Department of Interdisciplinary Life Sciences

University of Veterinary Medicine Vienna

Messerli Research Institute

Unit for Ethics and Human-Animal Studies

(Head: Univ.-Prof. Dr. Herwig Grimm)

Animals and the Harm of Moral Thwarting:

Assessing the Impact of Scientific Research on Moral Subjects

Master thesis

University of Veterinary Medicine Vienna

submitted by

Richard Long

Vienna, September 2020

Supervisor:

Univ.-Ass. Dr. Judith Benz-Schwarzburg

Ethics and Human-Animal Studies

Messerli Research Institute

Unit of Ethics and Human-Animal Studies

Veterinärplatz 1

1210 Vienna

Acknowledgements

Firstly, I would like to express my sincere thanks to my supervisor, Univ.-Ass. Dr. Judith Benz-Schwarzburg, for encouraging me to pursue this thesis and for all the time, input, feedback, and support that she has provided, both during the writing of this thesis, and throughout my time studying in Vienna.

I am also extremely grateful to Dr. Susana Monsó for her willingness to engage with and discuss this work throughout its development, and for her general support over the previous few years.

I would like to thank Univ.-Prof. Dr. Herwig Grimm for his overall approachability, his encouragement to involve myself with projects within the Unit of Ethics and Human-Animal Studies, and for the opportunities that he has afforded to me during my studies.

My thanks also to all of the staff at the Unit of Ethics and Human-Animal Studies for drawing me into the field of animal ethics, and for all of their assistance and encouragement.

I would like to express a special thank you to DDr. Regina Binder for her input regarding EU laws governing animal research.

A further thank you to all of the teachers and staff involved with the IMHAI master program. I feel incredibly lucky to have been able to spend the last years learning so much about topics that I find compelling and that I consider to be of great importance.

To all my family and friends, thank you for encouraging me and supporting me in my decision to move to Vienna and take part in this study program. Beyond that, I am extremely thankful for all of the positive impacts that you have on my life, and for the support, encouragement, and distraction that you have provided me during the completion of this study program.

Finally, I would like to thank Mariessa for all of the love, compassion and inspiration that she provides.

Abstract

It has recently been argued that some animals may be moral subjects, individuals capable of acting on the basis of moral motivations, and that the thwarting of their moral capacities is a morally problematic form of harm. However, there has yet to be thorough consideration of whether any of the many millions of animals used every year for scientific research undergo such a form of harm. Therefore, this thesis aims to address the question of whether the moral lives of some animals are negatively impacted upon as a result of their use in modern scientific research. The term *moral thwarting* is introduced to refer to such harmful negative impacts, and is characterised through an analysis of the conceptual forms that such thwarting may take. Following this, an analysis of recent scientific studies manipulating empathy and aggression in rats and mice is carried out. Evidence is presented and discussed regarding specific moral capacities of these species, and it is argued that these studies result in the moral thwarting of their animal subjects. Practices and conditions that result in moral thwarting are identified, as are some common characteristics of these. It is then claimed that such practices and conditions can also be found within scientific breeding and husbandry practices. The applicability of the analysis to other species is discussed, and, through a focus on non-human primates, it is shown how these findings help to uncover other likely cases of moral thwarting in scientific research. Finally, directions for further research are suggested and the wider relevance of this topic is considered. Overall, this thesis claims that, although currently available evidence does not allow us to draw any irrefutable conclusions, there is good cause to believe that some animals are morally thwarted as a result of their use in modern scientific research.

Contents

1. Introduction

1.1. Can animals be moral?

In February 2013, an Oklahoma-based news website ran a story detailing the actions of a Pit Bull named Baby (KOCO News 2013). Baby had alerted her sleeping owners to a house fire by repeatedly barking and pouncing on them, waking them up and allowing them to escape. A family member described how Baby, as well as successfully warning her owners of the danger, rescued another dog, who was hiding under a bed, by seizing its neck and dragging it outside to safety. Her owner exclaimed:

> “I'm so proud of her. She is my hero. She's the hero for all of us” (KOCO News 2013).

Baby’s owner’s pride in her dog’s behaviour, and her use of the term *hero* seem to suggest that the owner believes that there is something good, admirable, or respectable in the way that Baby has acted. Certainly, if events have played out as described in the article, one interpretation of Baby’s behaviour could be that she was motivated by something resembling concern for her owners and the other dog. If this were to be the case, could we recognise that Baby was *right* to experience this type of motivation, and to behave in the way that she did? Could we understand such concern as the *morally correct* thing to feel in such a situation, and the subsequent behaviour as *morally correct* behaviour?

Both observational accounts and controlled scientific experiments provide us with many more examples of nonhuman animals (hereafter *animals*) behaving in ways that seemingly align with common standards of moral correctness or goodness recognised by our society, or that suggest that animals may have various capacities relevant to behaving in such a way. The valuable task of gathering together reports and studies concerning such types of behaviour has been performed by authors including Bekoff and Pierce (2009), de Waal et al. (2009), Rowlands (2012), and Monsó et al. (2018). Anecdotal reports provide fascinating descriptions of animal acts such as a female gorilla rescuing an unconscious child from her enclosure in an Illinois zoo (Bekoff and Pierce 2009, pp. 1–2), an exhausted rat being led to water by another rat luring her[1]

---

[1] In this thesis, I have chosen to refer to animals using female pronouns, which is a gendering practice common in philosophical work. When discussing empirical studies, this may sometimes result in the use of pronouns that do not correspond with the reported sex of the animal subjects used in the studies; however, I do not believe that in these cases the specific sex of the animals is of importance for the general points that are being raised.

with food (Bekoff 2007, p. 12), and an elephant's attempts to provide assistance to, apparent distress at, and later seeming grieving for, an unrelated dying elephant (Douglas-Hamilton et al. 2006). Empirical studies likewise provide further evidence of the types of behaviour being discussed[2]. Seemingly altruistic behaviours, in which individuals help others despite no direct gain, and sometimes at direct cost, to themselves, have been seen in animals including some primate species (Masserman et al. 1964, Wechkin et al. 1964, Warneken and Tomasello 2006, Burkart et al. 2007, Warneken et al. 2007, Lakshminarayanan and Santos 2008, Cronin et al. 2010, Horner et al. 2011, Schmelz et al. 2017), rats (Church 1959, Rice and Gainer 1962, Evans and Braud 1969, Greene 1969, Ben-Ami Bartal et al. 2011, Sato et al. 2015) and pigeons (Watanabe and Ono 1986). Behaviours that appear consolatory in nature have been observed in primates (de Waal and Roosmalen 1979, Kutsukake and Castles 2004, Cordoni et al. 2006, Fraser et al. 2008, Clay and de Waal 2013, Palagi et al. 2014), corvids (Seed et al. 2007, Fraser and Bugnyar 2010), canines (Cools et al. 2008, Palagi and Cordoni 2009, Custance and Mayer 2012), elephants (Plotnik and de Waal 2014), horses (Cozzi et al. 2010), budgerigars (Ikkatai et al. 2016) and prairie voles (Burkett et al. 2016). Inequity aversion studies performed in chimpanzees (Brosnan et al. 2005, 2010), monkeys (Brosnan and de Waal 2003, Cronin and Snowdon 2008, Massen et al. 2012), dogs (Range et al. 2009) and rats (Oberliessen et al. 2016) have all suggested that these species possess a sense of fairness.

Can any of these examples or studies truly be said to show animals acting in a moral way? Can animals ever be said to be capable of acting morally?

1.2. Animals as moral subjects

Rowlands (2012) has argued that some animals may be capable of acting on the basis of moral motivations. He indicates two ways in which people may be sceptical of such a claim; they may raise empirical objections, questioning whether the available evidence for such a claim actually demonstrates such motivations, or they can question the very conceptual idea that such motivations, should they exist, can have moral content in the case of animals (Rowlands 2012, pp. 7–14). Empirical objections may take the form of specific alternative explanations for behaviour, or a more general sceptical outlook about how conclusive such evidence may be. As an example, an experiment showing that rats work to free seemingly distressed conspecifics

---

[2] My thanks to Monsó et al. (2018) for their identification and classification of the following studies.

from inside restrainers has been cited as evidence for empathy-motivated behaviour in rats (Ben-Ami Bartal et al. 2011); however, others claim that such a behaviour could instead be motivated by a desire for social contact rather than empathy (Silberberg et al. 2014). Rowlands' work, however, is concerned with addressing the conceptual aspects of whether some animals may be capable of acting on the basis of moral motivations.

Currently, it is common in philosophical thought to classify individuals of moral concern as either moral patients or moral agents, characterised by Rowlands as follows:

> "X is a moral *patient* if and only if X is a legitimate object of moral concern: that is, roughly, X is an entity that has interests that should be taken into consideration when decisions are made concerning it or which otherwise impact on it." (Rowlands 2012, p. 72)
>
> "X is a moral *agent* if and only if X is (a) morally responsible for, and so can be (b) morally evaluated (praised or blamed, broadly understood) for, its motives and actions." (Rowlands 2012, p. 75)

Among those who consider animals to be morally considerable beings, the view that animals are moral patients, rather than moral agents, is largely uncontroversial. Rowlands, however, proposes that some animals may also belong to a third, non-exclusive category, that of the moral subject, defined as follows:

> "X is a moral *subject* if and only if X is, at least sometimes, motivated to act by moral reasons." (Rowlands 2012, p. 89)

Rowlands (2012, pp. 71–123) discusses how orthodox philosophical thought has predominately led to the conflation of the categories of moral subjects and moral agents, despite the differing claims regarding each category; the claim regarding moral subjects is concerned with motivation, whereas the claim regarding moral agents focuses on responsibility and the ability to be evaluated for one's actions. After exploring the general distinction between motivations and evaluation, Rowlands considers the reasoning for why this general distinction has been traditionally thought not to apply in the cases of moral motivation and evaluation. By examining Aristotelian (Rowlands 2012, pp. 99-123, with reference to EN, 1105a27-35, 1103a19-b2, 1109a27-30, Hursthouse 1999, and an unspecified earlier version of Hursthouse and Pettigrove

2018) and Kantian (Rowlands 2012, p. 99-123, with reference to Korsgaard 2004, 2006) accounts of morality, Rowlands identifies a common connection between normativity and control over one's motivations, where control over a motivation is required for it to be considerable as a moral motivation; this control "consists in the ability to critically reflect on or scrutinize one's motivations" (Rowlands 2012, p. 122). Such reasoning denies animals the possibility of being moral subjects, as they are seemingly unable to control their motivations. Therefore, a key strand of Rowlands' argumentation that some animals may be moral subjects is focussed on challenging this connection between control and normativity.

Rowlands (2012, pp. 169–190) examines the claim that metacognitive abilities, such as the ability to critically scrutinise one's motivations, can grant control over one's motivations, and that this control transforms them into normative states. He argues that metacognitive abilities cannot confer control over motivations, and thus any claims that metacognitive abilities can confer normativity, via control, are therefore incorrect; to claim otherwise relies upon invoking the *miracle-of-the-meta*, a type of fallacy that "involves the attribution of miraculous powers to metacognition or metacognitive abilities" (Rowlands 2012, p. 178). To assume that second-order states allow us to control first-order motivations assumes that these second-order states are fully under our control; on what basis can we make such an assumption? How can we ensure that these second-order states are not subject to influencing factors of which we are not fully aware[3]? Seemingly, to guarantee control over our second-order thoughts would require the presence of fully controlled third-order thoughts in order to assess these second-order thoughts; but we face the same problem regarding control over these third-order thoughts. This process leads to an infinite regress, where every order of evaluation relies on the presence of a higher-order process. To assert that, at any of these levels, control, and therefore the ability to confer normativity, can simply be assumed is to invoke the *miracle-of-the-meta*.

Rowlands argumentation allows him to claim that the Aristotelian and Kantian reasoning that has led to the widespread conflation of the categories of moral subjects and moral agents is

---

[3] To illustrate how people's ability to evaluate their motivations could be unknowingly influenced by situational factors external to them, Rowlands (2012, pp. 184–185) draws attention to situationist accounts of moral psychology (see e.g. Zimbardo 2007); such accounts claim that a person's behaviour is heavily influenced by external, situational factors, as opposed to internal dispositions. The well-known Stanford Prison Experiment (Haney et al. 1973) is often used to illustrate how situational factors can influence individuals' behaviours.

flawed. The seeming invalidation of such a prominent argument creates a much stronger footing for claiming the theoretical possibility of moral subjects who are not moral agents; individuals who are motivated to act for moral reasons, even though they cannot be considered morally responsible for, and therefore cannot be morally evaluated for, their motives and actions.

Rowlands (2012, pp. 32–38) proposes that animals capable of displaying certain morally laden emotions should be considered moral subjects, as well as moral patients. As potential examples of such morally laden emotions, he states "[t]hese include emotional states such as sympathy and compassion, kindness, tolerance, and patience, and also their negative counterparts such as anger, indignation, malice, and spite" (Rowlands 2012, p. 32). I will discuss moral emotions further in chapter 4.

1.3. The capabilities approach, moral emotions and harm

Taken together, Rowlands arguments provide a compelling case for reconsidering orthodox views on what is required to act for moral reasons, and whether animals, or at least some animals, are capable of moral behaviour. Continuing from this conception of animals as moral subjects, Monsó et al. (2018) presuppose its correctness in order to consider what it means for a hypothetical animal, one who is a moral subject, to be exposed to some common agricultural practices. They employ the capabilities approach (Nussbaum 2004, 2006) to demonstrate how failure to recognise and treat such an animal as a moral subject can result in types of harms against that individual that would not be recognised by a typical welfare-focussed conception of harm.

The capabilities approach "find[s] harm in the thwarting or blighting of [central capabilities]" (Nussbaum 2004, p. 309); these *central capabilities* are understood as things that members of a species are typically "able to do and to be" (Nussbaum 2006, p. 70) and that can be "evaluated as both good and central" (Nussbaum 2004, p. 309). Monsó et al. (2018) elaborate on this idea of certain capabilities being *good and central*, by describing them as "intrinsically valuable, and […] essential to the flourishing of members of that species as the sort of thing they are" (Monsó et al. 2018, p. 294). Monsó et al. (2018) argue that moral emotions can either be understood as central capabilities[4] themselves, or as grounding central capabilities. Therefore, the capabilities approach recognises the thwarting or blighting of an individual's moral emotions as a type of harm.

1.4. Research aim

This previously discussed usage of the capabilities approach already provides a strong argument for why it is important for us to consider the potential effects of human actions on the moral lives of animals, a task that this thesis aims to contribute towards. Within the paper in which they utilise the capabilities approach, Monsó et al. (2018) focus mainly on the potential impact of common agricultural practices on moral subjects, but the authors also indicate other types of human practices that may potentially impact upon the moral lives of animals; one of these is the use of animals in scientific research. As I will discuss in more detail in chapters 3 and 6, every year many millions of animals are used by humans as part of scientific research (United States Department of Agriculture 2018, European Commission 2020a, Speaking of Research 2020). If any of these animals are moral subjects, then could the practices that they are exposed to as part of this research impose upon their moral lives?

In this thesis I aim to address the question of whether the moral lives of some animals are negatively impacted upon as a result of their use in modern scientific research. Going forward, I will use the term *moral thwarting* to refer to this process of negatively impacting upon the moral life of an animal. I will begin by expanding upon the concept of moral thwarting, characterising the term through an analysis of the conceptual ways in which it can occur. With a clearer understanding of how moral thwarting can be understood and can occur, I will turn my attention to analysing recent real-world scientific studies and practices. This will allow me discuss whether we have cause to believe that some animals used in scientific studies may be moral subjects, and, if so, whether we have cause to believe that some scientific practices result in the moral thwarting of these animals. Finally, I will discuss open questions and possible future research avenues that arise from this analysis, and how the findings of this thesis relate to wider ethical debates.

---

[4] The authors of the paper use the term *basic capabilities*, but subsequent personal communication between Nussbaum and the authors clarified that *central capabilities* is the expected terminology. From this point forwards, I will continue to use the expected terminology of *central capabilities*.

As my investigations into this topic will show, our current knowledge regarding the moral lives, behaviours and capacities of different species, and the ways in which these may be impacted upon by human action, is far from complete. Therefore, it may be difficult to reach any definitive conclusions on such a topic at this current time. Nevertheless, this is still a very timely and important topic to consider. As the argumentation of Monsó et al. (2018) has already shown, moral thwarting can be understood as a type of harm inflicted upon the thwarted individual. Given both this and the extremely large number of animals used for the purposes of scientific research, there exists the possibility that scientific research could have led to, and, if practices remain unchanged, could continue to lead to, very large numbers of animals being harmed in a way that is typically neither recognised nor acknowledged, let alone argued to be justifiable. It is my hope that the analysis in this thesis will help us to gain a clearer understanding of the likelihood of moral thwarting occurring in the discussed context, and therefore help to provide a more complete and considered basis from which we can reconsider and re-evaluate some of the current practices within our society.

PART I: Defining moral thwarting

2. Moral thwarting

Given the presupposition that some animals are moral subjects, it becomes possible to conceive that various human actions interfere with the moral lives of these animals. The purpose of this chapter is to develop a definition of *moral thwarting*, a term that I will use to try to capture potentially problematic human interferences in the moral lives of those animals who are moral subjects. I will develop definitions of the terms *moral disenhancement* and *moral preclusion*, both of which I identify as subcategories of moral thwarting. I have three main reasons for developing these definitions. The first is that the process of developing these definitions allows me to provide some initial reflection on ways that human actions may impact upon the moral lives of animals. The second is that these definitions and the reflection involved in arriving at them should greatly assist me in the upcoming chapters, where I will make use of them to help analyse whether some modern scientific experiments and practices result in potentially problematic interferences in the moral lives of animals. The third is that these definitions, and the work involved in arriving at them, may serve to assist others looking to consider or explain ethical problems related to moral thwarting, by highlighting the varying aspects that they may wish to reflect upon, such as the differing ways in which it may occur, and the differing ways individuals may be affected by it.

2.1. Generalising from the capabilities approach

As discussed in the previous chapter, Monsó et al. (2018) utilised the capabilities approach (Nussbaum 2004, 2006) to provide an explanation of how impositions into a moral subject's moral life can be considered harmful. Monsó et al. (2018) identify moral emotions as central capabilities, and the capabilities approach identifies the *thwarting* or *blighting* of central capabilities as a form of harm (Nussbaum 2004, p. 309). Consideration of the ways in which capabilities may be thwarted leads to the declaration that "an animal can have her moral capabilities thwarted (1) if she is precluded from the possibility of exercising them, or (2) if her moral capabilities are taken away from her" (Monsó et al. 2018, p. 300). If either of these occur, then the individual has been harmed.

My intention in this chapter is to develop a definition of moral thwarting that is not tied to one particular ethical theory, in order to ensure that a potentially problematic interference in the moral life of an individual is not excluded from my definition simply because it does not align to one specific theory. However, I have not been able to conceive of forms of moral thwarting which do not fit into the general understanding of thwarting provided by Monsó et al. (2018). Therefore, I will use this as a template for my definition of moral thwarting, albeit modified in such a way that its terminology is not specific to a particular ethical theory.

I see two additional benefits from creating a definition on the basis of the one derived from the capabilities approach. The first is that the distinction of thwarting into the two proposed types seems a useful one. This distinction need not imply anything about the respective *level of wrongness* of acts that fall under each category, but it does offer that opportunity to those who wish to consider such a topic[5]. This distinction also helps to emphasise that thwarting occurs in multiple ways, and that it can impact the individual in different ways; I believe that this helps to ensure the visibility of the whole scope of moral thwarting, hopefully preventing certain aspects from becoming overlooked or ignored. The second benefit to basing my definition on a generalised version of the one derived from the capabilities approach, is that, should we identify real-life examples of moral thwarting using this definition, we already have an ethical argument by which we can understand these examples as being morally problematic.

The first modification that I would like to make from the understanding of thwarting provided by Monsó et al. (2018) is generalising the references to moral capabilities. I feel that the continued use of the term *capabilities* would create an undesirably strong association between my theory-agnostic definition of moral thwarting and the capabilities approach. Therefore, I propose to refer instead to *moral capacities.* To some degree, I am reluctant to provide an explicit definition of moral capacities; there is the danger that an overly explicit definition may unintentionally exclude capacities related to moral motivation or behaviour in animals, either because I have overlooked them, or because they are currently unknown to us. However, my understanding of moral capacities seems to align with that of Monsó and Wrage (forthcoming) who have also utilised the term moral capacities, defining it in a way that I feel clearly conveys the sense in which I too understand and use the term:

---

[5] However, the choice to use this distinction should neither be interpreted as claiming that this is the only possible way of distinguishing types of moral thwarting, nor that there exists a *correct* way of distinguishing types of moral thwarting, nor that ethical theories need recognise any such distinction.

> “Since we do not want to circumscribe our claims to a particular account of moral capacities, the readers should understand this term in a broad sense, as capacities that imply a “sensitivity to [some of] the good- or bad-making features of situations” (Rowlands 2012, 230) or as those whose exercise conveys information about a being’s moral character (Parrott 2019). We understand moral capacities to include moral emotions (those that are involved both in pro-social and in anti-social behaviour), as well as other capacities that can’t be classified as emotions but could still be said to ‘track’ moral properties (in Rowlands’ [2012] sense), such as trust, care, or normative capacities.” (Monsó and Wrage forthcoming, p. 8)

With a theory-agnostic alternative to using the language of moral capacities now defined, I can begin to adapt the understanding of moral thwarting provided by Monsó et al. (2018). However, it does not seem appropriate to simply substitute the term capacities for capabilities in this understanding of moral thwarting. The definition of moral capacities that I have provided refers only to the characteristics of moral capacities, allowing them to be identified, but does not make any claim about how capacities are attributed to an individual. In the capabilities approach, capabilities are recognised on the basis of species norms; an individual is expected to possess a capability if it is typical of a member of its species, and that individual is harmed by the thwarting or blighting of such a capability (Nussbaum 2004, 2006, pp. 325–407). In this way, we might approximately think of moral capabilities as moral capacities that members of a species typically possess. This definitional difference could mean that simply substituting the terms could unintentionally result in a differing interpretation of moral thwarting. However, we can still make use of the characteristics used to discern the two different types of thwarting to further understand and define moral thwarting. I will now turn to this task, analysing both forms of thwarting proposed on the basis of the capabilities approach in order help further clarify how to define and understand them, to consider if they fully capture the scope required, and to consider some of the conceptual ways in which each type of moral thwarting may occur.

2.2. Moral disenhancement

The first form of moral thwarting that I will discuss could broadly be characterised as one in which the moral capacities of the individual are somehow negatively changed or eliminated. I will use the term *moral disenhancement* to refer to this type of thwarting. Monsó et al. (2018)

refer to this type of thwarting as occurring to an individual when “her moral capabilities are taken away from her” (Monsó et al. 2018, p. 300), and as “eliminating the animals’ ability to act morally” (Monsó et al. 2018, p. 301). As I have mentioned, with moral capabilities understood as being approximately equivalent to moral capacities typical of the species, it is important to recognise this can mean that under such an interpretation of moral thwarting, thwarting occurs not only when current moral capacities of an individual are eliminated but also when species-typical capacities are somehow absent or fail to manifest in an individual. This is an important consideration that I will further explore shortly. I will now turn to analysing and discussing differing aspects relevant to the topic of moral disenhancement to help more fully characterise this subcategory of moral thwarting.

2.2.1. The minimal moral subject

To consider the ways in which a moral subject may be morally disenhanced, it is first useful to consider what it is that can confer moral subjecthood on this individual. Expanding upon his conception of moral subjects, Rowlands (2012) develops a set of criteria for what he refers to as a *minimal moral subject* (Rowlands 2012, pp. 221–232). Meeting all of these criteria is a sufficient condition for declaring the individual who does so as a moral subject, but is not a necessary condition. Although I do not wish to imply that all animals who are moral subjects meet only these minimal criteria, I believe that an analysis of such an individual may already contribute to our understanding of moral disenhancement.

Rowlands describes the profile of the minimal moral subject as follows:

> “X is a moral subject if X possesses (1) a sensitivity to the good- or bad-making features of situations, where (2) this sensitivity can be normatively assessed, and (3) is grounded in the operations of a reliable mechanism (a “moral module”).” (Rowlands 2012, p. 230)

Criterion 1 refers to an ability to sense some of the objectively good- or bad-making features of the situation[6]. For brevity, I shall refer to these good- or bad-making features as *moral features*, and refer to sensitivity to these moral features as *moral sensitivity*. In the case for animal

---

[6] The assumption that there are objective moral facts regarding the goodness or badness of certain situational features is discussed shortly.

morality that Rowlands (2012) proposes, this sensitivity takes the form of moral emotions; these are further discussed in section 4.2.

Criterion 2 refers to the idea that a normative judgement can be made regarding the moral correctness or appropriateness of the subject's sensitivity to these moral features. In the case of the emotional moral sensitivity that Rowlands proposes some animals may possess, it is these emotional responses to moral features that can be evaluated as normatively correct or not; for example, we can assess whether experiencing sadness at another's pain, or happiness at another's joy are normatively appropriate responses (Rowlands 2012, pp. 221–232).

In criteria 1 and 2, Rowlands (2012, pp. 223–224) assumes an objective consequentialist theory of morality. In such a theory, good-ness or bad-ness are not determined by factors such as the intentions with which acts are performed, nor are they open to subjective interpretation; instead they are determined by objectively good- or bad-making features that comprise the situation. Rowlands (2012, pp. 223–224) does not promote any particular theory of this type, simply acknowledging that there are many competing accounts. He does, however, offer up some examples of such theories, such as hedonistic utilitarianism, where "elevation and diminution of overall happiness are, accordingly, the respective good- and bad-making features" (Rowlands 2012, p. 223), or approaches based around a concept of flourishing, such as that found in Martha Nussbaum's capabilities approach (Nussbaum 2004, 2006), that understand "the good- and bad-making features of a situation as ones that, respectively, promote or suppress flourishing". In the upcoming analysis of scientific practice, I too do not wish to stake my claims to any particular ethical theory, as I believe this would place unnecessary restrictions on my arguments. My aim is rather to use what I hope will be largely uncontroversial moral principles or claims to explain the moral character of certain animal emotions and behaviours. No ethical theory has received universal acceptance, despite the long history of philosophical debate, and it does not seem unreasonable to assume that this is something that will remain unchanged in the foreseeable future; therefore, explicitly tying my arguments to a particular theory would seem an unnecessary distraction that could lead to instant dismissal of these arguments by those who reject that particular theory, even if the underlying principle being defended could have been supported by alternative theories that they may accept. By instead utilising generally uncontroversial moral principles or claims, it is my hope that people inclined to various differing ethical theories may still find the argumentation agreeable.

Criterion 3 of the minimal moral subject definition refers to the reliability of the subject's moral sensitivity. This condition embodies the claim that to be a moral subject, one's sensitivity "must be exercised correctly a significant portion of the time" (Rowlands 2012, p. 229). For us to be able to consider an individual as a moral subject, they must be disposed to respond to the moral features of a situation "in a relatively systematic, although (of course) not necessarily error free, way" (Rowlands 2012, p. 230). The intent behind this condition is clear; accidentally having the correct sensitivity to a situation on rare occasions should not be enough to qualify one as a moral subject.

2.2.2. Existing moral capacities

From the set of criteria defining the minimal moral subject, we can identify several ways in which we are theoretically able to interfere with such an animal's existing moral capacities in ways that may leave her in a disenhanced state; we could reduce an animal's sensitivity to the moral features of situations, or the normative quality of this sensitivity, or we could lower the reliability of this sensitivity. Sensitivity could be impacted, for example, by reducing the performance of an individual's sensory organs, decreasing the individual's ability to receive information about the moral features of the environment or situation. Alternatively, the connection between the reception of environmental or situational information and the generation of forms of moral sensitivity, for example moral emotions, could somehow be altered; for example, learning processes such as habituation or conditioning might potentially be employed in ways that could reduce the intensity or even what we might choose to call the moral or normative quality or correctness of these responses, as could surgical or pharmaceutical methods. Concerning the reliability of the individual's moral sensitivity, we can conceive that for individuals whose moral sensitivity is an emotional sensitivity, as Rowlands (2012) proposes it may be for some animals, the reliability of the mechanism that grounds this sensitivity may be affected by processes that induce emotional instability.

Key points from this consideration of the minimal moral subject, can be applied more broadly in the case of more sophisticated moral capacities, whether these be interpreted as more complex forms of moral sensitivity, or as other moral capacities. Not only can moral capacities be eliminated, but they can also be reduced in their functioning, or made less reliable. Any of these changes to moral capacities should be recognised in our understanding of moral disenhancement. Additionally, even if these changes were to only be temporary, this disruption to moral capacities should also be recognised as moral disenhancement as it still impacts upon the moral life of the individual during that time.

2.2.3. Development of moral capacities

In the previous section I focussed on ways in which the existing moral capacities of an individual might be altered. However, we can also conceive that certain types of human intervention could interfere with development of moral capacities. One such way that this could occur is through human influence on environmental factors. Environmental factors, including those relating to the social environment, are known to play an important role in shaping how an individual will develop in terms of her behaviour, including her social behaviour[7], as well as affecting the development of other capacities of the individual; for example, separating young rodents from their mothers has been shown to affect their stress responses and result in them developing abnormal aggressive behaviour (see e.g. Haller et al. 2014), a topic that I will return to in chapter 5. Therefore, I feel it is important that effects of human action on the development of moral capacities be considered and represented in our understanding of moral disenhancement. Our previous analysis of how existing moral capacities may be negatively impacted upon allows us to conceive of differing ways in which the development of moral capacities may also be negatively impacted; the capacities may not develop at all, may develop in a reduced sense, their development may be impeded, or they may develop in such a way that they function less reliably.

It is apparent that some type of comparison is required to identify these cases of moral disenhancement. In order to be able to judge whether an individual's moral development has been impaired, we need to have a sense of how this individual may otherwise have developed.

---

[7] I have explicitly highlighted social behaviour here because, as I will discuss later, I suspect that many moral behaviours will occur within the social realm. I assume that many ethical theories that are compatible with the idea of animals as moral subjects will form normative judgements, at least in part, on the basis of an individual's responses to the states of others, and the effect that the individual's behaviours have, or will likely have, on others. Both of these aspects, responding to and affecting the states of others, are strongly associated with interactions within the social realm.

In cases of short-term interventions with immediately noticeable consequences, it may be easy to consider how the individual would likely have developed without the intervention. However, not all interventions will have these, or only these, short-term, immediate consequences. Consider for example an animal raised her entire life in captivity by humans. These humans are clearly intervening in this animal's life; decisions they make regarding her care and environment have the ability to affect her long-term development, including the development of her moral capacities. However, given that human influences, for example regarding care decisions and her environment, have had a sustained presence in the individual's life, how can we judge how she would otherwise have developed? To identify such cases of moral thwarting, we require some way of estimating, with reasonable certainty, how individuals may otherwise have developed.

We could, for example, try to utilise some idea of what *normal* development would have been for that individual, in order to compare this to the way that she has actually developed. We see this type of approach, for example, in the capabilities approach, where species norms are to be taken as a reference point to understand the ways in which individuals of that species should be able to flourish (Nussbaum 2004, pp. 309–310). However, attempting to utilise the concept of *normal* can prove troublesome. In the case of the capabilities approach, how are we to determine a subset of individuals whose development is sufficiently representative of *normal* for that species? One solution to this is to define normal development as being equivalent to the development that would occur if the individual were to develop under *normal developmental conditions*; this, however, leaves us with the task of defining what *normal developmental conditions* would be. I will now outline two possible interpretations of this term, and offer a brief critique of each, before considering an alternative reference point for comparisons.

Firstly, we could, understand the *normal developmental conditions* for an individual to be the most common or average conditions that individuals of her kind experience during development. However, if we consider, for example, the case of many farmed animals, the most common conditions that they experience are already those imposed by humans, meaning that this interpretation of normal would be incapable of detecting many of the effects of human interference. Not only this, but some of these common animal keeping practices are known to have significant effects on the development of these animals, including perhaps most relevantly for the topic being discussed, on their social behaviour. For example, in dairy production, calves are typically separated from their mothers shortly after birth; however, mother rearing of calves has been shown to result in calves that are more socially active (Weary and Chua 2000, Flower and Weary 2001, Wagner et al. 2013) and that display less behavioural disorders (Fröberg and Lidfors 2009, Roth et al. 2009). Therefore, this interpretation of *normal developmental conditions* seems a poor choice for estimating how an individual of a species whose life is heavily impacted by human acts could have otherwise have developed, as it has the potential to overlook large amounts of human interferences, including those that have the ability to majorly impact relevant aspects of animals' lives. Nevertheless, this interpretation may allow us to catch some cases of moral disenhancement where there is still a negative deviation from development under conditions adhering to this interpretation; however, we must remember and acknowledge that it may potentially cause us to overlook many cases of moral disenhancement*,* or fail to capture the full extent of moral disenhancement that has occurred.

Alternatively, we could try to define *normal developmental* conditions in terms of the type of conditions that the individual has evolved to develop within; conditions that we might crudely consider as its *natural environment*. There are also difficulties with such an approach. The evolutionary history of some species is intertwined with that of humans; we see this, for example, in the case of domesticated animals who have been selectively bred over many generations based on human priorities. Do such individuals have a recognisable *natural environment*, one free of human influence, for which they are adapted? If not, then we cannot always rely on such an understanding of *normal developmental conditions* to serve as a comparison point to determine how humans have impacted the lives of individuals of these species. We could instead look back across further generations, to the conditions typical of these species before humans influenced their evolution. However, this may be many generations, and there exists the possibility that in some cases the developmental needs of these species and their ancestors may now be different. Therefore, this understanding of *normal developmental conditions* may not be well suited to identifying cases of moral disenhancement for species whose evolutionary history is closely connected to that of humans. To be able to utilise such an understanding would also require significant knowledge of the moral lives of these animals when living in *natural* conditions, which is something that may not be available for all species.

