny that animals have moral significance. Quite the contrary. They gladly agree that animal enjoyment and suffering are relevant when discussing the morality of acts involving animals. What they believe is simply that they should be discounted with regards to human enjoyment and suffering.

This contention is important for a utilitarian assessment of animal experimentation. Indeed, depending on which perspective one endorses, the morality of certain experiments will differ. Consider the case of a given experiment judged morally wrong when treating the feelings of animal subjects on an equal footing. Now, if one starts discounting what is felt by the animals, one might reach a point where the discounting is such that the experiment in question is now justified on moral grounds. Therefore, and before proceeding any further, I must clarify which side of the debate I situate myself on. I will, in this thesis, stand in line with Singer. Indeed, I share the sentiment that equal consideration is the appropriate way to go when it comes to beings that – at least – possess a complex nervous system and exhibit traits commonly associated with complex life. This includes most animals used for human needs, laboratory monkeys first and foremost. The reason I have to share this sentiment lies in the fact that the discounting view strikes as particularly anthropocentric. In my eyes, this severely erodes its appeal. Proponents of this stance hold human sentience as the absolute reference for moral consideration and proceed to discount the moral significance of what is felt by other animal species based on their similarities with human beings. This might seem arbitrary and suspicious, the result of a self-attributed significance. After all, suffering and enjoyment can be very intense for many animals as well. It might very well be that species which show elevated levels of cognition but that are not affiliated with primates or the human line such as certain birds or marine animals will be refused a due appreciation of their interests on the ground that they appear alien to us in terms of shape or behaviour.

But if we now take some distance with this theoretical aspect and consider the particular case it will become relevant for – i.e., the use of monkeys in neuroeconomic experiments – it seems we can make the point that embracing equal consideration should not, for the matter at hand in this thesis, appear wholly nonsensical nor completely contentious for proponents of the discounting view. Indeed, neuroeconomists resort to non-human primates as subjects and, in so doing, experiment on the type of beings that most resemble humankind in terms of physiology, cognitive abilities, and social structures. A similar physiology which, as stressed in the previous chapter already, stems from a similar genetic background due to a close evolutionary vicinity. Monkey brains, in particular, are considered so similar to ours that not only are they used to further our understanding of human economic behaviour but of human neurodegenerative diseases as well[3]. Monkeys also live in highly social groups characterized by strong bonds between members, especially between mother and child.

Under the hypothesis that we agree with the discounting view, we must take human sentience as the absolute standard for moral importance – as previously indicated this sounds acutely anthropocentric but let us accept it for the sake of the argument – and it is on the basis of this very human standard that the discounting ought to be done. In other words, the more similar to humans the species, the less discounted the feelings of its members should be. Monkeys are primates just like us and the similarity can be enriched by all the features just enumerated and sketched. In light of this, we would be on solid grounds, it appears, if we argued that their suffering and their enjoyment must be the ones which most closely resemble what we can ourselves experience as human beings. And if we agree on the fact that monkey sentience is probably the closest type of sentience there is to human sentience, the discounting view tells us that whatever is felt by non-human primates ought to be the less discounted compared to every other type of beings. What I conclude from this, as a consequence, is that the use of monkeys in neuroeconomics – and in any type of laboratory experiment for all that matter – should reveal itself worthy of attention, not uniquely for those endorsing equal consideration, but for proponents of the discounting view as well.

[3] A point I will come back to towards the end of the thesis (section 5.4).

2.3.2. For knowledge's sake

The second crucial point I would like to mention about the utilitarian framework is the following. When assessing the morality of using animals for research it states that the only knowledge worth gaining is the one which contributes to maximizing the balance of happiness over available alternatives. Some might find this too restrictive. Shouldn't we, one could say, consider the enhancement of science as a goal worth pursuing in itself irrespective of its contribution to maximizing happiness? Isn't the increase in human knowledge rendered possible by animal experimentation a positive consequence that should be granted moral relevance even when such increase cannot be related to positive subjective feelings? Imagine that a given experiment involving animals allows us to discover X. Suppose further that X cannot be used to improve the life of any sentient being. Couldn't the mere fact of discovering X, something unbeknownst to anyone before, count as a benefit to be included in the moral calculus? Something that might justify the suffering, stress, and discomfort the animals went through while being experimented on? One might think that this should be the case. I do not, however, share this view. I believe that, although the valuation of knowledge in itself might not always be an issue, such a valuation should raise cautiousness insofar as the acquisition of the knowledge in question necessitates inflicting suffering upon sentient beings.

A first reason is to be found in the lurking speciesism. Before accepting to take unrelated-to-happiness developments of human knowledge into account and considering them apt to justify the suffering endured by animal subjects in labs, we first ought to make something clear. We need to ask: Are those endorsing such a view still willing to defend it when knowledge in the vein of X is acquired, instead, by means of human suffering? If X is gained after rats, dogs, or monkeys had to be painfully experimented on, and if X is valued by certain individuals, would those individuals still value X if they found out that X was obtained thanks to humans being experimented on in the very same painful way? Answering this question negatively might raise suspicions. It might mean that proponents of this stance are prone to give more weight to the interests of humans than to that of the animals. Given the threat posed to the finding of a morally relevant difference between humans and animals by the issue of marginal cases set out earlier, this preference can very well be totally arbitrary and therefore unjustifiable on philosophical grounds. Said otherwise, it might appear as a case of sheer speciesism.

A second reason for not finding the 'valuing knowledge for knowledge's sake' view convincing is simply that holding such a stance would put us in a position to possibly justify even the most atrocious of deeds simply because it contributes to the advancement of human science. Needless to say how problematic this can be in addition to being very much reminiscent of the darkest hours in history. At this point, however, one can point out that this might be the case with utilitarianism as well since, strictly speaking, utilitarianism might indeed tolerate the generation of a significant amount of pain and suffering. But drawing such an analogy between the two positions neglects the crucial difference that exists between them. Utilitarianism is built upon the core principle that, if pain needs to be inflicted, it ought to be somewhat 'compensated' by the creation of happiness so that, overall and across alternatives, good is maximized or bad is minimized. This constraint surrounding the generation of suffering is not present in the case of the valuing knowledge for its own sake position. Utilitarianism does not say "those animals were worth experimenting on because they allowed us to discover X, which we were not aware of" but "those animals were worth experimenting on because we are now aware of Y which we can use to improve the lives of sentient beings in a way that could not have been reached otherwise". With things presented that way I believe it is easy to see how more likely the former is to warrant an out-of-proportion amount of pain and suffering for the sake of scientific discoveries compared to the latter.

Both reasons combined, I think, do a good enough job at explaining why, as far as the utilitarian perspective defended here goes, only what contributes to maximizing happiness over available alternatives is to be deemed susceptible to morally justify the creation of pain and suffering of animals in labs, and why not including the sheer discovery of a piece of knowledge cannot be said to be overly restrictive.

2.4. Conclusion of Chapter 2

In this chapter, I aimed to detail the utilitarian framework I deem appropriate to investigate the ethics of using monkeys for neuroeconomic purposes. I argued that, from a utilitarian standpoint, the use of animals for given scientific purposes is morally justified if and only if (1) it results in a greater balance of happiness over unhappiness than available alternatives and (2) happiness and unhappiness are understood as subjective emotional states that can be experienced by all sentient beings involved. I then discussed two important implications of the utilitarian perspective. Those were the aggregation of happiness and unhappiness across species and the type of knowledge worth considering when assessing the ethics of animal experimentation. I argued first that I was a proponent of equal consideration but that the rivalry with the discounting view was less important when experimenting on monkeys. Second, I wanted to stress that the mere fact of increasing human knowledge is rather unfit to count as a benefit, in itself, for the moral assessment of animal experimentation. In the end, whether we have reasons to believe the use of monkeys in neuroeconomic research is morally justified within those utilitarian lines is the motivation behind this thesis. Answering this question will necessitate the help of the remaining chapters.

Chapter 3: The Harms of Monkey Experiments in Neuroeconomics

The first two chapters of the present work had the objective of setting the stage, so to speak. Now, after having offered an overview of the use of monkeys in neuroeconomics and of the ethical framework I deem appropriate to assess its morality, it is time to turn to the benefits and harms generated by this strand of research. For the time being I would like to focus on the harms. I shall, therefore, postpone the investigation of the benefits to the subsequent chapter. In this thesis, and as was stressed in the previous chapter, I side with equal consideration. That is, I consider the happiness and unhappiness of the monkeys to be as significant morally speaking as that of humans. It is something I would like the reader to keep in mind when reading this chapter. I believe this is required to fully grasp and picture the extent of the suffering we will be dealing with here. In this chapter, I would like to establish as plainly as possible that the way monkeys are raised, kept, and experimented on for neuroeconomic purposes generates a decent amount of pain. My goal is that by the end of this chapter the reader will have a good appreciation of what the monkeys have to go through to advance our knowledge in the field of neuroeconomics. The chapter opens up with a discussion on the transparency of monkey experiments in neuroeconomics before proposing a scrutiny of the methodology neuroeconomic experiments cited thus far rely on and of their pain-inducing feature. It then seeks to resolve an identified transparency issue by presenting the common fate of a laboratory monkey before and once it has reached a research facility. The chapter ends with a brief discussion of the precautions supposedly taken to reduce the suffering of the animals.

3.1. What we do and do not know

The first step to take while investigating the morality of a type of animal experimentation is to analyse how the subjects are treated in the lab, both in and out of the experiment. This crucially depends on how available such information is. Namely, on how explicit the researchers are about those very aspects in the work they publish. The problem, however, is that published articles – which represent the only thing at our disposal to understand how research is being conducted – are way too often vague about how animals are treated. This was already an issue for Singer ([1975], 2015) when he first published *Animal Liberation*. As he put it, “the experimenters will not emphasize the suffering they have inflicted unless it is necessary to do so in order to communicate the results of the experiment, and this is rarely the case. Most suffering therefore goes unreported” (p. 80). This “unreporting” of suffering but also the omission of any other relevant aspects for the matter at hand can be qualified as a lack of transparency. The fact that scientific articles rarely display extensive information about the living conditions of the animals used as subjects is a significant issue. Let me sketch why.

3.1.1. Why transparency matters

The main reason why lack of transparency is a problem is that it makes it exceedingly difficult to have a complete picture of the harms done to the animals. As a consequence, it becomes quite complex to satisfyingly compare them to the benefits obtainable from experimenting on them. Needless to say, this is particularly significant for what is at stake in this thesis. That is, for a utilitarian approach of experimenting on animals for certain given purposes. May the reader rest assured, this problem will be addressed in an upcoming discussion[4].

For now, it suffices to say that complete transparency would, in fact, necessitate having details regarding where the subjects are coming from, their captivity environments, what is being done to the animals during experiments, and what becomes of them once it has been properly carried out. If those aspects were to be systematically and thoroughly spelled out, they would represent a strong incentive for the researchers to engage with potential ethical concerns and to clearly detail the reasons that, for them, render the experiment worth the suffering inflicted. Allegedly, this could create an atmosphere more conducive for discussions and debates around the question of animal experimentation. This would also permit to better elicit the intention of the researchers and shed light on what they were prepared to do to successfully carry out their experiment.

Another reason why transparency can be said to be important is because people should be able to know how science is being made and at what cost. This is especially true when experiments receive public funding – as is often the case – because citizens have a right to know how their money is being spent. What is more, transparency would allow them to verify whether the ethical views they hold regarding animal experimentations are properly reflected by public institutions in charge of granting authorisations to such experiments. If scientific articles are being vague and/or silent about what the subjects of the experiments are going through, how could citizens know if their government is being too lenient or not?

Finally, one could also claim that individuals should keep themselves informed concerning what humans, as a species, inflict upon other sentient beings for scientific purposes. To know how far we are willing to go to advance the ends of their own species to the detriment of others. Indeed, the benefits that can be derived from whatever is being done to animals in labs will never, in most cases, accrue to them but solely to us. In this light, some consideration would not be overdue. In Singer's words, "If the animals have to undergo these experiments, the least we can do is read the reports and inform ourselves about them" (p.79). Lack of transparency represents a significant hurdle to that objective.

3.1.2. What is usually very obscure with neuroeconomic experiments

Truth be told, neuroeconomic papers are no exception to the lack of transparency often characterising animal research. As was just said, transparency necessitates being clear about three things. (1) where the monkeys are coming from and what their captivity environments are like, (2) what happens during the experiment and (3) what becomes of the animals afterwards. I would say that, based on the corpus of articles I read to prepare this work, neuroeconomic

[4] See section 3.3.

research in monkeys would gain being clearer about all three aspects, although not to the same extent since (2) is usually more developed.

(1) and (3) are definitely the most obscure. Concerning (1), it is highly difficult to find any detailed explanation of how the monkeys are held captive in the lab and what their origin is. For instance, we do not know whether they were bred and raised in the lab or whether they were purchased to specialized institutions. We also do not know whether they are allowed to go out of their cages every now and then to stretch their limbs. Nor do we know if they are given the possibility to have any social interaction with each other or if they are kept isolated in their boxes all day long when no experiment is being conducted. We are also mainly unaware of the size of the cages they are being kept in and regarding how often they are allowed to eat and drink. In brief, we are unable to determine the extent to which a monkey's fundamental needs are restrained by their current state of captivity.

When it comes to (3) things are mostly unspecified as well. In the wide majority of cases, this dimension of the lives of the animals isn't even mentioned. Here and there it is possible to read that the subjects used for a certain experiment were also utilized for the sake of another previous experiment. This suggests that, when the research agenda permits it, monkeys can be used for several experiments in a row. Fine, but their long-term fate remains a mystery. Given the invasiveness of the methodology – which I will detail later on – it is hard to imagine a possible convalescence for them. Euthanasia therefore appears to be a fairly safe bet to place when speculating on what happens to the animals after their service.

Finishing with (2), one must admit that things always get a bit more transparent when we touch upon the experimental setting *per se*. Indeed, it is a common requirement in science to be clear about the exact protocol used. As a consequence, the tasks monkeys have to perform are always quite detailed. The same thing can be said about the technical specificities of the recording devices employed as well as regarding the way the data was collected and processed. But even with that in mind, there is still much room for improvement. Firstly, although researchers often mention that monkeys have to be trained before the experimental trials begin, we never know what this training is like nor the form it takes. We can often deduce that it has to do with positive reinforcement techniques but that is all. Yet, training periods can span over several weeks. McCoy & Platt (2005) specify for instance in their paper that "Six weeks later, animals were habituated […] and trained to perform oculomotor tasks for liquid rewards". Secondly, and besides training, nothing is never specified as to whether the authors were able to smoothly carry out each and every trial of their experiment on the first attempt, or if some had to be untimely interrupted because one of the subjects showed signs of fatigue, intense stress, or illness.

(1), (2) and (3) are important aspects in the life of a monkey in a lab. All three dimensions have a direct effect on how the animal will subjectively feel from the moment it is born to when it becomes useless to the researchers. Unfortunately, most neuroeconomic research which depends on monkeys is far from being completely transparent on such matters. Someone quickly jumping to conclusions might say that this probably hides a serious lack of consideration for the animals and what they must go through.

