Investigating social behaviour in animals: The curious case of the prosocial and empathic rat

Magnus H. Blystad

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The curious case of the prosocial and empathic rat

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"No man is an island" – Jon Donne

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Abstract

Animal models of behaviour have been used since ancient Greece, both to study anatomy and behaviour. Social behaviour has also been modelled in non-human animals, and these models are especially important for the field of social neuroscience, which attempts to understand the neural mechanisms of social behaviour. One such animal model is the social release paradigm, which claimed to demonstrate empathy in rats via observations of prosocial behaviour. In this paradigm, a rat is trapped inside a plastic tube and another rat can release the trapped conspecific. Empathic distress in the free rat is suggested to be the reason why opening behaviour occurs. However, this claim of empathy in rats has been contested as findings point to social reinforcement being the most important factor for social release. Additionally, the interpretation in terms of empathy rests on a challenged premise that entrapment causes distress in the trapped rat. If entrapment is not distressing, then release from entrapment cannot be categorised as empathic or prosocial.

The thesis points out the lack of a behaviourally focused definition of empathy fitting for animal studies. This is addressed by a novel conceptualization of empathy based on basic principles of behaviour analysis. A systematization of previous research using the three-term contingency, also borrowed from the field of behaviour analysis, illustrates that little is known regarding antecedent stimuli in the social release paradigm. Until the discriminative stimuli for opening is thoroughly studied and analysed, it seems premature to conclude that empathic motivation underlies social release. The current work also demonstrates how increased experimental control allows for better understanding of what controls behaviour in the social release paradigm. Improvements to the experimental design are demonstrated in the first experimental study, and these address the lack of both baseline and training in the original social release study. Current findings show that latency to open the restrainer is lower for food than for a cagemate in food deprived rats. Additionally, the premise of aversiveness due to entrapment, fundamental to the suggested empathic motivation, is tested in a second experimental paper; results of both exploration and vocalizations indicate that entrapment is not aversive.

The main contribution of the present work, in addition to the empirical findings, is the novel conceptualization and definition of empathy usable for animal studies, and the suggestion of how to systematize and integrate previous findings to identify new areas for future research. In total, the most important takeaway message from this thesis is that an approach that focuses on what can be observed, rather than inferred, is a necessity in studies of social animal behaviour.

Keywords: *animal modelling, prosocial, empathy, rat, social behaviour*

Sammendrag

Dyremodeller for atferd har blitt brukt siden de gamle grekernes, både for å studere anatomi og atferd. Sosial atferd har også blitt modellert hos ikke-menneskelige dyr, og disse modellene er spesielt viktige for forskningsfeltet kalt sosial nevrovitenskap. Dette er et underfelt av nevrovitenskap som forsker på de nevrale mekanismene til sosial atferd. En dyremodell på sosial atferd er det sosiale frigjøringsparadigmet, som hevdet å demonstrere empati hos rotter via observasjoner av prososial atferd. I dette paradigmet er en rotte fanget inne i et plastrør, og en annen rotte kan frigjøre den fangede artsfrenden. Stress skapt av empati med den fangede rotta hevdes å oppstå i den frie rotta, og dette empati-stresset antydes å være grunnen til at åpningsatferd oppstår. Imidlertid har denne påstanden om empati hos rotter blitt bestridt. Andre funn peker på at sosial forsterkning er den viktigste faktoren for at den frie rotta skal slippe fri den fangede. I tillegg hviler empatiforklaringen på en forutsetning om at fangenskap forårsaker stress hos den fangede rotten. Nye funn indikerer at fangenskap kanskje ikke er stressende for rottene. Hvis fangenskap ikke er skaper stress, kan ikke det å slippe fri en fanget rotte kategoriseres som empatisk eller prososialt.

Denne avhandlingen peker på mangelen på en atferdsmessig fokusert definisjon av empati som passer for dyrestudier. Dette adresseres med en ny konseptualisering av empati basert på grunnleggende prinsipper fra atferdsanalyse. En systematisering av tidligere forskning ved bruk av tre-terms-kontingensen, også lånt fra feltet atferdsanalyse, illustrerer at det er lite kunnskap om stimuli i det sosiale frigjøringsparadigmet. Inntil det er kartlagt hvordan forskjellige stimuli i den eksperimentelle situasjonen påvirker åpning, synes det for tidlig å konkludere med at empatisk motivasjon ligger til grunn for sosial frigjøring. Avhandlingen demonstrerer også hvordan økt eksperimentell kontroll gir bedre forståelse av hva som styrer atferd i det sosiale frigjøringsparadigmet. Forbedringer av eksperimentell apparatur er demonstrert i den første eksperimentelle studien, og denne studien adresserer mangelen på både baseline og trening i den opprinnelige sosiale frigjøringsstudien. Den studien viser også at latenstiden for å åpne er lavere for mat enn for en rotte i mat-depriverte rotter. I tillegg blir forutsetningen om aversjon på grunn av fangenskap, som er et premiss for den foreslåtte empatiske motivasjonen, testet i et annet eksperiment. Der indikerer resultater fra både utforskning og vokaliseringer at fangenskap i sosial frigjørings paradigmet ikke er aversiv.

I tillegg til de empiriske funnene er bidraget til denne avhandlingen den nye konseptualiseringen og definisjonen av empati som kan brukes til dyreforsøk, og forslaget om hvordan man systematiserer og integrerer tidligere funn for å identifisere nye områder for fremtidig forskning. Til sist er den viktigste beskjeden i denne avhandlingen at det i studier av sosial atferd hos dyr er nødvendig med en tilnærming som vektlegger det som kan observeres snarere enn teoretiske antagelser.