Rather than considering how an individual may have developed under *normal developmental* conditions, we might try instead to hold ourselves to stricter standards and compare the individual's development with the way that she could have developed under *ideal developmental conditions*. Empirical data, such as that arising from the field of animal welfare science, provides us with a growing knowledge of the needs and preferences of various species of animals, and a better understanding of how the development and behaviour of individuals is influenced by whether these needs and preferences are met. For example, relevant findings are available concerning species whose lives are frequently impacted upon by human actions, such as rodents (see e.g. Smith and Corrow 2005, Kappel et al. 2017), non-human primates (see e.g. Hannibal et al. 2017), and farmed animals (see e.g. Nawroth et al. 2019). Therefore, we could utilise such knowledge to help understand what the ideal conditions for an individual may be, how she would develop under these conditions, and how she may be impacted if such conditions are not met. However, assuming that we were able to identify what such conditions would be, there may still be arguments against such an approach. For example, wild animals whose lives have not included human interventions[8] may still not actually experience the *ideal* conditions for their moral development, so it may be argued that it is unreasonable to hold humans to such high standards if they were to intervene in an animal's life in some way.

The preceding discussion, although far from being a complete representation of the debate and possible alternatives, serves to illustrate the complexity of assessing the impact of some human interventions on the development of an individual. I believe that there is benefit in not specifying a particular reference point within my definition of moral disenhancement. The definition should clearly represent the pure concept of moral disenhancement, which for this form of moral disenhancement is characterised by negative impacts on the development of the moral capacities of the individual, understood in relation to *how she would otherwise have developed*. The use of reference points for comparisons merely provides a practical way of estimating how the individual would otherwise have developed; the more appropriate the

---

[8] Given the pervasiveness of human activity and its associated consequences, many wild animals' lives may have been, and may continue to be, affected by human action, even if only indirectly, again complicating discussions around this topic.

reference point is, the more accurately we can assess the impact and evaluate the extent of moral thwarting.

In the following chapter, I will turn to considering possible cases of moral thwarting in modern scientific practice. To practically assess these, I will indeed need to be able to estimate the impacts that certain practices and procedures have had on the moral lives of individuals. The species that I will be mainly investigating, rats, mice and non-human primates, have been the subject of much scientific study, so I will be able to make use of scientifically informed knowledge concerning these species, their needs and preferences, and their behavioural capacities (particularly those capacities of a social nature). The use of control conditions in experiments will also provide a useful reference point for estimating the impact of the particular procedures being analysed in a given study; however, given that, outside of the procedures being investigated, these animals will be expected to have experienced the same conditions, it is unlikely that I will be able to detect moral thwarting occurring as the result of other human-influenced factors in their lives, such as imposed husbandry conditions, without making use of additional knowledge from outside of the study in question. Between these two approaches, utilising empirical knowledge concerning a species' needs, preferences and behaviours, and comparing experimental outcomes with control conditions, I believe that I will be able to reliably identify at least some of the cases of moral thwarting that may occur in modern scientific practice.

2.2.4. Future individuals and populations

Human interventions also have the potential to shape the moral capacities of future individuals and populations. Selective breeding practices or genetic engineering techniques are two examples of ways in which this could be achieved. In some, perhaps many or even all, of these cases, the non-identity problem (see e.g. Palmer 2011, Parfit 2011, pp. 217–231) prevents us from speaking of a specific individual being changed in such a way that her moral capacities are affected; in such cases the individual comes into existence *already altered* and would never have been brought into existence in an *unaltered* state. However, this does not mean that we must not consider such cases as examples of moral disenhancement, but simply means that ethical theories that consider this type of moral disenhancement as problematic should consider and explain this in their argumentation.

In order to identify cases of this form of moral disenhancement, we again face the problem that some kind of comparison is implicitly required. When only a small fraction of a population is disenhanced in this way, the disenhancement will likely be identifiable through comparisons with others in the wider population, or knowledge regarding the typical moral capacities of members of that population; here again though, we face issues regarding the selection of appropriate reference points to compare against.

The issue of detecting these types of cases of moral disenhancement, and of picking suitable reference points, may be particularly troublesome for forms of disenhancement that affect a large proportion of a population, that have historical precedent, or that occurred in past generations that have since propagated these changes; there may be a lack of suitable reference points for comparison, and this may even mean that we remain unaware of such cases. In situations such as these, utilising scientifically based knowledge of the needs and preferences of these species, if available, may be the only way of detecting moral disenhancement of this type. Furthermore, regarding the topic of changes to moral capacities being propagated to future generations, consideration must be taken as to whether each subsequent generation can also be considered morally disenhanced. In this thesis, I intend to consider such cases as forms of moral disenhancement, as clearly human intervention has shaped the moral lives of animals in such cases.

Here again, I feel that there is some benefit to not tying my general definition of moral disenhancement to a particular mode of comparison. However, as discussed in the previous section, I believe that in the upcoming analysis of modern scientific practices, scientific knowledge regarding the species being investigated, and control conditions of experiments, will provide suitable reference points, that will at least indicate thwarting has occurred, even if the exact extent of this thwarting cannot be specifically determined.

2.2.5. Moral disenhancement: Summary

At this point, I believe that I have sufficiently discussed possible forms that moral disenhancement may take, allowing me to arrive at a generalised definition.

Moral disenhancement occurs whenever human action results in negative changes to a moral subject's, or a population of moral subjects', moral capacities; examples of forms that moral disenhancement may take are the elimination or reduction of an individual’s existing moral capacities, a decrease in the reliable functioning of these capacities, impeding or impairing the development of an individual’s moral capacities, or affecting the moral capacities of future individuals in such ways.

As I have discussed, in order to identify some of these forms of moral disenhancement, one needs to be able to assess how an individual’s moral capacities would have differed if the human imposition had not occurred. Although in many of these cases we are unlikely to be able to know exactly how this specific individual could have differed in terms of her moral capacities, the use of suitable reference points, such as the typical moral capacities of members of this species, should allow us to estimate the effect of these impositions with reasonable certainty, or at least allow us to recognise cases where moral disenhancement has occurred. These reference points should be chosen with consideration and care to ensure that they are relevant to the individual being considered, and to try to minimise, or at least recognise, any effects of moral thwarting on the reference points themselves.

2.3. Moral preclusion

The second form of moral thwarting to be considered occurs whenever human action results in a moral subject being precluded from, or impeded in, the proper exercise of her moral capacities; for brevity, I will label such cases as *moral preclusion*. In such cases, an individual possesses moral capacities, but human intervention prevents her from properly employing these capacities to the same extent that she would otherwise be able to do.

Monsó et al. (2018) suggest several examples of ways in which this type of thwarting may occur. One example involves a moral subject witnessing the distress of conspecifics, something that creates an urge in the moral subject to perform caring behaviour towards the conspecific; however, environmental restrictions prevent her from carrying out the moral behaviour that she is motivated to perform. In this example, her moral capacities are intact and functioning reliably, as shown by her urge to care for her conspecific, but she is unable to carry out the morally appropriate behaviour that she is motivated to perform. As further examples of precluding the exercise of moral capacities, Monsó et al. (2018) discuss the impact of human influences on animals’ social environments. Some animals kept in captivity may be subject to unstable social situations, such as frequent regroupings, that prevent the formation of social relationships that may be a pre-requisite for greater displays of moral behaviour such as caring or helping behaviours. Some animals in captivity may also be kept in isolation, leaving them with significantly fewer options, or perhaps no options, to exercise their moral capacities, as they have no conspecifics that they can perform morally motivated behaviour towards.

As was the case for moral disenhancement, some cases of moral preclusion may be relatively easy to recognise; for example, when an individual has frequently demonstrated moral behaviour in the past and has now been prevented from doing so, or when an individual is showing clear attempts to engage in moral behaviour but is unable to do so. In other situations, cases of moral preclusion may be harder to detect; for example, an individual may never have had the preconditions necessary for the exercise of her moral capacities met and therefore we may have no direct experience of this individual's moral capacities. This could be particularly troublesome to detect for individuals of species that have long been raised by humans in conditions that do not meet the required pre-conditions for moral behaviour, as many people may have limited awareness of the moral behaviour that these animals could display under more sufficient conditions. As was discussed for moral disenhancement, this again points to the need for appropriate reference points to allow us to determine with reasonable certainty whether moral thwarting is occurring in such cases.

Before returning to summarise the two types of moral thwarting now identified, I would like to stress that moral thwarting of this form does not only occur at the extreme of an individual not being able to exercise a moral capacity to any extent. Any human interference that impedes or frustrates the exercise of moral capacities should also be considered to morally thwart that individual. The question of whether the extent to which an act impedes or precludes the exercise of moral capacities is relevant to understanding the level of harm or *wrongness* of such an act is one that I leave to individual ethical theories to consider.

2.4. Summary

At this point, I have explored and discussed *moral thwarting* in a way that I hope sufficiently characterises what can be understood by the term. In summary, moral thwarting occurs when human action negatively impacts upon the moral lives of animals who are moral subjects. We can identify *moral disenhancement* and *moral preclusion* as subcategories of moral thwarting. Moral disenhancement occurs whenever human action results in negative changes to a moral subject's, or a population of moral subjects', moral capacities. Moral preclusion occurs whenever human action results in a moral subject being precluded from, or impeded in, the proper exercise of her moral capacities. The preceding discussions of these terms should help to provide a more complete understanding of how they are to be understood.

A further point that I would like to raise regarding the characterisation of moral thwarting that I have provided is that the same act can result in both forms of moral thwarting. For example, isolating an individual in a location where she will witness a conspecific's distress may preclude her from engaging in moral behaviours, such as caring, that she would otherwise perform towards that conspecific (*moral preclusion*), but could also impact her moral capacities in ways such as habituating her to others' distress, meaning that she is less likely to display moral behaviour in the future (*moral disenhancement*). In situations such as these, the individual is being thwarted in multiple ways.

2.5. Regarding normative correctness

Before moving on I would like to briefly comment on two likely valuations that may be proposed for moral capacities. So far in my characterisation of moral thwarting, I have referred to moral capacities without discriminating between those that may be judged as normatively correct and those that could be judged as normatively incorrect. Recall that in the previously given broad definition of moral capacities, moral capacities can be understood, for example, in the sense of Rowlands (2012) or Parrott (2019). Rowlands permits the idea that a moral subject could be a "morally evil one" (Rowlands 2012, p. 231), one who is reliably sensitive to some moral features of an environment or situation but senses them in a way that we would consider normatively incorrect or inappropriate, such as feeling happiness when witnessing another's suffering. Likewise, if we are to use an understanding of moral capacities in the sense of Parrott (2019), then moral capacities are capacities whose exercise conveys information about a being's moral character; this could of course be *evil* or *immoral* aspects of her character. Therefore, I can conceive that those concerned with claiming the *wrongness* of moral thwarting may fall into two camps; those concerned with the thwarting of all moral capacities, and those concerned only with the thwarting of normatively correct moral capacities. This is not something that I wish to take a stand on in this thesis, but I believe that it is worth highlighting here as it is an important consideration for those looking to explain the harm or *wrongness* of moral thwarting.

In my upcoming analysis, I will focus exclusively on normatively correct moral capacities, meaning that my findings will be equally applicable to either interpretation.

PART II: Analysis of moral thwarting in modern scientific research

3. Introduction to the upcoming analysis

3.1. Overview of analysis

Over the course of chapters 3-6, I will turn my attention to analysing real-world scientific studies and practices in order to address the question of whether moral thwarting occurs as part of modern scientific practice. I will focus the majority of my analysis on two areas of scientific research that utilise animals; in chapter 4 I will focus on studies into empathy, and in chapter 5 I will focus on studies into abnormal aggression. In both cases I will analyse how the topics and procedures involved in these experiments relate to the issues of moral subjecthood, moral behaviour and moral thwarting. In these two chapters, I will focus specifically on studies that utilise rats and mice for reasons described in the following section. Having analysed rodent-based studies into empathy and abnormal aggression, I will explain in chapter 6 how my findings have wider relevance, helping to make us aware of further possible cases of moral thwarting within other aspects of scientific practice, and the potential moral thwarting of many more species used in this context.

Before beginning the first major part of the analysis, I will use the rest of this chapter to address some general points.

3.2. Why focus on rats and mice?

I have decided to primarily focus my upcoming analysis on studies involving rats and mice for three main reasons. The first of these is that rats and mice are used extensively for scientific research. In 2017, 9,388,162 animals were used for scientific purposes in the EU, of which approximately 61 % were mice and 12 % were rats (European Commission 2020a). Equivalent data for the US is not available (Speaking of Research 2020); mice, rats, birds and cold-blooded animals are among the list of animals not protected by the US Animal Welfare Act (Schaffner 2011, pp. 71–74), something which has itself been raised as problematic (see e.g. Frasch 2017), and usage data regarding these animals is not available in the United States Department of Agriculture reports (see e.g. United States Department of Agriculture 2018). Applying usage statistics from other countries to the available US data can give us cause to believe that in 2018 “the total number of vertebrates used in research in the US would be between 11 and 23 million”

(Speaking of Research 2020) and that a significant percentage of these animals would be rats and mice. The remaining two reasons why I have chosen to focus on rats and mice are inspired by similar reasoning in Monsó and Andrews (forthcoming). Rats and mice are not necessarily the typical animals that are considered in everyday conversations concerning moral behaviours such as helping or caring, so making the case for them may well help make the argument seem more credible for other less-considered species as well. Finally, rats and mice have been studied in numerous behavioural, neurobiological and neurochemical studies, meaning that there is a variety of existing empirical evidence from which I can draw.

3.3. Some general comments

Before continuing to the main analysis, I would like to briefly address two relevant points. The first is that I do not present the empirical data and discussion in this thesis as conclusive, irrefutable proof of the moral capacities and moral thwarting of these animals; seemingly there is not yet enough evidence on either side of the argument to accept or refute this. Rather my aim is to draw attention to the fact that there are credible reasons to consider such claims as plausible and a real possibility. This may hopefully give us cause to reconsider our past, present and future treatment of these animals.

The second point that I would like to briefly touch upon is that some, perhaps many, of the methods used to obtain the empirical data used here to support the claim of animals as moral subjects can be criticised from various ethical perspectives. For example, animal suffering, a commonly raised ethical concern, certainly results from studies into animal empathy, such as Church (1959), that intentionally place animals in distressing situations in order to observe the reactions of their conspecifics. While I do not wish to downplay other ethically problematic aspects of these studies, I will bracket these concerns in order to focus specifically on the topic of moral thwarting within scientific research.

4. Experimental manipulation of empathy: Rats and mice

4.1. Overview

In this chapter, it is my aim to discuss the manipulation of empathy in scientific experiments utilising rats and mice, and present an argument for why this should be considered as moral thwarting. I will briefly address the connection between moral emotions, the behaviours that they motivate, and moral thwarting, and then move on to discussing how a particular conception of empathy can be understood as a moral emotion. Following this, I will focus on a recent body of work concerning empathy manipulation in rats (Hernandez-Lallement et al. 2016, 2018) and argue that this work results in moral thwarting; discussing this work will afford me the opportunity to present empirical evidence of the empathic capacities of rats, and to provide a detailed analysis of how the manipulation of empathy in rats can be understood as a form of moral thwarting. I will then present other examples of recent scientific experiments that likely manipulate empathy in rats and mice, claiming that these too are examples of moral thwarting. Finally, I will discuss what we can learn from these analyses regarding the detection of further cases of moral thwarting in scientific experimentation and scientific practice.

4.2. Moral emotions, behaviour and moral thwarting

My upcoming argumentation concerning moral thwarting in scientific experimentation relies heavily upon the concept of moral emotions; therefore, it is important to establish the relation between moral emotions, behaviour and moral thwarting. In chapter 2, I developed a working definition of *moral thwarting*, which identified *moral disenhancement* and *moral preclusion* as types of moral thwarting. These types of moral thwarting were identified and characterised by the impact that they had on a moral subject's moral capacities. In the understanding of moral capacities provided in section 2.1, a subject's moral sensitivity, i.e. her sensitivity to good- or bad- making features of her environment, was indicated as one type of moral capacity, understood on the basis of Rowlands (2012). Rowlands identifies moral emotions as one possible form that such sensitivity may take. Given that moral emotions are a form of moral sensitivity, we can recognise them as moral capacities. This means that if human action affects moral emotions in any of the ways identified by my concepts of moral disenhancement or moral preclusion, then we can recognise that moral thwarting has occurred.

Rowlands characterises moral, or morally laden, emotions as follows:

> "An individual possesses a (nonmisguided) morally laden emotion when it is in a state that tracks a true evaluative proposition of a specific sort—a proposition that expresses a moral evaluation. This allows us to define the concept of a morally laden emotion as follows:
>
> An emotion, E, is *morally laden* if and only if (1) it is an emotion in the intentional, content-involving, sense, (2) there exists a proposition, *p*, which expresses a moral claim, and (3) if E is not misguided, then *p* is true." (Rowlands 2012, p. 69)

Within the preceding characterisation, Rowlands utilises the concept of an emotion *tracking* an evaluative proposition. *Tracking* denotes a truth preserving relationship; if an emotion *E tracks* a proposition *P*, then *E* guarantees the truth of *P*, so long as *E* is not misguided (Rowlands 2012, pp. 39–70). An emotion is considered misguided when its evaluative component is in some way erroneous (Rowlands 2012, pp. 67–68). Utilising this concept of tracking as part of his argumentation allows Rowlands (2012, pp. 39–70) to be able to claim that an individual can be capable of acting for moral reasons, without requiring that the individual possess the necessary capacities to form moral judgements, or consciously entertain the relevant propositions.

Due to their subjective nature, we cannot directly experience another's emotions. However, we can infer the existence of some moral emotions through the behaviour that they motivate; if an emotion motivates a behaviour, then that behaviour will in turn track the same proposition as the emotion (Monsó 2015, p. 676). Therefore, in this analysis, I will frequently utilise behavioural evidence to identify probable underlying motivations and their moral character, and I will utilise differences in behavioural responses to identify likely changes to underlying moral motivations. In this way, I can use behavioural evidence to understand how moral capacities may have been impacted upon by human actions, and to identify cases of moral thwarting.

4.3. Empathy as a moral emotion

Given that my argumentation is concerned with both empathy and morality, it may initially seem tempting to be drawn into addressing two existing debates; how exactly to understand empathy, and what is its role in morality. There exist differing interpretations of the term empathy, characterised by varying cognitive and non-cognitive requirements (for discussion, see e.g. Preston and de Waal 2002, de Vignemont and Singer 2006, Monsó 2015, Adriaense et al. 2020). Furthermore, there are varying views on empathy's role in morality (for discussion, see e.g. Maibom 2014, pp. 27–35). However, for the purposes of my argument, what is important is to establish that the type of emotion that I will discuss in this section, which I will identify as empathy, is a moral emotion. If this case can be made, then manipulations of this emotion, or precluding the exercise of this emotion, can be identified as cases of moral thwarting. Acceptance or rejection of the term *empathy* to describe this emotion would not affect any arguments concerning whether its manipulation corresponds to a type of moral thwarting.

Through analysis and discussion of differing definitions of empathy, Monsó (2015) developed a formulation of what she describes as *minimal moral empathy* (MME), an emotion which corresponds to Rowlands' definition of a moral emotion, and maintains what she believes many would recognise as the core characteristic of empathy (captured by condition 2 in the following characterisation). MME is characterised as follows:

"Creature C possesses *minimal moral empathy* (MME) if: it has (1) an ability to detect distress behaviour that, (2) due to the action of a reliable mechanism, results in an emotion that is directed towards the distress behaviour, and built into which is (3) an urge to change the situation that, together with the emotional reaction, (4) tracks a relevant moral proposition." (Monsó 2015, p. 681)

This definition only makes reference to empathy in the context of distress behaviour. Monsó notes, however, that her decision to refer only to the detection of behaviour indicative of negative emotions in the definition was made for the sake of simplicity, and that a form of MME could be recognised that involves the detection of behaviour indicative of joyful emotions (Monsó 2015, pp. 683–684). When it comes to considering the upcoming real-world examples, it could be the case that some of these examples deal with the ability of individuals to detect behaviour of others that is indicative of joyful emotions. Taking this into account, I have reformulated the above description of MME to also incorporate joyful behaviour:

> Creature C possesses *minimal moral empathy* (MME) if: she has (1) an ability to detect distress behaviour or joyful behaviour that, (2) due to the action of a reliable mechanism,

results in an emotion that is directed towards this behaviour, and built into which is (3) an urge to change the situation that, together with the emotional reaction, (4) tracks a relevant moral proposition.

4.4. Case study: "Towards an animal model of callousness"

Having established the relationship between moral emotions, behaviours and moral thwarting, and identified a definition of empathy that is recognisable as a moral emotion, I will now apply this knowledge to a real world set of related scientific studies to assess whether there is a strong case for considering them as cases of moral thwarting.

The main work that I will analyse is a paper entitled "Towards an animal model of callousness" (Hernandez-Lallement et al. 2018). Although itself only a review paper, it discusses recent work by its authors (Hernandez-Lallement et al. 2016) that I will argue resulted in the moral thwarting of the animal subjects who were experimented upon. Furthermore, the review paper argues that the types of manipulation performed in this work form the basis of an animal model that should be further utilised and developed in ongoing work, indicating that this type of work is likely to be performed many more times in the future. Among the argumentation given for the further utilisation of this animal model, the authors include a normatively laden claim that their approach of performing the suggested manipulation on rodents represents an "ethically less controversial alternative to non-human primate[s] [sic]" (Hernandez-Lallement et al. 2018, p. 124). In the following analysis, I aim to draw attention to one of the ways in which this type of work should still be recognised as ethically problematic, by arguing that the use of this model results in the moral thwarting of the animals involved. Furthermore, the arguments found within this thesis support claim that both rodents and non-human primates can be harmed via moral thwarting, and therefore illustrate ethically relevant similarities between these two types of animals.

The focus of Hernandez-Lallement et al. (2018) is to identify and propose a rodent model of callousness that can be used to further understand neurobiological aspects of callousness. The authors consider this work potentially important for the development of treatments for anti-social behaviour, conduct disorder and psychopathy in humans, all of which are associated with callousness, or callous-unemotional traits (Hernandez-Lallement et al. 2018, pp. 121–122). They identify several conditions that they believe should be fulfilled by an animal model of callousness (Hernandez-Lallement et al. 2018, p. 124) and propose that the prosociality reducing effects of amygdala lesions on the performance of rodents in a Prosocial Choice Task meet these conditions. This proposal is based on previous work by the authors (Hernandez-Lallement et al. 2015, 2016) that I will now briefly describe.

The Prosocial Choice Task that they have developed utilises a double T-Maze-based design to examine prosociality in rats. In this task, an actor rat can choose to visit one of two compartments of the maze. The actor rat receives an identical food reward regardless of the compartment that she chooses. However, choosing one of the compartments, designated the *mutual-reward option*, also results in a partner rat, separated from the actor in both compartments by a perforated, transparent wall, receiving a food reward. It has been shown that non-lesioned rats undergoing this task develop a significant preference for the mutual-reward option, which is taken as evidence of prosociality in rats (Hernandez-Lallement et al. 2015).

The authors have subsequently shown that lesioning rats' basolateral amygdalae has the effect that they will no longer develop this preference for choosing the mutual-reward option in the Prosocial Choice Task (Hernandez-Lallement et al. 2016). The lesioning process performed consists of a surgical procedure that involves the drilling of holes into the rat's skull and then the lesioning of the basolateral amygdala via an injection containing quinolinic acid. The further study of rats subjected to such amygdala lesions is central to the proposed animal model of callousness (Hernandez-Lallement et al. 2018).

My intention now is to show that the lesioning process, proposed for future use as part of the animal model of callousness (Hernandez-Lallement et al. 2018), and already performed on rats as part of the research under discussion (Hernandez-Lallement et al. 2016), results in moral thwarting. To do this, I will first show how the authors aim at, and achieve, the abolishment of emotional empathy, and then I will show how this also corresponds to the abolishment of minimal moral empathy.

4.4.1. Abolishment of emotional empathy

The authors intend to create an animal model of callousness, with callousness understood as "the absence of empathy" (Hernandez-Lallement et al. 2018, pp. 121–122), later defined as "the *absence* of emotional empathy" (Hernandez-Lallement et al. 2018, p. 122). Emotional empathy is described as "the ability to recognize affective displays in others and emulate the underlying emotion" (Hernandez-Lallement et al. 2018, p. 122) and "is thought to be supported by low-level emotional contagion/mimicry and direct perception" (Hernandez-Lallement et al. 2018, p. 122) [9].

When laying out the case for the model of callousness that they wish to propose, the authors suggest that "a promising approach to develop putative animal models of callousness is to capture experimentally-induced abolishment of an empathic reaction or other-regarding concern in a task in which behaviour is normally modulated by the affective state of a conspecific" (Hernandez-Lallement et al. 2018, p. 122). The reference in this quote to *experimentally-induced abolishment of an empathic reaction*, alongside the author's description of callousness, should leave us in little doubt that an animal model successfully corresponding to this description, such as the one developed by the authors, both intends and results in the removal of empathy from the animals involved.

Having established that the goals of the proposed model involve experimentally removing empathy, as understood by the authors, from the animals involved, I will now briefly summarise the evidence that the lesioning procedure will result in, and has already resulted in, the removal of empathy from the animals undergoing the procedure.

It seems clear that Hernandez-Lallement et al. (2018) believe that the absence of prosociality in their study corresponds to an absence of empathy. They describe social choice-based paradigms, such as the proposed Prosocial Choice Task as a "strong suit to establish a rodent model of emotional empathy" (Hernandez-Lallement et al. 2018, p. 125) and identify the absence of prosociality as a proxy for callous behaviour. Callousness is defined as "the *absence* of emotional empathy" (Hernandez-Lallement et al. 2018, p. 122), and their proposed approach to modelling callousness involves abolishing empathy. Numerous scientific studies involving rats are cited to help make the case that they possess empathic abilities (Hernandez-Lallement et al. 2018, pp. 124–125); references are made to early studies in which rats seem to display an emotional response to conspecifics in distress (Church 1959, Rice and Gainer 1962, Evans and

---

[9] Emotional empathy is contrasted with *cognitive* empathy; "imagining that another individual has thoughts and feelings separate from our own" (Hernandez-Lallement et al. 2018, p. 122) (a definition that binds cognitive empathy to the existence of a Theory of Mind).

Braud 1969), and to more recent studies investigating the informational value of freezing behaviour (Pereira et al. 2012), responses to the freezing behaviour of others (Knapska et al. 2006, Atsak et al. 2011), the effect of prior self-experience of aversive situations on emotional responses (Kavaliers et al. 2001, Atsak et al. 2011, Parsana et al. 2012, Sanders et al. 2013), the role of various neurological structures in the social transmission of fear (Knapska et al. 2006, Jeon et al. 2010, Ito et al. 2015), transfer of positive affect (Knutson et al. 1999, Popik et al. 2012, Kashtelyan et al. 2014, Willuhn et al. 2014), and both non-costly (Taylor 1975, Hernandez-Lallement et al. 2015, Márquez et al. 2015, Oberliessen et al. 2016) and costly (Ben-Ami Bartal et al. 2011, Sato et al. 2015) helping behaviours. Therefore, we can assume that if the lesioning process leads to a decrease in prosociality in the rats in the discussed studies, the authors will interpret this as illustrating a decrease in empathy.

As previously mentioned, Hernandez-Lallement et al. (2015) utilised their Prosocial Choice Task to show that actor rats significantly preferred to visit the compartment of a T-Maze that resulted in a reward for both themselves and a conspecific, as opposed to the compartment where only they themselves were rewarded. When partnered with a toy rat instead of a conspecific, actor rats did not develop this preference for the mutual-reward condition, providing evidence that there is something reinforcing about the effect of the outcome on an actual, living partner rat, and thus a prosocial motivation. The results imply that the actor rat is sensitive to the effect on the partner rat, suggesting an ability to recognize affective displays of conspecifics, and thus is strongly suggestive of (emotional) empathy.

This study design was then re-used in a subsequent study by Hernandez-Lallement et al. (2016). In this study, two groups of rats were used. The first group, the lesioned rats, were subject to the previously described surgical lesioning procedure. The second group, the sham-operated rats, underwent a similar surgical procedure, except only vehicle solutions were injected, meaning that no lesioning occurred. Both groups of rats were later tested in the previously described Prosocial Choice Task, with the results showing that the lesioned rats had a significantly lower preference for the mutual reward condition; in the authors' words "the integrity of basolateral amygdala (BLA) was necessary for the expression of mutual reward preferences" (Hernandez-Lallement et al. 2016, p. 7).

An additional experiment in the same paper (Hernandez-Lallement et al. 2016), focussing on the rats' reward discrimination capabilities, helped confirm that the deficits in the lesioned rats' behaviour corresponded to the social aspects of the task. Commenting on the results of this study in a later paper, the authors comment that "the BLA-lesion effects were characterized by the absence of pro-social tendencies, suggesting a disruption of the cognitive, emotional or motivational mechanisms underlying pro-social behavior" (Hernandez-Lallement et al. 2018, p. 126). This outcome shows that the lesioning leads to an absence of prosociality, and therefore the authors interpret this as the lesioning procedure having led to a reduction in empathy in the lesioned rats.

4.4.2. Abolishment of minimal moral empathy

I believe that the above evidence shows that the lesioning procedure reduces empathy, as understood by the authors, in the affected rats. However, to be able to argue that this constitutes moral thwarting, we need to show that the affected emotion is a moral one. To do this, I will present evidence to help make the case that the affected emotion conforms to the conditions of minimal moral empathy.

Earlier, I arrived at the following definition of minimal moral empathy, on the basis of (Monsó 2015):

> Creature C possesses *minimal moral empathy* (MME) if: she has (1) an ability to detect distress behaviour or joyful behaviour that, (2) due to the action of a reliable mechanism, results in an emotion that is directed towards this behaviour, and built into which is (3) an urge to change the situation that, together with the emotional reaction, (4) tracks a relevant moral proposition.

Does the behaviour of the rats in the discussed studies provide evidence of MME? Regarding condition (1), as already mentioned, a previous study by the authors has shown that the presence of a real partner rat, as opposed to an inanimate toy rat, is necessary for the rats to develop a preference for the option that rewards both itself and the partner (Hernandez-Lallement et al. 2015). This suggests that the actor rat's behaviour results from detecting the partner rat's behavioural response to the experimental situation. It is currently unclear whether the rats in this study are motivated to reward both themselves and the partner due to distress behaviour from the partner rat if not rewarded, or, for example, due to the pleasure expressed by the partner rat upon receiving the food reward (Hernandez-Lallement et al. 2018, p. 125), or even due to a combination of these. However, any of these three reasons is compatible with condition (1) of minimal moral empathy. More generally, in support of condition (1), there is a body of scientific evidence that shows rats modifying their behaviour due to affect-related signals of conspecifics (see e.g. Church 1959, Rice and Gainer 1962, Evans and Braud 1969, Greene 1969, Atsak et al. 2011, Ben-Ami Bartal et al. 2011, Sato et al. 2015, Lu et al. 2018).

Concerning conditions (2) and (3), results show that the rats establish a stable preference for the prosocial, mutual reward condition. They significantly prefer to choose this option and reliably develop a preference to act in this way (Hernandez-Lallement et al. 2015) supporting the idea that the underlying mechanism behind this behaviour, and the emotion that motivates it, is reliable and that the chosen option is not merely selected by chance. However, it is possible to argue that the behaviour shown by non-lesioned rats in the studies under discussion (Hernandez-Lallement et al. 2015, 2016) does not necessarily provide evidence of an emotion that is directed towards the partner rats' distressed or joyful behaviour, and could simply be an un-directed emotion, a *mood* as Rowlands describes it (Rowlands 2012, pp. 42–43), experienced as a result of this behaviour.

As an example of how this could be argued, consider that it may be the case that the mutual-reward option is preferred by the actor rats because in the alternative, own-reward condition, the partner rat is distressed as a result of not being rewarded, and her distress behaviour is experienced as aversive by the actor rat. The only way for the actor rat to avoid this aversive stimulus is to choose the both-reward condition. She might not choose the mutual-reward option because its emotional response and corresponding behaviour are concerned with addressing the distressed state of the partner rat but simply because it is the only way for the actor rat to avoid the more aversive situation. In this case, an experiment showing that the actor rat would still prefer mutual-rewards over a modified own-reward condition, in which the actor rat did not experience the aversive behaviour of the partner rat, could provide greater evidence that the underlying emotion motivating the behaviour is concerned with the addressing the partner rat's situation. I am not aware of such an experiment having been carried out within the same experimental setup; however, as I will now briefly discuss, an experiment by Carvalheiro et al.

(2019), utilising a modified version of an experimental setup developed by Ben-Ami Bartal et al. (2011), does provide evidence that suggests that prosocial behaviour in rats is not simply performed due to it being the only way to avoid aversive stimuli.

Ben-Ami Bartal et al. (2011) developed an approach for studying helping behaviour in rats, in which rats could choose between the option of freeing a conspecific trapped within a transparent restrainer, or differing control conditions such as opening an empty restrainer or a restrainer containing a toy rat. Rats significantly preferred to free trapped conspecifics, and their latency to do so decreased across sessions. A further modification showed that rats would still choose to free a conspecific even if they were prevented from socially interacting with the rat once it was free. Although this experiment seems to demonstrate helping behaviour, it also fails to differentiate whether the rats were acting with the intention of reducing distress in the conspecific or simply because it was the only option to reduce their own aversive experience[10]. However, a modified version of this experiment addresses this question.