3.2. A Pain-Inducing Methodology

After having highlighted what we are ignorant about concerning how monkeys are treated by neuroeconomists, let us now focus on what we do in fact know. As said earlier, researchers are a bit more explicit when it comes to (2). Namely, regarding what happens to the monkeys during the experiments themselves and the recording techniques involved. In this section, I will review the experimental methodology commonly used to investigate the brain areas underlying economic behaviour in monkeys. I will do so on the base of what can be found in the articles themselves, backed up with further research I did on my own. This research was mostly carried out with the help of articles directly cited in the neuroeconomic papers I focused on. They were particularly useful to elucidate what lurked behind what was for me nothing but cryptic jargon and specialised terminology. It is common knowledge that what is done to monkeys is greatly invasive. This invasiveness is fully recognized by the researchers themselves and is one – if not the main – reason why monkeys are used as subjects in neuroeconomics, as was already stressed. From what I was able to glean, I would contend that the methodology utilized on monkeys is pain-inducing because of three of its features. I will address them in turn.

3.2.1. Oculomotor tasks, saccades, and scleral search coils

There is a first striking resemblance between all the neuroeconomic experiments using monkeys evoked so far: most of them relied on oculomotor tasks. Indeed, monkeys were almost always presented visual targets or cues associated with different kinds of rewards that they could select by shifting their gaze. This process is known as "saccades" (figure 3). First, a fixation cue appears at the centre of the screen for calibration. Then, additional visual targets are made visible before the fixation cue disappears. Once done, only additional targets remain and the subject can proceed to choose by moving their eyes around and fixate one of them. Only after are they to receive a corresponding reward.

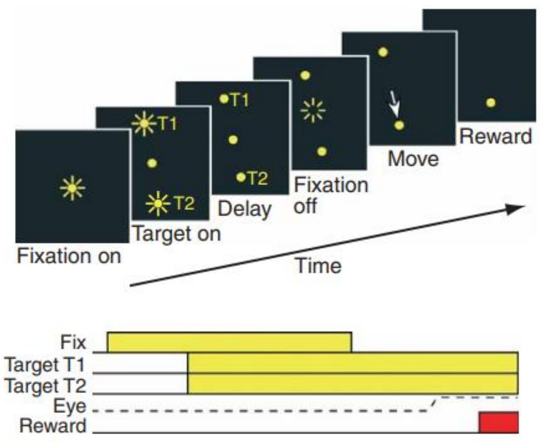

Figure 3. Schematic representation of an oculomotor task. Taken from McCoy & Platt (2005).

This protocol crucially depends upon the ability of the researchers to track eye movements of the subjects properly and accurately. This is evident. Not being able to do so would lead to an impossibility of eliciting choice and delivering rewards. The entire experiment would be at risk. To prevent that from happening, scientists resort to what is called a 'scleral search coil'. Scleral search coils are recording devices placed on the surface of the eyes. When the eye moves, the coil sends an electrical message to the computer assisting the experiment. It indicates the direction of the movement as well as its duration. When this data is correlated with the position of the additional targets relative to the fixation cue, it becomes possible to deduce which target the subject decided to look at and to deliver the corresponding reward.

Scleral search coils have been used in neuroscience for quite some time now. This includes neuroeconomics. Indeed, one of the founding articles of the discipline – i.e., the study of Platt & Glimcher (1999) – was already relying on oculomotor tasks and eye-tracking devices. However, and despite their particular efficiency, scleral search coils can be said to be problematic. The main reason for that pertains to how invasive they are to the subjects wearing them, especially animals. In humans, coils take the form of lenses that one is asked to merely apply on the eyes. In animals, coils are not only 'placed' on the eyes; they are surgically implanted. And although less invasive methods can be employed to track eyes non-invasively with good results (Kimmel & al., 2012), the scleral search coil is still widely regarded as the gold standard measurement technique for eye movements in animals. Proof being that recent neuroeconomic experiments still rely on it (Yamada & al., 2018).

Methodologically speaking, the first paper dealing with how to surgically install scleral search coils on monkeys was published in the mid 60's (Fuchs & Robinson, 1966) and an improved version of the protocol was proposed twenty years later (Judge & al., 1980). Essentially, the surgical procedure is performed as follows. Firstly, the eyes need to be maintained open. To that end, eyelids are retracted with tiny hooks piercing through them, weighted sutures, or metallic eyelid retractors. Then, a scalpel is used to make several incisions on the ocular globe. The coil is often made *in situ* by passing three turns of fine wire either under or in front of the insertions – depending on the exact method – of the extraocular muscles. Fuchs & Robinson (1966) recommend passing under the insertions (see figure 4) but Judge & al. (1980) noticed that passing the wires in front of them instead allowed researchers to get rid of the subsequent strabismus that the subjects were likely to develop after the implantation of the device. I am mentioning both techniques because the two of them are popular in neuroeconomic experiments with the papers making direct and systematic references to either one or the other. One can notice a slight preference for the methodology elaborated by Judge & al. (1980), however (see Figure 5). When the procedure is properly carried out, it has been observed that the coils remain satisfactorily in place for a period of time spanning from at least many months and up to several years. This gives even more support to the point made earlier that monkeys can be utilized for multiple experiments in a row.

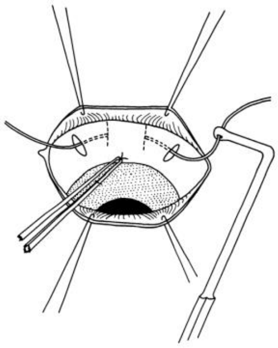

Figure 4. Detail of a monkey's eye showing the placement of incisions and the suture under the superior rectus insertion. Taken from Fuchs & Robinson (1966).

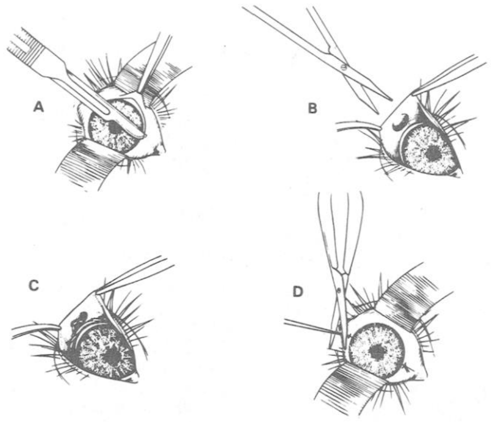

Figure 5. The various steps of the surgical procedure. Taken from Judge & al. (1980).

Truth be told, side-effects associated with implanting scleral search coils in animals – monkeys first and foremost – would deserve to be more systematically investigated. Indeed, research articles dealing with the issue seem to be very few and difficult to reach. Another striking example of the lack of transparency in neuroscience. It is however quite clear that, in light of what was developed regarding the implantation of scleral search coils, wearing implanted metallic wires in the eyes for long period of times is likely to have an effect not only on the organs themselves but on vision also. The strabismus generated by the coils when implanted à la Fuchs & Robinson is a good illustration.

In humans, for instance, wearing coil lenses is commonly associated with a variety of effects including ocular discomfort, hyperemia of the bulbar conjunctiva, buckling of the iris, corneal staining, and reduction in visual acuity (Irving & al., 2003). Those effects were observed as early as 15 minutes after insertion of the coils. Fortunately enough for the subjects, they were all transient and dissipated after the coils were removed. In animals, coils are never removed. They remain in the eyes for as long as needed, usually until the death of the subject. Yet, it would be unwise to believe and assume that animals are immune to such symptoms. That monkeys, whose physiology is so close to ours, are not likely to feel a constant ocular discomfort following the implantation procedure as well as suffer from the same side-effects as those observed in humans. The same side-effects which are likely to grow in severity as time passes, amplified by the non-removability of the devices, and which might even be more important from the start due to the very nature of the coil; being a surgical implant and not a mere lens.

Implants are generally associated with many downsides and we have *a priori* no reason to think that it should be otherwise with implanted coils. This is all the more true in a zone as fragile and delicate as the eyes. One can think of permanent discomfort of course but also of a sensation of itch or of an irritation of the pupil and related areas. Besides this, what can be mentioned as well are all the damage that can ensue from a miscarriage of the surgical operation and/or a bad positioning of the wires. This might include blindness, rapid deterioration of visual capacity, infections – which are always more likely for implanted individuals –, necrosis of ocular tissue, and so on and so forth. All of this combined with the invasiveness of the procedure possesses a pain-inducing feature which is particularly manifest.

3.2.2. Neuronal measurement and recording chambers

In chapter 1 I touched upon the fact that monkeys are used in neuroeconomics because of the specific recording method that can be employed on them[5]. This method, I specified, bears the name of 'single-unit recording'. It allows researchers to obtain an unmatched level of spatial resolution. While other techniques highlight the activation of entire brain regions, single-unit recording permits to tell which specific neurons or small groups of them are firing when given tasks are undertaken. This is rendered possible by the lowering of fine electrodes in the vicinity of the neurons of interest. Yet, lowering electrodes into the brain requires the installation of a recording device placed directly on the subject' skull. Such devices are called 'recording chambers' and are mostly made out of metal such as steel or titanium.

In the timeline of a typical experiment, installing a recording chamber necessitates a second surgical intervention which intervenes once the monkeys have been trained to perform oculomotor tasks and habituated to the scleral search coils (Figure 6). The first step of the operation consists in incising the skin of the head to expose the skull. The chamber is then fixated by being firmly screwed upon it, right on top of the opening just made. After that, trephination is performed. Namely, a hole is pierced in the skull to make the brain readily accessible. Trephination can either be carried out at the same time as the implantation of the chamber or a few weeks later.

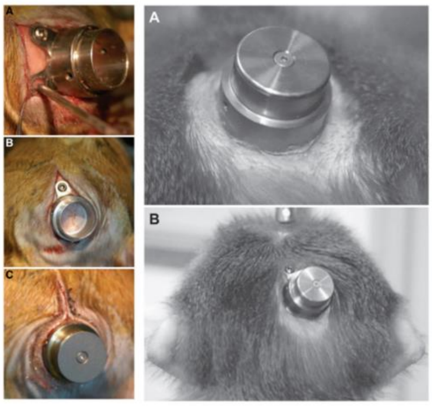

Figure 6. A recording chamber on a monkey's head while the implantation (left) and several weeks after (right). Taken from Adams & al. (2011).

[5] See section 1.2.2.

During the experiment, the recording chambers are connected to an additional supporting device utilized to insert the electrodes which – by passing through the implant – can easily reach the brain (figure 7). Interestingly enough, neuroeconomists seem to disagree regarding the effect that lowering electrodes in the brain has on the organ itself. Some like Camerer & al. (2005) acknowledge that it can cause problems. In their words: “a limitation of single neuron measurement is that, because insertion of the wires damages neurons, it is largely restricted to animals” (p.13). Others, however, contend that “the electrode itself does not cause appreciable damage to the brain” (Ruff & Huettel, 2014, p.80). Anyhow – and irrespective of whether it does indeed damage the brain or not – two things are certain. First, introducing electrodes in the brain is painless; the brain being an organ deprived of pain sensors. Second, opening the skull to gain access to the brain requires an invasive surgical procedure that always carries significant risk.

Figure 7. The lowering of the electrodes into the brain. Schematic representation (left) taken from Adam & al. (2011). Representation *in vivo* (right) taken from Lanz & al. (2013).

The risks of an open brain surgery are manifold. The worst case scenario, of course, is the death of the patient on the operating table. But even without going that far, one can think of all the possible complications that might ensue from a miscarriage of the intervention. This concerns possible damage to the brain, the skull, and nearby tissues that might be a source of chronic headaches, abscesses, and haemorrhage. In our case, the complications coming from surgically exposing the brain should be completed with those that can arise from implanting recording chambers and screwing them on the skull. If the device is misplaced or if a screw gets loose, additional surgeries will be necessary to correct or repair the implantation process. Yet, multiple major survival surgeries increase the risk that an animal subject experiences anaesthetic and post-surgical complications as well as post-surgical pain.

Even when risks surrounding the implantation of recording chambers are completely evaded by a proper and clean performing of the surgery, subjects are not free from pain. They will still have to spend the rest of their lives with a metal device fixated on their heads and a hole in their skulls, with the extent of discomfort and confusion that this entails. What is more, they will also be more prone to complications from bacterial contaminations. In fact, pathogenic contamination is one of the main causes of deleterious side-effects when implanting abiotic materials – which chambers are made of – and bacterial and fungal infections have been widely reported in cephalic implants (Dannemillier & al., 1995; Bergin & al., 2000; Venezia & al., 2012). In one study at the University of Pennsylvania, researchers cultured the interiors of nine recording chambers for evidence of microbial contamination and identified 13 different pathogens (Johnston & al., 2016).

But what is even more concerning, perhaps, is that in addition to the risk of localized microbial contamination, cranial implants can also allow infections to spread to deeper tissues of the skull, including the calvarium and the dura. Infection of the calvarium can produce painful periosteal damage and bone degeneration that results in bone loss. Over the long term, infection of the calvarium can cause the skull to become thin, soft, and spongy; this can allow the entire implant to become loose or dislodged and can even lead to failure of the implant. Failure of the implant can, in turn, lead to additional surgeries to repair or replace it and even to euthanasia if the monkey can no longer participate in neurophysiological experiments. The spread of infection to the dura is also a serious concern because it can endanger the health of experimental animals, delay experiments, promote the formation of scar tissue and cause pain as the electrode penetrates the inflamed dura. Other possible complications that arise from the spread of a local infection include meningitis and brain abscesses (Leblanc & al., 2013).

A last point worth mentioning when discussing the pain-inducing feature of implanting recording chambers concerns the use of dental acrylic. Dental acrylic is a product traditionally used to fixate prostheses and implants. When applied, it generates a reaction which is strongly exothermic. Yet, the resulting heat can potentially damage the bone – in our case the cranium – and underlying brain tissues (Hamlen & Olson, 1995). Dental acrylic also makes bleeding more likely by causing dilation of blood vessels which can interfere with the adherence of the acrylic to the bone screws (Gardnier & Toth, 1999). Evidence also suggests that sometimes the product can leak from the base of cranial implants and cause toxic effects in the bone, including disturbances, standstill of blood-flow, and intravascular hemolysis – the rupture of blood cells – (Albrektsson & Linder, 1984). Lastly, researchers often score the bone surface to encourage bonding of the acrylic. This procedure improves binding whereas dental acrylic is not very biocompatible with surrounding tissues. This can compromise the bone and prevent natural healing (Adam & al., 2007). The practice of bone scoring can lead to chronic inflammation, rejection of the implant and systemic disease sequelae. In turn, chronic inflammation can cause amyloidosis – a type of disease where abnormal proteins build up in tissues – with subsequent amyloid deposition in viscera, connective tissue and blood vessel walls damaging the tissues.

3.2.3. Primate chairs, head-restraints, and water deprivation

The last methodological features worth mentioning share a common trait. Contrary to implanted coils and chambers, their role is not to permit researchers to record data about the neurophysiology of the brain while involved in decision-making tasks. Their role is to ensure that the noise will be minimized while the experiment is being conducted. That is, that subjects will behave as expected and that the results will not be impacted by undesired external factors. Those features are (1) primate chairs, (2) head-restraints, and (3) water deprivation. The three of them have a straightforward ability to induce suffering and discomfort.