Carvalheiro et al. (2019) created a modified version of the experimental setup from Ben-Ami Bartal et al. (2011), in which the actor rat also had the option of retreating to a darkened room, avoiding potentially aversive stimuli associated with the trapped rat. Although they showed a higher latency to free the trapped conspecific and fewer door openings overall, the experiment shows that rats with an escape option do still choose to help a trapped conspecific. This provides evidence that the rats' behaviour is concerned with modifying the situation of the trapped rat, and not only with improving their own situation. Returning to the conditions of MME, we can certainly claim that there is some available scientific evidence that gives us cause to believe that the prosocial action of rats may be concerned with improving a conspecific's situation.

Addressing the final condition required for an emotion to qualify as MME, point (4), can we claim that the emotional reaction and behaviour of the rat track a relevant moral proposition? So long as it is not misguided, do the emotion and associated behaviour track a proposition

---

[10] Silberberg et al. (2014) have proposed an alternative explanation for the observed behaviours, claiming that they may instead be the result of rats' neophobia and desire for social contact. Whether rats are actually distressed by being restrained inside the restrainer has also recently been called into question (Hachiga et al. 2020).

expressing a true moral claim[11]? Working only from the context of the Prosocial Choice Task and the results of the authors' previous studies (Hernandez-Lallement et al. 2015, 2016), we could make the case that the emotion tracks the following proposition:

> *Given the choice between actions with the same associated benefit or cost to oneself, one should choose the action that most benefits others.*

Can we recognise this proposition as expressing a moral claim? When discussing moral emotions, Rowlands does not provide a definition for us to use, declaring "[w]hat makes a proposition a moral one is something that I shall not discuss. I shall assume we have a reasonable grasp on which propositions are moral ones and which are not" (Rowlands 2012, p. 71). Nevertheless, I would argue that on the grounds that this proposition expresses a normative judgement regarding the way in which one should act, it expresses a moral claim. Furthermore, does the proposition express a moral claim that resembles any typically recognised and accepted approaches to morality? As discussed in chapter 2, I wish to avoid staking my claim to one particular ethical theory in order to judge the *rightness* of a moral subject's actions. However, it seems to me that the proposition here expresses a rather uncontroversial moral judgement, commonly reflected in folk intuition. More concrete ethical theories can also support such a proposition; for example, if we interpret *benefiting* an individual as increasing their pleasure or reducing their suffering, an interpretation which is clearly applicable to the studies being discussed, then such a proposition is supported by hedonistic utilitarianism.

Additionally, there is evidence that may give us reason to believe that the previous proposition, although accurately characterising a proposition tracked by the emotion, may be too narrow an interpretation of the moral claim being tracked, potentially doing an injustice to both the scope to which rats may be capable of experiencing moral emotions, and as a result, the extent to which they may demonstrate morally motivated behaviour. Studies have shown rats modifying their behaviour in a way that not only benefits others but that is also costly to themselves (Church 1959, Ben-Ami Bartal et al. 2011, Sato et al. 2015). Therefore, it could be possible that the emotion tracks a more selfless proposition, one that captures the notion of the previous

---

[11] As described in section 4.2, to be able to claim that an individual's emotions (and behaviours motivated by these emotions) *track* moral propositions, does not require that that individual must be able to entertain and understand such propositions.

proposition but that also endorses the idea that *sometimes* one should act to benefit others, even at a cost to oneself. Although based on the available evidence we may not be able to fully define *sometimes* in this proposition at this current time, the evidence does suggest that a suitable definition may exist. Depending on the exact definition, such a notion could again be captured by ethical theories such as hedonistic utilitarianism, which would recognise that an action that causes a universal net gain in pleasure, even at a cost to the performer, is the right action to perform. Regardless of whether we choose to embrace this potentially broader proposition, or stick to the more conservative original proposition, I hope to have made the case that the emotion tracks a valid moral proposition.

Through discussing each of the conditions required for MME, I hope to have shown that, based on the available evidence from both within the study and from other scientific work, there are strong reasons to take seriously the claim that rats possess MME and that this emotion motivates the behaviours seen in the study.

4.4.3. Conclusion: The case for moral thwarting

I have now established that there is a strong case that the emotion being studied meets the conditions of minimal moral empathy, a moral emotion. By bringing together the various strands of my discussion concerning the work under discussion, I believe that this work can be shown to contain acts of moral disenhancement, a type of moral thwarting. I previously identified several forms that moral disenhancement may take; the first of these involved a moral subject's existing moral capacities being eliminated or reduced; for example the reduction of an individual's emotional moral sensitivity or the reliability of this sensitivity, would correspond to this form of moral thwarting. This is the type of moral disenhancement that I have identified in the discussed studies. I have shown that the authors of the work under discussion both intended and achieved the abolishment of empathy through the process of amygdala lesioning, as seen by the abolishment of the prosocial behaviour that it motivates. I established that there is strong evidence for understanding empathy here as a moral emotion, identified as *minimal moral empathy*. Therefore, the discussed work seemingly promotes and achieves the reduction, perhaps even the complete abolishment, of moral capacities underlying the prosocial helping behaviour of rats observed in these studies. This reduction of moral capacities clearly corresponds to an identified type of moral disenhancement, and is therefore identifiable as a type of moral thwarting.

4.5. Further examples

The previous case study gives us strong reasons to consider that rats may be moral subjects whose behaviour can be motivated by the moral emotion referred to here as empathy, and that moral thwarting does occur within modern scientific experimentation and is therefore a prospect to be taken seriously. I believe that this analysis also provides a starting point from which we may already begin to understand that the implications and scope of moral thwarting in scientific studies go well beyond what is seen in this specific example. I will therefore offer some additional discussion on further experiments and experimental procedures performed on rats and mice that I believe are also likely to have resulted in moral thwarting.

4.5.1. Amygdala lesioning of rats in other experiments

The lesioning of rats' basolateral amygdalae is not a niche process found only in the discussed model of callousness. There are many modern examples of scientific studies performing this manipulation on rats (see e.g. Dvorkin et al. 2010, Greenwood et al. 2010, Segura-Torres et al. 2010, Ostrander et al. 2011, Zeeb and Winstanley 2011, Zimmerman and Maren 2011, Chang et al. 2012, West et al. 2012, Blundell et al. 2013, Izquierdo et al. 2013, Zheng Li et al. 2013, Pelloux et al. 2013, Tavares et al. 2014, Holland 2016, Ranjbar et al. 2016, 2017, Schönfeld et al. 2019). Although these studies utilise a variety of different lesioning procedures, for example electrical lesioning or lesioning using various acids, in principle the studies seem to amount to the same kind of treatment. This list of studies is by no means meant to be a complete reference of all experiments performing this procedure but is rather used here to illustrate that basolateral amygdala lesioning occurs in many other experiments in addition to the rat model of callousness previously discussed. Given what we have discussed concerning basolateral amygdala lesioning resulting in deficits in empathy, it does not seem unreasonable to assume that moral thwarting occurs as a result of each of these experiments.

4.5.2. Empathy and amygdala lesioning in mice

As stated earlier, my intention for the majority of this chapter is to focus on examples of the moral thwarting of rats and mice. Having discussed empathy and amygdala lesioning experiments in rats, I would now like to briefly do the same for mice. There are recent examples of amygdala lesioning procedures being performed on mice (see e.g. Tzeng et al. 2017, Ferrazzo et al. 2019, Marincovich et al. 2019). Although we may not have such direct empirical evidence on the effects of lesioning on empathy in mice as we do for rats, as this does not seem to have been researched at this time, a combination of the effects of the previously discussed lesioning studies performed on rats (Hernandez-Lallement et al. 2016, 2018), existing evidence for empathy in mice, and scientific knowledge regarding the amygdala may give us good reasons to consider the possibility that this lesioning could inhibit empathy within mice. Therefore, I will now briefly introduce the current empirical evidence for empathy in mice, and relevant scientific knowledge concerning the amygdala.

The study of empathy in mice does not seem to have advanced as far as the study of empathy in rats. The majority of relevant studies that I have found focus on emotional contagion. Emotional contagion, the "adoption—in whole or in part—of another's emotional state" (de Waal 2008, p. 283) has been suggested as the most basic form of empathy (de Waal 2008). The emotional contagion of fear (see e.g. Chen et al. 2009, Jeon et al. 2010, Jeon and Shin 2011) and pain (see e.g. Langford et al. 2006, Smith et al. 2016) has been well demonstrated in mice.

There seem to have been less scientific papers published addressing whether behaviours, such as helping behaviours, are shown by mice in response to conspecifics' states. A study by Langford et al. (2010) observed that female mice more frequently chose to approach a familiar female conspecific who was in pain than one who was not in pain. A very recent study has shown that mice work to free conspecifics contained inside tubes, but not to open empty tubes, but it is unclear from the study whether the mice were motivated by the distress of the trapped mice or some other factor (Ueno et al. 2019a). A follow-up paper further investigated this topic using a variety of modified setups (Ueno et al. 2019b). Amongst their results, they showed that oxytocin administration does not affect rescue behaviour, that mice will also open opaque, but not transparent, tubes containing a ball of yarn, that the presence of a second unrestrained mouse does not affect the time taken to rescue a restrained conspecific, that mice more freely enter open tubes placed near restrained conspecifics than those positioned further away, that the time spent inside open tubes positioned at different distances to a restrained conspecific does not vary significantly, and that when two mice are restrained in separate tubes, an unrestrained mouse will rescue the first mouse with the same latency as previously observed, but will show a significantly longer latency to rescue the second mouse or will fail to do so within the experimental timeframe. These results pose challenges to the hypotheses that empathy motivates tube opening rescue behaviours in mice, particularly the lack of oxytocin-related effects and the longer latency to rescue a second trapped conspecific. The authors propose that the results provide evidence that tube-opening behaviour can be motivated by desire for social contact and interest in the restraint tubes. However, this does not necessarily rule out empathy as a motivation, as it is possible that mice may be subject to multiple motivating factors at one time. The authors do not rule out that mice show prosocial behaviour; they suggest that further studies and methods are required to investigate both rescue behaviour and prosociality in rodents.

Therefore, it appears that there is currently insufficient scientific knowledge available to allow us to claim with reasonable certainty whether mice do or do not meet the conditions for possessing minimal moral empathy. Further scientific research is required to be able to address the question with greater certainty. In the meantime, I propose that there still exist reasons for seriously considering the possibility; namely the existing evidence for emotional contagion and basic empathy-motivated behaviour in mice, and the evidence of empathy-motivated behaviours in rats that we have previously discussed.

If we were to assume that mice, or indeed other types of animals, used in scientific experiments are capable of experiencing empathy, or other moral emotions, do we have any reason to suspect that amygdala lesions would affect them in the same way as seen in rats? I believe that we do, given the amygdala's evolutionary history, and its roles in social processing and social learning.

Hernandez-Lallement et al. (2018) highlight how "[a]mygdala functions and circuitry are phylogenetically old and well conserved across vertebrates" (Hernandez-Lallement et al. 2018, p. 125) and that "evolutionary homologues of major amygdala clusters are found in most mammals including primates and rodents but also in birds, reptiles and fish" (Hernandez-Lallement et al. 2018, p. 125). This suggests a similar role is likely played by the amygdala in these species as in rats.

Hernandez-Lallement et al. (2018, p. 123) discuss how the amygdala is seemingly involved with processing social signals. They draw attention to scientific work (Adolphs et al. 1994, 1998, Adolphs 1999), focussed on humans, indicating that “[d]amage or atrophy of amygdala tissue is associated with selective deficits in affiliation and social signal processing” (Hernandez-Lallement et al. 2018, p. 123). They also discuss how “the role of the amygdala in emotional empathy could be facilitatory: in drawing or increasing attention to stimuli associated with emotions” (Hernandez-Lallement et al. 2018, p. 123). Given this information, we can conceive that, as was seen with rats, the social behaviour of mice, as well as other vertebrates, may well be affected by damage to the amygdala leading to deficits in social signal processing. Given the role of social signals in communicating aspects of an individual’s affective state, it seems clear that a compromised ability to process these signals could interfere with an individual’s empathic capacities. In cases where empathy, or other morally motivated behaviours are affected, moral thwarting occurs.

Hernandez-Lallement et al. (2018, p. 123) also draw a connection between the amygdala and their social reinforcement learning hypothesis (Hernandez-Lallement et al. 2017). “According to the social reinforcement learning hypothesis […], the likelihood of showing a particular behavior is increased or decreased, contingent on the type of social signals following the behavior” (Hernandez-Lallement et al. 2018, p. 123). Behaviours carrying positive valence would become reinforced, whereas those carrying negative valence would not. Due to its importance in emotional processing and associative learning, the amygdala is identified as likely very important to this learning process. Compromised amygdala function would likely reduce an individual’s ability to modify its behaviour according to social feedback from conspecifics. Among other effects, this could prevent the development of moral behaviour, as a result of not being able to experience and learn from the effect of one’s behaviour on others; as previously discussed, negatively impacting the existing moral capacities of a moral subject, or the development of these moral capacities, are forms of moral thwarting.

Taking together the evidence for empathy-motivated behaviours in mice and rats, the evolutionarily conserved functionality of the amygdala, the amygdala’s role in social signal processing and learning based on these signals, and the previously discussed effects of amygdala lesions in rats, I believe that we should seriously consider the prospect that moral thwarting is a possible outcome of basolateral amygdala lesions in mice, a process that occurs in modern scientific practice.

4.5.3. Other empathy-thwarting experimental procedures

I have been unable to find many more example studies that, through their own results alone, seem to specifically highlight their manipulation of empathy in rats and mice; in the subsequent section I will discuss why I believe that many existing cases of moral thwarting may be difficult to identify, at least without detailed analysis. Before discussing this however, I would like to draw attention to several additional studies that do clearly seem to show the manipulation of empathy, and then go on to discuss how empathic behaviour may also be affected in more subtle ways.

A study by Zhen Li et al. (2014) demonstrated that rats showed an enhanced paw flinch reflex after socially interacting with cagemates who had been subcutaneously injected with bee venom; this serves as evidence of emotional contagion of pain amongst rats. The study then went on to show that rats who were subjected to bilateral lesions of the medial prefrontal cortex would not display this enhanced paw flinch reflex, leading the authors to conclude that "the medial prefrontal cortex plays a critical role in processing the empathy-related enhancement of spinal nociception" (Zhen Li et al. 2014, p. 1253). This lesioning of the medial prefrontal cortex appears to prevent, or at least reduce, emotional contagion of pain in rats. Given the previously listed evidence for empathy-related behaviour in rats it seems reasonable to interpret this as reducing the rats' moral sensitivity, and to assume that it would lead to a reduction in morally motivated behaviour; therefore, this experiment would qualify as an example of moral thwarting[12]. Another recent experiment involved the pharmacological deactivation of the rats' anterior cingulate cortex, one of the areas comprising the medial prefrontal cortex, and showed that this procedure reduced rats' aversion to conspecifics' pain, resulting in less behaviour aimed at preventing others' pain (Hernandez-Lallement et al. 2020). The decreased sensitivity to others' pain and the associated change in behaviour seem to clearly correspond to a decrease in empathy and empathy-motivated behaviours, giving us good reason to identify this as another experiment that results in moral thwarting. As well as both of these studies themselves representing cases of moral thwarting, the evidence they provide may suggest to us that any other work that interferes with the working of the medial prefrontal cortex or anterior cingulate

---

[12] This experiment also included an additional condition in which rats' amygdalae were lesioned via injections of a chemical toxin. Given the previous discussion of amygdala lesioning and its effects in rats, it is likely that the rats undergoing this condition were also morally thwarted.

cortex, whether via lesioning or some other method such as drug administration, could also result in moral thwarting; again we see how the results of experiments that consider the effect of an intervention on the empathic abilities of animals can potentially make us aware of the moral thwarting that may occur in a host of other studies, even if those studies themselves may not indicate this, for example due to their alternative foci or choice of collected data.

A study by Ben-Ami Bartal et al. (2016) provides further evidence that pharmacological interventions can also result in moral thwarting. In their experiment they showed that rats injected with midazolam, an anxiolytic, showed reduced helping behaviour compared to rats in the control condition. This demonstrates one of the ways, namely pharmacological interventions, in which moral thwarting may occur through seemingly less invasive methods than the previously discussed lesioning procedures. Scientific research can involve the administration of various substances to animals for purposes such as drug development and testing, and, as I will discuss in the upcoming section on abnormal aggression, to study the effects of the use and abuse of substances such as alcohol. Once we take seriously claims about animals as moral subjects and about moral thwarting being problematic, then it becomes clear that the effects of these types of interventions on the moral lives of animals should not be overlooked. This study also serves as a useful illustration of the fact that, seemingly unlike in the case of the lesioning studies, moral thwarting can also involve changes that are temporary in nature; such cases are recognisable as moral thwarting, as the moral lives of animals are still impacted upon.

The studies that I have drawn attention to so far have largely featured invasive procedures or specific interventions, and the resulting moral thwarting may be somewhat obvious, for example through a noticeable alteration in behaviour that occurs rather suddenly and is obviously tied to the intervention that the animal has recently undergone. However, moral thwarting can occur in perhaps more subtle ways, which it may be easier to overlook or be unaware of. Ben-Ami Bartal et al. (2016) have shown that both low and high levels of stress or arousal lead to a lower amount of successful prosocial behaviour than a moderate of amount of stress, suggesting that exposing an individual to low or high arousal situations may thwart their motivation or ability to perform empathy-motivated behaviour. An early study into rat empathy by Church (1959) suggests that individuals may become habituated to indicators of others’ distress, suggesting that some level of exposure to others in distress could result in a decrease in moral sensitivity or moral behaviour; therefore interfering in animals' lives in such a way that they experience these conditions could also lead to moral thwarting. Social experiences have also been shown to impact empathic behaviour in rats (Ben-Ami Bartal et al. 2014, Lu et al. 2018), suggesting that interferences in the social lives of animals may impact upon their moral behaviour in this way and lead to moral thwarting. Although some researchers may choose to deliberately manipulate factors such as stress, exposure to others in distress, or social experiences as part of their scientific research, it could also be the case that these factors become unintentionally manipulated in other cases, for example as side-effects of scientific procedures or husbandry practices.

Furthermore, scientific procedures or husbandry practices may, whether intentionally or not, restrict individuals from acting on the basis of empathy, for example by restricting or preventing access to others that these individuals may be motivated to help; these represent cases of moral preclusion, a form of moral thwarting that we identified earlier.

In the upcoming chapters, I will discuss studies into abnormal aggression (chapter 5), and husbandry practices (chapter 6), where I will present examples of such potentially empathy-thwarting practices.

4.6. Detecting further cases of moral thwarting

As discussed in section 4.5.1, it is possible to find many recent examples of studies performing basolateral amygdala lesioning on rats. Looking into the topics of the example studies that I referenced in that section, we see that the research covers a variety of topics such as compulsive checking behaviour (Dvorkin et al. 2010), pain chronicity (Zheng Li et al. 2013) and spatial and cognitive memory (Ranjbar et al. 2016). Unlike the animal model of callousness paper (Hernandez-Lallement et al. 2018) these studies do not directly focus on how empathy is affected by the manipulations. Due to their alternate foci, the types of results these studies collect can likely often not address the effects on empathy and, therefore, if we were to consider any of these studies in isolation, we may remain unaware of their potential effects on the moral lives of their subjects and any associated harms. In the case of these studies, it is only through the existence and analysis of an additional existing study, one focussed specifically on this type of lesion and its effects on empathy, that we become aware of these potential further implications.

This draws attention to the fact that it may be very difficult for us to identify many cases of moral thwarting due to both a lack of knowledge concerning how the various scientific manipulations performed on animals may affect their moral lives, and due to the observations and results of these experiments not focussing on these aspects. In the preceding discussion, I have focussed on a few specific experimental procedures, particularly basolateral amygdala lesioning, because of fact that there is existing relevant research concerning the effects of these procedures, but it is important to remember that they represent only a few of the vast multitude of scientific procedures that animals are subjected to in the name of science. Given the sheer number of scientific manipulations performed on animals, the lack of knowledge regarding their effects on the moral lives of animals, and the lack of focus on this in the recorded results, we may currently be unable to detect many out of a potentially large number of cases of moral thwarting that have already occurred and that may continue to occur.

Nevertheless, combining philosophical reflection, the currently available empirical information regarding empathy and other moral emotions in animals, and knowledge regarding topics of scientific research may already help us to identify some features that may be common among scientific practices that are likely to result in moral thwarting, as well as helping us to identify areas of research where, if it occurs, moral thwarting may currently be detectable, or at least hinted at, by the types of results recorded. This is of use for my current purposes of trying to identify further existing scientific practices that may result in moral thwarting, but perhaps also useful in highlighting aspects of scientific practice where further empirical data could help us to better detect cases of moral thwarting.

Scientific practices that manipulate interactions between individuals may be a good candidate for further investigation regarding moral thwarting. I believe that there is good reason to consider that moral behaviour in animals may be strongly linked with interactions amongst individuals, and therefore manipulating the way in which individuals interact could affect moral behaviour. Not all ethical theories are consequentialist in nature, but Rowlands (2012, pp. 223–224) has linked his conception of moral subjects with objective consequentialist ethical theories. Although I have chosen not to focus on a particular ethical theory to underpin my arguments, it does not seem unreasonable to assume that a consequentialist ethical theory that broadly reflects common moral intuitions will likely place at least some weight on the outcomes of actions on other members of the moral community. Social interactions and social relationships provide animals with a direct opportunity to impact each other's lives, whether for better or worse. If a common feature of moral behaviour is that it has some effect on the lives of others, and if moral subjects can most directly affect others through social interactions, then it seems likely that moral behaviours may be strongly linked to behaviour that takes place in the social realm. Although this does not imply that all social interactions are moral in nature, it may give us reason to consider that many moral behaviours may be social in nature. Given this, manipulating the ways in which individuals typically interact may also affect morally motivated aspects of their behaviours and thus we might consider practices that do affect interactions between individuals as worthy of further investigation regarding their effects on animals' moral capacities. It is important to remember that manipulation of behaviour in this sense can refer to both manipulating the capacities of the animal that facilitate such behaviour, and to precluding the exercise of these capacities.

Where behaviour has been, or is being, manipulated, the consequences that follow from these manipulated behaviours may also hint towards moral thwarting. Reductions in prosocial or helping behaviour may be indicative of decreased empathy or the restriction of empathy-motivated behaviour. Likewise, behaviour that results in increased risk of harm or distress for others could be suggestive of a decrease in morally motivated behaviour, for example reflecting a decrease in empathy. This is not to claim that all behavioural changes with these characteristics represent changes to moral behaviour; instead I am simply stating that such consequences *could be indicative of* changes to moral behaviour, and so practices that result in these changes may warrant further investigation.

What may be problematic here is that behavioural changes can occur but go unnoticed or unrecorded due to factors such as a lack of attention on, focus on, or knowledge of behavioural effects, or due to the animals themselves lacking the opportunity to express their full behavioural repertoire. For the purposes of being able to detect further cases of moral thwarting from existing resources, this limits me to considering studies and practices where there is either existing evidence that aspects of these practices may result in moral thwarting, or where there is behavioural evidence reported that can indicate whether moral thwarting has occurred[13]. A further complication that arises here when discussing *changes* in behaviour, is that moral thwarting may occur, from, or even before, birth, so it may go unnoticed if only observing one individual's behaviour; this highlights why the study and awareness of animal behaviour and, more specifically, animals' moral lives, is of importance to being able to better detect some cases of moral thwarting.

Of course, further cases of moral thwarting in scientific practice may also be detected through the use of practices already identified as leading to moral thwarting. In my discussion of empathy, I have identified the following procedures as resulting in moral thwarting: basolateral amygdala lesioning, lesioning of the medial prefrontal cortex, pharmacological deactivation of the anterior cingulate cortex, and administration of the anxiolytic midazolam. Wherever these specific manipulations occur, we have good cause to suspect that moral thwarting will also occur. We may also wish to consider practices that may have relevant related effects; for example, if a pharmacological product is known to impact upon the functioning of the basolateral amygdala, we have cause to suspect that it could also lead to moral thwarting. I have also discussed evidence that stress, social experiences, and exposure to others in distress can impact upon empathy-motivated behaviour. Therefore, practices that expose animals to conditions where these factors are somewhat *abnormal* may also potentially lead to moral thwarting; these practices, and studies that utilise them, may be good candidates for further investigation regarding moral thwarting.

In summary, it appears that very few scientific studies currently consider or report on how they may impact the moral lives of animals. This means that it is difficult to search for and identify experiments that result in moral thwarting; without results that specifically focus on changes to moral emotions or behaviours, or results from which these can be inferred, we need to rely on additional evidence regarding how the procedures can impact upon moral emotions, and, in many cases, this is something that may never have been investigated. Nevertheless, my analysis

---

[13] It is important to understand that I do not claim anything about the likelihood of moral thwarting occurring as a result of studies that do not focus on behaviour or recording behavioural results. Rather, I am simply explaining how practical limitations will largely limit my analysis to focussing on studies that record behavioural interactions between individuals; in the absence of further data regarding how the specific manipulations of an experiment affect moral behaviours, changes to behaviours during inter-individual interactions may offer one of the only available ways to detect if moral thwarting has occurred as the result of a specific existing study.

suggests some ways in which we may proceed with the task of identifying and investigating some further cases of moral thwarting in scientific practice, in spite of these difficulties. We can look for uses of the specific practices that I have identified as likely leading to moral thwarting, as well as practices that may be expected to have related effects. We can search for experiments that subject animals to abnormal levels of stress, impact their social experiences, or expose them to others in distress. Moral thwarting may be indicated by changes to social behaviours, particularly by increases in harmful behaviour or decreases in prosocial behaviours, and so should be investigated where these occur. Finally, in the absence of external evidence, we may be reliant on behavioural evidence provided by studies themselves; therefore, we may find it useful to focus on studies where relevant behavioural evidence is reported.

4.7. Summary

In the preceding discussion, I have investigated the scientific manipulation of empathy in rats and mice. I have identified a conception of empathy that qualifies as a moral emotion in the sense of Rowlands (2012) and argued that negatively impacting upon a moral emotion such as empathy can be recognised as moral thwarting. I have discussed the evidence that rats and mice possess the identified form of empathy, and presented studies utilising rats and mice that I argued negatively impacted upon their empathic capacities, and therefore represent cases of moral thwarting. Currently, there seems to exist more direct scientific evidence to support this claim for rats than for mice, but in both cases there exist strong reasons to take seriously the claim that scientific experimentation can result in the moral thwarting of these individuals. Additionally, I have discussed the current difficulties faced when attempting to detect further cases of moral thwarting, and highlighted specific practices and aspects of scientific practice that may help us identify some further practices or types of practice that potentially result in moral thwarting.

5. Experimental manipulation of aggression: Rats and mice

5.1. Reasons for investigating abnormal aggression experiments

Through the preceding analysis of empathy manipulation in rats and mice I was able to identify some specific practices and more general types of manipulations that likely result in moral thwarting, as well as some aspects of scientific practices that may be common among practices that can lead to moral thwarting. Through these, I have identified animal-based experiments into abnormal aggression as worthy candidates for further analysis regarding whether they result in moral thwarting. As should become clear when I discuss these experiments in greater detail shortly, abnormal aggression experiments include several of the discussed aspects that associate with practices likely to result in moral thwarting. Behavioural interactions between individuals are changed, and changed in such a way that they pose a greater risk of harm. A variety of manipulations are performed, including ones that affect social experiences, expose the animals to stress, and involve repeated experiences of others in distress. Furthermore, behavioural data concerning inter-individual interactions is also typically recorded and presented, allowing for the possibility of further analysis concerning whether these results may indicate that moral thwarting has occurred. Therefore, in this chapter, I will investigate whether experiments focussed around inducing abnormal aggression in individuals may potentially result in moral thwarting.

5.2. Overview

After introducing the topics of aggression and abnormal aggression, and after introducing the experiments that I will focus on in this section, I will discuss two ways in which it could be claimed that moral thwarting occurs as a result of these experiments. The first of these is to claim that moral emotions are involved in the regulation of aggressive behaviour, and that the experimental manipulations performed in these studies result in the thwarting of these moral emotions. The second is to claim that these experimental manipulations result in the thwarting of moral emotions, irrespective of whether moral emotions directly influence aggressive behaviour.

5.3. Aggression

To begin with I will provide an overview of what can be understood by the term *aggression* and discuss the role that aggression plays in animals' lives. This will be important for my upcoming arguments concerning abnormal aggression experiments and moral thwarting.

Aggression serves important purposes within the lives of animals. De Boer states that "aggressive behavior is considered a highly functional form of social communication leading to active control of resources and the social environment, and thus is essential for individual and population survival" (de Boer 2018, p. 81) and that it is "the behavioral weapon of choice for both animals and humans to defend themselves and their offspring, secure food and mates, compete for limited resources, and maintain social status/hierarchies" (de Boer 2016, p. 22). He describes that "[i]t is characterized by a ritualized set of species-typical behaviors performed in close interaction with a conspecific opponent" (de Boer 2016, p. 25). These descriptions begin to draw attention to the important point that there is much more to aggression-related behaviours than simply attacks against another individual; it is an important form of social communication that also serves to facilitate competition amongst individuals.

Another key point regarding aggressive behaviours is the fact that many of these behaviours serve to limit the risk of harm:

> "Overt aggression and physical conflicts are potentially harmful not only for the victim but for the aggressor as well. Therefore, strong inhibitory control mechanisms have developed to minimize and control physical aggression in order to prevent its potentially adverse (i.e., injury or death) consequences. Such mechanisms include, for example, threatening behavior that often predicts aggressive arousal and intent and may thereby prevent actual physical attacks. Other mechanisms to keep aggression in control are taboos, ritualization, submission, reconciliation, and appeasement." (de Boer 2016, p. 25)

Concerning my upcoming analysis of whether abnormal aggression inducing experiments result in moral thwarting, the important points here are that aggression-related behaviours serve important social functions between individuals as they facilitate competition while seeking to limit the risk of harm, and that the inhibition of aggressive attacks is a key component of aggression-related behaviours working as a means of social communication.

5.4. Abnormal aggression

Having clarified key points about aggression and its role in animals' lives, I will now introduce the topic of abnormal aggression, and summarise the studies that I will be analysing, in terms of their general shared goal, methods used and effects on the animals involved. Once these have been introduced, I will progress to my analysis of whether the experiments that comprise these studies result in moral thwarting.

According to Haller (2017, p. 78), "aggression is abnormal when it has no identifiable aim, or when the potential benefits of competition are by far outweighed by highly predictable costs". De Boer (2018, p. 82) uses the term violence to describe "a pathological form of aggressive behavior that is not subjected to inhibitory control mechanisms and that has lost its function in social communication"; this again emphasises how species-typical aggressive behaviour has important social functions and is moderated by inhibitory mechanisms.

To try to better understand abnormal, violent and pathological forms of aggression, researchers have used various means to trigger abnormal aggressive behaviour among animals (de Boer 2018). Access to, administration of, and withdrawal from various substances such as glue (Bouchatta et al. 2016) or alcohol (A. Takahashi et al. 2010, Hwa et al. 2015, Mamiya et al. 2017, Newman et al. 2018), surgical removal of the adrenal glands (Tulogdi et al. 2010), optogenetic stimulation of various neurons (Lin et al. 2011, Lee et al. 2014, Biró et al. 2018), being subjected to stressful situations (Cordero et al. 2012, 2013, 2016, Márquez et al. 2013, Walker et al. 2018), enforced social isolation (Tóth et al. 2011, 2012, Tulogdi et al. 2014, Biró et al. 2017), and the continued breeding and use of aggressive strains of animals (Natarajan et al. 2009) are among the approaches that have been used in recent years to evoke abnormal forms of aggression in animals. The referenced studies in the previous sentence all involved the use of rats or mice, and are the studies that I will use as the basis of my analysis into moral thwarting and abnormal aggression experiments.

De Boer (2018) states that animal models of pathological aggression "should demonstrate excessive, injurious and impulsive aggressive behavior that exceeds and/or deviates from normal species-typical levels or patterns" (de Boer 2018, p. 82); these are indeed the type of results that we see in the previously referenced studies. As a result of these studies, the manipulated animals have demonstrated behaviour towards others that qualifies as abnormal aggression, such as increased quantity or frequency of attacks (Natarajan et al. 2009, A. Takahashi et al. 2010, Tóth et al. 2011, 2012, Cordero et al. 2012, 2013, 2016, Márquez et al. 2013, Bouchatta et al. 2016, Biró et al. 2017, 2018, Mamiya et al. 2017, Newman et al. 2018), increased attacks to vulnerable areas (Tulogdi et al. 2010, 2014, Tóth et al. 2011, 2012, Márquez et al. 2013, Biró et al. 2017, 2018, Newman et al. 2018), decreased social signalling before aggressive behaviour (Tulogdi et al. 2010, 2014, Tóth et al. 2011, 2012, Biró et al. 2017, 2018), increased attacking of individuals showing submissive behaviour (Márquez et al. 2013, Cordero et al. 2016), decreased latency to attack (Natarajan et al. 2009, Tóth et al. 2012, Bouchatta et al. 2016), increased or unprovoked defensive aggression (Tóth et al. 2011, 2012, Tulogdi et al. 2014), and increased attacks to non-typical victims such as females, castrated males or anaesthetised individuals (Natarajan et al. 2009, Lin et al. 2011, Cordero et al. 2012, 2016, Márquez et al. 2013, Lee et al. 2014). It should be noted here that I can only draw from the indicators of abnormal aggression that each set of researchers chose to observe and record in each study; this does not rule out the possibility that further unrecorded changes in aggression occurred as a result of each experiment.

There are various aspects of these experiments that can be considered morally questionable, such as the effects that they have on each individual's welfare; for example, practices such as keeping individuals in social isolation, confronting them with highly stressful situations, or placing them in inescapable situations where they will become attack victims for another animal, will all likely result in the increased suffering of these animals. However, for the purposes of this thesis, I intend to only focus on the question of whether these types of experiments represent cases of moral thwarting. I will discuss two ways in which it may be argued that moral thwarting has occurred as a result of these studies.

For clarity going forward, I will refer to acts where one individual attacks another as *aggressive attacks*. I will continue to use terms such as *aggression*, and *aggressive behaviours* to cover the whole scope of aggression-related behaviours, including threats and posturing, not just attacks. When referring to the *severity* of aggression, I believe that my usage of the term should be fairly intuitive; for example I view submissive displays as less severe than threatening displays, smaller amounts of threatening displays as less severe than larger amounts, aggressive displays as less severe than aggressive attacks, and fewer numbers of potentially harmful attacks as less severe than greater numbers of potentially harmful ones. In the context of aggression, I will use terms related to *escalation* to signify an increase in the severity of aggression.

5.5. The thwarting of aggression-regulating emotions

The first of the approaches towards claiming that these experiments result in moral thwarting that I will discuss is the claim that moral emotions regulate aggressive behaviour, and that the experiments under discussion result in the thwarting of these moral emotions. This is the argument that I will cover in this section. I will first discuss the evidence that such emotional inhibition of aggression occurs, then argue for why these emotions are morally laden, and then finally discuss how the abnormal aggression experiments in question result in the thwarting of these moral emotions.

Before continuing to this argumentation, however, I would quickly like to dismiss the line of argumentation that aggressive behaviour, or at least aggressive attack behaviour, is always immoral, and that therefore any increase in aggressive behaviour or aggressive attack behaviour always represents an increase in immoral behaviour. It seems unlikely to me that aggressive behaviour can always be interpreted as immoral. As an example, we would likely consider that a mother who acts aggressively towards an intruder in order to protect her children is acting in a morally correct way; indeed in this example, we may be likely to consider a mother who does not show aggression in such a situation to be acting in a less morally correct way than one who does. Therefore, this is an argument that I will not pursue.

5.5.1. Aggression-regulating emotions

To begin with, I would like to establish the potential role of emotions in regulating aggressive behaviour. Among the list of example moral emotions given by Rowlands (2012, p. 32), we find both tolerance, and patience, emotions that we may associate with some degree of inhibiting or holding-back a response, to give a situation time to further develop. In potential conflict situations, I would argue that it is easy to conceive of how an inhibitory emotion such as tolerance or patience could counteract an urge to aggress, resulting in an absence of aggressive behaviour, or the performance of less-severe aggressive behaviour (e.g. threatening as opposed to attacking). There are certainly precedents for acknowledging the importance of inhibition in connection to aggressive behaviour. As seen in an earlier used quotation, de Boer (2016) talks of the role of various species-typical behaviours such as taboos or rituals as "inhibitory control mechanisms" (de Boer 2016, p. 25) for aggressive behaviour. We also find theoretical models where inhibition plays a key role in influencing potentially aggressive behaviour, such as the following two examples.

The Violence Inhibition Mechanism (VIM) was proposed by Blair (1995) to explain the regulation and suppression of aggression in humans when faced with various distress cues from others. The VIM theory was influenced by observations from ethologists regarding how aggressor animals would cease attacks following certain cues from their opponents such as submission cues, and it is described as using a functionally similar mechanism to that found in such animals. The VIM is activated by "non-verbal communications of distress" (Blair 1995, p. 3) and predisposes the individual to withdraw from the source of activation, interrupting their current aggressive behaviour; however, the VIM is not the only influence on behaviour, so withdrawal or interruption of behaviour may not occur in every situation in which the VIM is activated. Blair has linked the VIM with the development of what he refers to as *moral emotions*, such as sympathy, guilt, remorse and empathy, and interprets the arousal triggered by the VIM as a moral emotion.

The I^3 metatheory or framework can be used to model the likelihood of various behaviours occurring, including behaviours linked to aggression (Finkel 2007, 2014, Finkel et al. 2012). The 'I's in the name refer to the three types of factors that are considered in the model; instigating factors, impelling factors, and inhibiting factors. In the context of aggressive behaviour, instigating factors are those that provide an urge to act aggressively, impelling factors increase the likelihood of aggressive behaviour occurring if instigated, and inhibitory factors, which can be situational or dispositional, are those that counter the urge to behave aggressively. It is the interaction between these factors that determines the likelihood of a particular behaviour occurring; "[w]hen the strength of inhibition exceeds the strength of the urge to aggress, people behave nonviolently; when the reverse is true, they behave violently" (Finkel et al. 2012, p. 534).

Having established that there are theoretical reasons for considering that emotions may play a role in inhibiting aggression, are there further reasons for suspecting that this is the case for the species under discussion? Emotional inhibition of aggression may not always be easy to identify through behavioural observations, because the resultant behaviour may be a lack of aggression, something that may not seem like a change in behaviour at all. The emotionally influenced behaviour in these cases may be very similar in nature to the behaviour that would occur if the individual was largely unaware of certain features of the environment that may potentially provoke an aggressive response, or if these features were absent. However, just because a drastic change in behavioural output might not be seen in many cases when a situational change occurs, for example when a conspecific is first sighted, this does not mean necessarily that there is a lack of sensitivity to the changes, or that emotions are not involved in preventing a noticeable behavioural shift. In other situations, emotional inhibition may still facilitate a change of behaviour, but this could be less-severe aggressive behaviour than if the emotion did not exist; the problem here is that from observation alone, we cannot know that a more-severe behaviour was avoided. However, the results of the abnormal aggression experiments being discussed, and knowledge regarding aggressive behaviours in differing contexts do demonstrate that a range of aggressive responses would be possible, and do correspond with the notion that internal processes moderate aggressive behaviours under typical circumstances.

The results of the abnormal aggression experiments provide evidence of the alternative behavioural responses that can occur in potential conflict situations. The changes in aggressive behaviour that occur in these experiments, listed previously in section 5.4, are all more severe than the typical aggressive behaviours shown by members of the species involved, and this escalated aggression is consistent with the decreased effect of an aggression-inhibiting emotion.

Furthermore, additional empirical data highlights the consistent way in which differing situational aspects result in different aggressive behaviour being displayed by members of these species. This demonstrates that they have a range of aggression-related behavioural responses that they are capable of displaying, and that these responses are somehow moderated based on situational factors. For example, in the case of rats, we can see that displays of aggressive behaviour are influenced by a variety of situational factors such as whether another rat is familiar or unfamiliar (see e.g. Alberts and Galef 1973, Blanchard et al. 1975), the characteristics of potential opponents (see e.g. Thor and Flannelly 1976), the presence of rats other than the potential opponent (see e.g. Erskine et al. 1978, Taylor and Weiss 1982), social cues signalling intentions from the potential opponents (see e.g. Barnett 1975, pp. 104–115, 122–125, Thor 1979), and whether they are within their own territory (see e.g. Barfield et al.

1972). Given that these species are capable of showing a variety of behavioural responses in aggressive situations, and that these responses vary based on situational factors, there does indeed seem to be some form of internal moderation performed which affects the severity of aggressive behaviours.

5.5.2. Are aggression-regulating emotions moral emotions?

If we were to accept that aggression can be regulated by inhibitory emotions, is there any reason to think of these as moral emotions? Is there anything about the regulation of aggressive behaviour of the species in question that suggests that it may be morally laden? I believe that we have reason to believe that it is. Let us consider again how Rowlands defines a moral emotion:

> "An emotion, E, is *morally laden* if and only if (1) it is an emotion in the intentional, content-involving, sense, (2) there exists a proposition, *p*, which expresses a moral claim, and (3) if E is not misguided, then *p* is true." (Rowlands 2012, p. 69)

5.5.2.1. Are these intentional, content-involving emotions?

Firstly, are the emotions under discussion emotions in the intentional, content-involving sense? I believe that they are and that such a claim should not be controversial. Aggressive behaviours, such as threats, posturing and attacks, do not occur at random; they are triggered by the presence of other individuals and, most importantly, targeted towards these individuals. This strongly suggests that the emotions underlying these behaviours occur in response to the presence of these individuals, and that the emotional output is directed towards these individuals. This claim is further enhanced by the fact that differing aggressive behaviour is displayed in response to differing individuals; as previously stated in section 5.5.1, rats respond differently based on factors such as the familiarity of a potential opponent, or the characteristics of potential opponents. Furthermore, as also stated, the behaviour of potential opponents impacts the aggressive behaviour that is subsequently directed towards them; for example, less aggression is shown towards individuals displaying submissive behaviours. The fact that aggressive behaviours are directed towards other individuals and vary based on factors relating to those individuals strongly suggests that the underlying motivation has the other individual, or at least aspects of them or their behaviour, as its intentional object(s).

5.5.2.2. Do these emotions track a valid moral proposition?

To uncontroversially claim that conditions 2 and 3 are met, would be to claim that the emotions in question track a generally accepted moral proposition. To be able to make a strong case for this, I need to be able to identify a relevant moral proposition relating to aggression or its inhibition and then show that these emotions reliably tracks this proposition. This poses difficulties for several reasons. Different individuals likely hold differing views on when aggression is acceptable and to what level, and therefore there are unlikely to be any universally accepted moral propositions regarding when or if aggression is appropriate. This is further complicated by the fact that the appropriateness of an aggressive act is likely highly context-dependent, and because appropriate levels of aggression may be hard to precisely identify and quantify, especially if the outcome of alternative behaviours are somewhat difficult to predict. Nevertheless, as I will now discuss, I believe that there are good arguments for interpreting the typical aggressive behaviour of these species as showing an acceptable degree of moral appropriateness, particularly when compared to the modified aggressive behaviour displayed as a result of the scientific manipulations in question.

5.5.2.3. The minimisation of harm

Although finding a universally accepted proposition regarding if and when aggression, and therefore the underlaying emotional motivations, can be viewed as morally appropriate may be an impossible task, I will focus on what I hope to be a relatively uncontroversial moral principle to help argue for the influence of moral emotions on aggressive behaviour. As previously stated, I do not wish to connect my argumentation with only one particular ethical theory in order to avoid my entire argument being dismissed by people who do not support such a theory. However, my following argument does rely on the presupposition that, generally speaking, and with all other things being equal, acts that result in less harm or suffering are morally more acceptable.

Such a claim would seem to be broadly supported by the examples of objective consequentialist theories listed by Rowlands (2012, p. 223); hedonistic utilitarianism and a theory based around the concept of flourishing. In hedonistic utilitarianism, acts that most decrease overall levels of suffering or that most increase overall levels of pleasure are the morally correct ones to perform. Objective consequentialist theories concerned with flourishing would likely focus on the extent to which flourishing is promoted or diminished in order to judge which is the morally correct action to perform. Although there may be differing conceptions of what flourishing involves, particularly across different species, I do not believe that it is unreasonable to claim that, other factors aside, suffering or injury are inhibitive to flourishing. Indeed, when laying out basic political principles that could apply in the case of animals, derived from consideration of what it means for these animals to flourish, Nussbaum (2004, pp. 314–316) includes several relevant categories of entitlements including entitlements to *life*, *bodily health*, *bodily integrity* and *senses, imagination and thought* (a category that recognises an "entitlement to pleasurable experiences and the avoidance of nonbeneficial pain" (Nussbaum 2004, p. 315)). Therefore, it seems to me that being able to show that species typical aggressive behaviour tracks such a principle of minimising suffering or harm would provide strong reasoning to underlie the claim that the emotions regulating aggressive behaviour are morally laden.

Given this, do we have cause to believe that the emotions regulating aggressive behaviour seek to minimise suffering or harm? As summarised earlier in section 5.3, normal patterns of aggression have evolved within a species in order to allow competition but also moderate the potentially adverse consequences of violent physical conflict. This would seem to suggest that diverging from these typical patterns of behaviour could lead to outcomes that likely result in greater risk of harm and suffering for the individuals involved. Indeed, many of the previously described behavioural changes resulting from the studies being discussed show the manipulated animals behaving in ways that cause a greater risk of harm to others, and perhaps themselves; this seems to be inherent in the idea of abnormal aggression. Through these changes in behaviour, we see more clearly how species-typical aggressive behaviours seemingly minimise suffering, which I have identified as a common goal of morally correct behaviour according to some common ethical theories.

5.5.2.4. A possible objection

However, a possible objection to this would be to point out that what was actually claimed earlier is not that that such behaviours exclusively seek to minimise harm, but rather that species-typical patterns of aggression aim to reduce the risk of harm while still facilitating competition; if our underlying moral principle does not place any moral importance on facilitating competition, then it is unlikely to reach judgements that completely align with behaviour that represents some level of compromise between facilitating competition and minimising harm. In other words, if aggressive behaviour is a compromise between facilitating aggression and minimising harm, it may not fully track the moral principle of minimising harm. I would be prepared to concede this point. For example, I believe that it is likely the case that at least in some percentage of aggressive encounters, more altruistic approaches, such as giving up a resource needed more urgently by the potential opponent, may lead to a morally more preferable outcome. I do not believe, however, that this means that we must rule out the idea that emotional motivations connected to aggressive behaviours can be morally laden.

One possible approach to addressing the raised objection would be to instead propose that aggressive behaviour tracks a more complex ethical theory, one that is not exclusively focussed on the minimisation of suffering. For example, some theories of flourishing may choose to recognise that being able to compete with conspecifics is an essential part of the flourishing of individuals belonging to certain species. Although proposing such an alternate theory may be a valid way of addressing the raised concerns, it risks alienating those who do not endorse such a theory. Therefore, I present this approach as an option for addressing such objections, but I do not believe that it is the only way to address such objections, and it is not an approach that I will rely upon here.

An alternate approach to addressing such concerns is to argue that the behaviour and its underlying motivation need not always fully align with a moral proposition in every case, in order for them to be considered moral. Rowlands (2012, pp. 229–232) does not argue that a moral subject's moral sensitivity must be infallible. Discussing the case of a hypothetical moral subject named Myshkin, Rowlands says the following regarding the condition of minimal-moral-subjecthood that requires moral sensitivity to be "grounded in the operations of a reliable mechanism" (Rowlands 2012, p. 230):

> "Getting it right a significant proportion of the time—exhibiting the correct emotional response to a given good- or bad-making feature of the environment—presumably amounts to getting it right some percentage of the time that lies between once and always. There is almost certainly no precise line here. Nevertheless, Myshkin's emotional response must dispose him to promote the good-making and mitigate the bad-

> making features of situations in a relatively systematic, although (of course) not necessarily error-free, way." (Rowlands 2012, pp. 229–230)

As this quote makes clear, it is not necessarily required that a moral subject's sensitivity flawlessly tracks a moral proposition; it may be sufficient for it to track such a proposition in a *relatively* error-free, and systematic way. The question of whether the emotional motivations underlying aggressive behaviours track a moral proposition in a relatively error-free way is difficult to address without either specific knowledge of how reliably individuals' actions correspond to a specific proposition, or what the required reliability would need to be in order to be considered as sufficiently reliable. Although, as a result of these unknowns, we seemingly cannot currently answer such a question, my point here is that even if aggressive behaviours do not track a moral proposition in every circumstance, this does not necessarily rule out the notion that these motivations are morally motivated. Furthermore, although the sensitivity underlying aggressive behaviours may not infallibly track a moral proposition, it certainly seems to be the case that the typical aggressive behaviours of the species in question more reliably track the relatively uncontroversial moral principle of minimising suffering than the behaviours that result from the manipulations performed in the abnormal aggression experiments do.

Another alternative way to address arguments that aggressive behaviours do not always sufficiently track the proposed moral proposition would be to propose that the expressed behaviour could be the result of multiple underlying, possibly conflicting, motivations, and that only some of these motivations may be morally laden. For example, perhaps an individual confronted by a potential opponent could be subject to both a moral motivation such as patience, tolerance or compassion towards the other individual, and a possibly amoral motivation such as trying to protect a resource at any cost. This idea is reflected in my earlier use of terms such as *aggression-regulating emotions* and *aggression-inhibiting emotions*; an individual could be subject to amoral motivations, but also subject to morally laden motivations that can regulate or inhibit the behaviours that would otherwise result from these amoral motivations. If an individual's behaviour is guided, to some degree, but not exclusively, by underlying moral motivations then that behaviour may not fully align with the moral propositions tracked by the underlying moral motivations; this does not, however, rule out that such moral emotional motivations exist and have some influence on the behavioural output.

Conceptual objections regarding multiple motivations aside, this is still difficult to prove conclusively. Behavioural observations are one of the few ways in which we can infer the various motivations that an animal is subject to. If the proposed moral motivations rarely function in isolation from other non-moral motivations, then it may be difficult to ever conclusively demonstrate the existence of such motivations in their pure form through the use of behavioural observations. However, the aspects of these species' behaviours that I have highlighted during this discussion, and the general concept that species typical aggressive behaviours show at least some intent to minimise the risk of harm, are both consistent with the claim that aggression is regulated by moral emotions. The idea of typical aggressive behaviours seeking to limit harm is further supported by the fact that the abnormal patterns of aggression brought about by the experiments being focussed on result in more harmful behaviour.

To further argue the case that moral emotions regulate aggressive behaviour, we can examine how members of the species under discussion appear to be sensitive and responsive to situational features that likely play a role in determining the level of aggression that is morally acceptable in such a situation.

5.5.2.5. Sensitivity to relevant situational features

As previously mentioned, I believe that contextual factors play an important role in determining whether an aggressive act can be considered morally appropriate. Using the example of a mother defending her children, I have already given an explanation for why I believe that we cannot always view acts of aggression as morally bad, and I believe that it is obvious why aggression cannot always be interpreted as morally good. Therefore, context seems to be important. As previously described, Rowlands' has connected his theory of moral emotions with objective consequentialist theories of morality, and in such theories it is the outcome of an action that determines its moral appropriateness; however, situational factors may play an important role in affecting or signposting what that outcome may be and therefore can strongly influence which act should be performed. I would like to propose that the level of threat posed by another individual is such a factor.

Why is the level of threat that a potential opponent poses likely relevant to determining what level of aggressive behaviour is morally acceptable? The more threat that is posed by a potential opponent to an individual, the greater the risk that the individual, or other individuals that this individual should protect, will be harmed or suffer as the result of the potential opponent's actions. As I have previously described, minimising suffering is a likely goal of moral behaviour, and therefore the presence of a threat may justify some level of aggressive behaviour when this serves to reduce the risk of harm or suffering. The level of threat is likely also relevant for determining the severity of aggressive behaviour that is morally justifiable; for example, if a threat can be avoided by some aggressive posturing, then more-severe aggressive behaviour, such as attacking a potential opponent, seems morally inappropriate, given that it will likely result in more harm and suffering than merely posturing. Therefore, it seems that sensitivity to the level of threat currently posed may be important for an individual to be able to behave in a morally acceptable way in potential conflict situations.

When talking of threats, I believe that we can consider what I will refer to as both *direct threats* and *indirect threats*. By direct threats, I mean those threats which pose a near-immediate risk to the individual's health, flourishing or survival. An obvious example of this would be in situations where an individual is currently being attacked or about to be attacked and will likely suffer physical harm; sensitivity to situational features such as attack behaviour or social signals indicating the intention to attack could allow an individual to respond in a morally appropriate way that limits suffering. However, it is also the case that an individual's health, flourishing or survival can be indirectly threatened; for example, the actions of another could lead to lack of resources that that individual requires to live a flourishing, healthy life. If we consider food as an example, a lack of this will ultimately lead to an individual dying, but even in the shorter-term it could also lead to other problems, such as physical weakness that causes suffering, and that may go on to result in an inability to defend oneself against further threats, or lead to a compromised immune system leading to a greater risk of illness. Therefore, it could be argued that the indicators of indirect threats, such as indicators of the resources that one has access to and threats to those resources, are also features of a situation that may help to inform an individual as to which is the morally correct action to take, as sensitivity to them is relevant to the awareness of threats to oneself.

Summarising the previous few paragraphs, sensitivity to the level of threat currently posed to oneself or others potentially informs one of the likelihood of upcoming increases in suffering, and can help inform decisions about how to counteract such threats in order to minimise suffering.

I believe that it should be uncontroversial to argue that the animals being discussed have sensitivity to features of the situations that they find themselves in, and that sensitivity to some situational features influences their behaviour, including their aggressive behaviour. To reiterate information given earlier, in the case of rats, we can see that displays of aggressive behaviour are influenced by a variety of situational factors such as whether another rat is familiar or unfamiliar (see e.g. Alberts and Galef 1973, Blanchard et al. 1975), the characteristics of potential opponents (see e.g. Thor and Flannelly 1976), the presence of rats other than the potential opponent (see e.g. Erskine et al. 1978, Taylor and Weiss 1982), social cues signalling intentions from the potential opponents (see e.g. Barnett 1975, pp. 104–115, 122–125, Thor 1979), and whether they are within their own territory (see e.g. Barfield et al. 1972). In all of these cases, I believe that it is clear that such factors can affect the degree to which another individual could be considered as a threat, and that the aggressive behaviour displayed varies dependent upon the level of threat. For example, an unfamiliar male entering an individual's territory clearly poses a greater potential threat than a familiar cagemate, and is therefore correspondingly subject to more-severe aggression. As another example, young individuals pose less of a threat than fully grown individuals, and are therefore subject to less-severe aggression. This evidence shows how members of these species are sensitive to situational features that influence whether an act of aggression can be considered morally appropriate, and that these features influence aggressive behaviour in a way that is consistent with the influence of aggression-regulating emotions.

Further evidence in support of this claim comes from the abnormal aggression studies themselves, where the results are consistent with a decreased influence of such threat-indicating features on behaviour, leading to behaviour that results in more suffering.

The majority of the example studies make use of the resident intruder paradigm, studying the aggressive behaviour of a resident individual in their home environment when a (typically unknown) conspecific is introduced to simulate an intruder (Natarajan et al. 2009, A. Takahashi et al. 2010, Tulogdi et al. 2010, 2014, Lin et al. 2011, Tóth et al. 2011, 2012, Márquez et al. 2013, 2013, Lee et al. 2014, Hwa et al. 2015, Bouchatta et al. 2016, Cordero et al. 2016, Biró et al. 2017, 2018, Newman et al. 2018, Walker et al. 2018). In such a situation, the intruder could potentially represent a threat, whether it be a direct threat, an indirect threat (if we consider the resident's home territory as a resource itself, or as an area containing resources that could be lost), or a combination of the two. The level of threat the intruder poses is important for determining determine what level of aggressive response is appropriate.

As previously summarised in section 5.4, the results of the various experiments include increased attacks on individuals showing submissive behaviour, increased attacks on non-typical victims such as females, castrated males or anaesthetised individuals, and unprovoked defensive aggression. The submissive behaviour of others is clearly relevant for detecting the level of threat posed as its very intention is to show that the individual performing it does not pose a threat. The increase in attacks to submissive individuals suggests that the experimentally manipulated individuals' behaviour was less influenced by submissive behaviour, a relevant situational feature for determining the level of threat, than the behaviour of unmanipulated members of their species, and consequently morally less-acceptable behaviour is performed. Likewise, the sex, castration status and anaesthetisation of potential victims affects their likelihood of posing a threat, so are relevant situational features in this case. Again, the increased attacks to these less-threatening individuals by the manipulated animals seems indicative of reduced sensitivity to the level of threat posed, and leads to more harmful behaviour. Unprovoked defensive aggression is also indicative of less-reliable sensitivity to the level of threat, as it seems to show a misunderstanding of the other animal's intentions, as it involves a defensive response to a perceived attack that was not occurring.

Decreased latency to attack and decreased social signalling could be further indicators of a decrease in the ability to accurately detect the level of threat, and again are behavioural changes more likely to result in greater harm. A decreased latency to attack could occur as a result of perceiving a greater threat than is actually presented, and thus feeling the need to respond with aggression sooner. Decreased social signalling suggests non-adherence to species typical behaviours used to moderate aggressive encounters, meaning that less time may be given to the process of threat assessment via the observation of social signals or responses from the competitor.

The experimentally induced behavioural changes also include increases in quantity or frequency of attacks, and an increased number of attacks to vulnerable areas. Given that species-typical patterns of aggression have evolved over time to minimise the potential harm inflicted on the involved individuals, it does not seem unreasonable to interpret species-typical behaviours as representing at least a reasonable approximation of the minimal amount of aggression required to address various threats. Therefore, these increases in aggressive attacks again seem disproportionate to the level of threat posed.

5.5.2.6. Summary: Are aggression-regulating emotions moral emotions?

Returning now to the overall argument, I have attempted to show how the emotional motivations that regulate aggressive behaviour can be considered morally motivated. I have discussed the intentionality of the motivations, highlighting how the emotions are both caused by the presence of another individual and result in behaviour directed towards that individual. To argue that these motivations are morally laden, I have highlighted the hopefully uncontroversial moral principle of minimising suffering, and argued that the typical aggressive behaviour of the species in question seemingly does seek to limit harm and suffering, given the proposed general purpose of aggressive behaviour, and as demonstrated by the fact that abnormal aggressive behaviour, behaviour that varies from species typical behaviour, results in a greater risk of harm and suffering.

I have proposed three counterarguments to objections that aggressive behaviour may not fully track such a principle of minimising suffering. The first, which I have touched upon but ultimately chosen not to rely upon due to the lack of a universally accepted moral theory, involves the claim that morality should actually be understood through a more complex moral theory than one that focuses entirely on the minimisation of suffering, such as one that balances the reduction of suffering with other principles such as those that are promoted through the facilitation of competition among individuals. The second argument highlights how a moral emotion, or the behaviour that it motivates, need not infallibly track a moral proposition, and that some degree of error is acceptable; however, the question of whether aggressive behaviour tracks the proposition within an acceptable margin of error seems unanswerable due to a lack of data, and no overall consensus on the acceptable margin of error. The third argument involves the claim that aggressive behaviour may be influenced by both moral and amoral motivations, and therefore it is possible for aggressive behaviour to still have some underlying morally laden motivations, motivations that do sufficiently track a moral proposition, even if the resulting behaviour does not fully track a moral proposition. It is this third approach that leads me to build my case around the concept of *aggression-regulating emotions.*

I have presented several arguments to support the idea that such regulating emotions exist and are morally laden. I have referred again to the way in which species typical behaviours seem to be influenced to at least some extent by a motivation to minimise harm and suffering. I have referred to the results of abnormal aggression studies in order to show how variations from this behaviour adhere less to such a principle, given that they result in increased risk of harm and suffering. Finally, I have discussed how members of the species in question are seemingly sensitive to situational features that can influence the level of aggressive behaviour that can be considered morally acceptable in a given situation, and shown how this sensitivity leads them to perform behaviours consistent with the influence of an emotion tracking the proposed moral proposition. I cannot claim that my arguments definitively prove the existence of moral emotions that regulate aggressive behaviour but what I do claim is that there is evidence that is strongly supportive of such an idea.

5.5.3. The case for moral thwarting

I have argued that moral emotions regulate aggressive behaviour by inhibiting aggression, resulting in less-severe aggressive behaviour that causes less suffering than the uninhibited behaviour. These aggression-regulating emotions track the moral principle of minimising harm. I will now argue that the experiments in question result in the moral thwarting of their animal subjects by thwarting these morally laden, aggression-regulating emotions.

As previously described, the abnormal aggression studies being discussed result in their animal subjects displaying a variety of abnormal aggression behaviours; increased quantity or frequency of attacks (Natarajan et al. 2009, A. Takahashi et al. 2010, Tóth et al. 2011, 2012, Cordero et al. 2012, 2013, 2016, Márquez et al. 2013, Bouchatta et al. 2016, Biró et al. 2017, 2018, Mamiya et al. 2017, Newman et al. 2018), increased attacks to vulnerable areas (Tulogdi et al. 2010, 2014, Tóth et al. 2011, 2012, Márquez et al. 2013, Biró et al. 2017, 2018, Newman et al. 2018), decreased social signalling before aggressive behaviour (Tulogdi et al. 2010, 2014, Tóth et al. 2011, 2012, Biró et al. 2017, 2018), increased attacking of individuals showing submissive behaviour (Márquez et al. 2013, Cordero et al. 2016), decreased latency to attack (Natarajan et al. 2009, Tóth et al. 2012, Bouchatta et al. 2016), increased or unprovoked defensive aggression (Tóth et al. 2011, 2012, Tulogdi et al. 2014), and increased attacks to non-typical victims such as females, castrated males or anaesthetised individuals (Natarajan et al. 2009, Lin et al. 2011, Cordero et al. 2012, 2016, Márquez et al. 2013, Lee et al. 2014). These changes seemingly increase the overall risk of harm and suffering for the individuals involved in aggressive interactions, as they represent more-severe forms of aggression that seem disproportionate to the situations where they occur. The earlier established claim that aggression serves to minimise harm while facilitating competition gives us further cause to believe that changes from species-typical aggressive behaviours to more-severe ones will result in more suffering.

If, as I have claimed, aggression-regulating emotions inhibit aggressive behaviour and serve to minimise associated suffering, then changes in aggressive behaviour that result in less inhibited, more harmful aggressive behaviour seem to indicate that the aggression-regulating moral emotions have been somehow eliminated, reduced or made less reliable, either in terms of their ability to manifest or to influence behaviour. As previously described, moral emotions are a form of moral capacity, and the effects of these experimental manipulations on these moral capacities reflect those found in my definition of moral disenhancement, a subcategory of moral thwarting. Therefore, so long we accept that aggression is regulated by moral emotions, the results of the abnormal aggression studies seem to show that moral thwarting has occurred.

5.5.4. Additional thwarting of aggression-regulating emotions

The studies in question focus on how particular manipulations lead to abnormal aggressive behaviour in the manipulated individuals. However, there are additional aspects of these studies that may also potentially result in the further thwarting of aggression-regulating moral emotions.

As previously mentioned in section 5.5.2.5, the resident-intruder paradigm is used in the majority of the studies that I am currently discussing. In many of these studies individuals undergo the process multiple times (Natarajan et al. 2009, A. Takahashi et al. 2010, Lin et al. 2011, Cordero et al. 2013, Márquez et al. 2013, Lee et al. 2014, Tulogdi et al. 2014, Hwa et al. 2015, Bouchatta et al. 2016, Biró et al. 2017, 2018, Newman et al. 2018). In these experiments, the resident-intruder tests are typically being used as a way to assess changes in aggressive behaviour caused by the various types of experimental manipulations being investigated. However, there is evidence that resident-intruder tests themselves can also lead to changes in the aggressive behaviour of some mice and rats, that may correspond to further moral thwarting. In male mice, it has been shown that the attack latency decreases after one (Oyegbile and Marler 2005) or multiple (Caramaschi et al. 2008) experiences of being the winning resident. For male mice of the SAL strain, a strain that has been artificially selected for in order to produce individuals who display increased aggression, it has been shown that the more experience males have as winning residents in resident-intruder tests, the more likely they are to subsequently display the abnormal behaviour of attacking females (Benus et al. 1991). In male rats, it has been shown that a subcategory of the medium- to high-aggression rats exposed to multiple resident-intruder sessions showed a decrease in investigative or threatening behaviour, and proceeded sooner to attacking intruders (de Boer et al. 2003). If the use of resident-intruder tests in these studies does lead to abnormal aggressive behaviours, as the evidence I have listed suggests they can, then the previously presented argument regarding moral thwarting and abnormal aggression is also seemingly valid here.

I believe that it is also possible to make the case that the *intruders* used in the resident-intruder tests may be being morally thwarted. As far as I am aware, in the resident-intruder paradigm used by many of the discussed studies, intruders do not have an option to retreat from the situation. When describing the associated motor patterns of defensive aggression in rodents, de Boer (2016, p. 24) includes *flight*. A study by L. K. Takahashi et al. (1980) modified a colony-intruder procedure to show that when an escape chamber was provided, intruder rats would take refuge there, resulting in less fighting, fewer wounds, and fewer deaths. If we were to accept my earlier arguments regarding the role of moral emotions in regulating aggressive behaviour, then we can see how the intruder rats will likely be motivated to perform a behaviour, fleeing, that seems to better adhere to the earlier proposed moral proposition regarding minimising suffering, as opposed to not retreating. If the emotional motivation to flee is morally laden, then placing these individuals in a situation where they are unable to act on the basis of such a motivation can be identified as moral preclusion, a type of moral thwarting.

In some of the studies under discussion, we also see how manipulations that are performed on individuals can affect aggressive behaviour across generations. Not only did peripubertal stress protocols lead to increased aggressive behaviour in the male rats subjected to it, their future male offspring also displayed increased aggression, even when the offspring had not interacted with their fathers (Cordero et al. 2012, 2016). In the case of animals that have been selectively bred to show higher aggression, such as those used in the study by Natarajan et al. (2009), these characteristics will also be passed on to future generations. The affected individuals in the following generations can also be seen as having been morally thwarted.

5.5.5. An interesting example of moral preclusion

The use of the resident-intruder paradigm in these studies also leads me to consider an example of moral preclusion that is somewhat different from the examples that I have so far provided, but that nevertheless should be acknowledged as moral preclusion and, therefore, moral thwarting. I would like to specifically draw attention to this here to ensure that it is not overlooked by others who may wish to utilise the concept of moral thwarting as presented in this thesis. This form of moral preclusion occurs when the external situation of an individual is manipulated in such a way that her moral capacities are misled, misinformed or confused, meaning that although they may not be obstructed from functioning, the situation still impacts upon their ability to generate motivations or behaviour of the normative quality that they otherwise could do in a more suitable or typical environment. Although the moral subject's moral capacities may remain unchanged, environmental factors impact upon her current ability to undergo motivations of the same normative quality. For example, this could be achieved by placing an individual into a situation or environment for which her moral sensitivity has not evolved to correctly understand or interpret, essentially causing her to act on the basis of misinformation which could lead to less morally appropriate behaviours. This seems to fall within my definition of moral preclusion, as although it could be argued that the individual is exercising her moral capacities, the important point is that she has been precluded from, or impeded in, the *proper* exercise of her moral capacities; that is these capacities are precluded from, or impeded in, the promotion of behaviour that is of the normative quality that they could otherwise promote.