In neuroscientific experiments with alert monkeys the animals very often need to be seated in primate chairs during the span of all the experimental trials. In reality, part of the pre-experiment training – about which it is difficult to know much – is devoted to rendering the subjects accustomed to being installed in the chairs. Primate chairs are, as the name suggests, chairs specifically designed to receive monkeys (Figure 8). Although they might take several forms, their main goal is always to restrict the animal's movements to the necessary extent; to ensure that the moving and stretching of a limb will not interfere with the task undertaken nor with the recording devices. There are built on several levels and highly configurable to best fit the dimensions of the subject.

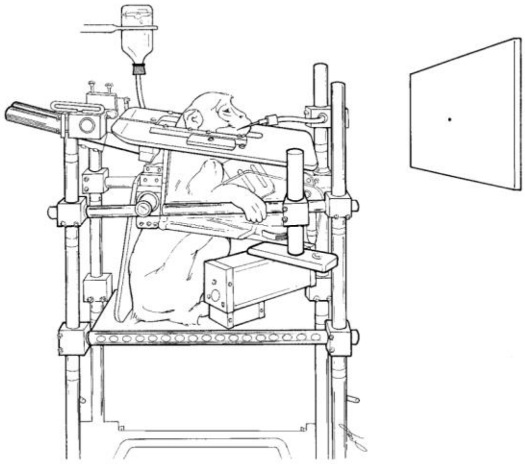

Figure 8. Schematic view of a monkey performing a dimming-detection fixation training task. Taken from Foeller & Tychsen (2002).

Non-human primates used in labs spend most weekdays in chairs (MacMillan & al., 2017). And this stops in the weekends simply because researchers are out of office. But if primate chairs are engineered to maintain the subjects in a desired position for sustained periods of time, it has also been observed that the common response of the animals to immobilization includes abnormal levels of stress, anxiety, and fear. This is especially the case during the beginning of the accommodation training. In addition, this immobilization also produces a reduction of tone in all limbs, a reduction of spontaneous behaviour, and the appearance of eye closure (Holcombe & al., 1979). Those are signs of monkeys finding themselves in a state similar to lethargy; in a situation wherein they barely respond to external stimuli from their environment such as the approach of the experimenter. An additional study even concludes that "the behaviour of monkeys in this position was considerably altered […] in contrast with their active behaviour when left free to move about in their cage" (Bouyer & al., 1978). In the wild, monkeys are very energetic creatures. They have evolved specialised limbs which allow them to be highly mobile in their natural habitats, be it to climb trees or wander the land. As a consequence, it would be difficult to find a situation any worse than what is being done to them during experiments which necessitate constant restraint, where a monkey's natural condition and urges are so intensely and so fundamentally thwarted.

Speaking about restraints, primate chairs usually go on par with head-restraints. In monkeys, head-restraints are surgically implanted just like recording chambers. They are metallic implants fixated on the skull with screws even before the training for the experiment begins (Figure 9). Their extremity is formed of what is called a headpost – a longitudinal cylinder protruding from the head – that is to be inserted into the primate chair. Once done, the headpost becomes able to maintain the head stationary. This is particularly useful as sudden rotations of the head would cause the brain to move relative to the electrode tip, destabilizing the recording. Furthermore, even when electrode recordings are not being made, a headpost remains useful to make monitoring of gaze position during psychophysical experiments much easier by eliminating head movement which would parasite the results.

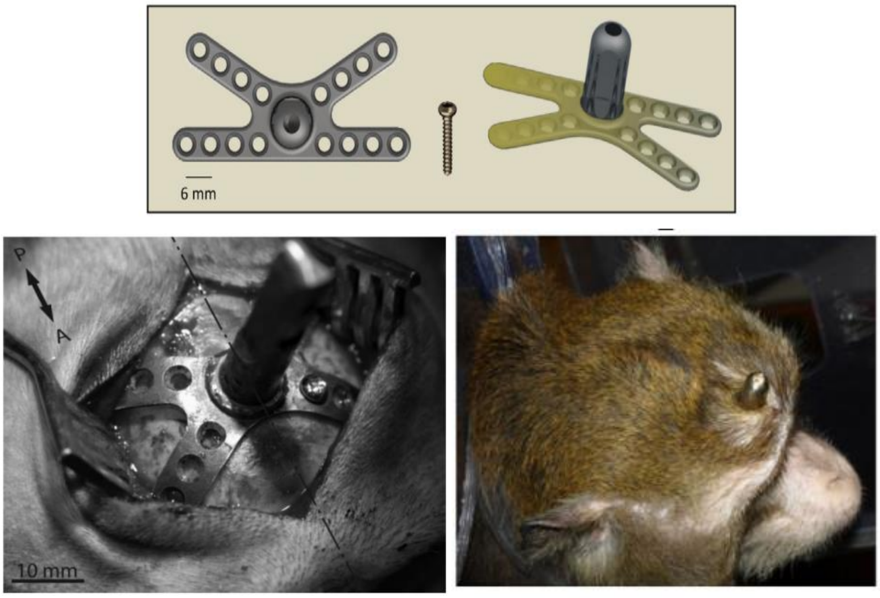

Figure 9. Implantation of a head-restraint prosthesis before (top), while (left), and after (right) the procedure. Taken from Adams & al. (2007) and Lanz & al. (2013).

Given that head-restraints are metallic implants they are subject to the very same inconveniences as recording chambers. They can be associated with discomfort, itch, and irritations. They make infections more likely by increasing the risk of a pathogen entering the body of the animal. And they need a risky surgical intervention to be installed which might lead to complications endangering the life or degrading the health of the subject.

The last methodological aspect necessary for the experiment to unfold properly but unpleasant for the subjects is water deprivation. In neuroeconomic research involving monkeys, the animals' access to water is always scrupulously controlled. The reason being that water or juice rewards are used during experimental trials as means to motivate subject performance. Monkeys, evidently, have to crave liquids in order to perceive their rewards as valuable and for the results obtained to be meaningful. In consequence, water control is exercised as long as monkeys are seated in their chairs performing tasks. As previously seen, this represents a period of minimum five days a week. As an example, this is present in McCoy & Platt (200) who wrote that: "in our experiments, access to fluids was limited during the week but freely available on weekends". Yet, it appears that sometimes the number of days spent being water-deprived by the subjects can be pushed from 5 to 6. This was the case for the animals in O'Neill & Schultz (2010) where "during training and testing, the monkeys were on a restricted water schedule 6 days of the week with 24 hr water *ad libitum*". While on this low-water-regime monkeys are given a fixed minimal daily allocation which is often separated in two separate rations; the behavioural ration which is the cumulation of everything obtained during the behavioural task and an additional one-take ration which cannot be smaller than 25% of the total.

A first thing which is intriguing about water-deprivation, however, is that for quite some time it was performed even though it was not clear whether animals were able to regulate their fluid balance appropriately under these experimental settings (Yamada & Glimcher, 2010). A second preoccupying aspect is simply that, in labs, monkeys are able to satisfy a need as basic as quenching their thirst freely as little as one or two days weekly. Finally, one can also point out that organisms exposed to prolonged periods of water deprivation are more easily associated with fatigue, fainting, and even delirium in extreme cases. But even without going this far, when one knows how unpleasant the sensation of thirst is, how powerful an urge it can be, and how annoying and difficult it would be to sustain it for five days straight, it is sufficient for one to have a good idea of how difficult and draining it must be for the monkeys.

3.3. Remedying the Transparency Issue

At the beginning of this chapter, I alluded to the fact that the acute lack of transparency exhibited by neuroeconomic articles relying on monkey experimentation rendered a complete depiction of the suffering of the subjects difficult. In this section, I shall attempt to remedy this situation by filling up the void created by this lack of transparency the best I can. To be more precise, my plan is to expose what was gleaned here and there – mostly by NGOs defending the animal cause – regarding the breeding, selling, and treating of the monkeys used for research purposes. I will, therefore, try to engage with (1). That is, give more information concerning the origin of the monkeys and the environment they are kept in. Doing so will allow us to greatly supplement the already extensive list of harms derived from using monkeys as subjects in neuroeconomics.

I am fully aware that what will be revealed here concerns the use of monkeys in research in general. Some might say, as a consequence, that I take the risk of being unfair towards neuroeconomics for working under the hypothesis that the typical monkey subject in neuroeconomic research is treated as badly as those whose fate will be described below. After all, this might not be entirely true. Perhaps neuroeconomists are very thoughtful of those things and always try to do their best to be 'cruelty-free' when purchasing or breeding their subjects. This might be, but it is difficult to verify. Indeed, the widespread lack of transparency in the field makes it virtually impossible to determine the extent by which what will be said below applies – or not – to neuroeconomic investigation. On another note, I also believe that suspecting neuroeconomic subjects of being as poorly treated as in any other domain of science is far from being unjustified. Given the invasiveness of the methodology used and how far the researchers are already willing to go to obtain results, it might not be a completely absurd nor exaggerated position to hold.

3.3.1. The typical life of a laboratory monkey: before the lab

The life of monkeys used as research subjects can begin in two possible ways: they are either captured in the wild or bred in captivity. In theory, the purchasing of monkeys captured in the wild by laboratories is illegal. In practice, however, the exact traceability of where a monkey is coming from is difficult to operate. As NGOs such as PETA deplore, it is not uncommon for trappers in countries of South-East Asia – Laos and Cambodia first and foremost – to hunt down macaques and sell them to scientific facilities or primate breeding centres for profit. In order to abduct primates from their homes in the wild, it has been reported that trappers often shoot mothers from trees – stunning the animals with dart guns – before capturing the babies who are still clinging, panic-stricken, to their mothers' bodies. Some wildlife traders even catch whole primate families in baited traps. Once captured, the animals are often packed into tiny crates with little to no food or water in the wait of being sold and taken somewhere else.

When primates are bred in labs or dedicated facilities, things are far from being any better for them. In labs, the animals are raised in an environment made of barren steel cages wherein females are usually artificially inseminated. After several months of gestation in a stressful and unfit environment, they give birth directly in the confined space of their cages. Usually within a span of three days after delivery, new-born babies are forcibly torn from their mothers who were reported to, as a result, loudly scream and exhibit behaviour that can easily be associated with panic and fear. In dedicated facilities – often referred to as 'monkey farms' – things are rather similar. Monkey farms are, unlike laboratories, institutions which are solely dedicated to the breeding and trading of non-human primates purchased by scientific facilities to serve as research subjects. Although many of them are located in Asia where the monkeys are from, more developed countries like the US also possess similar institutions on their soil.

In an article published online by *The Dodo* in 2017, photojournalist Jo-Anne McArthur recounted the experience she had had visiting three macaque breeding facilities in Laos where men in charge took pride in telling her they sold monkeys to labs from all across the globe. Without much of a surprise, monkeys were kept in horrific conditions in all three. "These animals are basically just being kept alive," the journalist said. "They're not getting much food, and there's a hierarchy in each cage. So the older monkeys get all the food, and the younger ones are left to scramble and fend for themselves. So there's a lot of starvation in these cages". To make matters worse cages are filthy, the workers carry the animals from places to places showing very little to no consideration and all, and they don't always remove the bodies of the monkeys who could not survive (Figure 10).

Figure 10. Living conditions in a primate breeding facility in Laos. © Jo-Anne McArthur/We Animals.

In the United States, the Primate Products Inc. (PPI) is a notorious Florida-based primate dealer importing, warehousing, and selling monkeys destined for experiments. It is one of the biggest in the business and was awarded federal contracts worth more than $13 million dollars by the National Institutes of Health, the Army, and several prestigious universities. Recently, the PPI was investigated by PETA and the report is alarming. Inside the buildings, monkeys are constantly chased, roughly-handed, and severely stressed by employees. Workers with no formal veterinary training "grabbed terrified monkeys by their sensitive tails […] they aggressively swung nets at them, yanked them off the fences that they desperately clung to, and even hurled them into nets". Most of the time monkeys were in pain and denied adequate care. As the report stresses: "some monkeys with painful injuries, including exposed bones, were left to suffer for days. One monkey was denied adequate veterinary care for an exposed vertebra in her tail for at least seven days, despite the witness's having verbally notified a supervisor, a PPI manager, and another worker repeatedly about the injury". Most of those injuries were either caused by the violent handling of the workers or by the monkeys themselves. Indeed, the psychological stress of being imprisoned and given nothing to keep them occupied increased the occurrence of fights. This was particularly true for subordinate monkeys who, with no escape available, lived in fear of both staff and other animals. In the end, "dozens of reports documented that the monkeys were attacked, were held down and mounted, and had open wounds and extensive hair loss". To top it all off, living conditions in the enclosures were terrible. The monkeys were confined to barren concrete pens often filled with "days' worth of accumulated waste and even, apparently, black mold". Moreover, monkeys kept outside were denied heat throughout the winter which led to several reported cases of frostbites.

Be they captured in the wild or bred and warehoused in Asia or the US, monkeys used for research are likely to go through a lot already before they even reach the lab. This remains true until the very last step of their journey when the animals are shipped in the cargo holds of airplanes. Monkeys are crammed into crates which are usually too small for they to stand up. The animals have to endure poor ventilation, loud and unfamiliar noises as well as extremes of temperature and humidity. They may become ill or die in transit and are made worse if there are delays en route. With such adverse conditions tragedies automatically appear. In an article published in 2021 by the journal *The Independent*, news was made public that many monkeys had died in a plane flying around 720 long-tailed macaques as cargo from Cambodia to Houston for research purposes. This is, however, only the fraction of a tip of a gigantic iceberg.

3.3.2. The typical life of a laboratory monkey: inside the lab

Now that I touched upon what monkeys go through before they get into a lab – that is if they are not directly born into one – let me turn to what happens to them once they are the property of a research facility. Whenever they are not used for experiments – including investigating the brain mechanisms responsible for decision-making – monkeys are kept in locked barren cages made out of stainless steel (Figure 11).

The precise dimensions of a cage may vary from product to product but they are all mainly devised to contain a single individual in a confined space; the room available being barely sufficient for the animal to turn around. Keeping animals isolated in a small space has two main advantages. On the one hand, animals are prevented from harming each other. Indeed, and as already alluded to, the psychological cost of captivity fuels violent attitudes and fights can erupt between the subjects. Separating them is a way to cope with this difficulty. On the other hand, small cages permit labs to make the most out of all the available storing space they possess. When elaborating a proper space with all the minimum comfort necessary for one single monkey would probably require an important surface, laboratories prefer optimizing. They pile up monkey cages and squeeze as many of them as possible inside cold white rooms. In that way, labs ensure that they will always be able to carry out a maximum of experiments simultaneously with the number of subjects they have.

Figure 11. Three monkeys being kept in a lab (Top) and a pair of two empty lab monkey cages (Bottom). © PETA & PrettyIndustries.