To further help understand this form of moral preclusion, we can consider how it may be understood in terms of moral emotions. Rowlands (2012, pp. 67–68) describes two ways in which emotions may *misfire*, something he describes as "roughly, the analogue of what it is for a belief to be false" (Rowlands 2012, p. 67); an emotion misfires when it is either *misplaced* or *misguided*. An emotion is *misplaced* if is "grounded in a factual assertion that is, in fact, false" (Rowlands 2012, p. 67) and is *misguided* when it involves an erroneous evaluation. Manipulating an individual's external situation so that her moral emotions misfire to a greater extent would thus be identifiable as the form of moral preclusion being discussed.

I believe that this form of moral preclusion occurs in the case of resident-intruder tests, such as those used as part of the abnormal aggression studies, and particularly in the case of studies that repeat the test multiple times for each resident. In these tests, we are aware that the *intruder* is not really a persistent intruder seeking to claim the resident's territory. We are also aware that the intruder has no means to escape when threatened. However, the resident rat likely does not have awareness of these factors; she may perceive that the intruder is a persistent threat that refuses to retreat, and thus her morally laden, aggression-regulating emotions permit a level of aggression towards the other individual that may be objectively judged as morally inappropriate, given that the intruder cannot actually retreat and does not mean to threaten the resident. In effect, we have placed the resident rat in a situation where her moral emotions seemingly misfire[14]. Although the resident rat's moral capacities operate as before, the situation that she has been placed in leads to her performing morally questionable behaviour.

5.5.6. Summary: The thwarting of aggression-regulating emotions

In this section, I have discussed one approach to claiming that abnormal aggression experiments result in moral thwarting. I have argued that aggression is regulated by inhibitory emotions that are morally laden and track a moral principle concerned with the minimisation of suffering. The manipulations performed on these animals results in them performing more-severe aggressive

---

[14] Depending on how exactly we choose to consider the situation, it could be possible to interpret the emotions in question as being either misplaced or misguided. It could be argued that the resident rat's moral emotions encapsulate a factual inaccuracy, such as interpreting the other rat as a persistent intruder who does not wish to retreat, and that these emotions are therefore misplaced. Alternatively, it could be claimed that these emotions encapsulate an erroneous evaluation, such as incorrectly evaluating the other rat's behaviour as threatening, and that these emotions are therefore misguided. However, either of these interpretations is compatible with the main point being argued in this section.

behaviour, indicating that the moral emotions that regulate their aggressive behaviour have been thwarted.

5.6. The thwarting of other moral emotions

As stated previously, this chapter will discuss two ways in which it may be argued that moral thwarting has occurred as a result of abnormal aggression studies, such as the ones highlighted earlier. The first, which I have just discussed at length, was to recognise moral emotions as important in the regulation of aggressive behaviours and show that these emotions have been thwarted by these experiments. The second, which I will now discuss, is to focus on how the experimental procedures may have affected other moral emotions, regardless of whether they are connected to aggressive behaviour. The purpose of this section is not to exhaustively list either all of the moral emotions that may have been thwarted by these experiments, nor to list all of the different ways in which they are thwarted. Rather, making use of the earlier analysis of empathy and the thwarting of empathy in mice and rats, I will simply aim to show that there do exist some further reasons to claim that these abnormal aggression experiments result in the moral thwarting of the animals being experimented upon.

When previously discussing the ways in which empathy in rats and mice may be thwarted, I highlighted evidence indicating that interventions that expose individuals to others in distress, that introduce abnormal levels of stress, and that impact social experiences, can all impact upon empathy-motivated behaviour. As I will now describe, these types of interventions can all be identified within the abnormal aggression experiments under discussion.

5.6.1. Exposure to others to distress

Evidence was presented that individuals exposed to others in distress may become habituated to this distress and therefore be less motivated to perform behaviour concerned with addressing or preventing this distress (Church 1959). As described, the majority of the studies in question utilised resident-intruder tests to assess aggressiveness, and many of these studies performed the tests multiple times. In these studies, the residents typically aggress towards the *intruder*, resulting in the intruder's distress; the intruder's level of distress will also likely be higher than usual in these cases, given that abnormal aggressive behaviour is likely to cause greater harm than species-typical aggressive behaviours. In the case of repeated resident-intruder tests, the resident will experience repeated incidents of others in distress, due to their own aggressive behaviours when responding to the perceived threats that the experimenters introduce. Additionally, although there is nothing in the papers to indicate that the following did occur, if it were the case that others rats or mice were somehow able to witness other resident-intruder tests being carried out, then they would no doubt be exposed to the distress of the aggressed-upon individuals. As I will discuss in the following section, other manipulations performed in these experiments also place individuals in stressful situations. In any of these cases, whenever individuals are exposed to others in distress, we have reasons to suspect that this could negatively impact upon empathy in these individuals, and thus morally thwart them.

5.6.2. Abnormal levels of stress

I have also presented evidence that abnormal levels of stress can impact upon the empathic capacities of rodents (Ben-Ami Bartal et al. 2016). In the abnormal aggression experiments under discussion, it is certainly the case that we can find animals experiencing stressful situations. Some of the studies focus specifically on the effect of subjecting individuals to high levels of peripubertal stress (Cordero et al. 2012, 2013, 2016, Márquez et al. 2013, Walker et al. 2018). However, it could be argued that any experiment that places an individual in a situation where she will be involved in aggressive encounters will result in her experiencing a high level of stress. In the case of the commonly used resident-intruder test, it should be noted that the situation may be stressful for both residents and intruders. In the case of the residents, they will likely perceive the presence of the intruder as a threat, and thus something clearly stressful; this may be particularly true in the case of repeated resident-intruder tests, where the residents likely perceive a repeated, persistent threat. In the case of the intruders, they are placed into a conflict situation, typically against larger animals, and are unable to act upon their species-typical instinct to flee. Another treatment found in these studies is the use of enforced social isolation (Tóth et al. 2011, 2012, Tulogdi et al. 2014, Biró et al. 2017), a situation that may be highly stressful for these individuals. Given that stress can impact upon the empathic capacities of rats and mice, we have strong reasons to believe that experiments utilising the practices just outlined may morally thwart their animal subjects.

5.6.3. Impacting social interactions

I have also suggested that interferences in the social lives of animals can impact upon their empathic capacities. As mentioned earlier, it has been shown that rats' prior social experiences influence the expression of helping behaviour towards certain types of individuals (Ben-Ami Bartal et al. 2014, Lu et al. 2018); this could imply that social experiences are important for empathy-motivated behaviour. Furthermore, if a manipulation reduces an individual's sociability or leads to alterations in her social behaviours or understanding, then it may interfere with that individual's ability to form social relationships and with her ongoing social development; therefore, it may reduce both her empathy-motivated behaviours towards others, and others' empathy-motivated behaviours towards her.

Specific practices used in the abnormal aggression experiments have been shown to impact the social behaviour of the animals involved. The effects of socially isolating individuals is the main focus of some of the discussed experiments (Tóth et al. 2011, 2012, Tulogdi et al. 2014, Biró et al. 2017) but also occurs in some others as part of the experimental procedure (Bouchatta et al. 2016, Mamiya et al. 2017). Three of these experiments isolated individuals from when they were 21 days old until they reached the age of 70 days old (Tóth et al. 2012, Tulogdi et al. 2014, Biró et al. 2017). Another appears to have isolated individuals when they were 21 days old until they reached an age of approximately 82 days old (Tóth et al. 2011). In the remaining two experiments individuals were isolated for 4 (Mamiya et al. 2017) or 6 weeks (Bouchatta et al. 2016), but I cannot determine how old they were at this time. The identified isolation ages correspond to a sensitive/critical period for rats during which they typically engage in large amounts of social play, considered important for the development of normal behaviour, social organisation, social communication skills and conflict management skills (Kaliste and Mering 2004, pp. 155–158, Koolhaas 2010, p. 319). Isolation during this period has been shown to lead to the development of abnormal social, sexual and aggressive behaviours (Kaliste and Mering 2004, pp. 157–158). As expected, the experiments being discussed all recorded data showing changes in aggressive behaviour, but Tulogdi et al. (2014) also examined changes in other social behaviours, recording increased defensiveness and decreased huddling when sleeping. As well, as arguing that social isolation morally thwarts the isolated individuals by impacting their empathic capacities, it is also clearly the case that it can result in the subcategory of moral thwarting that I have referred to as moral preclusion, as the involved individuals are physically prevented from performing empathy-motivated behaviour towards others. Among the other abnormal aggression studies that I discussed, there is evidence that peripubertal stress (Walker et al. 2018) and alcohol withdrawal (Hwa et al. 2015) also lead to reductions in social behaviour.

It can also be argued in general for all of the abnormal aggression experiments that they impact upon the social lives of animals and therefore potentially impact upon these animals' empathic capacities. As was discussed in section 5.3, aggressive interactions represent a form of social communication, and so any changes to patterns of aggressive behaviour represent changes to the ways in which individuals interact. Some of the specific changes in aggressive behaviour that were observed, such as decreased social signalling before aggressive behaviour, increased attacking of individuals showing submissive behaviour, decreased latency to attack, unprovoked defensive aggression, and increased attacks to non-typical victims such as females, castrated males or anaesthetised individuals, seem to preclude other types of social interactions that could otherwise potentially have occurred or developed in the absence of this abnormal aggression. Furthermore, although I have chosen to focus specifically on examples of empathy thwarting here, I previously indicated how moral emotions and behaviours may be strongly linked to interactions in the social realm in the case of animals; if this is indeed the case, then interferences such as those just discussed may be likely to affect other moral emotions and behaviours that these animals may possess.

5.6.4. Summary: The thwarting of other moral emotions

I have shown how the findings of the previous analysis of empathy thwarting in scientific experiments can be applied to the abnormal aggression experiments being discussed, in order to show further ways in which these studies result in moral thwarting. The claims that these studies morally thwart their animal subjects by negatively impacting upon their empathic capacities is independent of the prior argument that moral emotions regulate aggressive behaviour. If the prior claim regarding emotional regulation of aggression is accepted, then the discussion of empathy thwarting here shows evidence of further ways in which moral thwarting occurs in these experiments and thus indicates additional harms inflicted upon these animals. Even if the prior claim regarding aggression regulation is refuted, then this discussion still gives us reason to claim that these experiments morally thwart their animal subjects.

The application of the findings of my analysis into empathy thwarting further demonstrates the point that moral thwarting can occur in experiments where moral capacities are not the focus of the experiment, nor the presented results, and shows how further study and analysis of moral emotions in animals and the ways in which they can be thwarted, will likely help us to detect further cases of moral thwarting in scientific practice.

5.7. Summary

In this chapter I have investigated two approaches to claiming that moral thwarting occurs as the result of experiments into abnormal aggression. In the first, I argued that there are strong reasons to believe that moral emotions are involved in the regulation of aggressive behaviour, and then argued that the experiments in question thwart these moral emotions. In the second, I argued that, irrespective of whether moral emotions directly influence aggressive behaviour, the manipulations performed in these experiments do thwart other moral emotions; to help illustrate this, I used the findings of my previous analysis of empathy thwarting to provide examples of the way in which these experiments thwart the empathic capacities of their experimental subjects.

6. Beyond the experimental manipulation of rats and mice

6.1. Overview

In the previous two chapters, I have analysed various types of studies that perform experimental manipulations on rats and mice, and argued that these manipulations morally thwarted the animal subjects involved. However, there are other areas of scientific practice beyond experimnetation that impact upon the lives of animals that are used for scientific research, and there are many more species than just rats and mice that are used in scientific research. Therefore, in this chapter, I will discuss each of these topics with relation to moral thwarting, focussing on how the findings of my thesis so far can be applied to each of these in order to assess whether we have reasons to suspect or claim that the scope of moral thwarting extends beyond the scope of experimental manipulations on rats and mice.

6.2. Moral thwarting outside of experimental procedures

Up until now, I have focussed on the potential moral thwarting of rats and mice that arises as part of experimental procedures that they undergo. However, it is important to remember that animals used in scientific research will have their entire lives shaped by this usage. They will likely have been intentionally bred and then born into captivity, with the human-designated purpose of being used for scientific experimentation. Their lives will be dictated by breeding decisions, the various husbandry procedures of the various institutions that they pass through, as well as the scientific procedures that they will undergo. At any of these stages moral thwarting could potentially occur, and it may have a lasting effect on individuals. In this section, my aim is to briefly highlight some of the ways in which moral thwarting could occur in the lives of animals used for scientific research, outside of the experimental procedures themselves.

Human moderation of animals' reproduction certainly has the potential to result in moral thwarting. I have already discussed how certain strains of mice are intentionally bred to express high levels of aggression, such as the SAL mice used in the experiment by Natarajan et al. (2009), and how this may represent the thwarting of morally laden aggression-regulating emotions. As another example of how breeding can result in moral thwarting, a currently available mouse model of autism is described as exhibiting "reduced social interactions" (Charles River 2020); I have already discussed how social relations may be important for the expression and development of empathy, therefore, these animals may be thwarted in this respect. Breeding decisions that introduce other impairments, such as the breeding of mice for blindness (see e.g. The Jackson Laboratory 2020a, 2020b, 2020c, 2020d, 2020e) or deafness (see e.g. The Jackson Laboratory 2020f, 2020g, 2020h, 2020i, 2020j) also have the potential to impact upon the moral capacities of animals; they may limit these individuals' abilities to perceive morally relevant sensory data, or impact their ability to live normal social lives.

I have already discussed studies showing how exposure to stress can lead to increased aggression (Cordero et al. 2012, 2013, 2016, Márquez et al. 2013, Walker et al. 2018) and how this corresponds to moral thwarting. I have also highlighted studies showing how stress can affect helping behaviour in rats, with a moderate level of arousal promoting the most helping behaviour (Ben-Ami Bartal et al. 2016). Therefore, husbandry practices that subject individuals to high levels of stress, or low-arousal environments likely result in moral thwarting.

The keeping of animals in isolation is another situation that can occur during general animal husbandry and not just during specific experimental procedures. I have already discussed how isolation can result in moral thwarting, by inducing abnormal aggression, preventing the formation of social bonds that may be important to the expression and development of empathy, and by preventing or inhibiting individuals from performing morally motivated behaviours towards others.

As highlighted by Monsó et al. (2018), animals used for research may experience a variety of distressing situations, and this distress may be detected by others. As previously discussed, being exposed to others in distress has the potential to habituate individuals to this, impacting upon their empathic capacities; this could occur if animals are able to witness distressing procedures carried out to others, but also, for example, if husbandry or handling techniques cause distress to the animals, or if individuals are returned to home cages still in a distressed state following distressing procedures. Furthermore, if animals witnessing this distress are motivated to help their distressed conspecifics, as my discussion of empathy in rodents suggests they are, then preventing them from doing so would preclude them from exercising their moral capacities, and therefore morally thwart them.

Finally, I would like to emphasise that although a situation, manipulation or experimental procedure that results in moral thwarting may only last a small amount of time, the effects of these on the animals and their lives may extend far beyond the end of a given manipulation, potentially being long-lasting or even permanent. For example, in the experiment by Tulogdi et al. (2014), it was shown that the effects of social isolation lead to changes in aggression that remained even after the rats were resocialised. The rest of the lives of animals who have been morally thwarted can be affected by the manipulations and treatments that they undergo, and this will continue to influence how they interact with others, how others interact with them, and potentially how they are viewed, and consequently treated, by others such as ourselves. Therefore, it is important to remember that moral thwarting is generally not a discrete event confined to the moment where the thwarting occurs, but rather it can have a sustained, harmful impact on the lives of the thwarted animals.

6.3. Moral thwarting of other species

So far in my analysis, I have largely focussed on examples of rats and mice being used in ways which may lead to them being morally thwarted. However, as mentioned earlier, many other species of animals are also used in scientific research. In 2017, 9,388,162 animals were used for scientific purposes in the EU (European Commission 2020a). Approximately 27 % of the animals used were species others than rats and mice; other types of rodents, rabbits, cats, dogs, pigs, goats, sheep, cattle, non-human primates, fish, birds, reptiles and cephalopods were among the many species used. In the US, data shows that, excluding mice, rats, birds or fish, 792,168 other animals of numerous species were used for research in the 2017 fiscal year (United States Department of Agriculture 2018)[15].

It would be beyond the scope of this thesis to fully analyse the moral subjecthood of each of these species. However, some authors have already began the important task of gathering together the empirical evidence for relevant abilities in various species, such as emotional contagion (Monsó et al. 2018) and capacities of care, autonomy and normative capacities (Monsó and Andrews forthcoming). Although the findings of this thesis so far concerning rats and mice cannot simply be assumed to apply in the case of all species, hopefully the available empirical evidence concerning moral capacities in other species, and the case presented for rats

---

[15] As described in section 3.2, mice, rats, birds and cold-blooded animals are among the list of animals not protected by the US Animal Welfare Act (Schaffner 2011, pp. 71–74), something which has itself been raised as problematic (see e.g. Frasch 2017). Usage data is not available for these animals in the United States Department of Agriculture reports (see e.g. United States Department of Agriculture 2018).

and mice so far in this thesis, will help convince the reader that the case for morally motivated behaviours in animals is one that should be taken seriously and not dismissed out of hand.

When members of a species consisting of moral subjects are used in scientific research, then they too are at risk from moral thwarting, which, as I have discussed, can occur as a result of the various experiences they undergo during this usage. Although it would also be beyond the scope of this thesis to assess the moral thwarting of all species used for scientific research, I would now like to discuss the specific case of non-human primate (NHP) use in research.

6.3.1. Moral thwarting of non-human primates

There are several reasons why I have chosen specifically to discuss the moral thwarting of NHPs. Firstly, many NHPs are still used for scientific research and so discussion regarding their treatment continues to be relevant. In the US 2017 fiscal year, 75,825 NHPs were used for scientific research (United States Department of Agriculture 2018). In the EU in 2017, 8235 non-human primates were used for scientific purposes; this number includes only individuals used for the first-time in animal research (European Commission 2020b, p. 12). NHPs are also recognised as a “species of particular public concern” (European Commission 2020a, p. 5) by a European Commission report regarding the use of animals for scientific purposes; I believe that this public concern, combined with NHPs’ evolutionary closeness to humans, and the available scientific evidence for moral behaviours in these animals (which I will discuss shortly), may help to capture the publics’ attention and concern regarding the issue of moral thwarting, and thus help introduce the topic into broader public discussion.

Discussing the topic of whether the moral thwarting of NHPs occurs in scientific practice will also provide a practical example of how the findings from my analysis thus far, mainly focussed around the moral thwarting of rats and mice, can be applied in alternative contexts to help recognise additional cases of moral thwarting. Showing that the issue of moral thwarting applies to NHPs as well as to rats and mice will also help to demonstrate ethically relevant similarities between rodents and NHPs that are commonly overlooked when justifying the different levels of protection that these species receive in scientific practice. In the animal model of callousness study that I previously discussed, the authors state that “[r]odents offer a cheap, convenient and ethically less controversial alternative to non-human primate[s] [sic]” (Hernandez-Lallement et al. 2018, p. 124). In my analysis so far, I hope to have drawn attention to one of the ways in which the usage of rodents can still be considered morally problematic, that is if it results in moral thwarting; looking into the case of moral capacities in NHPs should help to illustrate that there may not be as much separation between these two species in terms of their morally relevant capacities as some may claim or believe.

Finally, there already exists a body of evidence to help support the claim that NHPs may be capable of acting in morally motivated ways. Studies and reports focussing on NHPs have provided evidence of seemingly altruistic behaviour (Masserman et al. 1964, Wechkin et al. 1964, Warneken and Tomasello 2006, Burkart et al. 2007, Warneken et al. 2007, Lakshminarayanan and Santos 2008, Horner et al. 2011, Schmelz et al. 2017), consolation behaviour (de Waal and Roosmalen 1979, Kutsukake and Castles 2004, Cordoni et al. 2006, Fraser et al. 2008, Clay and de Waal 2013, Palagi et al. 2014), inequity aversion (Brosnan and de Waal 2003, Brosnan et al. 2005, 2010, Cronin and Snowdon 2008, Massen et al. 2012) and mourning behaviour (Hosaka et al. 2000, Warren and Williamson 2004, Sugiyama et al. 2009, Anderson et al. 2010, Biro et al. 2010, Fashing et al. 2011, Campbell et al. 2016, van Leeuwen et al. 2016, Yang et al. 2016)[16]. Although I do not claim that this evidence provides irrefutable proof of the moral subjecthood of these animals, I do believe that it does provide us with reasons to take seriously such a possibility.

6.3.1.1. The Harlow studies

Before moving on to the discussion of more recent scientific usage of NHPs, I would like to first discuss a series of experiments carried out by US researcher Harry Harlow and colleagues beginning in the 1950s. Although discussion of these older studies may initially seem somewhat irrelevant to an analysis of modern scientific practice, I believe that this is not the case. These studies provide a powerful example of how human experimentation on NHPs can have serious consequences that may include moral thwarting. These studies also provide evidence of practices that can result in the moral thwarting of NHPs, and therefore may be relevant for the upcoming consideration of more recent NHP studies. Furthermore, they also bear noteworthy similarities to some of the modern rodent studies that I have discussed.

---

[16] For further discussion regarding the connection between these types of behaviour and animal morality, see Monsó et al. (2018), Monsó and Andrews (forthcoming), and Monsó and Wrage (forthcoming).

Harlow became famous for his primate experiments like few other scientists. In one set of his experiments, Harlow (1958) utilised maternal separation in order to "study the development of affectional responses of neonatal and infant monkeys to an artificial, inanimate mother" (Harlow 1958, p. 675). Baby rhesus macaques were taken from their mothers shortly after birth and raised alone in metal cages. They were given access to *surrogate mothers*, inanimate objects covered in cloth or made of bare wire, some of which provided milk, in order to research and understand the importance of physical contact to the mother and access to food; the infants spent significantly more time in contact with the cloth mother, regardless of whether it provided milk, suggesting that body contact to the mother is highly important for young monkeys. Additional experiments reported as part of this study further utilised the cloth mothers in order to research the importance of the mother to the young monkeys as a safe haven for exploration, an object of visual interest, and to assess the retention of affection.

In a later summary of these experiments, the researchers describe how "[t]hese monkeys suffer total maternal deprivation and, even more important, have no opportunity to form affectional ties with their peers" (Harlow et al. 1965, p. 90). The effects of the experiments on the monkeys, as shown by their behaviours, were extreme. The young monkeys showed "[c]ompulsive nonnutritional sucking, repetitive stereotyped movements, detachment from the environment, hostility directed outwardly towards others and inwardly toward the animal's own body, and inability to form adequate social or heterosexual attachments to others" (Harlow et al. 1965, p. 90).

Another focus of the researchers was the effect of total social isolation on young monkeys. Several hours after birth, monkeys were isolated in a stainless-steel chamber, without contact to any other individuals, animal or human, for periods of 3, 6 or 12 months; an additional group underwent a condition referred to as *partial isolation*, where individuals were raised in bare wire cages for 6 months, before then being subjected to 6 months total isolation. Upon release from isolation, the researchers investigated the effects upon the individuals' social, sexual and play behaviours, their intellectual development and the maternal care skills of isolated females, and they investigated various approaches to try to rehabilitate isolated monkeys after they were released from isolation (Seay et al. 1964, Harlow et al. 1965, Sackett 1965, Arling and Harlow 1967, Harlow and Suomi 1971).

Again, these experiments had devastating effects on the monkeys. They showed clear signs of fear and distress, such as self-clutching and freezing. Two monkeys refused to eat; one starved to death after 5 days, the other was force-fed to prevent this. There were significant effects on social behaviour that were shown to be long-lasting; the researchers describe how social isolation during the first 6 months "severely impairs the potentiality for socialization" (Harlow et al. 1965, p. 92). They go on to state that:

> "The effects of 6 months of total social isolation were so devastating and debilitating that we had assumed initially that 12 months of isolation would not produce any additional decrement. This assumption proved to be false" (Harlow et al. 1965, p. 94)

Monkeys showed changes in aggressive behaviours, varying between isolation conditions and individuals. Some monkeys became hyper-aggressive, showed "suicidal aggression towards adults" (Harlow et al. 1965, p. 96), or aggressed towards infants. Other monkeys displayed an abnormal lack of aggression; monkeys raised in partial isolation showed increasingly aggressive behaviour towards those raised in total isolation for 12 months, who were described as helpless, to the point that, after 10 weeks, the experimenters stopped further interactions to prevent deaths occurring.

The researchers had little success in getting previously isolated females to mate. They state that "[b]y methods dark, dismal, and devious we impregnated several of these reluctant females over a period of years" (Harlow and Suomi 1971, p. 1535). These mothers, who never had contact or experience with their own mothers, "completely ignored or abused their initial offspring" (Harlow and Suomi 1971, p. 1535), and in some cases killed them. Although some mothers later showed some maternal behaviour towards subsequent offspring, "[m]ost of the motherless mothers that had abused or ignored their first infants throughout a predetermined 6-month postpartum period continued to be inadequate, brutal, or lethal mothers to subsequent progeny" (Harlow and Suomi 1971, p. 1535).

Clearly there is much to critique here from a welfare perspective, such as the extreme distress and fear experienced by the monkeys, the use of procedures such as force-feeding and the implied forced impregnation of females, young monkeys being abused and even killed by their mothers, monkeys starving themselves to death after removal from social isolation, and the hyper-aggression induced in the monkeys and allowed to play out. However, applying the concept of moral thwarting allows us to understand that there may have been additional harms occurring here, as well as those related to welfare.

The noticeable similarities between the aims, methods, and outcomes of these studies and the previously discussed modern studies involving rats and mice should immediately give us strong reasons to suspect that moral thwarting occurs as a result of these experiments. Such similarities include the use of social isolation, the resulting decreases in social behaviour, and the increased aggressiveness that was induced. I believe that many of the arguments I have already raised in detail can be applied to these experiments. Isolation physically prevents individuals from engaging in empathy-motivated behaviour towards others and from forming social ties that may be a necessary precursor for morally motivated behaviour. Likewise, obstructing the development of social skills may leave individuals unable to form social bonds, or to correctly interpret the intentions of others. Increased aggression may be a symptom of a reduction in aggression-inhibiting emotions, and likely interferes with the ability of an individual to form social bonds.

I believe that the impacts of these experimental procedures on maternal care also likely constitute cases of moral thwarting. I have not discussed the connection between maternal care and moral emotions up until this point; I will not make a detailed case for this here but simply state that there seems to be a *prima facie* connection between the two. If an individual is sensitive to the state of another, and motivated, for example by emotions such as empathy, compassion or love, to act in such a way that protects, helps or fosters that other individual, then that motivation seems likely to qualify as morally good[17]. In every case where an infant was taken from its mother, that mother has been prevented from performing the caring behaviour that she is likely motivated to perform towards her child. We also see the thwarting of maternal care in the case of females who were isolated and then later impregnated; these manipulated females displayed a lack of maternal care, going so far as to violently abuse and sometimes kill their offspring. To me, this represents a particularly persuasive example of the

---

[17] For a larger discussion regarding the caring capacities of animals, including the connection between caring behaviour, body contact and touch, see Botero (2014, 2016, 2017, 2018), Monsó and Andrews (forthcoming), and Monsó and Wrage (forthcoming).

harms of moral thwarting; even putting aside the harm suffered by the infant, does there not still seem to be something intuitively wrong with taking away a mother's motivation to care for and raise her infants?

As a final point, I would like to return again to the similarities between these experiments and the previously discussed studies involving rodents. As I have argued, there are strong reasons to believe that moral thwarting occurs as a result of both these past NHP experiments, and the more recent rodent studies. If rats and NHPs are indeed moral subjects, then the same type of moral-thwarting-related harms that resulted from highly controversial animal experimentation are seemingly still being committed today, albeit in a species that perhaps has less public sympathy. It is my hope that highlighting these similarities may help to persuade more people that moral thwarting is a harm that should not be overlooked.

6.3.1.2. Recent primate studies

As well as moral thwarting being a feature of older studies utilising NHPs, there are also strong reasons to claim that moral thwarting still occurs as part of modern scientific research.

Maternal separation of NHPs is still used as part of modern scientific practice, as discussed in critiques that have addressed its ongoing use over the past 30 years; these critiques focus on both the cruelness of the approach and the limited relevance of the data that can be obtained (Medical Research Modernization Committee n.d., Novak 2014, King 2015). Maternal separation is also used as an approach to create *specific-pathogen-free monkeys*; babies are removed from their mothers within the first day of life and individually housed (Solnick et al. 1999). Recent examples of this practice can be found in which newborn monkeys were isolated for the first 28 days of their lives, after which they were paired with another individual (Rommeck et al. 2009b, 2011); this process is described as "part of the yearly SPF breeding program" (Rommeck et al. 2009b, p. 397) at the institution where it took place. I believe that it should be clear how my previous arguments concerning moral thwarting and maternal separation can be applied here. If maternal care is motivated by moral emotions, or other forms of moral motivation, then preventing a mother from caring for her baby is a form of moral thwarting. If the separation goes on to affect the separated individuals in ways that impacts upon their ability to act morally, such as by reducing their social capacities, including their own maternal skills, then this too qualifies as moral thwarting.

We also find examples of moral thwarting connected to the housing situations of NHPs used for scientific research. Hannibal et al. (2017) discuss recent regulations and recommendations promoting the use of social housing for NHPs but note that "[w]hile social housing is the default, many investigators request and receive exemptions" (Hannibal et al. 2017, p. 10). They also state that "animals may experience many housing changes in their lifetime" (Hannibal et al. 2017, p. 1). To further attest to this, there are many modern studies assessing the impacts of individual housing (Doyle et al. 2008, Cole et al. 2009, Rommeck et al. 2009a, Gilbert and Baker 2011, Vandeleest et al. 2011, Baker et al. 2012, Gottlieb et al. 2013, Xie et al. 2014) and social change (for example, due to regrouping practices) (Capitanio et al. 2008, Cole et al. 2009, Rommeck et al. 2011, Gottlieb et al. 2013, Capitanio and Cole 2015) in NHPs, showing that this is still relevant to modern practice. As was discussed in the case of mice and rats, physical separation from others can be considered as moral thwarting when it prevents an individual from interacting with others on the basis of moral motivations. Furthermore, physical separation and the regrouping of individuals prevent the formation and maintenance of social relationships and the development of social skills, both of which may be important for the development and expression of empathy or other moral emotions.

It would be beyond the scope of this thesis to assess all of the various experimental procedures that NHPs have undergone in recent research. However, for the sake of example, I will end this discussion of NHP use in scientific research by briefly drawing attention to the fact that there are recent studies in which rhesus macaques have been subjected to basolateral amygdala lesioning, much like the rodents in the earlier-described studies; recent NHP studies include those that either specifically described having lesioned areas including the basolateral amygdala (see e.g. Izquierdo and Murray 2007, Rhodes and Murray 2013, Rudebeck et al. 2013, Dal Monte et al. 2015, Fiuzat et al. 2017, Pagliaccio et al. 2019), or that involved the lesioning of very large areas, or the entirety, of the amygdala (Bauman et al. 2004a, 2004b, Machado and Bachevalier 2006, Bliss-Moreau et al. 2011a, 2011b, 2013, 2017, Goursaud et al. 2014, Moadab et al. 2015, 2017). As was the case in many of the rat lesioning studies referenced earlier, not all of these studies focussed on how empathy or social behaviours were affected. Among the potentially relevant effects that were reported are blunted responding to both positive and negative stimuli (Bliss-Moreau et al. 2011a), behavioural changes that preclude positive social interactions (Machado and Bachevalier 2006), altered threat responses (Machado and

Bachevalier 2006), abnormal fear of conspecifics (Bauman et al. 2004b), and abnormal patterns of social behaviour (Bliss-Moreau et al. 2013, 2017, Moadab et al. 2015).

Given the previously made arguments connecting moral thwarting and changes to social and aggressive behaviour, it should be clear why the reported behavioural changes should give us cause to suspect that moral thwarting has occurred. Furthermore, as was discussed earlier in the case of mice, although these studies may not provide much in the way of direct evidence of the effects of lesioning on empathy in NHPs, the previously discussed work in rats (Hernandez-Lallement et al. 2015, 2016, 2018), scientific knowledge regarding the role of the amygdala in social signal processing and social-signal-related learning, the previously discussed evidence for moral emotions in NHPs, and the effects of these experiments on relevant capacities such as social skills, should give us further reasons to claim that this lesioning negatively impacts empathy, or other moral emotions, within NHPs, and therefore results in moral thwarting.

6.4. Summary

In this chapter, I have discussed how the scope of moral thwarting in scientific research extends well beyond the experimental manipulation of rats and mice discussed up until this point. Using the findings from my previous chapters, I have discussed the potential of various breeding and husbandry practices to result in moral thwarting, highlighting various ways in which this likely already occurs. Following this, I have focussed on considering whether other species may be morally thwarted by current scientific practice. Using the example of non-human primates, I have shown how the findings of my analysis can be applied to scientific research utilising other species, in this case indicating some of the ways in which historical and modern treatment of these animals has resulted in their moral thwarting. This analysis also highlighted similarities between highly controversial primate research from the past, and modern rat-based studies, and draws attention to ethically relevant similarities between these two types of animals that may be commonly overlooked.

PART III: Outlook and conclusion

7. Open questions, future research avenues, and related debates

7.1. Overview

Over the course of the previous chapters, I have made use of philosophical and ethical theories, frameworks and debates, as well as findings from empirical research, in order to support the claim that modern scientific practice leads to the moral thwarting of animal subjects. As well as allowing me support this claim, the analysis that I have presented also serves as a starting point from which we can consider how this and related topics can be further addressed and expanded upon moving forward, and how various debates and disciplines can contribute to, and benefit from, further work on the topic of moral thwarting. Therefore, in this chapter, I will discuss open questions relating to the topics focussed upon in this thesis, highlight related possible future research avenues, and discuss how analysis and discussion of moral thwarting can contribute to, and be informed by, other areas of applied ethical debates. I will first discuss how further contributions from empirical researchers could contribute towards our understanding of moral thwarting, then proceed to discuss aspects relating to moral theory, before finally highlighting relevant debates in applied ethics. This division of topics is somewhat artificial, as there is a great deal of interconnectedness and crossover between these topics, but I have opted to use it here to help provide structure to the points raised.

7.2. Empirical research

The results of prior empirical research form an essential part of the argumentation presented in this thesis, lending support to the claims that some animals possess moral capacities, and that some scientific practices result in the moral thwarting of these animals. However, there remain many opportunities for empirical researchers to further contribute towards our understanding of this topic.

As was seen from the discussion regarding empathy in rats, although there is a growing body of empirical evidence regarding rats' empathic abilities, there is still not sufficient data for us to be able to definitively state the extent of these abilities; therefore, there is a need for further empirical research on this specific topic. However, rats are far from the only species used in scientific research, and empathy is only one of a number of possible moral emotions that animals could possess. To fully understand the possible scope and scale of moral thwarting in scientific research, more empirical data would be required regarding the moral capacities of all of the species utilised for this purpose. As well as this, additional empirical data would be important for fully understanding which scientific practices, such as experimental or husbandry practices, impact upon the moral capacities of these animals. Such work would undoubtedly benefit from cooperation with ethicists and philosophers with expertise in these areas, who may be able to assist with the identification of relevant aspects of animals' behaviour or experimental effects. When considering further research into the moral capacities of animals, various questions with normative elements also arise; this topic is discussed further in section 7.4.1.2.

As well as conducting further research into the moral capacities of animals and how they may be impacted upon by different practices, scientific researchers can further contribute by working across specialities and disciplines to combine domain-specific knowledge. As an example, consider the finding that basolateral amygdala lesions have been shown to result in deficits in empathy in rats (Hernandez-Lallement et al. 2016, 2018). It may be the case that combining this information with knowledge from other research areas could lead to the identification of other practices that could have similar effects. For example, other researchers may be aware of additional interventions, perhaps pharmaceutical or surgical, that also interfere with the development or functioning of the basolateral amygdala. Combining this knowledge would allow for the recognition of further practices likely to result in moral thwarting. These kinds of discoveries would no doubt be aided by wider awareness of the issue, and good communication between researchers and others concerned with the topic.

An additional key contribution that empirical researchers could make, where practical, would be the wider reporting of data relevant to the topic of moral thwarting, even when it is not a focus of the research in question. For example, recording any changes to social interactions between conspecifics that occur following a scientific procedure may allow those concerned with the issue to detect cases of moral thwarting, or they may at least provide hints that a practice could result in moral thwarting occurring.

7.3. Moral theory

As highlighted by this thesis, relevant work concerning moral theory has already contributed heavily towards the debate concerning animal morality. Philosophical and ethical reflection has resulted in the claim that it is theoretically possible for some individuals to be moral subjects, individuals who can act on the basis moral motivations, even if they lack control or understanding of their actions. Furthermore, it has allowed us to claim that some animals may meet the criteria to be considered moral subjects, for example, by identifying and characterising specific moral emotions that may be attributable to some animals (Monsó 2015, 2017). Building upon such work, further analyses, such as the work of Monsó et al. (2018) and this thesis, allow us to recognise the ways in which moral thwarting may occur as a result of everyday human treatment of animals, and provide ethical arguments as to why moral thwarting should be considered problematic. Going forward, all of the aforementioned topics could be further explored.

Argumentation that permits the notion of animals being able to act on the basis of moral motivations, such as that of Rowlands (2012), could be further proposed, analysed and debated, to identify whether any weaknesses or shortcomings are present in the existing argumentation, and if so, to modify such arguments in order to strengthen their claims. For example, the reliance on an objective consequentialist ethical theory to underlie claims of animal morality in Rowlands theory may be a controversial point to some. Monsó (2015) has touched upon such a point but suggested that some anti-realist stances may also be compatible with the requirements of Rowlands' theories. Therefore, new work aimed at identifying further compatible ethical perspectives could serve to increase the palatability of Rowlands' theory for a wider range of individuals holding different ethical views.

Further work concerning the identification and characterisation of other moral emotions, particularly those relevant to the capacities of animals, has the potential to provide us with a more complete picture regarding the moral capacities of various species, and, as a consequence, also raise our awareness of other ways in which our current treatment of these animals may result in moral thwarting. Work concerning the identification and characterisation of other moral emotions that may be found in animals would likely both drive, and be driven by, further complimentary empirical investigation into the moral capacities of animals.

Perhaps one of the key issues that moral theory has the potential to help address is the question of whether and how moral thwarting can be considered morally problematic. As previously described, Monsó et al. (2018) have already utilised the capabilities approach to argue that moral thwarting is morally problematic; moral emotions can be understood both as central capabilities, or as grounding central capabilities, and the capabilities approach recognises harm in the thwarting or blighting of such central capabilities. However, there may also be additional ethical theories that utilise different reasoning to explain the morally problematic nature of moral thwarting. To address the full scope of moral thwarting as defined in this work, such a theory would need to be able to address effects on an individual's existing moral capacities, the development of moral capacities, the proper exercise of moral capacities, and on the moral capacities of future individuals and populations. Such a theory would also need to be capable of recognising that practices can be morally problematic even if the individuals affected by them do not subjectively experience harm.

The use of differing ethical theories may be informed by, and lead to, consideration of further related issues. One such consideration could be whether we can understand the capacity to act on the basis of moral motivations as having a different value or importance than other morally considerable aspects of an individual and, if so, how such a difference could be understood. Differing answers to these questions could result in different judgements when addressing questions such as whether an act that impacts negatively upon a moral subject's welfare can be seen as justifiable if it has been carried out in order to avoid that individual being morally thwarted (or vice versa).

The choice of theory may also affect whether we are able to recognise degrees of wrongness. Is an act that slightly reduces an individual's moral capacities less problematic than one that greatly reduces them, or are moral capacities to be viewed an inviolable? Does the duration or permanency a case of moral thwarting affect the level of wrongness? Is an act that precludes an individual from performing morally motivated behaviour less problematic than one which impacts upon the underlying moral capacities of an individual? Is a greater wrong committed if an individual fully loses the capacities that bestow moral subjecthood upon her and is perhaps therefore no longer identifiable as a moral subject?

Another aspect to be considered concerns the intentionality behind an act of moral thwarting. Does the wrongness of an action resulting in moral thwarting vary depending on whether this was an intended outcome, a foreseeable or predictable outcome, or if it occurred unintentionally? Can an act be considered morally wrong if it aims at achieving the moral thwarting of an individual but fails to do so? Reliance on a consequentialist ethical theory would suggest that intentions are irrelevant, but some may find such a claim at odds with their moral intuition.

Different ethical theories may even lead to differing judgements on topics such as whether it is wrong to change the morally motivated behaviour of an animal at all, even if it is in such a way that promotes morally good behaviour, for example by training individuals to respond to moral features in a more normatively correct way. Theories that value *naturalness* or *natural behaviour* may find it difficult to justify such interventions. An interesting thought experiment also arises when we consider the case of a (hopefully hypothetical!) morally evil moral subject of the type identified by Rowlands (2012, p. 231); an individual with sensitivity to good- or bad-making features, whose sensitivity is grounded in the operations of a reliable mechanism, but who is motivated to promote bad-making features or reduce good-making features. Would manipulating such an individual to promote morally better behaviour be permissible, or would this be considered problematic; theories valuing naturalness, or that value an individual's ability to flourish as the type of being it is, may find such interferences problematic.

We may also want to consider whether the method of moral thwarting affects our judgement as to how problematic an act of moral thwarting is. For example, are non-invasive techniques such as training any more or less problematic than the use of more invasive or *unnatural* approaches such as pharmaceutical or surgical interventions?

Work focussing on addressing any of the questions or topics listed in this section could provide meaningful insights and developments concerning the topic of moral thwarting, and help inform related debates.

7.4. Debates in applied ethics

In this section, I will touch upon some of the ongoing debates in applied ethics that have the potential to be informed by discussions concerning moral thwarting, or that can potentially contribute to discussions on this topic. I will comment on relevant aspects of these debates and, where appropriate, I will indicate some potential directions that future research in these debates could take.

7.4.1. The usage of animals in scientific research

Beginning with the main focus of this thesis, it should be clear to the reader that discussions concerning moral thwarting are highly relevant to the topic of animal usage in scientific research. I have focussed on showing that there are strong reasons to claim that moral thwarting does occur in this context, identified some of the ways that it likely occurs, and identified some features characteristic of practices that may lead to moral thwarting. However, there remain various aspects of this usage of animals that could benefit from further ethical discussion.

7.4.1.1. The justifiability of experiments resulting in moral thwarting

If the arguments in this thesis and related work successfully make the case that moral thwarting occurs in scientific practice, and that it is a morally problematic practice, then perhaps one of the key questions that arises is how this should be taken into consideration going forward when considering the justifiability of animal-based research. The claims that animals can suffer, and that this suffering is morally relevant, are almost certainly more established and less controversial than the claims made in this thesis regarding animals' moral capacities and moral thwarting, and yet people still hold various different views regarding the justifiability of animal research that results in suffering. Therefore, we can likely expect a similar range of ethical stances on the justifiability of research that results in the moral thwarting of animals. No doubt contributions from ethical theory will help to illuminate various perspectives on this issue, and to provide reasoned argumentation for these different viewpoints.

Although ethical arguments may provide good reasons for certain stances regarding the issue of moral thwarting and scientific research, it is ultimately the legal protections afforded to animals that will most impact their usage and treatment in this context. Ethical reflection on the topic can provide reasoned argumentation for how moral thwarting may be best considered by the law, and analysis of existing laws can determine whether they sufficiently address the issue of moral thwarting, both in theory and in practice. Legal change may be in part directly informed and influenced by ethical arguments and analyses, but it can also be driven by public opinion. Mepham (2000) has argued that in democratic societies, acceptance into the *common morality*, the generally accepted, unphilosophically determined morality shared by members of a society, is an important first step for an idea to be eventually incorporated into public policy. Rollin (2006) has also highlighted the role of public concern in shaping policy, describing how the emergence of a new social consensus ethic featuring increased concern for the treatment of animals played a key role in driving legislative changes regarding animal use. Indeed, in EU Directive 63/2010/EU, the main EU legislation regulating the use of animals for scientific purposes, the ethical concerns of the general public are given as one of the bases for the protections that it grants (European Parliament, Council of the European Union 2010, preamble [12,17,26])[18]. Therefore, achieving, and demonstrating, public support could be of vital importance for achieving legal recognition of moral thwarting as a morally problematic practice. As ethical argumentation can help inform public opinion, the further public discussion of moral thwarting will likely play a role in affecting any future legal changes that may occur regarding this issue.

If moral thwarting is to be taken into account when considering the justifiability of a piece of scientific research involving animals, we still have to contend with the fact that our current knowledge regarding moral thwarting and the ways in which it can occur is far from complete, as made clear through the analysis in this thesis. This gives rise to the question of how we should determine whether a scientific practice can be justified in cases where we have incomplete knowledge regarding the involved animals' moral capacities or the ways in which they may be thwarted by this practice. Should an act only be considered to result in moral thwarting if it has been previously proven to do so, or should moral thwarting be considered a potential outcome of any acts that have not yet been proven to not result in moral thwarting?

The decision as to how cautious to be when considering the justifiability of performing acts whose impact on moral capacities is unknown has the potential to affect the progress of scientific research, and may also affect how incentivised different individuals are to further investigate the likelihood of moral thwarting occurring. Requiring proof, or at least reasonable certainty, that an act does not result in moral thwarting would likely incentivise further investigation into the topic by scientific researchers who may otherwise be reluctant to address these issues if it were not in immediate interests of their ongoing research to do so. However,

---

[18] It is worth noting, however, that despite listing public concern as an important influence on the legislation, it has been argued that the current legislation does not fully capture public concerns. Röcklinsberg et al. (2014) have discussed how animal ethics committees responsible for project authorisations typically only consider the effects of practices on animals in terms of how their welfare is impacted, whereas public concerns for animals go beyond merely these welfare concerns. They argue that incorporating a concept such as integrity into ethical assessments would better allow for public concerns to be more fully represented.

requiring such proof would likely impact negatively on the progress of scientific research in areas other than the moral behaviour of animals. If proof, or at least reasonable certainty, that a practice does result in moral thwarting is required for a practice to be considered problematic, then it may be difficult to incentivise further empirical investigation; scientific researchers working in areas closely related to procedures that may result in moral thwarting may be among those best placed to provide scientific insight that helps to address these issues, but it may not be in the immediate interests of their ongoing research to provide evidence that their intended work may result in moral thwarting. Those perhaps most concerned with the topic, such as animal welfare and animal rights advocates, as well as a subset of animal ethicists, may not be those most capable of providing the further required empirical evidence, and may therefore find it difficult to pursue such a topic without the support of empirical researchers.

7.4.1.2. Scientific research into moral capacities and moral thwarting

As I discussed in section 7.2, there are many ways in which further ongoing empirical research could contribute towards increasing our understanding of the moral capacities of animals, and the ways in which these may be thwarted by various scientific practices. These contributions may help to give us a much more complete overview of moral thwarting in various contexts, and in turn allow us to more carefully consider practices that result in moral thwarting. However, various questions with normative aspects arise when considering such ongoing research into the moral capacities of animals.

What priority should be given to research addressing animals’ moral capacities and the effects of procedures on them when compared with other research with alternate aims? How should different aspects of research into moral thwarting be prioritised? For example, should we prioritise research into the most commonly performed practices, such as routine husbandry practices, into the most commonly used species, into the species most likely to be moral subjects, into procedures identified as most likely to result in moral thwarting, or based upon some other metric?

Questions concerning further research into the moral capacities of animals are further complicated by the fact that this research may rely on practices that are themselves morally problematic; for example the classic study by Church (1959), investigating rats’ responses to others in distress, involved subjecting rats to electrical shocks, and, as previously argued, the study showing the effect of basolateral amygdala lesions on rats' empathic capacities (Hernandez-Lallement et al. 2016) resulted in moral thwarting. Can the harm of further research into the topic of moral thwarting be justified by the eventual benefits to other animals if it leads to greater respect for their moral capacities? How much proof of a species' moral capacities is necessary before moral thwarting is considered a likely consequence? Is near certainty required? Is there a threshold of certainty beyond which moral thwarting should be considered as a likely consequence, or beyond which the harm of further research outweighs the potential gain in certainty?

Theories explaining the wrongness of moral thwarting can no doubt contribute to addressing questions such as these but it seems clear that to fully address such questions, other relevant normative factors, such as the priority of other research and opinions of the general public, need to be considered.

7.4.1.3. Identification of practices likely to lead to moral thwarting

As has hopefully been demonstrated by this thesis, ethical analysis can also lead to contributions such as the identification of practices likely to result in moral thwarting, or the identification of features characteristic of such practices. Such investigations are crucial for understanding the ways in which our real-world treatment of animals may lead to moral thwarting. This thesis has largely focussed on a small subset of possible moral emotions, scientific practices and species that could be investigated. Further detailed analysis into these topics could help identify further practices that result in moral thwarting, increasing our knowledge of the ways in which our actions may negatively impact animals' lives, and allowing us to more accurately reconsider such actions. This analysis of moral thwarting within the context of scientific research also has the potential to help us understand how moral thwarting may occur in other areas of human-animal interaction, and vice versa, as I will now describe.

7.4.2. Other human practices impacting animals

Scientific research is just one of many types of human practice that impact upon the lives of various animals. The issue of moral thwarting may be applicable to many of these practices, and could contribute to ongoing ethical debates regarding them. For example, Monsó et al. (2018) have already discussed how the issue of moral thwarting is a relevant concern regarding common farming practices. Farming practices impact upon the lives of many billions of animals each year; therefore, where moral thwarting occurs as a result of commonly used practices, it will likely occur on a massive scale. Looking at the kinds of farming practices identified by Monsó et al. (2018) as potentially resulting in moral thwarting, we see some commonality with those identified in this thesis; for example, both draw attention to practices that involve isolating individuals, regrouping individuals, restricting social interactions, and exposing individuals to others in distress. Therefore, we see how analyses of moral thwarting in one specific context will likely help to inform discussion of moral thwarting in other contexts.

Even a superficial consideration of other human practices that impact upon animals can give us cause to believe that they have the potential to result in moral thwarting. For example, if we consider the case of animals used for different forms of entertainment, such as those kept in zoos, used in sports, or trained as fighting animals, we can immediately identify some types of treatment that they may potentially experience, or in some of these cases, definitely will experience, that correspond to practices already linked to moral thwarting. Examples of such practices are when animals are kept without a suitable social environment, when they are prevented from forming long-term social bonds, when they are exposed to others in distress, when they themselves are subjected to stressful experiences, or when they are manipulated into displaying abnormal aggressive behaviour.

Even practices that some may initially consider as reflecting positive human-animal relationships, such as the keeping of pets, could potentially involve practices that could result in moral thwarting if performed in an unconsidered way. For example, some practices connected to the breeding, sale or keeping of pet animals may involve the early separation of young from their mother, the disruption of social groups when rehoming individuals, and the keeping of social animals in isolation.

As these passing examples hopefully show, there is much to be gained from further consideration of moral thwarting in the context of other human practices that impact upon the lives of animals. We may gain a greater understanding of how our current treatment of animals can harm them, allowing us to reconsider aspects of how we act towards and treat animals, and we may also discover additional ways in which moral thwarting may occur.

7.4.3. Bioethics debates

7.4.3.1. Animal disenhancement

The topic of moral thwarting also overlaps with some current bioethics debates. Perhaps one of the most pertinent of these is the topic of animal disenhancement. Broadly speaking, debates around animal disenhancement attempt to address the question of whether it is ever morally justifiable to modify animals in such a way that they are somehow reduced in their capacities. One paradigmatic example of such a modification concerns the breeding of blind chickens, as discussed by Sandøe et al. (1999); these chickens seem to suffer less welfare-related problems when living in the cramped conditions commonly found in poultry farming, and therefore it has been argued that breeding blind chickens for use in these conditions could be morally justified, given that it reduces overall levels of suffering. Another classic example, discussed by Bovenkerk et al. (2002), commonly associated with the term *brave new birds*, involves hypothetical genetically engineered non-sentient organisms, derived from chickens, that consume food and produce eggs; being non-sentient, these organisms do not suffer and therefore it could be argued that their use is preferable to that of normal chickens under typical farming conditions. In both examples, the manipulations would result in less overall suffering, but still many people seemingly feel uncomfortable with such propositions. Debates such as these continue to have ongoing relevance to current human practice; for example, a recent argument has been made for the use of gene editing technology in livestock farming, in order to produce animals who suffer less under intensive confinement (Shriver and McConnachie 2018).

Arguments concerning moral thwarting add a new aspect to these debates concerning animal disenhancement. They provide additional reasons as to why certain types of disenchantment can be considered problematic, bringing in an ethical perspective other than animal welfare concerns. For example, in the case of breeding and farming blind animals that are seemingly less distressed by unpleasant conditions, we should also consider whether these impairments affect the moral lives of these animals; perhaps they impair these individuals' abilities to perceive morally relevant features of their environments, their ability to form social bonds that may be a prerequisite for moral behaviour, or impact upon their ability to perform moral behaviour. In the case of the brave new birds, these animals are seemingly stripped of all moral capacities.

Debates into animal disenhancement, and related topics such as genetic modification, can also contribute to discussions regarding moral thwarting. Arguments claiming the wrongness of animal disenhancement need to address relevant issues such as the reduction or removal of animals' capacities, the wrongness of acts that do not necessarily lead to subjectively experienced harms, and the wrongness of effects on future-individuals or populations who would otherwise not have been brought into existence.

By way of an example, one such approach to addressing such issues in the context of animal disenhancement and genetic engineering debates has been to utilise the concept of integrity. Generally understood, integrity may reflect notions of intactness, wholeness, completeness, or being in an unharmed, undamaged or untouched state (Vorstenbosch 1993, Röcklinsberg et al. 2014). Integrity-based ethical theories have included various interpretations of the concept, such as individual integrity, species integrity and genetic integrity (De Vries 2006). It would be interesting to assess whether various integrity-based theories can satisfactorily capture ethical objections to moral thwarting, for example through theories valuing the integrity of species-characteristic-behaviours, or whether a separate theory focussed around a concept such as *integrity of moral capacities and behaviour* is needed to fully capture these ethical objections. Integrity may also be of particular interest to investigate as it has previously been included in aspects of Dutch policy concerning biotechnology (Bovenkerk 2012, pp. 158–161), and because it has recently been argued that its inclusion in EU animal ethics committee assessments would better allow them to capture wider ethical concerns of the public than is currently achieved when only taking animal welfare considerations into account (Röcklinsberg et al. 2014).

7.4.3.2. Moral enhancement

Another area of bioethical debate that may be able to help inform discussion on the topic of moral thwarting is that of moral enhancement. According to Raus et al. (2014, p. p263), "there is no consensus on what precisely constitutes moral enhancement"; however, we might approximately characterise it as the bringing about of an "improvement in the way in which we act or reflect morally" (Raus et al. 2014, p. p263). Unsurprisingly, given the orthodox philosophical position that humans are the only (non-theoretical) moral beings, existing discussions on this topic typically focus around human morality. Nevertheless, despite this, and the fact that the focus of such discussions largely concerns something that is quite the opposite of moral thwarting, there may be much that we can take from these debates, as demonstrated by the following examples.

Raus et al. (2014) carried out an analysis of the differing uses of the term *moral enhancement*, exposing different perspectives that can be taken, and that themselves lead to differing normative implications. The types of intervention considered as moral enhancement vary among interpretations, with some focussing more narrowly on bioenhancements, such as biomedical or genetic approaches, while others also consider practices such as moral education as forms of moral enhancement. Some choose to differentiate between *moral treatment*, something which, roughly speaking, restores a morally lacking individual to *normal* levels of moral motivation or behaviour, and *moral enhancement*, which elevates an individual's moral motivation or behaviour beyond *normal* levels. Different understandings of the term also vary concerning whether to consider interventions that *aim* at morally enhancing an individual, regardless of whether this is actually achieved, or interventions that actually *do* result in moral enhancement, even if this was not intended. The arguments given for and against these differing perspectives could help inform analyses of moral thwarting, for example by providing useful justifications for differing approaches, or by highlighting opposing views that may need to be addressed or considered when discussing moral thwarting and its related harms.

Another topic that arises in the context of moral enhancement debates is the connection between moral traits and identity (see e.g. Crutchfield 2018). Crutchfield cites work that proposes a person's identity is most closely associated with their moral traits, and therefore proposes that moral enhancement can induce a loss of identity. The term *moral traits* is presented in a broad sense that can include "moral beliefs or other attitudes, moral motivation, dispositions, or emotions" (Crutchfield 2018, p. 569). In this thesis, I have discussed work that proposes that capacities conforming to moral motivations, dispositions and emotions may be attributable to individuals of certain species of animals, so this could be an interesting line of thought to pursue regarding the moral thwarting of animals, particularly in cases of moral disenhancement. Such work would likely involve consideration of topics including the moral capacities of animals, personal identity among animals and its connection to their moral traits, the valuation of such personal identities, and the harms of modifying them.

The preceding examples are provided to illustrate some of the ways in which debates concerning moral enhancement may help contribute towards further work on the subject of the moral thwarting of animals, but not presented as the only relevant aspects. It may well be the case that further inter-related aspects can be found between these two topics.

7.5. Summary

In this chapter, I have highlighted some of the open questions, possible future research avenues, and related ethical debates that arise in connection with the topics covered in this thesis. I have provided examples of how further contributions from empirical research, moral theory, and applied ethics debates could help to address questions concerning the scope, scale, and moral significance of moral thwarting. Furthermore, I have discussed how ongoing work into the topic of moral thwarting can additionally provide insights that can contribute towards other ongoing ethical debates.

8. Conclusion

In this thesis, I have aimed to address the question of whether the moral lives of some animals are negatively impacted upon as a result of their use in modern scientific research.

I first arrived at a characterisation of the term *moral thwarting*, a term that I have introduced to refer to the ways in which a moral subject's moral capacities may be negatively impacted upon by human action. The characterisation of this term took inspiration from the work of Monsó et al. (2018) and was further established through reflection upon the ways that such thwarting could theoretically occur. Two subcategories of moral thwarting, *moral disenhancement* and *moral preclusion*, were identified, distinguished by the way that they impacted upon a moral subject's moral capacities.

I went on to show that there is strong evidence in support of the claim that specific experiments have morally thwarted rats, and potentially mice, by impacting upon their empathy-related capacities, with empathy understood here as a moral emotion. Analysis of these experiments revealed practices and conditions that result in the moral thwarting of the animals that undergo them, as well as revealing several characteristics that may be typical of practices that result in moral thwarting.

Scientific experiments that aimed at inducing abnormal aggression in animals were then discussed, as many of the identified practices and characteristics could be found in such experiments. I presented two different arguments for how such experiments could be considered to result in moral thwarting. In the first of these, I discussed how aggression could be viewed as being regulated by moral emotions, and how the effects of the experiments in question on their animal subjects were consistent with the thwarting of these aggression-regulating emotions. The second approach to claiming that these experiments result in moral thwarting was to ignore the issue of whether moral emotions directly influence aggressive behaviour, and to instead focus on how other moral emotions may be thwarted by these experiments. I highlighted how various aspects of these experiments involved practices that I had previously argued resulted in moral thwarting, such as exposing individuals to stressful situations, exposing them to others in distress, and socially isolating individuals. Furthermore, I argued that, in the case of animals, moral behaviour likely takes place mainly in a social context, and that, given that these experiments modify social interactions, these experiments likely impact upon moral behaviours that these animals may otherwise have performed in a social context.

Moving away from the specific focus on the experimental manipulation of rats and mice, I then discussed how certain scientific husbandry and breeding practices include practices or conditions already identified as resulting in moral thwarting. Finally, I considered the applicability of these findings to other species used in scientific research, and, through a focus on non-human primates, showed how these findings helped us to discover cases where these species had likely been morally thwarted as a result of scientific work. This also demonstrated ethically relevant similarities between rodents and non-human primates that are commonly overlooked.

By focussing on a few specific species in this thesis, I have been able to discuss the evidence for certain moral capacities in these species and elaborate on some specific ways in which they may be morally thwarted. Given the evidence gathered and the arguments presented, I feel justified in claiming that we have good cause to believe that modern scientific practice can and does result in the moral thwarting of some animals, both as a result of some experimental procedures and some husbandry practices.

Although I have discussed available evidence and how it supports the claims of this thesis, I cannot claim that such evidence conclusively proves the claims of this thesis. Analyses into moral thwarting, such as the one found in this thesis, are complicated by non-conclusive or lacking empirical data regarding the moral capacities of different species, lack of awareness of how these moral capacities can be impacted upon, and a lack of focus on how scientific practices impact upon these animals. Furthermore, I cannot claim that the findings of this thesis with regards to the focussed-upon species can simply be assumed to apply for all species that are used for the purposes of scientific research. Fully addressing the topic of moral thwarting for all such species, and for all scientific practices that they may undergo, is clearly a significantly larger task than can be achieved in this thesis alone. There remains much empirical, philosophical, and ethical work that can be done to better understand this topic, and to properly identify and address all of the associated morally problematic practices.

While there remains much more to be researched and learned concerning the various facets of moral thwarting, this thesis highlights that, based on the currently available evidence, moral thwarting should be considered as a very likely outcome of some scientific practices. Given that many millions of animals are used every year for scientific research, the importance and relevance of this topic should not be understated; hesitancy to address this topic could lead to the ongoing use of harmful practices in an overlooked, unconsidered, and non-justified way, impacting upon the moral lives of a great number of morally considerable individuals. Moving beyond the context of scientific research, many other areas of human activity also have the potential to impact upon the moral lives of a great number of animals; this again highlights the urgent need to further consider the ways in which our actions may subject animals to the harm of moral thwarting.

Rowlands (2012) has described how, although they cannot be praised for their actions, moral subjects are worthy of our moral respect, an attitude that recognises that when a moral subject acts in such a morally good way it is “a good thing that the world contains a subject like this, an individual who acts in this way” (Rowlands 2012, p. 254). We might pause to consider whether the current treatment of those animals in our society who may be moral subjects currently demonstrates such an attitude of moral respect.

9. References

Adolphs R. 1999. Social cognition and the human brain. Trends in Cognitive Sciences, 3(12):469–479. DOI 10.1016/S1364-6613(99)01399-6 (Accessed 27.03.2020).

Adolphs R, Tranel D, Damasio H, Damasio AR. 1994. Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. Nature, 372:669–672. DOI 10.1038/372669a0 (Accessed 27.03.2020).

Adolphs R, Tranel D, Damasio AR. 1998. The human amygdala in social judgment. Nature, 393:470–474. DOI 10.1038/30982 (Accessed 27.03.2020).

Adriaense JEC, Koski SE, Huber L, Lamm C. 2020. Challenges in the comparative study of empathy and related phenomena in animals. Neuroscience & Biobehavioral Reviews, 112:62–82. DOI 10.1016/j.neubiorev.2020.01.021 (Accessed 24.03.2020).

Alberts JR, Galef BG. 1973. Olfactory cues and movement: Stimuli mediating intraspecific aggression in the wild Norway rat. Journal of Comparative and Physiological Psychology, 85(2):233–242. DOI 10.1037/h0035050.

Anderson JR, Gillies A, Lock LC. 2010. Pan thanatology. Current Biology, 20(8):R349–R351. DOI 10.1016/j.cub.2010.02.010 (Accessed 11.02.2020).

Aristotle. 1999. Nicomachean ethics. (T Irwin, Tran). 2nd ed. Indianapolis: Hackett Pub. Co.

Arling GL, Harlow HF. 1967. Effects of social deprivation on maternal behavior of rhesus monkeys. Journal of Comparative and Physiological Psychology, 64(3):371–377. DOI 10.1037/h0025221 (Accessed 05.07.2019).

Atsak P, Orre M, Bakker P, Cerliani L, Roozendaal B, Gazzola V, Moita M, Keysers C. 2011. Experience modulates vicarious freezing in rats: a model for empathy. PLoS ONE, 6(7):e21855. DOI 10.1371/journal.pone.0021855 (Accessed 26.03.2020).

Baker KC, Bloomsmith MA, Oettinger B, Neu K, Griffis C, Schoof V, Maloney M. 2012. Benefits of pair housing are consistent across a diverse population of rhesus macaques. Applied Animal Behaviour Science, 137(3):148–156. DOI 10.1016/j.applanim.2011.09.010 (Accessed 13.02.2020).

Barfield RJ, Busch DE, Wallen K. 1972. Gonadal influence on agonistic behavior in the male domestic rat. Hormones and Behavior, 3(3):247–259. DOI 10.1016/0018-506X(72)90038-4 (Accessed 21.01.2020).

Barnett SA. 1975. The rat: a study in behavior. Rev. ed. Chicago: University of Chicago Press.

Bauman MD, Lavenex P, Mason WA, Capitanio JP, Amaral DG. 2004a. The development of mother-infant interactions after neonatal amygdala lesions in rhesus monkeys. Journal of Neuroscience, 24(3):711–721. DOI 10.1523/JNEUROSCI.3263-03.2004 (Accessed 18.02.2020).

Bauman MD, Lavenex P, Mason WA, Capitanio JP, Amaral DG. 2004b. The development of social behavior following neonatal amygdala lesions in rhesus monkeys. Journal of Cognitive Neuroscience, 16(8):1388–1411. DOI 10.1162/0898929042304741 (Accessed 18.02.2020).

Bekoff M. 2007. The emotional lives of animals: a leading scientist explores animal joy, sorrow, and empathy--and why they matter. Novato: New World Library.

Bekoff M, Pierce J. 2009. Wild justice: the moral lives of animals. Chicago: University of Chicago Press.

Ben-Ami Bartal I, Decety J, Mason P. 2011. Empathy and pro-social behavior in rats. Science, 334(6061):1427–1430. DOI 10.1126/science.1210789 (Accessed 31.10.2019).

Ben-Ami Bartal I, Rodgers DA, Bernardez Sarria MS, Decety J, Mason P. 2014. Pro-social behavior in rats is modulated by social experience. eLife, 3:e01385. DOI 10.7554/eLife.01385 (Accessed 04.02.2020).

Ben-Ami Bartal I, Shan H, Molasky NMR, Murray TM, Williams JZ, Decety J, Mason P. 2016. Anxiolytic treatment impairs helping behavior in rats. Frontiers in Psychology, 7:850. DOI 10.3389/fpsyg.2016.00850 (Accessed 07.10.2019).

Benus RF, Bohus B, Koolhaas JM, van Oortmerssen GA. 1991. Heritable variation for aggression as a reflection of individual coping strategies. Experientia, 47(10):1008–1019. DOI 10.1007/BF01923336 (Accessed 27.01.2020).

Biro D, Humle T, Koops K, Sousa C, Hayashi M, Matsuzawa T. 2010. Chimpanzee mothers at Bossou, Guinea carry the mummified remains of their dead infants. Current Biology, 20(8):R351–R352. DOI 10.1016/j.cub.2010.02.031 (Accessed 11.02.2020).