In research facilities, living conditions are in total opposition to the type of environment the monkeys have evolved to face in their natural habitat. Barren steel cages are a far cry from the lush forests and savannahs where they would live in otherwise. In the wild, non-human primates may travel for miles, foraging for a variety of foods, socializing with family and friends, climbing hills, swinging from vines, swimming in rivers, scampering across fields, and cavorting with their companions. All of this is refused to them. In laboratories, these animals have barely enough room to sit, stand, lie down, or turn around. The rich days full of sensory stimulation that they could be experiencing are here replaced by days that are devoid of colour, scent, and almost every other type of environmental enrichment. The only comfort that primates might have access to from time to time is very meagre; being given cheap plastic toys, scratched mirrors, and occasional slices of apple or banana by researchers.

The joint influence of social isolation and lack of stimulation for sustained periods of time leads to the development of abnormal behaviours that cannot all be contained by putting the monkeys apart from each other. Many go insane, rock back and forth, pace endlessly in their cages, engage in repetitive movements, or bang against the bars. Acts of self-mutilation are also very common. Monkeys often tear out their own hair, compulsively lick or bite their own flesh, gnaw their own tail, or break some of their teeth against the structure of their cage. In the end, seating the animals in primate chairs during experiments is far from being the only type of pain-inducing restraints that they will have to face. From almost beginning to end, the life of a monkey subject is one of confinement and associated traumas.

3.4. The Considerations for Animal Welfare

To end this chapter I wish to briefly touch upon a passage that can be found in every research article resorting to non-human subjects. This includes, of course, all the neuroeconomic papers cited thus far. This passage is made out of one or two sentences taking the following form: "All procedures were approved by the Duke University Institutional Animal Care and Use Committee and were designed and conducted in compliance with the Public Health Service's Guide for the Care and Use of Animals". This passage is present to reassure the reader on the fact that all procedures were performed according to current guidelines and appease any potential ethical considerations they may have. It makes clear that the experimental protocol was reviewed and approved by a specialized ethics committee. The role of such committees is to ensure that the treatment of the animals for the purposes of the experiment at hand strictly respects the rules concerning their handling which were allegedly elaborated to restrict animal suffering as much as possible during experimentation; to make sure that, for instance, the subjects are to receive minimal medical attention before, while, and after all necessary surgeries. They are also in charge of assessing whether the experiment to be performed is acceptable in light of what we can expect it to teach us.

For some people, this control and reviewing process is enough to dissipate doubts regarding the desirability of any type of animal research. After all, if it was authorized by the experts who make up those committees, and who judged that it could be conducted, what is there more to say? Here, I do not seek to elaborate a detailed criticism of the reliability of committee-reviewing processes. Such work can be found elsewhere (Plous & Herzog, 2001; Schuppli & Fraser, 2005). What I will do, instead, is simply stress that such a criticism can be associated with the fact that the existence of committees do not entirely preclude – and this is unfortunate given their main objective – the conducting of badly designed experiments. Many experiments, indeed, can be found in the animal experimentation literature for which, although the procedure had them being approved by a committee, several flaws can still be found (Festing, 1994; Festing & Altman, 2002). For instance, it is not uncommon for studies on animal subjects to lack adequate precaution to reduce statistical bias in animal selection and outcome assessment (Kilkenny & al., 2009) as well as to exhibit methodological unclarity which greatly impairs their reproducibility (Glasziou & al., 2014).

On another note, nothing prevents committees to approve of painful methods. Think about what was just touched upon regarding the use of non-human primates in neuroeconomics. Across the years, everything detailed in this chapter was submitted to different committees times and times again, everything was reviewed times and times again, and everything was approved times and times again. From the implantation of metallic threads on the eyes to the opening of the skull, from being restrained in chairs to being water-deprived for several days. Committees tolerated all of this and judged that it was justified in the context of neuroeconomic investigation. However, the sheer fact that certain people agreed on monkeys being experimented on in such ways does not make it any less painful nor any less invasive for the animal subjects themselves. So, in the end, one's questioning of the morality of such practices on utilitarian grounds can still very much be legitimate despite the support they received by committees simply because their pain-inducing feature does not, evidently, disappear.

3.5. Conclusion of Chapter 3

In this chapter I did my best to demonstrate the harms that using monkeys for neuroeconomic experiments generates. Scrutinizing the methodology neuroeconomists rely on, I made it clear that it was particularly invasive and more than likely to induce a decent amount of pain, stress, fear, and discomfort to the animals. This is so because the monkeys are greatly restrained, water-deprived, and have to undergo several surgical interventions which involve the creation of openings in the eyes and the skull to be implanted with recording devices. Yet, every intervention is delicate and puts the health of the animals at risk, opening up the possibility for death, infections, and other complications. Besides experimental procedures, I also argued that this list of harms could be completed when investigating further and seeking to resolve parts of the transparency issue exhibited by neuroeconomic articles. I made the point that we had no reasons to consider researchers in this specific strand of research as obtaining and treating their subjects any differently than any other domain of the neurosciences. As a result, it is fair to say that experimenting on monkeys for neuroeconomic purposes can also be associated with alienating captivity environments detrimental to both the mental and physical health of the subjects and with the promotion of an industry of breeding, warehousing, purchasing, and shipping of sentient beings which shows very little to no consideration at all for what the monkeys might be feeling.

Chapter 4: The Benefits and Why They Can Be Mitigated

After having scrutinized the harms inflicted to the monkeys when they are used as subjects for neuroeconomic experiments, let us turn to how those harms can potentially serve to improve the lives of sentient beings. From my understanding of the literature, it appears to me that the types of benefits to be derived from monkeys in neuroeconomics fall into two categories. Each category can, in turn, be divided into several subsections. The problem, however, is that each of those benefits can be mitigated. In other words, the strength of the positive effects associated with this strand of research are not as significant as they might appear at first glance. I open this chapter with two important preliminary comments defining what will count as a benefit for the issue at hand and how they are to be classified. I then continue by presenting the different types of benefits to be derived from monkeys in neuroeconomics before explaining why they can be qualified.

4.1. Preliminary Comments

4.1.1. Precision and insights cannot count as benefits in themselves

In the first chapter I presented the reasons adduced to justify experimenting on monkeys for neuroeconomic purposes. More particularly, I said that two of them were (1) the precision of the results obtained – all the more important under the assumption that the neuronal processes under investigation are similar in both humans and monkeys – and (2) the evolutionary insights we can gain regarding the emergence of human decision-making. What is worth stressing even more, however, is that those two specific reasons explain why the knowledge derived from monkey experiments is important. They explain why it has value for neuroeconomists. This is well reflected, for instance, in the words of Paul Glimcher. In a book chapter he wrote to present the discipline, the forefather of neuroeconomics stated that: "these studies of monkeys are of importance for two reasons. First, they demonstrate the surprising similarities in the economic behaviour of humans and our nearest relatives. Second, they employ highly precise brain measurement technologies that cannot be used in humans." (Glimcher, 2009, p.271).

As highlighted in the previous chapter, utilitarian ethics is consequentialist. This has an important consequence on how we should appreciate the advantages of experimenting on monkeys spelled out by Glimcher and listed above. Indeed, from a utilitarian standpoint, what matters is not merely the inherent properties of a practice or a deed such as its precision or the evolutionary perspective it grants us. What matters is the positive and/or negative effects the practice under investigation and its properties generate on the overall level of happiness. The corollary is that one cannot, therefore, consider the precision and the insights associated with experimenting on monkeys as benefits in themselves. That is, as features carrying positive moral worth *per se*. Doing so, indeed, requires establishing a link between the advantages of such research – which explains why it has value for the scientists – and a beneficial contribution to happiness in general.

To remain consistent with what has been said concerning the specificities of the utilitarian framework detailed in chapter 2 – and also just quickly recalled above – I will in this chapter only focus on the ways neuroeconomic knowledge obtained in monkeys can be used to improve the lives of sentient beings. Monkeys undoubtedly bring us precise insights and results. But those results need to be addressed in light of their practical applications – that is how they can be truly utilized – in terms of generating happiness and/or reducing pain. Such consequences are the only ones that can, according to utilitarian ethics, be rightfully labelled as 'benefits'.

4.1.2. Two categories of benefits

Before discussing the benefits of using monkeys in neuroeconomic experiments, I wish to say that I decided to organize them into two categories. This way, I hope, things will be easier to spell out. To make up the categories, I decided to operate a distinction between (1) the benefits that accrue to monkey experimentation alone and (2) those that can be associated with neuroeconomics as a whole but for which monkey experimentation can be said to contribute.

Monkey research – via its precision and what it teaches us about human economic behaviour and its origin – helped neuroeconomics develop to the stage it is at today. It would be fair, as a consequence, to hold monkey experiments at least partly accountable for any positive impact on happiness the neuroscience of decision-making may possess. I take this view seriously. Indeed, omitting this dimension would be taking the risk of developing an incomplete and/or biased view of the benefits of monkey research in neuroeconomics. This is particularly true because – as we shall see – most of its benefits are of this kind.

Reverting to the distinction made above, and although both aspects are important, there exists a crucial difference between a benefit that we owe exclusively to experimenting on monkeys and a benefit only partly imputable to it. In the case of the former, the benefit in question would have never been obtained had the practice never existed. In the case of the latter, if experimenting on monkeys had never been performed, it is – in principle at least – solely the magnitude of the benefit that would have been diminished. To be more precise, this decrease in magnitude would have been in proportion to the significance of the contribution but the benefit itself would have probably still remained, in one way or another. This is important to keep in mind while considering the two categories of benefits I want to rely on.

Logically enough, in the first category of benefits I will regroup those of the first kind. That is, those that are exclusive to monkey experiments in neuroeconomics. In the second category, I will regroup those of the second kind. Namely, the benefits of neuroeconomic research in general for which the results obtained in monkeys offered relevant insights. I will now address the two categories in turn.

4.2. The Benefits Exclusive to Experimenting on Monkeys: Impacting Researchers and Subjects

As far as I am concerned, I have identified two ways the neuroeconomic experimentation of monkeys and its characteristics can alone improve the lives of sentient beings. The first one pertains to the thrilling and excitement that might be felt by the researchers while performing the experiments and observing the results. The second one has to do with what we learn about the monkeys themselves. Knowing more about their brains, indeed, is probably valuable for anyone seeking to improve the quality of their lives; be it because of probable therapeutic benefits or simply because it allows us to have a better grip of what brings about happiness in monkeys.

4.2.1. The thrill of research

Researchers are, just like the subjects of their experiments, sentient beings. They are capable of feeling pleasure, enjoyment, pride, and excitement. The consequence is that, if there exists a way by which experimenting on monkeys can stimulate or promote such positive emotions in researchers, then the hedonistic approach tells us it ought to be taken into account.

First off, devoting one's life to research is a path very few walk down. What I take from this observation is that building a career as a scholar is a matter of passion. One has to very much appreciate what one is doing research on to have been through the difficult task of obtaining a Ph. D, the struggle of finding position at a university, and being willing to deal with the demanding rules of the academic world more generally. For this reason, I believe, it is safe to assume that scientists find what they do pleasant and stimulating. Be it otherwise, they would have probably chosen a different course for their lives.

But if doing research brings joy to the researchers, why is experimenting on monkeys any different than experimenting with human subjects? Both situations offer an opportunity for the scientists to do what they love. They can set up experiments, perform them, and obtain data allowing them to know more about the complexity of the decision-making process and its neural substrates. This is true. Yet, although this 'thrill of research' is probably also here while studying humans, using monkeys may exacerbate it because it is more challenging and the results obtained more precise. Those two aspects are often of prime significance for scholars.

When it comes to the challenge it represents, it is hardly deniable that using non-human subjects necessitates a decent amount of expertise on the part of the researchers if the experiments are ever to be properly carried out. Indeed, it is usually easier to perform experiments in humans because they have a far better comprehension of what is expected of them, know how to limit their movements when recording is under way to prevent interfering with the instruments, and can control their temper if the experiment requires calmness, patience, and/or supporting discomfort. Experimenting with monkeys, on the contrary, is always more delicate. Monkeys need to be trained for long periods of time and several precise surgical interventions are necessary to correctly "prepare" them for their tasks.

Actually, finding ways to elaborate experiments with monkeys which lead to meaningful results regarding a specific dimension of decision-making is quite an achievement. It is something worth getting excited and prideful about. Such an achievement takes advantage of a researcher's skills to an extent which is not always this important while setting up experiments with human subjects. To study humans playing games, for instance, one generally 'simply' needs to place electrodes on the scalp or use fMRI while the subject is performing. To do the same thing with monkeys, in comparison, scientists need to resort to their surgical skills and detailed knowledge of the brain to identify where to precisely lower the electrodes and then carefully proceed to do it. This state of affairs, it can be assumed, is both enriching and intellectually stimulating for some of them.

In addition to the thrilling challenge it represents for the researchers, experimenting on monkeys also permits them – as was stressed already – to work with more precise instruments. It would not be absurd, however, to conceive that operating such technology could potentially be enjoyable for neuroeconomists. In science, there is always a unique satisfaction to uncover the precise cause behind a given phenomenon. In the case of investigating what occurs in the brain when decisions are made, precise causes lie in specific neuronal activity and it is this very type of activity which is best explored with electrodes placed directly inside the brain, next to the neurons of interest. Monkey experimentation can therefore be said to contribute to unveiling the mysteries of the brain to a point hardly reachable otherwise. This state of affairs can constitute a source of enjoyment and satisfaction for individuals dedicating their lives to brain research.

4.2.2. For the monkeys' sake

In addition to what it can do for the researchers, one can make the point that using non-human primates in neuroscientific research has the unique advantage of allowing us to better understand the monkeys themselves. Most of the time, the brains of monkeys are envisaged as nothing more than mere proxies for us to learn more about human neural processes. We ought not to forget, however, that such an investigation also teaches us a great deal about the neural processes of the animals. After all, their brains are what is being studied first-hand.

If the knowledge we derive from their brains can be beneficial to humans, it can also have positive spillovers for the subjects. A first example of this lies in the study of valuation. Indeed, knowing how monkeys come to value certain things – and under what circumstances – is supposedly valuable for anyone seeking to promote the happiness they feel in one way or another. In fact, neuroeconomic experiments are a very good tool to observe how physical reactions in the brain can be associated with states of pleasure/pain and how to, in turn, promote/discourage such reactions.

Another way neuroeconomic knowledge can improve the life of captive animals is via the enhancement of training methods which have always raised concerns regarding the welfare of animals (Laule & al., 2003). Captive monkeys are, for various reasons, almost systematically trained to perform several tasks. In labs, monkeys are trained to perform the tasks researchers want to study. In zoos, the animals are trained to remain calm in the vicinity of veterinarians. Usually, training is operated with positive reinforcements methods and, depending on the task, the training process can be quite long, laborious, and a source of stress for the animal (Prescott & al., 2003). Such methods rely on a combination of rewards and punishments for the subject to associate the desirability of an act with a treat – something positive – and the undesirableness of another with something they do not like. The investigation of how punishments and rewards are processed by the brain is a living research area in the field of neuroeconomics which is often referred to as 'reinforcement learning' (Daw & Tobler, 2014). Reinforcement learning frequently relies on monkey subjects (Lee & Seo, 2007). Arguably, such research can be useful to elaborate and improve training techniques making animals more responsive by taking advantage of the brain areas associated with valuing rewards and fearing punishments.