Biró L, Tóth M, Sipos E, Bruzsik B, Tulogdi Á, Bendahan S, Sandi C, Haller J. 2017. Structural and functional alterations in the prefrontal cortex after post-weaning social isolation: relationship with species-typical and deviant aggression. Brain Structure and Function, 222(4):1861–1875. DOI 10.1007/s00429-016-1312-z (Accessed 23.08.2019).

Biró L, Sipos E, Bruzsik B, Farkas I, Zelena D, Balazsfi D, Tóth M, Haller J. 2018. Task division within the prefrontal cortex: distinct neuron populations selectively control different aspects of aggressive behavior via the hypothalamus. Journal of Neuroscience, 38(17):4065–4075. DOI 10.1523/JNEUROSCI.3234-17.2018 (Accessed 01.10.2019).

Blair RJR. 1995. A cognitive developmental approach to morality: investigating the psychopath. Cognition, 57(1):1–29. DOI 10.1016/0010-0277(95)00676-P (Accessed 10.01.2020).

Blanchard RJ, Fukunaga K, Blanchard DC, Kelley MJ. 1975. Conspecific aggression in the laboratory rat. Journal of Comparative and Physiological Psychology, 89(10):1204–1209.

Bliss-Moreau E, Bauman MD, Amaral DG. 2011a. Neonatal amygdala lesions result in globally blunted affect in adult rhesus macaques. Behavioral Neuroscience, 125(6):848–858. DOI 10.1037/a0025757 (Accessed 26.08.2019).

Bliss-Moreau E, Toscano JE, Bauman MD, Mason WA, Amaral DG. 2011b. Neonatal amygdala lesions alter responsiveness to objects in juvenile macaques. Neuroscience, 178:123–132. DOI 10.1016/j.neuroscience.2010.12.038 (Accessed 26.08.2019).

Bliss-Moreau E, Moadab G, Bauman MD, Amaral DG. 2013. The impact of early amygdala damage on juvenile rhesus macaque social behavior. Journal of Cognitive Neuroscience, 25(12):2124–2140. DOI 10.1162/jocn_a_00483 (Accessed 26.08.2019).

Bliss-Moreau E, Moadab G, Santistevan A, Amaral DG. 2017. The effects of neonatal amygdala or hippocampus lesions on adult social behavior. Behavioural Brain Research, 322:123–137. DOI 10.1016/j.bbr.2016.11.052 (Accessed 26.08.2019).

Blundell P, Symonds M, Hall G, Killcross S, Bailey GlynisK. 2013. Within-event learning in rats with lesions of the basolateral amygdala. Behavioural Brain Research, 236:48–55. DOI 10.1016/j.bbr.2012.08.030 (Accessed 04.11.2019).

de Boer SF. 2016. Animal models: implications for human aggression and violence. In: Bushman BJ, ed. Aggression and violence: a social psychological perspective. 1st ed. New York: Routledge, 22–43.

de Boer SF. 2018. Animal models of excessive aggression: implications for human aggression and violence. Current Opinion in Psychology, 19:81–87. DOI 10.1016/j.copsyc.2017.04.006 (Accessed 12.08.2019).

de Boer SF, van der Vegt BJ, Koolhaas JM. 2003. Individual variation in aggression of feral rodent strains: a standard for the genetics of aggression and violence? Behavior Genetics, 33(5):485–501. DOI 10.1023/A:1025766415159 (Accessed 29.01.2020).

Botero M. 2014. How primate mothers and infants communicate, characterizing interaction in mother-infant studies across species. In: Pina M, Gontier N, eds. The evolution of social communication in primates. Cham: Springer International Publishing, 83–100.

Botero M. 2016. Tactless scientists: Ignoring touch in the study of joint attention. Philosophical Psychology, 29(8):1200–1214. DOI 10.1080/09515089.2016.1225293 (Accessed 13.08.2020).

Botero M. 2017. Primates are touched by your concern. In: Andrews K, Beck J, eds. The Routledge handbook of philosophy of animal minds. 1st ed. New York: Routledge Taylor & Francis Group, 372–380.

Botero M. 2018. Bringing touch back to the study of emotions in human and non-human primates: a theoretical exploration. International Journal of Comparative Psychology, 31. https://escholarship.org/uc/item/4qf475c2#author. (Accessed 13.08.2020).

Bouchatta O, Ouhaz Z, Ba-Mhamed S, Kerekes N, Bennis M. 2016. Acute and chronic glue sniffing effects and consequences of withdrawal on aggressive behavior. Life Sciences, 152:14–20. DOI 10.1016/j.lfs.2016.03.013 (Accessed 22.08.2019).

Bovenkerk B. 2012. The biotechnology debate. Dordrecht: Springer Netherlands.

Bovenkerk B, Brom FWA, van den Bergh BJ. 2002. Brave new birds: the use of “animal integrity” in animal ethics. The Hastings Center Report, 32(1):16. DOI 10.2307/3528292 (Accessed 26.03.2019).

Brosnan SF, de Waal FBM. 2003. Monkeys reject unequal pay. Nature, 425:297–299. DOI 10.1038/nature01963 (Accessed 11.02.2020).

Brosnan SF, Schiff HC, de Waal FBM. 2005. Tolerance for inequity may increase with social closeness in chimpanzees. Proceedings of the Royal Society B: Biological Sciences, 272(1560):253–258. DOI 10.1098/rspb.2004.2947 (Accessed 11.02.2020).

Brosnan SF, Talbot C, Ahlgren M, Lambeth SP, Schapiro SJ. 2010. Mechanisms underlying responses to inequitable outcomes in chimpanzees, Pan troglodytes. Animal Behaviour, 79(6):1229–1237. DOI 10.1016/j.anbehav.2010.02.019 (Accessed 11.02.2020).

Burkart JM, Fehr E, Efferson C, Schaik CP van. 2007. Other-regarding preferences in a non-human primate: Common marmosets provision food altruistically. Proceedings of the National Academy of Sciences, 104(50):19762–19766. DOI 10.1073/pnas.0710310104 (Accessed 11.02.2020).

Burkett JP, Andari E, Johnson ZV, Curry DC, Waal FBM de, Young LJ. 2016. Oxytocin-dependent consolation behavior in rodents. Science, 351(6271):375–378. DOI 10.1126/science.aac4785 (Accessed 25.03.2020).

Campbell LAD, Tkaczynski PJ, Mouna M, Qarro M, Waterman J, Majolo B. 2016. Behavioral responses to injury and death in wild Barbary macaques (Macaca sylvanus). Primates, 57(3):309–315. DOI 10.1007/s10329-016-0540-4 (Accessed 11.02.2020).

Capitanio JP, Cole SW. 2015. Social instability and immunity in rhesus monkeys: the role of the sympathetic nervous system. Philosophical Transactions of the Royal Society B:

Biological Sciences, 370(1669):20140104. DOI 10.1098/rstb.2014.0104 (Accessed 14.02.2020).

Capitanio JP, Abel K, Mendoza SP, Blozis SA, McChesney MB, Cole SW, Mason WA. 2008. Personality and serotonin transporter genotype interact with social context to affect immunity and viral set-point in simian immunodeficiency virus disease. Brain, Behavior, and Immunity, 22(5):676–689. DOI 10.1016/j.bbi.2007.05.006 (Accessed 14.02.2020).

Caramaschi D, de Boer SF, de Vries H, Koolhaas JM. 2008. Development of violence in mice through repeated victory along with changes in prefrontal cortex neurochemistry. Behavioural Brain Research, 189(2):263–272. DOI 10.1016/j.bbr.2008.01.003 (Accessed 27.01.2020).

Carvalheiro J, Seara-Cardoso A, Mesquita AR, de Sousa L, Oliveira P, Summavielle T, Magalhães A. 2019. Helping behavior in rats (Rattus norvegicus) when an escape alternative is present. Journal of Comparative Psychology, 133(4):452–462. DOI 10.1037/com0000178 (Accessed 31.10.2019).

Chang SE, McDannald MA, Wheeler DS, Holland PC. 2012. The effects of basolateral amygdala lesions on unblocking. Behavioral Neuroscience, 126(2):279–289. DOI 10.1037/a0027576.

Charles River. 2020. Autism spectrum disorder mouse model. https://www.criver.com/products-services/discovery-services/pharmacology-studies/neuroscience-models-assays/psychiatric-disease-studies/autism-spectrum-disorder-mouse-model?region=3696. (Accessed 06.02.2020).

Chen Q, Panksepp JB, Lahvis GP. 2009. Empathy is moderated by genetic background in mice. PLoS ONE, 4(2):e4387. DOI 10.1371/journal.pone.0004387 (Accessed 15.11.2019).

Church RM. 1959. Emotional reactions of rats to the pain of others. Journal of Comparative and Physiological Psychology, 52(2):132–134.

Clay Z, de Waal FBM. 2013. Bonobos respond to distress in others: consolation across the age spectrum. PLoS ONE, 8(1):e55206. DOI 10.1371/journal.pone.0055206 (Accessed 11.02.2020).

Cole SW, Mendoza SP, Capitanio JP. 2009. Social stress desensitizes lymphocytes to regulation by endogenous glucocorticoids: insights from in vivo cell trafficking dynamics in rhesus macaques. Psychosomatic medicine, 71(6):591–597. DOI 10.1097/PSY.0b013e3181aa95a9 (Accessed 14.02.2020).

Cools AKA, Hout AJ-MV, Nelissen MHJ. 2008. Canine reconciliation and third-party-initiated postconflict affiliation: do peacemaking social mechanisms in dogs rival those of higher primates? Ethology, 114(1):53–63. DOI 10.1111/j.1439-0310.2007.01443.x (Accessed 19.05.2020).

Cordero MI, Poirier GL, Márquez C, Veenit V, Fontana X, Salehi B, Ansermet F, Sandi C. 2012. Evidence for biological roots in the transgenerational transmission of intimate partner violence. Translational Psychiatry, 2(4):e106. DOI 10.1038/tp.2012.32 (Accessed 23.08.2019).

Cordero MI, Ansermet F, Sandi C. 2013. Long-term programming of enhanced aggression by peripuberty stress in female rats. Psychoneuroendocrinology, 38(11):2758–2769. DOI 10.1016/j.psyneuen.2013.07.005 (Accessed 23.08.2019).

Cordero MI, Just N, Poirier GL, Sandi C. 2016. Effects of paternal and peripubertal stress on aggression, anxiety, and metabolic alterations in the lateral septum. European Neuropsychopharmacology, 26(2):357–367. DOI 10.1016/j.euroneuro.2015.11.017 (Accessed 23.08.2019).

Cordoni G, Palagi E, Tarli SB. 2006. Reconciliation and consolation in captive western gorillas. International Journal of Primatology, 27(5):1365–1382. DOI 10.1007/s10764-006-9078-4 (Accessed 11.02.2020).

Cozzi A, Sighieri C, Gazzano A, Nicol CJ, Baragli P. 2010. Post-conflict friendly reunion in a permanent group of horses (Equus caballus). Behavioural Processes, 85(2):185–190. DOI 10.1016/j.beproc.2010.07.007 (Accessed 19.05.2020).

Cronin KA, Snowdon CT. 2008. The effects of unequal reward distributions on cooperative problem solving by cottontop tamarins, Saguinus oedipus. Animal Behaviour, 75(1):245–257. DOI 10.1016/j.anbehav.2007.04.032 (Accessed 11.02.2020).

Cronin KA, Schroeder KKE, Snowdon CT. 2010. Prosocial behaviour emerges independent of reciprocity in cottontop tamarins. Proceedings of the Royal Society B, 277(1701):3845–3851. DOI 10.1098/rspb.2010.0879 (Accessed 19.05.2020).

Crutchfield P. 2018. Moral enhancement can kill. The Journal of Medicine and Philosophy, 43(5):568–584. DOI 10.1093/jmp/jhy020 (Accessed 29.05.2019).

Custance D, Mayer J. 2012. Empathic-like responding by domestic dogs (Canis familiaris) to distress in humans: an exploratory study. Animal Cognition, 15(5):851–859. DOI 10.1007/s10071-012-0510-1 (Accessed 19.05.2020).

Dal Monte O, Costa VD, Noble PL, Murray EA, Averbeck BB. 2015. Amygdala lesions in rhesus macaques decrease attention to threat. Nature communications, 6:10161. DOI 10.1038/ncomms10161 (Accessed 19.02.2020).

De Vries R. 2006. Genetic engineering and the integrity of animals. Journal of Agricultural and Environmental Ethics, 19(5):469–493. DOI 10.1007/s10806-006-9004-y (Accessed 26.03.2019).

Douglas-Hamilton I, Bhalla S, Wittemyer G, Vollrath F. 2006. Behavioural reactions of elephants towards a dying and deceased matriarch. Applied Animal Behaviour Science, 100(1–2):87–102. DOI 10.1016/j.applanim.2006.04.014 (Accessed 25.05.2019).

Doyle LA, Baker KC, Cox LD. 2008. Physiological and behavioral effects of social introduction on adult male rhesus macaques. American Journal of Primatology, 70(6):542–550. DOI 10.1002/ajp.20526 (Accessed 14.02.2020).

Dvorkin A, Silva C, McMurran T, Bisnaire L, Foster J, Szechtman H. 2010. Features of compulsive checking behavior mediated by nucleus accumbens and orbital frontal cortex. European Journal of Neuroscience, 32(9):1552–1563. DOI 10.1111/j.1460-9568.2010.07398.x (Accessed 04.11.2019).

Erskine MS, Barfield RJ, Goldman BD. 1978. Intraspecific fighting during late pregnancy and lactation in rats and effects of litter removal. Behavioral Biology, 23(2):206–218. DOI 10.1016/S0091-6773(78)91814-X (Accessed 21.01.2020).

European Commission. 2020a. Report from the Commission to the European Parliament and the Council: 2019 report on the statistics on the use of animals for scientific purposes in the Member States of the European Union in 2015-2017.

https://ec.europa.eu/transparency/regdoc/rep/1/2020/EN/COM-2020-16-F1-EN-MAIN-PART-1.PDF. (Accessed 18.02.2020).

European Commission. 2020b. Commission staff working document part 1/5 accompanying the document report from the Commission to the European Parliament and the Council 2019: report on the statistics on the use of animals for scientific purposes in the Member States of the European Union in 2015-2017. https://ec.europa.eu/environment/chemicals/lab_animals/pdf/Statistical%20report_SWD_p1_EN.pdf. (Accessed 18.02.2020).

European Parliament, Council of the European Union. 2010. Directive 2010/63/EU of the European Parliament and of the Council of 22 September 2010 on the protection of animals used for scientific purposes. Official Journal of the European Union, 276:33–79. https://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=CELEX:32010L0063&from=EN. (Accessed 23.04.2020).

Evans VE, Braud WG. 1969. Avoidance of a distressed conspecific. Psychonomic Science, 15(3):166–166. DOI 10.3758/BF03336261 (Accessed 25.03.2020).

Fashing PJ, Nguyen N, Barry TS, Goodale CB, Burke RJ, Jones SCZ, Kerby JT, Lee LM, Nurmi NO, Venkataraman VV. 2011. Death among geladas (Theropithecus gelada): a broader perspective on mummified infants and primate thanatology. American Journal of Primatology, 73(5):405–409. DOI 10.1002/ajp.20902 (Accessed 11.02.2020).

Ferrazzo S, Gunduz-Cinar O, Stefanova N, Pollack GA, Holmes A, Schmuckermair C, Ferraguti F. 2019. Increased anxiety-like behavior following circuit-specific catecholamine denervation in mice. Neurobiology of Disease, 125:55–66. DOI 10.1016/j.nbd.2019.01.009 (Accessed 05.11.2019).

Finkel EJ. 2007. Impelling and inhibiting forces in the perpetration of intimate partner violence. Review of General Psychology, 11(2):193–207. DOI 10.1037/1089-2680.11.2.193 (Accessed 20.01.2020).

Finkel EJ. 2014. The I^3 Model: metatheory, theory, and evidence. In: Olson JM, Zanna MP, eds. Advances in experimental social psychology. Academic Press, 1–104.

Finkel EJ, DeWall CN, Slotter EB, McNulty JK, Pond RSJ, Atkins DC. 2012. Using I^3 theory to clarify when dispositional aggressiveness predicts intimate partner violence perpetration. Journal of Personality, 102(3):533–549. DOI 10.1037/a0025651.

Fiuzat EC, Rhodes SEV, Murray EA. 2017. The role of orbitofrontal–amygdala interactions in updating action–outcome valuations in macaques. Journal of Neuroscience, 37(9):2463–2470. DOI 10.1523/JNEUROSCI.1839-16.2017 (Accessed 06.11.2019).

Flower FC, Weary DM. 2001. Effects of early separation on the dairy cow and calf:: 2. Separation at 1 day and 2 weeks after birth. Applied Animal Behaviour Science, 70(4):275–284. DOI 10.1016/S0168-1591(00)00164-7 (Accessed 30.06.2020).

Frasch PD. 2017. Gaps in US animal welfare law for laboratory animals: perspectives from an animal law attorney. ILAR Journal, 57(3):285–292. DOI 10.1093/ilar/ilw016 (Accessed 12.08.2020).

Fraser ON, Bugnyar T. 2010. Do Ravens Show Consolation? Responses to Distressed Others. PLoS ONE, 5(5). DOI 10.1371/journal.pone.0010605 (Accessed 19.05.2020).

Fraser ON, Stahl D, Aureli F. 2008. Stress reduction through consolation in chimpanzees. Proceedings of the National Academy of Sciences, 105(25):8557–8562. DOI 10.1073/pnas.0804141105 (Accessed 11.02.2020).

Fröberg S, Lidfors L. 2009. Behaviour of dairy calves suckling the dam in a barn with automatic milking or being fed milk substitute from an automatic feeder in a group pen. Applied Animal Behaviour Science, 117(3):150–158. DOI 10.1016/j.applanim.2008.12.015 (Accessed 30.06.2020).

Gilbert MH, Baker KC. 2011. Social buffering in adult male rhesus macaques (Macaca mulatta): Effects of stressful events in single vs. pair housing. Journal of Medical Primatology, 40(2):71–78. DOI 10.1111/j.1600-0684.2010.00447.x (Accessed 14.02.2020).

Gottlieb DH, Capitanio JP, McCowan B. 2013. Risk factors for stereotypic behavior and self-biting in rhesus macaques (Macaca mulatta): Animal’s history, current environment, and personality. American Journal of Primatology, 75(10):995–1008. DOI 10.1002/ajp.22161 (Accessed 13.02.2020).

Goursaud A-PS, Wallen K, Bachevalier J. 2014. Mother recognition and preference after neonatal amygdala lesions in rhesus macaques (Macaca mulatta) raised in a semi-naturalistic environment. Developmental Psychobiology, 56(8):1723–1734. DOI 10.1002/dev.21233 (Accessed 19.02.2020).

Greene JT. 1969. Altruistic behavior in the albino rat. Psychonomic Science, 14(1):47–48. DOI 10.3758/BF03336420 (Accessed 26.03.2020).

Greenwood BN, Strong PV, Fleshner M. 2010. Lesions of the basolateral amygdala reverse the long-lasting interference with shuttle box escape produced by uncontrollable stress. Behavioural Brain Research, 211(1):71–76. DOI 10.1016/j.bbr.2010.03.012 (Accessed 06.11.2019).

Hachiga Y, Silberberg A, Slotnick B, Gomez M. 2020. Rats (Rattus norvegicus) find occupancy of a restraint tube rewarding. Journal of the Experimental Analysis of Behavior, 113(3):644–656. DOI 10.1002/jeab.596 (Accessed 22.06.2020).

Haller J. 2017. Studies into abnormal aggression in humans and rodents: Methodological and translational aspects. Neuroscience & Biobehavioral Reviews, 76:77–86. DOI 10.1016/j.neubiorev.2017.02.022 (Accessed 23.08.2019).

Haller J, Harold G, Sandi C, Neumann ID. 2014. Effects of adverse early-life events on aggression and anti-social behaviours in animals and humans. Journal of Neuroendocrinology, 26(10):724–738. DOI 10.1111/jne.12182 (Accessed 29.06.2020).

Haney C, Banks C, Zimbardo P. 1973. Interpersonal dynamics in a simulated prison. International Journal of Criminology & Penology, 1(1):69–97.

Hannibal DL, Bliss-Moreau E, Vandeleest J, McCowan B, Capitanio JP. 2017. Laboratory rhesus macaque social housing and social changes: Implications for research. American Journal of Primatology, 79(1):e22528. DOI 10.1002/ajp.22528 (Accessed 11.07.2019).

Harlow HF. 1958. The nature of love. American Psychologist, 13(12):673–685. DOI 10.1037/h0047884 (Accessed 24.06.2019).

Harlow HF, Suomi SJ. 1971. Social recovery by isolation-reared monkeys. Proceedings of the National Academy of Sciences, 68(7):1534–1538. DOI 10.1073/pnas.68.7.1534 (Accessed 24.06.2019).

Harlow HF, Dodsworth RO, Harlow MK. 1965. Total social isolation in monkeys. Proceedings of the National Academy of Sciences, 54(1):90–97. DOI 10.1073/pnas.54.1.90 (Accessed 24.06.2019).

Hernandez-Lallement J, van Wingerden M, Marx C, Srejic M, Kalenscher T. 2015. Rats prefer mutual rewards in a prosocial choice task. Frontiers in Neuroscience, 8. DOI 10.3389/fnins.2014.00443 (Accessed 23.10.2019).

Hernandez-Lallement J, van Wingerden M, Schäble S, Kalenscher T. 2016. Basolateral amygdala lesions abolish mutual reward preferences in rats. Neurobiology of Learning and Memory, 127:1–9. DOI 10.1016/j.nlm.2015.11.004 (Accessed 23.10.2019).

Hernandez-Lallement J, van Wingerden M, Schäble S, Kalenscher T. 2017. A social reinforcement learning hypothesis of mutual reward preferences in rats. In: Wöhr M, Krach S, eds. Social behavior from rodents to humans: neural foundations and clinical implications. Cham: Springer International Publishing, 159–176.

Hernandez-Lallement J, van Wingerden M, Kalenscher T. 2018. Towards an animal model of callousness. Neuroscience and Biobehavioral Reviews, 91:121–129. DOI 10.1016/j.neubiorev.2016.12.029 (Accessed 30.06.2019).

Hernandez-Lallement J, Attah AT, Soyman E, Pinhal CM, Gazzola V, Keysers C. 2020. Harm to others acts as a negative reinforcer in rats. Current Biology, 30(6):949-961.e7. DOI 10.1016/j.cub.2020.01.017 (Accessed 19.06.2020).

Holland PC. 2016. Enhancing second-order conditioning with lesions of the basolateral amygdala. Behavioral Neuroscience, 130(2):176–181. DOI 10.1037/bne0000129 (Accessed 06.11.2019).

Horner V, Carter JD, Suchak M, de Waal FBM. 2011. Spontaneous prosocial choice by chimpanzees. Proceedings of the National Academy of Sciences, 108(33):13847–13851. DOI 10.1073/pnas.1111088108 (Accessed 11.02.2020).

Hosaka K, Matsumoto-Oda A, Huffman MA, Kawanaka K. 2000. Reactions to dead bodies of conspecifics by wild chimpanzees in the Mahale Mountains, Tanzania. Primate Research, 16(1):1–15. DOI 10.2354/psj.16.1 (Accessed 11.02.2020).

Hursthouse R. 1999. On virtue ethics. Oxford: Oxford University Press.

Hursthouse R, Pettigrove G. 2018. Virtue ethics. In: Zalta EN, ed. The Stanford encyclopedia of philosophy. Winter 2018 ed. Metaphysics Research Lab, Stanford University. https://plato.stanford.edu/archives/win2018/entries/ethics-virtue/ (Accessed 08.05.2020).

Hwa LS, Nathanson AJ, Shimamoto A, Tayeh JK, Wilens AR, Holly EN, Newman EL, DeBold JF, Miczek KA. 2015. Aggression and increased glutamate in the mPFC during withdrawal from intermittent alcohol in outbred mice. Psychopharmacology, 232(16):2889–2902. DOI 10.1007/s00213-015-3925-y (Accessed 22.08.2019).

Ikkatai Y, Watanabe S, Izawa E-I. 2016. Reconciliation and third-party affiliation in pair-bond budgerigars (Melopsittacus undulatus). Behaviour, 153(9/11):1173–1193. DOI 10.1163/1568539X-00003388 (Accessed 19.05.2020).

Ito W, Erisir A, Morozov A. 2015. Observation of distressed conspecific as a model of emotional trauma generates silent synapses in the prefrontal-amygdala pathway and enhances fear learning, but ketamine abolishes those effects. Neuropsychopharmacology, 40(11):2536–2545. DOI 10.1038/npp.2015.100 (Accessed 25.03.2020).

Izquierdo A, Murray EA. 2007. Selective bilateral amygdala lesions in rhesus monkeys fail to disrupt object reversal learning. Journal of Neuroscience, 27(5):1054–1062. DOI 10.1523/JNEUROSCI.3616-06.2007 (Accessed 19.02.2020).

Izquierdo A, Darling C, Manos N, Pozos H, Kim C, Ostrander S, Cazares V, Stepp H, Rudebeck PH. 2013. Basolateral amygdala lesions facilitate reward choices after negative feedback in rats. The Journal of Neuroscience, 33(9):4105–4109. DOI 10.1523/JNEUROSCI.4942-12.2013 (Accessed 04.11.2019).

Jeon D, Shin H-S. 2011. A mouse model for observational fear learning and the empathetic response. Current Protocols in Neuroscience, 57(1):8.27.1-8.27.9. DOI 10.1002/0471142301.ns0827s57 (Accessed 15.11.2019).

Jeon D, Kim S, Chetana M, Jo D, Ruley HE, Lin S-Y, Rabah D, Kinet J-P, Shin H-S. 2010. Observational fear learning involves affective pain system and Ca v 1.2 Ca 2+ channels in ACC. Nature Neuroscience, 13(4):482–488. DOI 10.1038/nn.2504 (Accessed 25.03.2020).

Kaliste E, Mering S. 2004. The welfare of laboratory rats. In: Kaliste E, ed. The welfare of laboratory animals. Dordrecht: Kluwer Academic Publishers, 153–180.

Kappel S, Hawkins P, Mendl MT. 2017. To group or not to group? Good practice for housing male laboratory mice. Animals, 7(12):88. DOI 10.3390/ani7120088 (Accessed 24.09.2020).

Kashtelyan V, Lichtenberg NT, Chen ML, Cheer JF, Roesch MR. 2014. Observation of reward delivery to a conspecific modulates dopamine release in ventral striatum. Current Biology, 24(21):2564–2568. DOI 10.1016/j.cub.2014.09.016 (Accessed 25.03.2020).

Kavaliers M, Choleris E, Colwell DD. 2001. Learning from others to cope with biting flies: social learning of fear-induced conditioned analgesia and active avoidance. Behavioral Neuroscience, 115(3):661–674.

King BJ. 2015. Plight of baby lab monkeys reaches congress. https://www.npr.org/sections/13.7/2015/01/29/382326538/plight-of-baby-lab-monkeys-reaches-congress. (Accessed 14.02.2020).

Knapska E, Nikolaev E, Boguszewski P, Walasek G, Blaszczyk J, Kaczmarek L, Werka T. 2006. Between-subject transfer of emotional information evokes specific pattern of amygdala activation. Proceedings of the National Academy of Sciences, 103(10):3858–3862. DOI 10.1073/pnas.0511302103 (Accessed 25.03.2020).

Knutson B, Burgdorf J, Panksepp J. 1999. High-frequency ultrasonic vocalizations index conditioned pharmacological reward in rats. Physiology & Behavior, 66(4):639–643. DOI 10.1016/S0031-9384(98)00337-0 (Accessed 25.03.2020).

KOCO News. 2013. Pit bull hailed hero, saves Oklahoma family from fire. https://www.koco.com/article/pit-bull-hailed-hero-saves-oklahoma-family-from-fire/4292024?source=KOCO%5D. (Accessed 06.05.2020).

Koolhaas JM. 2010. The laboratory rat. In: Hubrecht R, Kirkwood J, eds. The UFAW handbook on the care and management of laboratory and other research animals. 8th ed. Chichester: John Wiley & Sons, Ltd, 311–326.

Korsgaard CM. 2004. Fellow creatures: Kantian ethics and our duties to animals. The Tanner Lectures on Human Values, 24:77–110. http://nrs.harvard.edu/urn-3:HUL.InstRepos:3198692. (Accessed 05.05.2020).

Korsgaard CM. 2006. Morality and the distinctiveness of human action. In: Ober J, ed. Primates and philosophers. Princeton: Princeton University Press, 98–119.

Kutsukake N, Castles DL. 2004. Reconciliation and post-conflict third-party affiliation among wild chimpanzees in the Mahale Mountains, Tanzania. Primates, 45(3):157–165. DOI 10.1007/s10329-004-0082-z (Accessed 11.02.2020).

Lakshminarayanan VR, Santos LR. 2008. Capuchin monkeys are sensitive to others’ welfare. Current Biology, 18(21):R999–R1000. DOI 10.1016/j.cub.2008.08.057 (Accessed 11.02.2020).

Langford DJ, Crager SE, Shehzad Z, Smith SB, Sotocinal SG, Levenstadt JS, Chanda ML, Levitin DJ, Mogil JS. 2006. Social modulation of pain as evidence for empathy in mice. Science, 312(5782):1967–1970. DOI 10.1126/science.1128322 (Accessed 15.11.2019).

Langford DJ, Tuttle AH, Brown K, Deschenes S, Fischer DB, Mutso A, Root KC, Sotocinal SG, Stern MA, Mogil JS, et al. 2010. Social approach to pain in laboratory mice. Social Neuroscience, 5(2):163–170. DOI 10.1080/17470910903216609 (Accessed 14.11.2019).

Lee H, Kim D-W, Remedios R, Anthony TE, Chang A, Madisen L, Zeng H, Anderson DJ. 2014. Scalable control of mounting and attack by Esr1$^+$ neurons in the ventromedial hypothalamus. Nature, 509(7502):627–632. DOI 10.1038/nature13169 (Accessed 23.08.2019).

van Leeuwen EJC, Mulenga IC, Bodamer MD, Cronin KA. 2016. Chimpanzees’ responses to the dead body of a 9-year-old group member. American Journal of Primatology, 78(9):914–922. DOI 10.1002/ajp.22560 (Accessed 11.02.2020).

Li Zheng, Wang J, Chen L, Zhang M, Wan Y. 2013. Basolateral amygdala lesion inhibits the development of pain chronicity in neuropathic pain rats. PLoS ONE, 8(8):e70921. DOI 10.1371/journal.pone.0070921 (Accessed 04.11.2019).

Li Zhen, Lu Y-F, Li C-L, Wang Y, Sun W, He T, Chen X-F, Wang X-L, Chen J. 2014. Social interaction with a cagemate in pain facilitates subsequent spinal nociception via activation of the medial prefrontal cortex in rats. PAIN®, 155(7):1253–1261. DOI 10.1016/j.pain.2014.03.019 (Accessed 15.11.2019).

Lin D, Boyle MP, Dollar P, Lee H, Lein ES, Perona P, Anderson DJ. 2011. Functional identification of an aggression locus in the mouse hypothalamus. Nature; London, 470:221–6. DOI 10.1038/nature09736 (Accessed 23.08.2019).

Lu Y-F, Ren B, Ling B-F, Zhang J, Xu C, Li Z. 2018. Social interaction with a cagemate in pain increases allogrooming and induces pain hypersensitivity in the observer rats. Neuroscience Letters, 662:385–388. DOI 10.1016/j.neulet.2017.10.063 (Accessed 14.11.2019).

Machado CJ, Bachevalier J. 2006. The impact of selective amygdala, orbital frontal cortex, or hippocampal formation lesions on established social relationships in rhesus monkeys (Macaca mulatta). Behavioral Neuroscience, 120(4):761–786. DOI 10.1037/0735-7044.120.4.761.

Maibom HL, Ed. 2014. Empathy and morality. New York: Oxford University Press.

Mamiya PC, Matray-Devoti J, Fisher H, Wagner GC. 2017. Mice increased target biting behaviors 24h after co-administration of alcohol and fluoxetine. Brain Research, 1662:110–115. DOI 10.1016/j.brainres.2017.02.007 (Accessed 22.08.2019).

Marincovich A, Bravo E, Dlouhy B, Richerson GB. 2019. Amygdala lesions reduce seizure-induced respiratory arrest in DBA/1 mice. Epilepsy & Behavior, 106440. DOI 10.1016/j.yebeh.2019.07.041 (Accessed 04.11.2019).

Márquez C, Poirier GL, Cordero MI, Larsen MH, Groner A, Marquis J, Magistretti PJ, Trono D, Sandi C. 2013. Peripuberty stress leads to abnormal aggression, altered amygdala and orbitofrontal reactivity and increased prefrontal *MAOA* gene expression. Translational Psychiatry, 3(1):e216. DOI 10.1038/tp.2012.144 (Accessed 23.08.2019).

Márquez C, Rennie SM, Costa DF, Moita MA. 2015. Prosocial choice in rats depends on food-seeking behavior displayed by recipients. Current Biology, 25(13):1736–1745. DOI 10.1016/j.cub.2015.05.018 (Accessed 26.03.2020).

Massen JJM, Berg LMVD, Spruijt BM, Sterck EHM. 2012. Inequity aversion in relation to effort and relationship quality in long-tailed Macaques (Macaca fascicularis). American Journal of Primatology, 74(2):145–156. DOI 10.1002/ajp.21014 (Accessed 11.02.2020).