On another note, investigating the brains of monkeys in neuroeconomics can also lead to therapeutic benefits for the animals. Generally speaking, such experiments enrich our knowledge of the brain and of what a "proper" functioning of this organ is supposed to be under given circumstances. We know for instance that such and such decision-making setting is going to involve the activation of such and such neurons. By comparison, we can utilize this information to more easily detect deviations from typical and expected reactions in the brain which might be caused by certain mental disorders and neurodegenerative pathologies. Scrutinizing the neurons firing in monkeys in response to external stimuli and under normal circumstances is relevant to better understand, diagnose, and treat brain affiliated diseases that may befall upon the animals.

4.3. Neuroeconomic Benefits Monkey Experiments Contribute To (1): Promoting Good Health

When it comes to the ways experimenting on monkeys can contribute to the benefits of neuroeconomic science, one can first mention the promotion of good health. For utilitarians, the prospects of curing diseases and/or alleviating the negative aspects of poor health conditions is highly valued. This is all the truer when what we seek to promote – i.e., happiness – is understood in hedonistic terms. Indeed, someone's mental and physical health is so closely intertwined with the emotions subjectively felt that improving them is an undeniable – perhaps even the greatest – source of happiness. As was just touched upon, neuroeconomic research on monkeys can possibly have positive therapeutic consequences for the animals. But it can also, by supplementing typical neuroeconomic results obtained in humans, be of some help in the fight against certain human health problems. To show exactly how this can be the case, let me consider two papers. One is by Platt & al. (2010) and the other by Kishida & al. (2010). In the first one, the authors argue that neuroeconomic developments are useful to better understand addictive behaviours. In the second one, it is claimed that neuroeconomic game theory can serve as an interesting tool to approach mental disorders. Although different in many aspects, the two articles share something crucial in common. In both of them, the researchers made their point relying on a corpus of studies including experiments in both humans and non-human primates. Whereas mentioning experiments conducted with human subjects is expected – given that results obtained in humans are evidently helpful to tackle diseases in humans – referring to findings in monkeys to elaborate their argument shows, explicitly, how relevant the researchers take such results to be for the issues they are dealing with.

4.3.1. Monkey experiments and addiction

In their article, Platt & al. (2010) evoke three aspects of addictive behaviours for which neural processes investigated in neuroeconomics are particularly rich in insights and testable predictions. They are (1) the encoding of value in the brain, (2) the processing of social context, and (3) what happens in the brain when risky decisions are made. In what follows, and to stay in line with the topic of this thesis, I will simply restrict myself to highlighting the type of contribution that monkey experimentation makes for all three.

The study of valuation is important for the clinical investigation of addictive behaviours. Indeed, from a certain perspective, addiction can be perceived as an unhealthy and completely out of proportion valuation of certain substances and/or habits. Chapter 1 already features an overview of how the study of valuation is performed on monkeys and of the knowledge we can derive from it. I will, obviously, not recap everything here. I will solely bring to the reader's attention that it is for our present concern that such knowledge might come in handy. To make things more vivid, just consider the famous work of Padoa-Schioppa & Assad (2006, 2008). As previously noted, the authors stressed the importance of dopamine neurons in the orbito-frontal cortex of rhesus macaques in transforming information into a common currency of subjective value. What can be advanced is that such knowledge is of some importance to understand how this system of value might be highjacked or overridden when dependencies emerge. Something similar can be said about neurons associated with related concepts but located somewhere else in the brain.

When it comes to the role played by social context in addiction, it is evident for many. Decisions to consume alcohol, do drugs, or start to smoke, are often initiated by social context and the behaviour of those around us. Consequently, having a better understanding of what happens in the brain when such contextual factors are integrated into the decision-making process is helpful to better grasp the phenomenon of addiction. From the literature, a good way to investigate how social context influences individual behaviour seems to be measuring the value individuals confer to social stimuli. That is, to signals possessed or emitted by others which have the potential to prompt one's actions. With that objective in mind, Deaner & al. (2005) set up an experiment in which male rhesus macaques had to choose between two visual targets. Selecting one target yielded fruit juice while selecting the other yielded both a juice reward and the picture of a familiar monkey. By systematically changing the juice payoffs for each target and the pools of images revealed, the authors could conclude that male monkeys were willing to forgo larger juice rewards in order to view female sexual signals or faces of high-ranking males. Yet, both signals are especially relevant for guiding behaviour – to prompt mating or fighting responses of an individual – depending on the reaction of others. On a neurobiological scale, those results are completed by monkey studies revealing the central place occupied by the amygdala in processing visual stimuli (Adolphs & Spezio, 2006). This part of the brain appears to be particularly involved in how diverse and complex social influences steer individual actions. This is a good way to start to better understand how individuals are pressured by their peers into adopting certain habits.

Given the fact that most addictive substances have adverse effects on health which are commonly well-known, consuming such substances represents a case of risk-taking. As a consequence, having a better grasp of the neuronal activity responsible for the perception of risk is relevant to improve our knowledge on the mechanisms of addiction. Similar to the study of valuation, an overview of the neural study of risk on non-human primates can be found in chapter 1 of this thesis. I will therefore, and here again, simply make things tangible by focusing on one single mechanism. The reader needs to keep in mind, once again, that a similar reasoning would also apply for the rest of the brain areas implicated in the appreciation of risk and investigated on monkeys. The mechanism I will focus on is the implication of neurons firing in the posterior cingulate cortex (CGp) in risk preferences. The role of the CGp in favouring risky rewards was famously highlighted by McCoy & Platt (2005) but also further investigated in following years. In an experiment in which two monkeys had to perform oculomotor tasks, Hayden & al. (2008) studied the contribution of the CGp to behavioural modifications subsequent to certain actions. Neuronal activity was recorded while the subjects had to visually choose between targets whose rewards differed in magnitude and certainty. The reward outcome of each choice was such that it strongly influenced the following decisions. The conclusions of the researchers were that neuronal firing in the CGp on any one trial could be used to consistently predict switching to the alternative option – the safe option if the risky was chosen previously or *vice versa* – on the next trial by the subject. Furthermore, and even more important, microstimulation in the CGp right after a risky choice encouraged a preference reversal for the safe option on the subsequent trial. If anything, such results are important to highlight the neural cause of appreciating risk and safety. This is crucial for all activity individuals engage in and which might be dangerous in one way or another. Consuming illicit substances or not moderating one's consumption when it comes to what is authorized legally such as sugar, alcohol, and tobacco, and which is known to be addictive and unhealthy, is one example of that.

4.3.2. Monkey experiments and mental disorders

For Kishida & al. (2010) a neuroeconomic approach to mental disorders can be developed on the basis of game-theoretic insights provided by neuroeconomic studies. To be more precise, the idea the authors defend is that gambling and economic games can be used as probes to investigate mental diseases like schizophrenia, multiple personality disorder, depression, Alzheimer's, and so on and so forth.

Game-theory has the advantage of granting us with simple and well-studied frameworks to examine how individuals do and should behave when they are interacting with others in games. Such games typically possess concrete notions of what an 'optimal' play is, to what someone's move ought to be. This permits us to easily track and determine whether the choices of a subject match or deviate from the optimal. Yet, by examining the brain of subjects playing games it is possible to highlight the type of neuronal activity commonly associated with normal and optimal attitudes on the one hand and to detect deviations from such behaviour which might be the indication of a mental disorder on the other.

It would make sense, indeed, to suppose that any recurrent problem arising in the course of playing a game – in estimating the value of an option or the risk associated with the payoffs – will reveal itself throughout constant losses. This is precisely the situation that one would expect to witness in the presence of brain damage, and psychopathologies. When the biological substrates responsible for typical strategic interaction are damaged or altered in a significant way, abnormal behaviour is certain to be expressed. Put otherwise, individuals with mental disorders tend to play games differently and this attitude is mirrored in the activity of their brains. The neuroeconomic study of economic games, it is contended, provides ways to capture and quantify this behaviour as well as its associated neural correlates to produce novel biomarkers of mental diseases.

This is where experiments with monkeys appear on stage. The findings obtained when monkeys play games – some of which were overviewed in chapter 1 – contribute to enrich our models of what exactly happens in the brain when decisions have to be taken in a strategic environment. They allow us to identify the biological substrates responsible for typical strategic behaviour. On the matter, experimenting on monkeys completes the results obtained in humans by relying on precise neuronal measurements. Not only are we able to determine which parts of the brain activate when individual play games but which group of neurons are firing in response to this or that aspect of the game. Such insights are useful to refine the precision of biomarkers of mental diseases down to the neuronal scale. This can be key to increase the capacity we have to detect brain related issues early and to improve diagnosis.

4.4. Neuroeconomic Benefits Monkey Experiments Contribute To (2): Improving Policy-Making and the Law

Public policies and laws have an impact on the lives of many individuals and an undeniable capacity to foster happiness. They are instigated by public officials who often claim that their objective is to better serve the public's interests by steering their behaviour in one direction or another. They also structure societal life and can be promulgated to discourage criminal acts and foster cooperation amongst citizens. In recent years, the importance of neuroeconomic results for laws and policy-making has been often stressed (Chorvat & al., 2005; Zak, 2004, 2007). Indeed, elaborating better laws and policies can be said to depend on a better comprehension of how the brain reacts when people make decisions and adapt their behaviour in response to certain policy features or modifications in the law. On the matter, one can find neuroeconomic studies on monkeys producing results which are possibly useful for such an objective. More accurately, what can be mentioned are the insights acquired regarding the processing of rewards and punishments and those that can be employed to foster pro-social behaviours.

4.4.1. Fostering pro-social behaviours and cooperative interaction

The brain regions involved in pro-social behaviour and cooperative interaction is yet another insight derivable from neuroeconomic experiments in game-theoretic settings. Allegedly, this knowledge can be seen as valuable for law and policy-makers to best promote pro-sociality, taking advantage of its underlying brain mechanisms. Under the assumption that selfishness and extreme individualism generate dissatisfaction – especially in circumstances where cooperation would have been optimal for the parties involved – reducing their prevalence can be perceived positively.

In monkeys, interesting results can be found regarding issues of trust and cooperation in experiments where they had to play games more complex than rock-paper-scissors or matching pennies. Chang & al. (2015), for instance, trained macaques to play a modified version of the classic dictator game while recording from single neurons in the basolateral amygdala. In this version of the game a monkey (the dictator) was given the opportunity to either donate or withhold rewards from another one. Sometimes, the allocation was automatically made by a computer. With their setting, the authors identified neurons that signalled the value of rewards for both self and the game partner when dictators made overt decisions to give or withhold reward. A similar neuronal activation was, however, not observed when the computer made the decisions. This suggests, the researchers concluded, an active role for these neurons in social decision-making. It also consolidates what had been obtained two years prior. With a similar methodology, Chang & al. (2013) demonstrated that neurons in the orbitofrontal cortex (OFC) mainly encoded rewards delivered to oneself; that neurons in the anterior cingulate gyrus (ACCg) encoded reward allocations to the other monkey, to oneself or to both; and that neurons in the anterior cingulate sulcus (ACCs) signalled reward allocations to the other monkey.

This role of neurons in the anterior cingulate cortex (ACC) in strategic cooperation was also observed when monkeys played the prisoner's dilemma game. In a study by Haroush & Williams (2015) monkeys were trained to perform an iterated version of this game while neuronal activity in the dorsal anterior cingulate cortex (dACC) of one of the players was recorded. As is customary for a prisoner's dilemma, monkeys had to decide between defecting for a small certain reward or choosing to cooperate and receive a larger uncertain reward. Remarkably, the authors identified some neurons selective for the monkey's own choice, some selective for the partner's choice, and a third subgroup of neurons selective for the predicted choice of the partner monkey. An additional hypothesis was that neurons selective for the predicted intentions of others might contribute to the computations necessary for strategic social behaviour. The authors tested this idea by using microstimulation to disrupt normal patterns of neuronal activity in the dACC, which impaired cooperation. This deficit was specific to cooperative interactions, but did not impair the capacity to retaliate following defection by the partner, nor to engage in zero-sum behaviour, in which there was no possibility of mutual benefit. These results strongly implicate the dACC in computations necessary for strategic cooperation.

Thanks to such studies we can have a better grasp of the different pathways in the brain associated with the perception of payoffs not only for oneself but for one's game partner as well. This is important if we seek to encourage individuals to be willing to give more to others or, similarly, to be less bothered when they receive less.

4.4.2. Processing rewards and punishments

Another part of neuroeconomic research in monkeys that can be helpful to improve policy-making and law-enactment is the processing of rewards and punishments. Indeed, both policies and laws aim at steering individual behaviour in certain directions. They do so by using different instruments to encourage or discourage certain courses of action. One can think of granting subsidies to promote eco-friendly deeds or heavily punishing violent acts. Gathering knowledge regarding the neural processes responsible for valuing rewards and fearing punishments can therefore permit us to find ways to strengthen their efficiency.

In monkeys, two sets of studies have the advantage of investigating, at the same time, the neuronal activity involved in processing rewards and the one involved in processing punishments. The first set of findings demonstrates the importance of neurons in core areas of the brain in evaluating both rewards and punishments (Kobayashi, 2012). This is for instance the case of neurons in medial basal forebrain (Monosov & al., 2015) or in the amygdala (Peck & Salzman, 2014). The second set of results highlights, *a contrario*, groups of neurons that seem to be specialized in one or the other.

Matsumoto & Hikosaka (2009), for instance, found that a population of lateral habenula neurons was most strongly excited by a conditioned stimulus associated with the most unpleasant events. That is, the absence of rewards or the presence of punishments. In addition, this neuronal population was also excited by the punishment itself and inhibited by the reward itself, especially when they were less predictable. The idea that punishments and rewards are processed differently in the brain was also investigated in prefrontal cortex. By recording neuronal firing in the ventromedial prefrontal cortex (vmPFC) of monkeys, Monosov & Hikosaka (2012) noticed that neurons in the ventral part were persistently more active in the appreciation of rewards. Conversely, neurons in the dorsal part were persistently more active in the aversion towards punishment.

4.5. The Mitigation of the Benefits

Now that I have presented the different domains where experimenting on monkeys for neuroeconomic purposes can potentially generate happiness, I would like to end this chapter by spelling out the reasons I have to believe that this generation of happiness can be mitigated. I will do so relying on the distinction made at the beginning of the chapter regarding the two types of benefits associated with monkey experiments in neuroeconomics and put both of them into perspective. Let me deal, first, with benefits I said were exclusive to it. That is, let me deal with its positive impact on the lives of researchers and subjects.

4.5.1. The thrill of research: revisited

In a nutshell, I said that experimenting on monkeys could generate pride and enjoyment in researchers because it takes advantage of two aspects of a scholar's life which are usually valued. On the one hand, it is more challenging and permits them to employ their skills more fully because using monkeys as subjects is more complex and delicate. On the other hand, it gives them the possibility to investigate the neural substrates of decision-making into more details. This is potentially thrilling for anyone whose life is dedicated to elucidating the mysteries of the brain by unveiling its underlying mechanisms. It appears to me, however, that the positive feelings that might be generated for certain targeted individuals can be more than outweighed – even perhaps completely belittled – by the negative feelings others might feel. Indeed, if we are willing to include the positive things experimenting on monkeys makes some researchers feel, we should also be willing to include the negative ones felt by those being appalled by the way monkeys are treated[6].