Masserman JH, Wechkin S, Terris W. 1964. “Altruistic” behavior in rhesus monkeys. American Journal of Psychiatry, 121(6):584–585. DOI 10.1176/ajp.121.6.584 (Accessed 19.11.2019).

Medical Research Modernization Committee. n.d.. A critique of maternal deprivation monkey experiments at the State University of New York Health Science Center. http://www.mrmcmed.org/mom.html. (Accessed 14.02.2020).

Mepham B. 2000. ``Würde der kreatur'' and the common morality. Journal of Agricultural and Environmental Ethics, 13(1):65–78. DOI 10.1023/A:1009587116907 (Accessed 26.02.2020).

Moadab G, Bliss-Moreau E, Amaral DG. 2015. Adult social behavior with familiar partners following neonatal amygdala or hippocampus damage. Behavioral Neuroscience, 129(3):339–350. DOI 10.1037/bne0000062 (Accessed 26.08.2019).

Moadab G, Bliss-Moreau E, Bauman MD, Amaral DG. 2017. Early amygdala or hippocampus damage influences adolescent female social behavior during group formation. Behavioral Neuroscience, 131(1):68–82. DOI 10.1037/bne0000181 (Accessed 26.08.2019).

Monsó S. 2015. Empathy and morality in behaviour readers. Biology & Philosophy, 30:671–690. DOI 10.1007/s10539-015-9495-x (Accessed 25.10.2019).

Monsó S. 2017. Morality without mindreading. Mind & Language, 32(3):338–357. DOI 10.1111/mila.12146 (Accessed 10.04.2020).

Monsó S, Andrews K. forthcoming. Animal moral psychologies. In: Doris JM, Vargas M, eds. The Oxford handbook of moral psychology. Oxford University Press.

Monsó S, Wrage B. forthcoming. Tactful animals: How the study of touch can inform the animal morality debate. Philosophical Psychology.

Monsó S, Benz-Schwarzburg J, Bremhorst A. 2018. Animal morality: what it means and why it matters. The Journal of Ethics, 22:283–310. DOI 10.1007/s10892-018-9275-3 (Accessed 28.03.2019).

Natarajan D, de Vries H, Saaltink D-J, de Boer SF, Koolhaas JM. 2009. Delineation of violence from functional aggression in mice: an ethological approach. Behavior Genetics, 39(1):73–90. DOI 10.1007/s10519-008-9230-3 (Accessed 20.08.2019).

Nawroth C, Langbein J, Coulon M, Gabor V, Oesterwind S, Benz-Schwarzburg J, von Borell E. 2019. Farm animal cognition—linking behavior, welfare and ethics. Frontiers in Veterinary Science, 6. DOI 10.3389/fvets.2019.00024 (Accessed 24.09.2020).

Newman EL, Terunuma M, Wang TL, Hewage N, Bicakci MB, Moss SJ, DeBold JF, Miczek KA. 2018. A role for prefrontal cortical NMDA receptors in murine alcohol-heightened aggression. Neuropsychopharmacology, 43(6):1224–1234. DOI 10.1038/npp.2017.253 (Accessed 22.08.2019).

Novak B. 2014. Animal research at NIH lab challenged by members of Congress. Reuters. https://www.reuters.com/article/us-nih-ethics-baby-monkeys-idUSKBN0K300120141225. (Accessed 14.02.2020).

Nussbaum MC. 2004. Beyond ‘compassion and humanity’: justice for nonhuman animals. In: Sunstein CR, Nussbaum MC, eds. Animal rights: current debates and new directions. New York: Oxford University Press, 299–320.

Nussbaum MC. 2006. Frontiers of justice. Cambridge: Harvard University Press.

Oberliessen L, Hernandez-Lallement J, Schäble S, van Wingerden M, Seinstra M, Kalenscher T. 2016. Inequity aversion in rats, Rattus norvegicus. Animal Behaviour, 115:157–166. DOI 10.1016/j.anbehav.2016.03.007 (Accessed 26.03.2020).

Ostrander S, Cazares VA, Kim C, Cheung S, Gonzalez I, Izquierdo A. 2011. Orbitofrontal cortex and basolateral amygdala lesions result in suboptimal and dissociable reward choices on cue-guided effort in rats. Behavioral Neuroscience, 125(3):350–359. DOI 10.1037/a0023574.

Oyegbile TO, Marler CA. 2005. Winning fights elevates testosterone levels in California mice and enhances future ability to win fights. Hormones and Behavior, 48(3):259–267. DOI 10.1016/j.yhbeh.2005.04.007 (Accessed 29.01.2020).

Pagliaccio D, Pine DS, Leibenluft E, Dal Monte O, Averbeck BB, Costa VD. 2019. Cross-species convergence in pupillary response: understanding human anxiety via non-human primate amygdala lesion. Social Cognitive and Affective Neuroscience, 14(6):591–599. DOI 10.1093/scan/nsz041 (Accessed 06.11.2019).

Palagi E, Cordoni G. 2009. Postconflict third-party affiliation in Canis lupus: do wolves share similarities with the great apes? Animal Behaviour, 78(4):979–986. DOI 10.1016/j.anbehav.2009.07.017 (Accessed 19.05.2020).

Palagi E, Dall'Olio S, Demuru E, Stanyon R. 2014. Exploring the evolutionary foundations of empathy: consolation in monkeys. Evolution and Human Behavior, 35(4):341–349. DOI 10.1016/j.evolhumbehav.2014.04.002 (Accessed 11.02.2020).

Palmer C. 2011. Animal disenhancement and the non-identity problem: a response to Thompson. NanoEthics, 5(1):43–48. DOI 10.1007/s11569-011-0115-1 (Accessed 27.03.2019).

Parfit D. 2011. On what matters. Oxford: Oxford University Press.

Parrott WG. 2019. Emotions as signals of moral character. In: Hess U, Hareli S, eds. The social nature of emotion expression: what emotions can tell us about the world. Cham: Springer International Publishing, 161–177.

Parsana AJ, Moran EE, Brown TH. 2012. Rats learn to freeze to 22-kHz ultrasonic vocalizations through autoconditioning. Behavioural Brain Research, 232(2):395–399. DOI 10.1016/j.bbr.2012.03.031 (Accessed 25.03.2020).

Pelloux Y, Murray JE, Everitt BJ. 2013. Differential roles of the prefrontal cortical subregions and basolateral amygdala in compulsive cocaine seeking and relapse after voluntary abstinence in rats. European Journal of Neuroscience, 38(7):3018–3026. DOI 10.1111/ejn.12289 (Accessed 04.11.2019).

Pereira AG, Cruz A, Lima SQ, Moita MA. 2012. Silence resulting from the cessation of movement signals danger. Current Biology, 22(16):R627–R628. DOI 10.1016/j.cub.2012.06.015 (Accessed 25.03.2020).

Plotnik JM, de Waal FBM. 2014. Asian elephants (Elephas maximus) reassure others in distress. PeerJ, 2:e278. DOI 10.7717/peerj.278 (Accessed 19.05.2020).

Popik P, Potasiewicz A, Pluta H, Zieniewicz A. 2012. High-frequency ultrasonic vocalizations in rats in response to tickling: The effects of restraint stress. Behavioural Brain Research, 234(2):223–227. DOI 10.1016/j.bbr.2012.06.028 (Accessed 25.03.2020).

Preston SD, de Waal FBM. 2002. Empathy: Its ultimate and proximate bases. Behavioral and Brain Sciences, 25(1):1–20. DOI 10.1017/S0140525X02000018 (Accessed 25.10.2019).

Range F, Horn L, Viranyi Z, Huber L. 2009. The absence of reward induces inequity aversion in dogs. Proceedings of the National Academy of Sciences, 106(1):340–345. DOI 10.1073/pnas.0810957105 (Accessed 19.05.2020).

Ranjbar H, Radahmadi M, Alaei H, Reisi P, Karimi S. 2016. The effect of basolateral amygdala nucleus lesion on memory under acute,mid and chronic stress in male rats. Turkish journal of medical sciences, 46:1915–1925. DOI 10.3906/sag-1507-7 (Accessed 04.11.2019).

Ranjbar H, Radahmadi M, Reisi P, Alaei H. 2017. Effects of electrical lesion of basolateral amygdala nucleus on rat anxiety-like behaviour under acute, sub-chronic, and chronic stresses. Clinical and Experimental Pharmacology and Physiology, 44(4):470–479. DOI 10.1111/1440-1681.12727 (Accessed 04.11.2019).

Raus K, Focquaert F, Schermer M, Specker J, Sterckx S. 2014. On defining moral enhancement: a clarificatory taxonomy. Neuroethics, 7(3):263–273. DOI 10.1007/s12152-014-9205-4 (Accessed 29.05.2019).

Rhodes SEV, Murray EA. 2013. Differential effects of amygdala, orbital prefrontal cortex, and prelimbic cortex lesions on goal-directed behavior in rhesus macaques. Journal of Neuroscience, 33(8):3380–3389. DOI 10.1523/JNEUROSCI.4374-12.2013 (Accessed 19.02.2020).

Rice GE, Gainer P. 1962. “Altruism” in the albino rat. Journal of Comparative and Physiological Psychology, 55(1):123–125. DOI https://doi.org/10.1037/h0042276 (Accessed 14.11.2019).

Röcklinsberg H, Gamborg C, Gjerris M. 2014. A case for integrity: gains from including more than animal welfare in animal ethics committee deliberations. Laboratory Animals, 48(1):61–71. DOI 10.1177/0023677213514220 (Accessed 26.03.2019).

Rollin BE. 2006. The regulation of animal research and the emergence of animal ethics: a conceptual history. Theoretical Medicine and Bioethics, 27(4):285–304. DOI 10.1007/s11017-006-9007-8 (Accessed 22.04.2020).

Rommeck I, Anderson K, Heagerty A, Cameron A, McCowan B. 2009a. Risk factors and remediation of self-injurious and self-abuse behavior in rhesus macaques. Journal of Applied Animal Welfare Science, 12(1):61–72. DOI 10.1080/10888700802536798 (Accessed 14.02.2020).

Rommeck I, Gottlieb DH, Strand SC, McCowan B. 2009b. The effects of four nursery rearing strategies on infant behavioral development in rhesus macaques (Macaca mulatta). Journal of the American Association for Laboratory Animal Science, 48(4):395–401. https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2715931/. (Accessed 14.02.2020).

Rommeck I, Capitanio JP, Strand SC, McCowan B. 2011. Early social experience affects behavioral and physiological responsiveness to stressful conditions in infant rhesus macaques (Macaca mulatta). American Journal of Primatology, 73(7):692–701. DOI 10.1002/ajp.20953 (Accessed 14.02.2020).

Roth BA, Barth K, Gygax L, Hillmann E. 2009. Influence of artificial vs. mother-bonded rearing on sucking behaviour, health and weight gain in calves. Applied Animal Behaviour Science, 119(3):143–150. DOI 10.1016/j.applanim.2009.03.004 (Accessed 30.06.2020).

Rowlands M. 2012. Can animals be moral? New York: Oxford University Press.

Rudebeck PH, Mitz AR, Chacko RV, Murray EA. 2013. Effects of amygdala lesions on reward-value coding in orbital and medial prefrontal cortex. Neuron, 80(6):1519–1531. DOI 10.1016/j.neuron.2013.09.036 (Accessed 06.11.2019).

Sackett GP. 1965. Effects of rearing conditions upon the behavior of rhesus monkeys (Macaca mulatta). Child Development, 36(4):855–868. DOI 10.2307/1126929 (Accessed 04.07.2019).

Sanders J, Mayford M, Jeste D. 2013. Empathic fear responses in mice are triggered by recognition of a shared experience. PLOS ONE, 8(9):e74609. DOI 10.1371/journal.pone.0074609 (Accessed 25.03.2020).

Sandøe P, Nielsen BL, Christensen LG, Sorensen P. 1999. Staying good while playing god--the ethics of breeding farm animals. Animal Welfare (South Mimms, England), 8(4):313–328. https://www.researchgate.net/publication/11431664_Staying_good_while_playing_God_-_The_ethics_of_breeding_farm_animals. (Accessed 20.08.2020).

Sato N, Tan L, Tate K, Okada M. 2015. Rats demonstrate helping behavior toward a soaked conspecific. Animal Cognition, 18(5):1039–1047. DOI 10.1007/s10071-015-0872-2 (Accessed 08.11.2019).

Schaffner J. 2011. An introduction to animals and the law. Basingstoke: Palgrave Macmillan.

Schmelz M, Grueneisen S, Kabalak A, Jost J, Tomasello M. 2017. Chimpanzees return favors at a personal cost. Proceedings of the National Academy of Sciences, 114(28):7462–7467. DOI 10.1073/pnas.1700351114 (Accessed 11.02.2020).

Schönfeld L-M, Zech M-P, Schäble S, Wöhr M, Kalenscher T. 2019. Lesions of the rat basolateral amygdala reduce the behavioral response to ultrasonic vocalizations. Behavioural Brain Research, 112274. DOI 10.1016/j.bbr.2019.112274 (Accessed 04.11.2019).

Seay B, Alexander BK, Harlow HF. 1964. Maternal behavior of socially deprived rhesus monkeys. The Journal of Abnormal and Social Psychology, 69(4):345–354. DOI 10.1037/h0040539 (Accessed 04.07.2019).

Seed AM, Clayton NS, Emery NJ. 2007. Postconflict third-party affiliation in rooks, Corvus frugilegus. Current Biology, 17(2):152–158. DOI 10.1016/j.cub.2006.11.025 (Accessed 19.05.2020).

Segura-Torres P, Aldavert-Vera L, Gatell-Segura A, Redolar-Ripoll D, Morgado-Bernal I. 2010. Intracranial self-stimulation recovers learning and memory capacity in basolateral amygdala-damaged rats. Neurobiology of Learning and Memory, 93(1):117–126. DOI 10.1016/j.nlm.2009.09.001 (Accessed 04.11.2019).

Shriver A, McConnachie E. 2018. Genetically modifying livestock for improved welfare: a path forward. Journal of Agricultural and Environmental Ethics, 31(2):161–180. DOI 10.1007/s10806-018-9719-6 (Accessed 27.03.2019).

Silberberg A, Allouch C, Sandfort S, Kearns D, Karpel H, Slotnick B. 2014. Desire for social contact, not empathy, may explain "rescue" behavior in rats. Animal Cognition, 17(3):609–618. DOI 10.1007/s10071-013-0692-1 (Accessed 11.11.2019).

Smith AL, Corrow DJ. 2005. Modifications to husbandry and housing conditions of laboratory rodents for improved well-being. ILAR Journal, 46(2):140–147. DOI 10.1093/ilar.46.2.140 (Accessed 24.09.2020).

Smith ML, Hostetler CM, Heinricher MM, Ryabinin AE. 2016. Social transfer of pain in mice. Science Advances, 2(10):e1600855. DOI 10.1126/sciadv.1600855 (Accessed 15.11.2019).

Solnick JV, Canfield DR, Yang S, Parsonnet J. 1999. Rhesus monkey (Macaca mulatta) model of Helicobacter pylori: noninvasive detection and derivation of specific-pathogen-free monkeys. Laboratory Animal Science, 49(2):197–201. https://www.ingentaconnect.com/content/aalas/cm/1999/00000049/00000002/art00012#. (Accessed 14.02.2020).

Speaking of Research. 2020. US statistics. https://speakingofresearch.com/facts/statistics/. (Accessed 17.02.2020).

Sugiyama Y, Kurita H, Matsui T, Kimoto S, Shimomura T. 2009. Carrying of dead infants by Japanese macaque (*Macaca fuscata*) mothers. Anthropological Science, 117(2):113–119. DOI 10.1537/ase.080919.

Takahashi A, Kwa C, DeBold JF, Miczek KA. 2010. GABAA receptors in the dorsal raphé nucleus of mice: escalation of aggression after alcohol consumption. Psychopharmacology, 211(4):467–477. DOI 10.1007/s00213-010-1920-x (Accessed 22.08.2019).

Takahashi LK, Grossfeld S, Lore RK. 1980. Attack and escape in the laboratory rat: a modification of the colony-intruder procedure. Behavioral and Neural Biology, 29(4):512–517. DOI 10.1016/S0163-1047(80)92806-X (Accessed 27.01.2020).

Tavares TF, Judice-Daher DM, Bueno JLO. 2014. Large neurotoxic amygdala lesion impairs reinforcement omission effects. Behavioural Brain Research, 266:1–6. DOI 10.1016/j.bbr.2014.02.026 (Accessed 04.11.2019).

Taylor CJ. 1975. Study of altruism in rats in an appetitive situation. Psychological Reports, 36(2):571–574. DOI 10.2466/pr0.1975.36.2.571 (Accessed 26.03.2020).

Taylor GT, Weiss J. 1982. Presence of intact and gonadectomized juveniles and the reduction of fighting between adult male rats. Physiology & Behavior, 29(6):1019–1023. DOI 10.1016/0031-9384(82)90293-1 (Accessed 21.01.2020).

The Jackson Laboratory. 2020a. Strain 000385. https://www.jax.org/strain/000385. (Accessed 11.08.2020).

The Jackson Laboratory. 2020b. Strain 000635. https://www.jax.org/strain/000635. (Accessed 11.08.2020).

The Jackson Laboratory. 2020c. Strain 000656. https://www.jax.org/strain/000656. (Accessed 11.08.2020).

The Jackson Laboratory. 2020d. Strain 000659. https://www.jax.org/strain/000659. (Accessed 11.08.2020).

The Jackson Laboratory. 2020e. Strain 002130. https://www.jax.org/strain/002130. (Accessed 11.08.2020).

The Jackson Laboratory. 2020f. Strain 001276. https://www.jax.org/strain/001276. (Accessed 11.08.2020).

The Jackson Laboratory. 2020g. Strain 002894. https://www.jax.org/strain/002894. (Accessed 11.08.2020).

The Jackson Laboratory. 2020h. Strain 004768. https://www.jax.org/strain/004768. (Accessed 11.08.2020).

The Jackson Laboratory. 2020i. Strain 004771. https://www.jax.org/strain/004771. (Accessed 11.08.2020).

The Jackson Laboratory. 2020j. Strain 006274. https://www.jax.org/strain/006274. (Accessed 11.08.2020).

Thor DH. 1979. Threat and attack in the alpha male rat. Bulletin of the Psychonomic Society, 14(3):146–148. DOI 10.3758/BF03329428 (Accessed 21.01.2020).

Thor DH, Flannelly KJ. 1976. Age of intruder and territorial-elicited aggression in male Long—Evans rats. Behavioral Biology, 17(2):237–241. DOI 10.1016/S0091-6773(76)90546-0 (Accessed 21.01.2020).

Tóth M, Mikics É, Tulogdi Á, Aliczki M, Haller J. 2011. Post-weaning social isolation induces abnormal forms of aggression in conjunction with increased glucocorticoid and autonomic stress responses. Hormones and Behavior, 60(1):28–36. DOI 10.1016/j.yhbeh.2011.02.003 (Accessed 04.10.2019).

Tóth M, Tulogdi Á, Biró L, Soros P, Mikics É, Haller J. 2012. The neural background of hyper-emotional aggression induced by post-weaning social isolation. Behavioural Brain Research, 233(1):120–129. DOI 10.1016/j.bbr.2012.04.025 (Accessed 04.10.2019).

Tulogdi Á, Tóth M, Halasz J, Mikics É, Fuzesi T, Haller J. 2010. Brain mechanisms involved in predatory aggression are activated in a laboratory model of violent intra-specific aggression. European Journal of Neuroscience, 32(10):1744–1753. DOI 10.1111/j.1460-9568.2010.07429.x (Accessed 23.08.2019).

Tulogdi Á, Tóth M, Barsvári B, Biró L, Mikics É, Haller J. 2014. Effects of resocialization on post-weaning social isolation-induced abnormal aggression and social deficits in rats. Developmental Psychobiology, 56(1):49–57. DOI 10.1002/dev.21090 (Accessed 11.07.2019).

Tzeng W-Y, Cherng C-FG, Yu L, Wang C-Y. 2017. Basolateral amygdalar D2 receptor activation is required for the companions-exerted suppressive effect on the cocaine conditioning. Neurobiology of Learning and Memory, 137:48–55. DOI 10.1016/j.nlm.2016.11.007 (Accessed 05.11.2019).

Ueno H, Suemitsu S, Murakami S, Kitamura N, Wani K, Matsumoto Y, Okamoto M, Ishihara T. 2019a. Helping-like behaviour in mice towards conspecifics constrained inside tubes. Scientific reports, 9(1):5817. DOI 10.1038/s41598-019-42290-y (Accessed 11.11.2019).

Ueno H, Suemitsu S, Murakami S, Kitamura N, Wani K, Takahashi Y, Matsumoto Y, Okamoto M, Ishihara T. 2019b. Rescue-like behaviour in mice is mediated by their interest in the restraint tool. Scientific Reports, 9(1):10648. DOI 10.1038/s41598-019-46128-5 (Accessed 22.06.2020).

United States Department of Agriculture. 2018. Annual report animal usage by fiscal year. https://www.aphis.usda.gov/animal_welfare/downloads/reports/Annual-Report-Animal-Usage-by-FY2017.pdf. (Accessed 10.02.2020).

Vandeleest JJ, McCowan B, Capitanio JP. 2011. Early rearing interacts with temperament and housing to influence the risk for motor stereotypy in rhesus monkeys (Macaca mulatta). Applied Animal Behaviour Science, 132(1):81–89. DOI 10.1016/j.applanim.2011.02.010 (Accessed 14.02.2020).

de Vignemont F, Singer T. 2006. The empathic brain: how, when and why? Trends in Cognitive Sciences, 10(10):435–441. DOI 10.1016/j.tics.2006.08.008 (Accessed 25.10.2019).

Vorstenbosch J. 1993. The concept of integrity. Its significance for the ethical discussion on biotechnology and animals. Livestock Production Science, 36(1):109–112. DOI 10.1016/0301-6226(93)90144-7 (Accessed 27.03.2019).

de Waal FBM. 2008. Putting the altruism back into altruism: the evolution of empathy. Annual Review of Psychology, 59(1):279–300. DOI 10.1146/annurev.psych.59.103006.093625 (Accessed 15.11.2019).

de Waal FBM. 2009. Primates and philosophers, how morality evolved. (S Macedo and J Ober, Eds). Princeton: Princeton University Press.

de Waal FBM, Roosmalen A van. 1979. Reconciliation and consolation among chimpanzees. Behavioral Ecology and Sociobiology, 5(1):55–66. https://www.jstor.org/stable/4599217. (Accessed 11.02.2020).

Wagner K, Barth K, Hillmann E, Palme R, Futschik A, Waiblinger S. 2013. Mother rearing of dairy calves: Reactions to isolation and to confrontation with an unfamiliar conspecific in a new environment. Applied Animal Behaviour Science, 147(1):43–54. DOI 10.1016/j.applanim.2013.04.010 (Accessed 30.06.2020).

Walker SE, Wood TC, Cash D, Mesquita M, Williams SCR, Sandi C. 2018. Alterations in brain microstructure in rats that develop abnormal aggression following peripubertal stress. European Journal of Neuroscience, 48(2):1818–1832. DOI 10.1111/ejn.14061 (Accessed 23.08.2019).

Warneken F, Tomasello M. 2006. Altruistic helping in human infants and young chimpanzees. Science, 311(5765):1301–1303. DOI 10.1126/science.1121448 (Accessed 11.02.2020).

Warneken F, Hare B, Melis AP, Hanus D, Tomasello M. 2007. Spontaneous altruism by chimpanzees and young children. PLoS biology, 5(7):e184. DOI 10.1371/journal.pbio.0050184 (Accessed 11.02.2020).

Warren Y, Williamson EA. 2004. Transport of dead infant mountain gorillas by mothers and unrelated females. Zoo Biology, 23(4):375–378. DOI 10.1002/zoo.20001 (Accessed 11.02.2020).

Watanabe S, Ono K. 1986. An experimental analysis of “empathic” response: Effects of pain reactions of pigeon upon other pigeon’s operant behavior. Behavioural Processes, 13(3):269–277. DOI 10.1016/0376-6357(86)90089-6 (Accessed 19.05.2020).

Weary DM, Chua B. 2000. Effects of early separation on the dairy cow and calf: 1. Separation at 6 h, 1 day and 4 days after birth. Applied Animal Behaviour Science, 69(3):177–188. DOI 10.1016/S0168-1591(00)00128-3 (Accessed 30.06.2020).

Wechkin S, Masserman JH, Terris W. 1964. Shock to a conspecific as an aversive stimulus. Psychonomic Science, 1(1):47–48. DOI 10.3758/BF03342783 (Accessed 19.11.2019).

West EA, Forcelli PA, Murnen AT, McCue DL, Gale K, Malkova L. 2012. Transient inactivation of basolateral amygdala during selective satiation disrupts reinforcer devaluation in rats. Behavioral Neuroscience, 126(4):563–574. DOI 10.1037/a0029080 (Accessed 04.11.2019).

Willuhn I, Tose A, Wanat MJ, Hart AS, Hollon NG, Phillips PEM, Schwarting RKW, Wöhr M. 2014. Phasic dopamine release in the nucleus accumbens in response to pro-social 50 kHz ultrasonic vocalizations in rats. Journal of Neuroscience, 34(32):10616–10623. DOI 10.1523/JNEUROSCI.1060-14.2014 (Accessed 25.03.2020).

Xie L, Zhou Q, Liu S, Xu F, Shively CA, Wu Q, Gong W, Ji Y, Fang L, Li L, et al. 2014. Effect of living conditions on biochemical and hematological parameters of the cynomolgus monkey. American Journal of Primatology, 76(11):1011–1024. DOI 10.1002/ajp.22285 (Accessed 14.02.2020).

Yang B, Anderson JR, Li B-G. 2016. Tending a dying adult in a wild multi-level primate society. Current Biology, 26(10):R403–R404. DOI 10.1016/j.cub.2016.03.062 (Accessed 11.02.2020).

Zeeb FD, Winstanley CA. 2011. Lesions of the basolateral amygdala and orbitofrontal cortex differentially affect acquisition and performance of a rodent gambling task. Journal of Neuroscience, 31(6):2197–2204. DOI 10.1523/JNEUROSCI.5597-10.2011 (Accessed 06.11.2019).

Zimbardo P. 2007. The Lucifer effect: Understanding how good people turn evil. New York: Random House.

Zimmerman JM, Maren S. 2011. The bed nucleus of the stria terminalis is required for the expression of contextual but not auditory freezing in rats with basolateral amygdala lesions. Neurobiology of Learning and Memory, 95(2):199–205. DOI 10.1016/j.nlm.2010.11.002 (Accessed 04.11.2019).

10. List of abbreviations

BLA:	basolateral amygdala
MME:	Minimal moral empathy
NHP:	Non-human primate

11. Zusammenfassung[19]

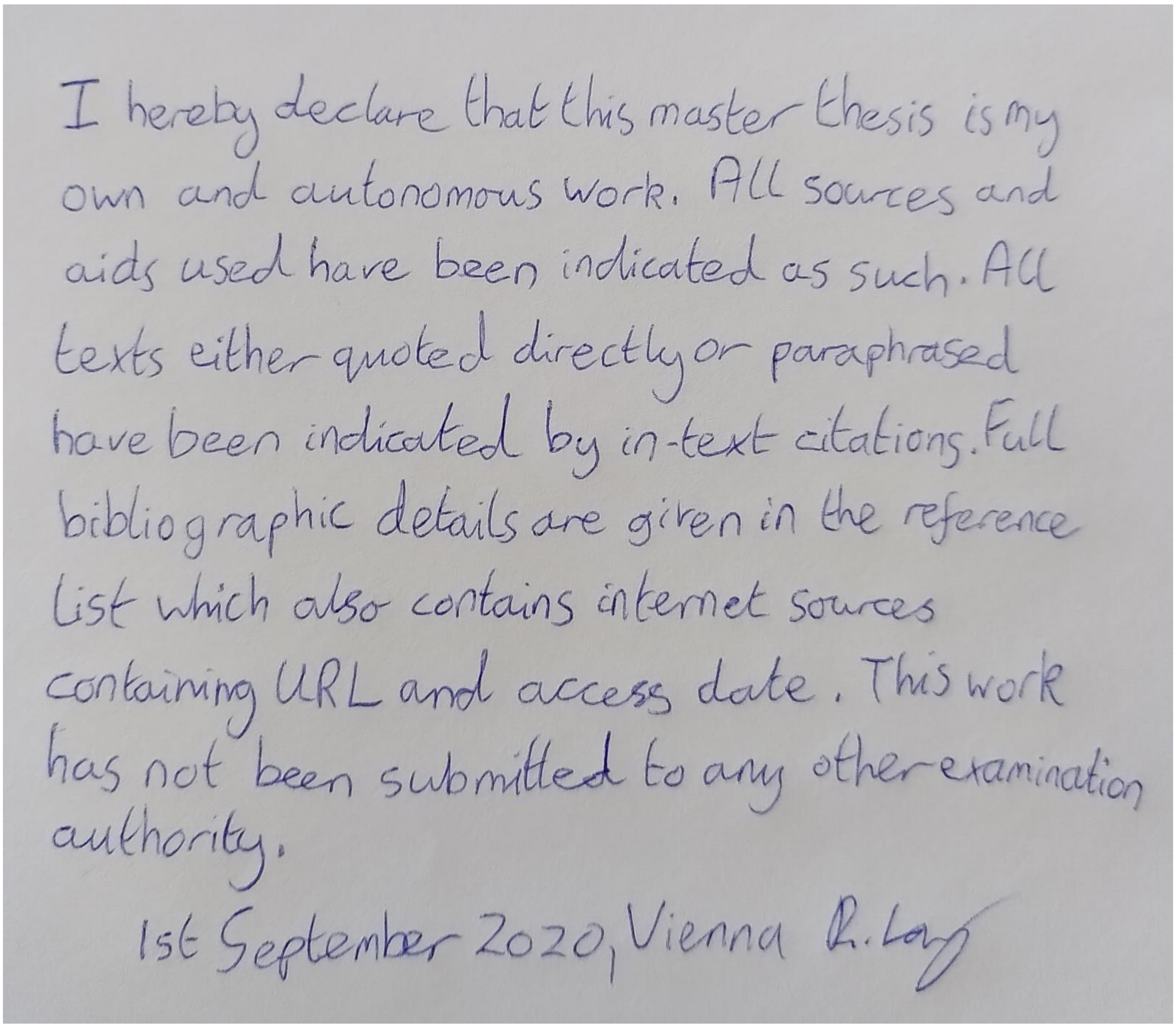
In den letzten Jahren haben Philosophen dahingehend argumentiert, dass auch nichtmenschliche Tiere moralische Subjekte sind, also Individuen, die auf der Basis moralischer Emotionen handeln können. Dies würde bedeuten, dass sie auch in ihrem moralischen Verhalten oder ihrer Moralfähigkeit eingeschränkt oder verletzt werden können, was eine problematische und neuartige Form der Schadenszufügung gegenüber Tieren darstellen würde. Ob zum Beispiel Millionen Versuchstiere, die weltweit für die Forschung verwendet werden, hiervon betroffen sind, wurde bisher nicht beachtet und ist eine weitestgehend offene Frage. Diese Masterarbeit untersucht, ob das moralische Leben mancher Tiere durch ihre Verwendung in der modernen wissenschaftlichen Forschung negativ beeinträchtigt wird. Der Begriff *„moral thwarting“* wird eingeführt, um mögliche Schädigungen dieser Art zu beschreiben, die dann über eine Analyse der verschiedenen konzeptuellen Formen, die sie annehmen können, inhaltlich bestimmt werden. Die theoretischen Annahmen werden auf zwei Typen von Versuchen mit Ratten und Mäusen angewendet und an diesen erprobt: Versuche zur Manipulation von Empathie und von Aggression. Empirische Evidenz zur Moralfähigkeit von Ratten und Mäusen wird präsentiert und diskutiert und es wird dahingehend argumentiert, dass die Versuche die Moralfähigkeit bzw. das moralische Verhalten der Tiere beeinträchtigen. Die Praktiken und Bedingungen, die zu *moral thwarting* führen, werden identifiziert und einige zentrale Charakteristika einer solchen Beeinträchtigung werden benannt. In einem zweiten Schritt wird dargestellt, inwiefern dieselben Praktiken und Bedingungen nicht nur in den Versuchen selbst, sondern auch in der an die Forschung angeschlossenen Zucht und Haltung der Tiere vorherrschen. Die Argumentation wird also auf diese Bereiche übertragen. Schließlich wird die Übertragbarkeit der Argumentation auf andere Tierarten erprobt und am Beispiel von nichtmenschlichen Primaten aufgezeigt, inwiefern die Argumentation dabei helfen kann, andere mögliche Fälle von *moral thwarting* in der Forschung sichtbar zu machen. Abschließend werden mögliche Forschungsfragen für die Zukunft vorgeschlagen und die Relevanz der Ergebnisse in den Blick genommen. Zusammenfassend zeigt diese Masterarbeit, dass— trotz noch ausstehender eindeutiger Evidenz hierfür— gute Gründe dafür bestehen, anzunehmen, dass manche Tiere

---

[19] Translated with the assistance of Univ.-Ass. Dr. Judith Benz-Schwarzburg.

durch ihre Verwendung als Versuchstiere in ihrem moralischen Verhalten oder in ihrer Moralfähigkeit, und damit *als moralische Subjekte,* geschädigt werden.

12. Declaration of autonomous work



I hereby declare that this master thesis is my own and autonomous work. All sources and aids used have been indicated as such. All texts either quoted directly or paraphrased have been indicated by in-text citations. Full bibliographic details are given in the reference list which also contains internet sources containing URL and access date. This work has not been submitted to any other examination authority.

1st September 2020, Vienna R. Lay