One can think, first and foremost, of all the animal rights activists. Without them, most of what we do know of the treatment of animals in labs would still be shrouded in mystery. One can also think of certain researchers who either oppose animal experimentation – therefore sticking to working with humans – or who experiment on them but without deriving any type of satisfaction whatsoever. Lastly, we have informed citizens who, without knowing everything

[6] On purely technical grounds, this point might be subjected to an issue of 'double-counting'. We must therefore be careful not to count what is felt by the monkeys twice when considering their pain of being experimented on and people's interest for them.

in detail, may know enough to be horrified and saddened thinking of the circumstances under which animals are being bred, kept, and used to increase human scientific knowledge.

Claiming that what the above-listed individuals feel outweigh what certain researchers feel means one thing. It means that I take the intensity of negative sentiments to be arguably superior to the intensity of positive sentiments derived from using monkeys in neuroeconomics. The reason I would give for that lies in numbers. First of all, the research community isn't really the largest professional community there is. There are, for instance, way more construction workers than scientists and only a fraction of this already small community is working with monkeys in the field of neuroeconomics. What is more, only a fraction of this fraction is potentially deriving positive things out of it. Certain researchers, as just discussed, might very well experiment on monkeys without appreciating it or finding it thrilling.

On the other side of the spectrum, the number of those strongly opposing or criticizing the way humans treat other animals – including non-human primates in labs – has been ever growing over the past few decades. One simply needs to think of the momentum and the visibility that the vegan movement managed to obtain in recent years to see my point. What was perceived as nothing more than an extreme subculture is now on the path of being included as part of the norm. Concerns about animal welfare preoccupy more and more people daily and associated feelings of disgust, sadness, and anger grow in proportion. With that in mind, it would be difficult to see, at least to me, how the thrill of using monkeys in neuroeconomics – which is specific to such a small population of individuals – would have any chance of exceeding this rising tide in terms of intensity of the feelings it creates in people.

4.5.2. For the monkeys' sake: revisited

The second type of benefits exclusive to monkey experiments in neuroeconomics that I touched upon relates to how the knowledge obtained can be utilized to improve the lives of the animals themselves. I mentioned the fact that investigating their brains can be useful to know more about what makes them happy, to ameliorate training methods, and that it could have potential therapeutic benefits for them. The problem with such benefits, however, is that it is difficult to consider them as anything more than just purely hypothetical. That is, as benefits that can probably be obtained – lying in the results – but that are never quite seized and sometimes not even really identified in the first place.

When reading what has been done in neuroeconomic research involving non-human primates so far, it is tough to find any clear mention of how it could concretely serve the interests of the subjects. Arguably, benefits of the kind could be derived from experimenting on monkeys, presenting them was therefore necessary, in my opinion, to avoid offering a biased and incomplete discussion of everything positive that we can rightfully expect from this strand of research. But this state of affairs does not change the fact that no research article in the field clearly elaborates much about the benefits for monkeys in the short, middle, or long run.

Consider the potential therapeutic benefits for instance. As we have already seen, one can find scientific articles proposing ways neuroeconomics – which experimenting on monkeys is a part of – can be helpful to improve human health. However, I systematically failed to find any discussion of the kind concerning how neuroeconomic results can be helpful to improve monkey health. Something similar can be said regarding neural studies highlighting what brings about happiness in monkeys. For researchers, the value of such studies lies in what they allow us to deduce about human enjoyment, not about what monkeys enjoy. As a result, the attention is mainly directed towards applying those findings in areas where human happiness can be increased, not where monkey happiness can be increased.

This is precisely why I say that benefits for monkeys, although they most likely exist, are deemed to remain purely theoretical. No one seems to be very interested in further developing them nor in orientating one's research towards this direction. Doing so does not – and in fact never quite did – seem to be in any neuroeconomist's intentions. No one in the field of neuroeconomics ever said or wrote in one of their paper: "I hereby present an experiment involving two rhesus macaques to study the neural substrates of decision-making. The results obtained are promising to better understand the animals. This is important, in turn, to better serve their interests". Quite the contrary, the attention of the researchers has always been way more focused on what neuroeconomic results can do for humans than on what can be done for the animals they use as subjects. The result of this is an underspecification of the benefits that might accrue to the monkeys and a decreased chance of ever seeing them being implemented in the real world. This is so because not only is work needed to identify how certain results might generate happiness, but also to put them into practice. Yet, the lack of attention that neuroeconomists devote to improving the lives of the subjects is a hurdle to both.

Actually, this obvious lack of attention and consideration on the part of neuroeconomists for investigating and implementing what can be done for the happiness of the animals is also very much present in how they are treated in labs. Surely, if a clear objective of neuroeconomic research on monkeys were to increase their happiness, they would probably not be kept and experimented on the way they usually are. And given that nothing has very much changed on this aspect during the twenty years that passed since monkeys were first experimented on for neuroeconomic purposes, the prospects of this changing in the future can be questioned. This is bad news for all the potential benefits the animals could enjoy but which necessitate a level of consideration on the part of the scientists which does not seem to be improving.

4.5.3. The contribution of monkey experiments to beneficial neuroeconomic results: revisited

Beyond the possibility of increasing happiness all on its own, monkey experimentation also contributes to neuroeconomic benefits. However, this contribution can be also put into perspective. First of all, it can almost always be seen as coincidental; as being the result of a favourable turn of events for the researchers performing such experiments. Proof being that, when reading the papers, one can barely find amongst the reasons enumerated by the scientists to motivate their experiments, the promotion of good health or the aid of policy-making. In fact, scientists seem way more motivated by developing our knowledge of the physiological reactions in the brain responsible for decision-making in itself. Positive impacts of this strand of research on happiness are lucky by-products. They are often obtained or theorized some time after the experiments were performed. Once it was realised that the results gained could be used in other ways, not only to enrich a pre-existing corpus of knowledge.

At this point, one could remark that this reasoning applies to neuroeconomics as a whole – including experiments with humans – and not solely to what is done to monkeys. This is true.

But while it is barely an issue for human experiments to positively influence happiness in a coincidental way because most of them do not generate extreme suffering to the subjects, the same thing cannot be said for monkey experimentation. Experimenting on monkeys for neuroeconomic purposes induces a decent amount of pain to sentient beings and not attempting to directly employ this pain in areas of research where we have good reasons to believe that goodness will be created as a result may be seen as a moral tragedy.

An objector, however, might point out that intentions have little moral worth in a utilitarian assessment. From a utilitarian perspective, only the consequences of an act matter to evaluate its morality, not the motivations of those committing it. Once again, this is true. But the truth is, even when it comes to the consequences that can ensue the obtention of neuroeconomic knowledge, things are far from always being positive. Lucky enough for neuroeconomists, their findings can possibly lead to certain positive spillovers. But it turns out that the very same findings can also be utilized to serve negative purposes. In brief, neuroeconomic findings are a double-edged sword. Yet, if we agree, like we did in this chapter, that monkey experiments should share the credit of certain neuroeconomic benefits via its contribution to key aspects of decision-making, we also need to concede the fact that it ought to share the blame for certain negative consequences that can be associated with neuroeconomic knowledge and knowing more about those key aspects of decision-making.

More specifically, the precise insights experimenting on monkeys grant us about the neural substrates of choice is particularly relevant in the field of neuromarketing. Neuromarketing, as the name suggests, is the application of neuroscientific knowledge to marketing (Weber, 2016). It seeks to incorporate and take advantage of the brain mechanisms responsible for the choices of consumers to increase the efficiency of marketing strategies. For obvious reasons, neuromarketing is often frowned upon. Indeed, it can be perceived as a particularly intrusive and morally questionable attempt on the part of compagnies to manipulate consumers into buying their products, irrespective of whether they might want or even need them. This is done by somewhat "hijacking" the brains of consumers to make what those compagnies sell appear more desirable. Given that experiments involving monkeys are at the forefront of brain research when it comes to the study of valuation and that this is important knowledge for neuromarketing, it is difficult not to link this strand of research to the potential manipulation of consuming behaviour.

What is more, the better steering of individual behaviour possibly permitted by neuroeconomic insights, to which experimenting on monkeys contributed, can be questioned as well. In fairness, when I said that neuroeconomic knowledge could be beneficial by improving policies and laws I was relying on the underlying assumption that both shared the objective of orientating individuals towards what is good for them. This need not be the case. Upgraded laws and policies are also very much useful tools for government only seeking obedience and compliance on the part of their citizens. On the matter, the neuroeconomic study of the processing of rewards and punishments – enriched by monkey experiments – is still particularly relevant. On another note, laws and policies that take advantage of the neural processes of citizens to better reach their goals, even if it is to promote their own good, can fall under the range of vivid paternalist critiques. They represent controversial situations wherein institutions force or encourage individuals into certain courses of action because it is in their supposed interest. This can be said to be detrimental to freedom and autonomy (Kleinig, 1983).

In the end, the contribution of monkey experiments to neuroeconomic benefits can be mitigated for the sheer reason that, even though what is found can possibly serve positive ends, it can also be of some use for purposes which are mostly negative. This does not mean, however, that the happiness possibly generated by the contribution of monkey experiments to the beneficial applications of neuroeconomic results is completely outweighed by its contribution to neuromarketing or paternalism. What it means simply is that it can, at least, be partly outweighed and its strength as a benefit, therefore, partly reduced.

4.6. Conclusion of Chapter 4

In this chapter I discussed the possible ways experimenting on monkeys for neuroeconomic purposes could increase the happiness of sentient beings. I first separated them into two categories with a distinction between what the practice can do on its own and the relevant insights it offers to contribute to neuroeconomic benefits. I mentioned its effect on researchers and possible applications to improve the lives of monkeys as well as its contribution to the fight against mental disorders or to the improvement of laws and policies. Then, towards the end, I introduced the reasons we can have to mitigate those benefits. The conclusion reached here, therefore, is that if monkey experiments can be linked to some benefits, this link is often quite tenuous and can always be questioned.

Chapter 5: The Utilitarian Principle and the Use of Monkeys in Neuroeconomics

In chapter 2, I advanced the utilitarian moral principle I deem relevant for the ethical assessment of using monkeys for neuroeconomic purposes. As a reminder, it states that the use of animals for given scientific purposes is morally justified if and only if (1) it results in a greater balance of happiness over unhappiness than available alternatives and (2) happiness and unhappiness are understood as subjective emotional states that can be experienced by all sentient beings involved. With everything we have seen in the previous two chapters, we are finally equipped to properly confront the neuroeconomic study of monkeys to this principle. The first part of this chapter offers a discussion regarding the state of the balance of happiness over pain that can be associated with the scientific practice at hand. The rest is used to provide an investigation of whether or not this balance can be said to be maximized in light of available alternatives.

5.1. The Balance of Happiness Over Pain

Considering the ethical principle just spelled out we can directly see the importance of the balance of happiness over pain for what is at stake here. Everything will depend on whether or not it can be said to reach its maximum when monkeys are used in neuroeconomics compared to other competing courses of action. However, before comparing this balance of happiness over pain to the ones affiliated with feasible alternatives, one needs to specify it first. One needs to provide a discussion of the way the benefits and the harms of neuroeconomic research on monkeys, both understood in hedonistic terms, can be weighed against each other and what conclusion this weighting process is likely to lead to. Will the balance be positive? That is, can the benefits be said to outweigh the harms? Or, conversely, do we have reasons to believe that the unhappiness and suffering endured by the monkeys are superior to the positive consequences we can expect them to have on the overall level of happiness? Furthermore, once it has been established that one side is outweighing the other, we need to determine whether it is by a great or a small extent. If we, for example, reach the conclusion that the benefits are superior to the harms would that be because they are indisputably greater or because they are just barely sufficient?

Questions like this are always difficult to approach. Complex situations can never be totally and easily synthesized in a nicely organized table where points are attributed to benefits and penalties given to the harms in accordance with their magnitude; where scores are added and subtracted until we obtain a clear, objective, and undisputed mathematical result in the end; and where the sign of this result gives us the answer we need. Unfortunately, we will never really find ourselves in a situation where in the capacity to meaningfully – as in non-arbitrarily – say: “the contribution of neuroeconomic knowledge obtained in monkeys to better understand and fight mental disorders grants it 10 points while the surgical implantation of recording chambers and its consequences costs 8 points”. As a result, and instead of relying on mathematical calculations, I will here resort to a combination of reason and intuition to present the position I hold concerning the state of the balance of happiness over pain that can be associated with monkey experimentation in neuroeconomics. Fortunately enough for us, I do not think this state of affairs is an important limitation. I believe that, with what we have at our disposal already, the picture of the state of the balance can be sufficiently depicted to make my point.

5.1.1. The state of the balance

Let me bring all the pieces of the jigsaw puzzle back together by jointly considering the conclusions reached in chapters 3 and 4. Chapter 3, on the one hand, exposed the pain-inducing methodology employed when monkeys are experimented on for neuroeconomic purposes and made clear that this methodology was greatly detrimental to the health and happiness of the subjects. Moreover, it was also argued that this pain-inducing feature could be supplemented by what laboratory monkeys usually have to go through before and once they are the property of research facilities. In general monkeys are bred, warehoused, shipped, and detained in conditions which show no consideration for what they might be feeling and we have, *a priori*, no reason to believe that things are any different for those used in neuroeconomic experiments. Chapter 4, on the other hand, presented the types of benefits we could possibly expect from this strand of research. Importantly, it was pointed out that such benefits could be mitigated. The happiness researchers feel while conducting experiments can be opposed by the negative feelings it generates in other individuals, the potential benefits for the monkeys are merely hypothetical, and the results we obtain thanks to them contribute not only to the benefits of neuroeconomic knowledge but also to the bad ends it can serve.

In the end, what we have here is nothing more than two separate observations which point towards the same direction. (1) The harms are extensive and can even be worsened when we seek to resolve the transparency issue found in neuroeconomic papers. (2) The benefits we can possibly derive from this suffering can be qualified. Yet, if the intensity of the harms can be increased while – at the same time – the strength of the benefits can be diminished, we have every right to be sceptical about the balance being positive; about the ability of the benefits to clearly and indisputably outweigh what the subjects of those experiments have to endure. This doubtful attitude would simply be the logical and rightful consequence of jointly considering the two claims. It can even be reinforced in light of the equal consideration of interests promoted by the utilitarian framework endorsed here. Indeed, it grants the suffering of the monkeys a moral weight which is as significant as that of human suffering.

In fact, one's intuition regarding the state of the balance of happiness over pain associated with monkey experiments in neuroeconomics could go beyond mere scepticism. When having in mind the invasiveness of the methodology and the vague and uncertain prospects for the results obtained to improve policies or health, it might seem evident that, not only are the benefits not clearly outweighing the harms but that the latter are largely outweighing the former. After all, the magnitude of the harms generated to non-human primates in this field of neuroscience can be associated with death, severe lesions of delicate organs, and huge psychological traumas. Most of the benefits, on their side, and even if we consider them as having been concretely reached, cannot really be associated with positive consequences for sentient beings of the same magnitude. What experiments make researchers feel, the improvement of training methods for captive animals, or the improvement of laws and policies cannot be said to save lives or relieve individuals from atrocious pain. This is a fair point and I share this intuition. But I also think that two obstacles might prevent us, as it stands, to turn this intuition into a definitive assertion; to conclude that the balance is undeniably largely negative.

The first obstacle is the possible acquisition of therapeutic benefits for both the monkeys and human beings whose extent has the potential to significatively favour happiness compared to the other types of benefits. The second one is what can be referred to as 'an issue of sheer numbers'. Namely, the fact that the suffering of an after all quite restricted number of monkey subjects might be offset by even the tiniest improvement it might cause in the lives of a number of individuals simply because this number is large enough. For instance, consider slightly improving the lives of millions of citizens by enhancing the efficiency of a certain national policy. Arguably, this may make up for the suffering of the animals which might have contributed to improving the policy in question.

Here, I will respond to those two points in a similar fashion. I will simply say that, although they might be a hurdle to address the state of the balance with anything more than founded scepticism, given that we seem to have enough at our disposal already to soundly doubt its positivity and the ability of the benefits to clearly be sufficient to outweigh the harms, they are no hurdle to address the morality of using monkeys in neuroeconomic experiments. Indeed, and as we shall see, there are possible alternatives to this practice that offer far better prospects at maximizing the balance of happiness over pain, notably by rendering the acquisition of therapeutic benefits far more likely, and without even needing a recourse to sheer numbers to support the positivity of their respective balance.

5.2. Maximizing Over Alternatives?

Making the point that the balance of happiness over pain associated with the use of monkeys in neuroeconomics is in a questionable state is but the first step to question the morality of the practice. Now that it has been done, let us proceed to the crucial part of the ethical assessment we are concerned with. Let us move to the investigation of how this balance fares compared to those associated with other available alternatives. This is crucial because as Bass (2012) puts it: "before concluding that we've gotten a good deal [with any animal research program] we need to ask if we couldn't have achieved as great or greater gains from the same resources, used some other way" (p.86). In what follows, I shall attempt to make the point that monkey experiments in neuroeconomics, despite the precision and insights it brings us, cannot really be considered "a good deal". The reason being that two potential alternatives seem to offer better prospects for obtaining a maximization of the balance of happiness over pain. Considering everything said so far, and the utilitarian principle I am working with, this observation represents the last piece of the puzzle that will put me in the position to offer a conclusion vis-à-vis the morality of this strand of research from a utilitarian perspective.

5.2.1. Two Available Alternatives

Let me first clarify what I have in mind when I speak of the type of alternatives that using monkeys for neuroeconomic purposes can be compared to for its ethical assessment. Here, by 'alternative', I mean nothing more than what is commonly understood from an everyday usage of the term. That is, whatever else could have been done, had we not decided to employ certain resources the way they are currently being utilized. In addition to that definition, the utilitarian principle fleshed out in chapter 2 and recalled at the beginning of this chapter adds a constraint regarding which alternatives are primarily concerned. It says that the balance of happiness over pain needs to be maximized over *available* alternatives. For what I will develop here, this notion of 'availability' is to be conceived in terms of how easy it is for all the resources employed – financial, human, and material – to be redirected in order to serve other purposes. The easier it is to do so the more available an alternative can be said to be.

Reverting to neuroeconomic experimentation on monkeys, this condition of maximization over available alternatives asks us to, in priority, compare it other possible utilizations of the same resources to limit waste and seek to make the most out of what we already have, no matter what, at our disposal. Here, I take such available alternatives to be of two kinds: (1) Stop experimenting on monkeys and focus solely on neuroeconomic experiments on humans instead. (2) Restricting investigating the brains of monkeys to the direct study of brain diseases. In both cases, neuroscientific knowledge and recording technologies are still needed – although not to the same extent – and put to use in domains where the balance of happiness over pain offers better prospects of being maximized; or so I shall attempt to argue. To do so, let me address both alternatives in turn.

5.3. Experimenting Only with Humans

In this section I will give support to the claim that, from a utilitarian standpoint, experimenting solely in humans for neuroeconomic purposes is an alternative to be preferred to the resort of monkey subjects. I indeed believe the associated balance of happiness over pain to be in better shape because this alternative would allow us to (1) greatly reduce the harms while (2) obtaining rather similar benefits.

5.3.1. Greatly reducing the harms

The reduction of the harms is evident when considering the difference in the methodology used in humans compared to the one generally adopted when subjects are non-human primates. However, whereas the latter was discussed in great length in chapter 4, the former was only quickly touched upon in chapter 1. Let me, therefore, say a little more on the matter. Indeed, understanding how exactly humans are experimented on is quite essential for the reader to realize the amount of pain which is spared to the subjects.

In neuroeconomic settings, human subjects are – very much like monkeys – asked to perform tasks precisely set up to investigate certain aspects of economic decision-making. While performing, the activity of their brains is usually studied with five main techniques. Those techniques are electro-encephalography (EEG), magnetoencephalography (MEG), positron emission topography (PET), transcranial magnetic stimulation (TMS), and of course the well-known functional magnetic resonance imaging (fMRI).

The aim of an EEG study – see Gehring & Willoughby (2002) for a famous example in neuroeconomics – is to record changes in electrical potential using electrodes positioned on the scalp. Typical electrodes consist of an electrically conductive disk connected to a long, light wire and conductive gels or pastes are often applied between those electrodes and the scalp to improve the quality of electrical connection. EEG has a good temporal resolution and is inexpensive. In other words, it allows researchers to satisfactorily separate changes in brain activity occurring in the span of a few hundred milliseconds at a low cost. The problem, however, is its poor spatial resolution. As the EEG signal is greatly attenuated by the skull, it is difficult to precisely pinpoint the source of the brain activity being recorded.

fMRI, on the other hand, offers a good combination of spatial and temporal resolutions. This is necessary to map complex cognitive functions in the brain and explains its widespread acceptance and use amongst the research community. Neuroeconomics is no exception (Huettel & al., 2006). During a fMRI study, subjects are placed and asked to lay still in a scanner using magnetic resonance to produce a live image of their brains. Subjects have to remain immobile in the confined and loud bore of the MRI scanner because even slight head movements are likely to introduce noise in the signal. This particularity renders any experiment which is not very basic in kind difficult to perform. That is, any experiment which requires more from individuals than the watching of a screen and the pressing of a few buttons.

A middle-ground, as it were, between EEG and fMRI can be found in magnetoencephalography. The point of a MEG study is to detect and record the variations in the weak magnetic fields associated with brain activity. Participants are asked to sit upright in the MEG system where a large helmet-like device surrounds their heads. They are – very much like in an fMRI study – positioned in front of a screen where visual stimuli appear and can respond thanks to a button box on their lap. MEG offers better temporal and spatial resolutions than fMRI in addition to placing subjects in a more open environment than the confined space of an MRI scanner. The utilisation of MEG in neuroeconomics can notably be found in Hunt & al. (2012) but remains greatly restricted because of the price of the technology.

A last recording method which is used in neuroeconomics is called positron emission tomography (Hakyemez & al., 2008). PET requires researchers to inject a quantity of a radioactive isotope into the venous system of participants. The isotope will then travel to the brain and binds itself to a particular type of neuron; the isotope being chosen in accordance with the neurons scientists have an interest in. Participants are then installed in a PET scanner which, by emitting gamma rays, will activate the isotope and reconstruct a 3D image of the brain. PET imaging necessitates a complex array of equipment and a respect of strict safety rules when it comes to the creation, handling, and administration of the radioactive material. But beyond its complexity this technology is, obviously, completely safe for the subjects.

Beside recording techniques, what can also be done is to stimulate targeted areas of the brain to better understand their involvement in certain aspects of decision-making. In animals, this is generally done invasively by stimulating neurons thanks to electrodes lowered inside the brain. In humans, researchers resort to transcranial magnetic stimulation (Knoch & al., 2006). With TMS, brain stimulation is obtained via the placing of a looped copper coil against the part of the scalp right above the site to be stimulated and running a strong, rapidly changing electrical current through the coil. This electric current acts on the underlying neurons in order to trigger their activity. TMS thereby permits a non-invasive manipulation of neural processes with high spatial and exceptional temporal resolutions. The main limitation of the technique is that it is presently only possible to target brain areas on the cortical surface. Deeper brain areas can simply not be reached by the magnetic field generated by the coil.

Although all five methods of investigation differ in precision, cost, and availability, they have something in common. They are all way less invasive than single unit recording methods utilized on monkeys. First of all, none of them necessitate surgical interventions to implant metallic devices on delicate areas such as the eyes or the skull. They are, as a consequence, not exposing the subjects to the pain and health-related risks associated with it. Second of all, the recording of brain activity is effectuated externally meaning that the risk of the subject’s brain being damaged by the lowering of an instrument inside of it is also avoided. Arguably, the recording methods described above might be associated with a slight discomfort stemming from the wearing of electrodes (EEG) or of a copper coil (TMS) on the scalp or having to stay in a relatively confined space in the case of an fMRI, PET, and MEG study. But this discomfort is belittled by the wearing of implants and having to stay restrained and water-deprived in primate chairs. On another note, whatever negative sentiments might be felt during the experiments, the subject knows that everything will be dissipated once the experiment is over. The same thing cannot be said for monkeys. For them, being done with an experiment means being put back inside a small barren cage which, as we have seen already, fuels harmful behaviours.

Because we previously identified recording methods used in non-human primates as well as their breeding and captivity environments as particularly pain-inducing for the subjects, focusing on experimental protocols that do not rely on such aspects is a great improvement in the maximization of happiness over pain. Humans are not bred, raised, and held in cages for exclusive research purposes. Being experimented on is but a tiny part of their lives, to which they explicitly consented to. In experimental neuroeconomic settings human subjects do not have their eyes, skulls, and brains surgically tinkered with. They are not forcibly restrained in chairs so that only their eyes can move nor are they water-deprived for five or six days. The activity of their brains is recorded non-invasively and they are sent back to the comfort of their homes when the experimental trials they were involved in are over. But if harms are greatly reduced while experimenting on humans, we also lose the advantages that encouraged researchers to experiment on monkeys in the first place. As stressed in chapter 1 already[7], those advantages are the precision of the results and the evolutionary insights we gain. Would this loss be dramatic for neuroeconomics? That is, would losing those advantages be truly detrimental to the benefits we might expect from investigating the neuronal processes of decision-making in monkeys? This is what I will now touch upon.

5.3.2. Obtaining similar benefits

In chapter 4 we have seen how experimenting on monkeys contributed to certain benefits of neuroeconomic research. More particularly, we saw how it could be associated with therapeutics benefits as well as with the improvements of laws and policies. Yet, the reason why it was nothing more than a contribution, why monkey experiments were not single-handedly responsible for those benefits, is because results obtained in humans – with the type

[7] See section 1.2.

of technology just evoked – are also useful for such purposes. In fact, for every domain of neuroeconomic research where monkey experiments could be said to bring relevant insights, similar findings were obtained with human subjects.

Consider therapeutic benefits first. It was argued, in summary, that experimenting on monkeys in neuroeconomics could serve the fight against addiction and mental disorders via the investigation of (1) the encoding of value in the brain, (2) the processing of social context, (3) the encoding of risk and uncertainty, and (4) how they play games. Yet, human imaging studies have provided – just like single-unit recording studies in monkeys – strong evidence that (1) prefrontal cortex and the striatum encode the subjective value of goods and actions (Plassmann & al., 2007; Hare & al., 2008; Kable & Glimcher; 2007). They showed that (2) humans were equally prepared to pay more to obtain information about others (Hayden & al., 2007) and that the amygdala was strongly implicated in social cognition (Adolphs & al., 1998; Adolphs, 2003; Gothard, 2020). They also reached the conclusion that (3) preferences for risky options was associated with neuronal activity in the striatum and posterior cortex (Kuhnen & Knutson, 2005; Preuschoff & al., 2006; Tom & al., 2007) and in prefrontal cortex and parietal cortex (Hsu & al., 2005; Huettel & al., 2006). And, finally, human brains were also (4) widely studied while subjects were asked to play an array of different games including trust games (McCabe & al., 2001; Dominique & al., 2004), ultimatum games (Sanfey & al., 2003), and prisoner's dilemma games (Singer & al., 2004). When it comes to improving laws and policies, I pointed out that experimenting on monkeys provided evidence regarding (5) the brain areas involved in fostering pro-social behaviour and in (6) the processing of rewards and punishments. But yet again, experimenting on humans offered very insightful results about (5) what happens in the brain during the making of altruistic decisions (Hare & al., 2010; Zaki & Mitchell, 2011; Waytz & al., 2012) and (6) the perception of social rewards and punishments (Delgado & al., 2000; Ernst & al., 2005; Martins & al., 2021).

With all that in mind, that is if both methods of experimentation i.e., studying the brain of humans and studying the brain of monkeys offer such similar and converging results, it becomes quite difficult to see how the contribution of the results obtained in monkeys to neuroeconomic benefits could be truly indispensable. Arguably, this contribution very well exists – as what is obtained remains relevant to highlight the type of brain activity associated with certain aspects of decision-making – but it appears difficult to see why the gap that would be left, if monkey experiments were to be stopped, could not be satisfactorily filled by the new findings derived from studying human brains. This is where we stumble upon somewhat of a paradox regarding the use of non-human primates in neuroeconomics. On the one hand, the similarity and convergence of the results obtained in monkeys with what we observe in humans give support to the idea that those animals are perfect models to study the neural substrates of human decision-making. But, on the other hand, they also cast doubt on why we need such experiments exactly.

Another point worth mentioning is that, although experimenting on monkeys has its own advantages, so does experimenting on humans. Such advantages play a role in the acquisition of neuroeconomic benefits which is as – and perhaps even more – important than those affiliated with monkey experiments. Monkeys are used for the precision of the results we can derive from investigating their brains invasively and because they bring evolutionary insights. Whereas evolutionary insights are more of the domain of 'pure science' and therefore less easily associated with improving lives, it is the loss of precision which might be a bigger concern. To illustrate how advantages pertaining to human experimentation are important for neuroeconomic benefits and how they can potentially make up for its less accurate results, consider once again the therapeutic benefits whose value for utilitarians is particularly high.

The loss of precision in neuronal measurements while subjects are playing games that would ensue the interdiction of using monkeys in neuroeconomics might be an issue, first and foremost, for the refinement of bio-markers of mental disorders (Kishida & al. 2010). As I have argued, monkey experiments can be useful for such a refinement. That much is granted. But this point overlooks that refining bio-markers of mental disorders greatly benefits from the inherent features of human experiments as well. First of all, human brain imaging permits us to examine the decision processes in the species we are most interested in, ourselves. Needless to say, this is important when we seek to understand, detect, or cure the development of disorders affecting the human brain. Second of all, more sophisticated games can be employed to examine in more depth the neuronal activity associated with social preferences and related concepts such as fairness, reciprocity, and trust. Using monkeys, in comparison, will always be limited by the level of comprehension of the subjects and by their experience of social interactions which, although quite elaborate, is never as developed as that of humans. For instance, humans are the only species known to exhibit reciprocal fairness, which implies the punishment of other individuals' unfair behaviours even if it hurts the punisher's economic self-interest (Knoch & al., 2006). Thirdly, all of that can be supplemented with the steady increase in the precision of neuroimaging techniques (Wintermark & al., 2018) and with neuroeconomists having subjects actually suffering from mental disorders play those games; something that can't be done – or at least not to the same extent – with monkeys. Yet, it is one of the great strengths of neuroeconomic approaches to mental disorders and undoubtedly significant to better understand those disorders (Lis & Kirsch, 2016).

Taken together, all those aspects can make us put into perspective the loss of monkey experiments and their precision. They make us realize that studying humans brings about insights which are similarly relevant not only to improve laws and policies but also – and above all – to obtain therapeutic benefits.

5.4. Restricting Investigating on Monkeys to the Study of Brain Diseases

After having argued a little in favour of focusing solely on human experiments in terms of maximizing the balance of pleasure over pain, let me touch upon the second alternative. Let me consider restricting the invasive investigation of the brains of the monkeys to the study and treatment of neurodegenerative diseases. Arguably, whereas experimenting on humans offered us prospects to greatly diminish the harms when conserving the benefits, this second alternative does the opposite. It would (1) maintain the harms while (2) seeking to greatly improve the benefits.

5.4.1. Maintaining the harms

The direct study of neurodegenerative diseases and mental disorders in monkeys, very much like the neuroeconomic research we have been scrutinizing so far, relies on an invasive methodology. To make this point I will simply sketch what is done when Alzheimer's disease (AD), Parkinson's disease (PD), and strokes are investigated using non-human primates. Of course, the study of brain-related health conditions on monkeys is not limited to those three. But focusing on such targeted examples has the advantage of giving a good overview of the type of methodology employed in the field.

The use of monkeys in neurosciences – whatever the objective – can always be confronted with the harms generated by the way subjects are bred, warehoused, and then transferred to research facilities, as well as by the manner the animals are being kept inside laboratories. Experimenting on monkeys to better understand and cure brain diseases is no exception to that rule. Interestingly enough, and when it comes to captivity environments, certain papers reach an admirable level of transparency by making clear most of the aspects that I pointed out as obscure in neuroeconomic articles. It is indeed not uncommon to find detailed descriptions regarding the dimensions of the stainless steel cages monkeys are kept in, whether they are alone or by pair, and what they are fed and how often. From time to time, information is even disclosed about the temperature, humidity level, and light (day/night cycle) in the room monkeys were kept in (Shi & al., 2020). But despite its importance, this level of transparency does not change the fact that the nature of captivity environments in labs remains hostile to the subject's health and happiness. That put aside, let us enter the discussion on what monkeys have to go through while being experimented on to further our understanding of brain diseases starting with the study of Alzheimer's disease (AD).

Aged monkeys, just like aged humans, develop over time behavioural and cellular abnormalities which, for some of them, resemble AD (Albert, 2002). Thus, a first way to proceed to better understand the disease is simply to study its known pathological hallmarks in aging non-human primates. The problem is that some key hallmarks – such as the cerebral accumulation of amyloid beta – cannot easily be investigated *in vivo*. What is often done, then, is to acquire several subjects, to separate them in different age groups, and to harvest their brains. Said differently, monkeys are put to sleep with an overdose of anaesthetics for targeted parts of their brains to be dissected, analysed, and compared *post-mortem* (Zhao & al., 2017). For the hallmarks that can be studied *in vivo* such as memory impairment and other cognitive deficits, they can indeed be studied in aged monkeys but are also mainly recreated in healthy subjects for investigation. This is done by researchers surgically intervening in order to create lesions in the hippocampal region of the monkeys' brains. This induces impaired recognition memory (Zola & al., 2000; Teng & al., 2000). In a similar vein, the loss of cholinergic basal forebrain neurons generated by AD and associated with the loss of cognitive capacities such as attention and learning can be obtained by stereotaxic injections of cytotoxin ibotenic acid directly into the basal forebrain to damage it (Voytko & al., 1994) or by transection – a type of precise surgical incision – of the fornix (Kordower & Fiandaca, 1990).

In essence, the study of AD in non-human primates is very similar to the study of Parkinson's disease. Just like AD, several risk factors of PD were identified including ageing, neurotoxins, and genetics. Experiments involving monkeys are thus focused on investigating the relationship between those risk factors and the disease *per se*. When it comes to aging, aged monkeys have proven to be useful subjects to understand the role it plays in PD. Like humans, they develop age-related dysfunctions associated with the disease (Emborg & al., 1998). The influence of ageing on the development of PD and associated symptoms is studied by harvesting, analysing, and comparing the brains of euthanised monkeys of different ages (Collier & al., 2011). On another note, neurotoxins can also be injected into healthy subjects to induce neurodegeneration. What is widely used, for instance, is a substance named MPTP. This substance is notably famous for attacking the brain and generating a syndrome that clinically and pathologically resembles PD. Monkeys 'infected' with Parkinson in this way can then be studied to examine the development of parkinsonian symptoms and associated brain activity. Such studies generally have the subjects performing tasks while monitoring their brains. This involves the use of primate chairs and implanted recording chambers for neuronal measurement (Wichmann & al., 1994; Bergman & al., 1994). Lastly, the study of the genetic roots of PD on non-human primates is only in its infancy. It is an emerging field, which revolves around the genetic modification of fertilized eggs to obtain transgenic subjects. Firstly, the success of the operation is attested by the researchers via the examination of aborted monkeys to search for the expression of the altered gene. Once done, other transgenic monkeys are raised and behaviourally investigated throughout their lives. The results are then compared to what is obtained with paired non-transgenic subjects (Niu & al., 2015).

In line with the study of AD and PD, the study of strokes in non-human primates chiefly relies on inducing what is to be investigated in healthy subjects. Waiting for the monkeys to develop strokes on their own would be too arbitrary and a huge hurdle to a conscientious study of the phenomenon. Roughly, two surgical approaches are used to generate both transient and permanent strokes in animals (Howells & al., 2010). The aim of both of them is to occlude the middle cerebral artery (MCA) to mimic the most common subtype of human stroke. The first group of methods requires opening of the skull to allow direct access to the cerebral arteries permitting the MCA to be ligated, clipped, or sealed (Crowell & al., 1981). Although craniotomies provide consistent strokes, they are associated with a painful incision site and taking the transorbital route permanently damages the eye of the subject in addition to producing marked oedema requiring prolonged intensive care of the animal (Cook & Tymianski, 2012). To avoid opening the skull, the second group of methods relies on an intra-arterial introduction of specific material to occlude cerebral arteries. The most commonly used of such methods involves introducing an occluding thread into the extracranial internal carotid artery (ICA) and advancing it until its tip occludes the origin of the MCA (Feret & al., 2008). More realistic models of embolic strokes can also be obtained with the introduction of blood clots to achieve vessel occlusion (Kuge & al., 2001). The corollary of artificially inducing strokes, however, is a significant percentage of poststroke mortality amongst the subjects. Remarkably enough, the endovascular technique – occlusion by thread or clot – appears to have increased variability in stroke size and a higher mortality rate when compared to open vascular occlusions (D'Arceuil & al., 2006). Once the strokes have been generated, their consequences are studied by having monkeys performing neurobehavioral tasks to assess the state of their cognitive abilities. Neurological dysfunctions and recovery are then examined under anaesthesia with brain imaging techniques such as fMRI or PET. In a last step, monkeys are euthanised for their brains to be dissected and scrutinized in more depth (Bihel & al., 2010).

5.4.2. Improving the benefits

As we have just seen, using the brains of monkeys to better understand neuronal issues is very invasive. Very much like neuroeconomic experiments, the subjects are submitted to conditions which are highly detrimental to their health and well-being. Not only are the animals kept in small cages inside a lab but their brains are also damaged on purpose to mimic neurodegenerative diseases or induce strokes before being killed for dissection. For this reason, serious ethical concerns can, and actually have been, raised (Garett, 2012; Rollin, 2012). The main difference with neuroeconomics, however, is that this type of research offers very clear prospects of improving the lives of those suffering from particularly scary and/or invalidating neuronal conditions by contributing to the development of treatments. It is also quite useful to improve prevention by isolating what makes such conditions more likely to arise in the first place (Capitanio & Emborg, 2008). Although such research is conducted with the objective of curing human patients, its usefulness can be extended to any being likely to suffer from similar brain problems and that we would like to see cured. One can think of pets like cats and dogs but also of animals kept in zoos including, of course, the monkeys themselves.

Consider Alzheimer's disease first. It is the most common age-related neurodegenerative disorder and form of dementia. Patients present cognitive or intellectual symptoms such as amnesia, aphasia, apraxia, and agnosia as well as psychiatric ones like personality changes, depression, hallucinations, and delusions. Yet, *post-mortem* brain analyses of monkeys were helpful to understand the precise impact of lifestyle modifications in decreasing AD risk. Such modifications include calorie-restricted diets (Katsman & al., 2012; Willette & al., 2013) and exercising (Rhyu & al., 2010). Studies on non-human primates have also been crucial in determining and establishing the efficiency and safety of potential future treatments for AD like nerve growth factor gene therapies (Tuszynski & al., 1990; 1996; 2015) or those targeting β-amyloid (Godyń & al., 2016). Something similar can be said about PD.

After AD, Parkinson's disease is the second-most common age-related neurodegenerative disorder. Symptoms of the disease most generally include the presence of typical motor impairments like tremors, rigidity, slowness of movement, and postural instability. As a consequence, the progression of the disease over time severely affects walking, talking, or completing simple tasks. Similar to AD, PD patients also present non-motor symptoms such as orthostatic hypotension, fatigue, urinary problems, constipation, and sleep disruptions. Once again, experimenting on non-human primates has proven to be essential for the development of safe and efficacious therapeutic strategies to treat PD. The most famous of them is probably deep brain stimulation (Dorval & al., 2008; Drouot & al., 2004) but one can also mention surgical ablation of targeted brain areas (Bergman & al., 1990), symptomatic treatments such as dopamine agonists (Jenner, 2003), or gene therapies (Hadaczek & al., 2010; Emborg & al., 2007).

Finally, the study of strokes on monkeys' brains have greatly contributed to a better understanding of a leading cause of disability and death around the globe. In the US, strokes impact approximately 3% of the population and ranks 3rd amongst all causes of death (Lloyd-Jones & al., 2010). Moreover, survivors of strokes often have to live with subsequent dysfunctions of variable severity affecting motor and non-motor faculties alike. In this context, experiments on monkeys are particularly relevant to identify substances reducing the occurrence of strokes (Sugidachi & al., 2016; Yoshikawa & al., 2008), those that can reduce the coming of long-term disabilities and limit post-stroke brain damage (Marshall & al., 1999, 2000; Liston & al., 2022), and to improve treatments like thrombolytic therapy (Findlay & al., 1988, 1989).

All in all, the contribution of non-human primate research to brain-related medical issues – here I gave the examples of AD, PD, and strokes but they are by no means limited to those – has yielded a number of advancements towards the understanding of neural networks affected by each disorder. It also provided valuable data to assess the safety and feasibility of novel therapies. As neuroeconomic experiments cannot be affiliated with such direct and established ways to increase happiness and relieve pain – mainly in humans but also arguably in animals – there seems to be enough room to argue that, if we are to investigate the brains of monkeys invasively, we would have reasons to limit it to the study of brain diseases.

5.5. Conclusion of chapter 5

In this chapter I offered, as is requested by the ethical principle spelled out in chapter 2, a discussion around the possibility for monkey experiments in neuroeconomics to maximize the balance of pleasure over pain over available alternatives. I started by specifying the state of the balance of happiness over pain and argued that we could rightfully doubt its positivity. I then proceeded to investigate how this balance would likely fare against two available alternatives of the use of monkeys in neuroeconomics. They are (1) experimenting only with human subjects in neuroeconomics and (2) limiting the invasive study of monkeys to medical brain research. The conclusion I reach is that the two of them offer better prospects at maximizing the balance of pleasure over pain. Indeed, alternative (1) gives us the possibility to greatly reduce the harms to obtain fairly similar benefits while alternative (2) maintains the harms but for the acquisition of way better benefits.

General Conclusion

What I had in mind while starting this project was to apply insights inherited from Singer's *Animal Liberation* as well as other utilitarian developments to the case study of neuroeconomic experimentation on monkeys. I hope to have done it in an appropriate manner and to therefore be convincing when I say that the prospects of this practice being morally justified from a utilitarian standpoint are very dim. The harms are extensive, clear, and immediate towards highly sentient and social beings. The benefits are uncertain, delayed, and can be put into perspective. Certain available alternatives, at least two of them, seem to offer better prospects at maximizing the balance of happiness over pain. With all of that in mind, I tend to believe that we have a strong case to conclude that the use of monkeys in neuroeconomics does not abide by the ethical principle I have been working with; in other words, to conclude that the practice can be seen as immoral.

That being said, I do not take the reasoning employed here and the conclusion arrived at to be without limitations. First of all, the conclusion reached evidently depends on the utilitarian principle endorsed. The one I spelled out seeks maximization and promotes hedonism. However, and although I tried to defend this principle as well as its relevance to assess any type of animal experimentation, the flexibility of utilitarianism makes it possible to work with different features. Think about mere outweighing instead of maximizing or preference-based happiness in lieu of hedonism. In light of this, it is possible that a different utilitarian investigation yields to a conclusion differing from mine. I suspect, nonetheless, that if difference there might be, it would be one of degree rather than one of kind. Second of all, some developments in animal ethics have emphasized the limitation of focusing solely on pain (Gruen, 2021). Pain, after all, surely isn't the only thing worth considering when interrogating the way humans treat other species but it is, arguably, a good start. Yet, and even though my notion of 'unhappiness' is a bit broader than mere pain in the sense that it also includes discomfort, frustration, boredom, and every other negative feeling, it is true that it does not take into consideration the deprivation, for instance, of the inherent value of relationships or freedom that might go beyond mere sentiments. Lastly, and for the sake of space and clarity, I had to leave out from this thesis the use of rodents in neuroeconomics. Monkeys are, because of the complexity of their brains, more esteemed subjects than rodents. But this does not change the fact that rats and mice are experimented on with an equally invasive methodology. As a consequence, there is little doubt that an investigation regarding the treatment of such subjects in neuroeconomic labs and following the same logic could supplement my own very well. My intuition is that such an investigation would likely aggravate the moral situation of using animals in neuroeconomic experiments which was already questioned in this thesis. Very much, in fact, like the incorporation of unrelated-to-pain features would; a result that going in the direction of what was developed here rather than against it.

At any rate, I do hope that the present thesis did justice to the feelings of those concerned about animal welfare. I hope it succeeded in shedding light upon some of the perhaps less well-known ethical aspects of neuroeconomics. If anything, I would be glad if the present work adorned the informative power I wanted it to have when I undertook its writing. I would be glad if its content, at least, allowed the reader to be acquainted with a way of using monkeys in neuroscience which, in addition to being most likely unbeknownst to the general public, is probably also very much obscure to many experts, especially in the field of economics.

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