Nøkkelord: *dyremodeller, Prososial, empati, rotte, sosial atferd*

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Mexican Journal of Behavior Analysis, 45(2), 199–222. doi: 10.5514/rmac.v45.i2.75563

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PLOS ONE, 14(10): e0223039. doi: 10.1371/journal.pone.0223039

Study 3: Empathy or not empathy, that's the question - a pragmatic behavior analytical approach

Blystad, M. H. & Hansen, S.

Submitted, 2020. *Behavior Analysis Research and Practice*

Study 4: The social release paradigm: Investigating restrainer aversion by restrainer entries and positive ultrasonic vocalizations

Blystad, M. H., Asare, P., Andersen, D., & Johansen, E. B.

Submitted, 2020. *Journal of Comparative Psychology*

Overview of abbreviations used in the thesis

Abbreviations listed below are also described in the text(s).

L-D	Experimental condition with change in illumination from light to dark.
D-L	Experimental condition with change in illumination from dark to light.
CM1/CM2	Cagemate condition 1 and 2.
USV	Ultrasonic vocalizations.
FELASA	Federation of European Laboratory Animal Science Associations
ASD	Autism Spectrum Disorders
fMRI	Functional magnetic resonance imaging
ToM	Theory of Mind
EO	Establishing operation
SE	Setting events
RFT	Relational frame theory
US/CS/NS	Unconditioned, conditioned, and neutral stimuli
UR/CR	Unconditioned and conditioned response
SDB	Social desirability bias
SD	Discriminative stimulus
TAT	Thematic apperception test
EQ	Empathy quotient

PAM	Perception action model

Introduction

‘Empathy, along with cooperation and pair-bonding, exemplify the typical topics of social neuroscience.’ (Bartal & Mason, 2018, p. 159)

‘If we fail to understand the **behavior**, we will probably also fail to understand how the **brain** serves it.’ (Catania, 2000, p.1, author’s emphasis)

Biology teaches that organisms are products of evolution in terms of natural selection. Traits in a species are selected and survive across generations only if the individuals who carry those traits reproduce at a higher rate than other members of the species (Darwin, 1859). This idea of selection has since been introduced to psychology, particularly by Skinner, who proposed and proved that selection by consequences governs human behaviour (Skinner, 1981). However, Skinner also points out that not only is human behaviour caused by evolutionary and behavioural selection; there is also the matter of changes in social environment (Skinner, 1981). The social environment creates social behaviour wherein stimuli from other members of the same species occasion behaviour (Skinner, 1953). A subset of social behaviours concerns empathy and prosociality, and these two terms are at the heart of the current thesis. Empathy, and to some extent prosociality, are also key terms for the research field known as social neuroscience (Bartal & Mason, 2018; Cacioppo & Berntson, 1992; Matusall et al., 2011) from which the experimental animal model in this thesis originates. However, for research on social behaviour, perhaps especially on empathy and prosocial behaviour, there are both conceptual and experimental hurdles. The current thesis therefore concerns both how to define and use empathy and prosociality in animal research, and how best to model social behaviour in non-human animals. Thus, the thesis attempts to answer the call for better animal models in social neuroscience (Keysers & Gazzola, 2016, 2018) and the need for better measurement of behaviour in neuroscience in general (Krakauer et al., 2017).

Empathy and prosociality I: Why study empathy and prosociality?

Research is focused not only on understanding, but also on bettering both society and individual lives. Empathy and prosociality research are no exception, and a few examples can illustrate this. A first example is how empathy is known to be relevant for schizophrenia (Montag et al., 2007; Shamay-Tsoory et al., 2007). The relationship between empathy and schizophrenia may be connected to poor insight, which sufferers of schizophrenia tend to have (Bell et al., 2007). It is suggested that schizophrenia-related empathy problems are caused by dysfunctional neural circuits thought to exist in empathy networks of schizophrenic brains (Bora et al., 2008). Furthermore, schizophrenic patients have problems with social behaviour, prosocial behaviour included, due perhaps to their dysfunctional cognition (Dodell-feder et al., 2016). Another example is in autism spectrum disorders (ASD), where theory of mind (ToM) is proposed to be missing or dysfunctional, and since ToM is necessary for empathy, empathy is also dysfunctional (Baron-Cohen et al., 1985; Baron-Cohen & Wheelwright, 2004; Montgomery et al., 2016; A. Smith, 2009). Many patients with ASD also lack prosocial behaviour (Oerlemans et al., 2018). ASD is estimated to cost society between USD 1.4–2.4 million per individual across their lifespan (Buescher et al., 2014), while the economic cost of schizophrenia ranges from USD 94 million to USD 102 billion (Chong et al., 2016). Research into amelioration of these disorders certainly seems warranted. It should also be noted that schizophrenia and ASD are just two of many clinical conditions (e.g. psychopathy, anxiety, bipolar disorder) where empathy is affected (Rum & Perry, 2020).

Additionally, in a non-clinical setting it seems logical that a lack of understanding of the emotions of others, i.e. poor empathic ability, could influence many day-to-day social situations. Research supports this, with empathy emerging as a relevant factor in bullying behaviour (Gini et al., 2007; Stavrinides et al., 2010; van Noorden et al., 2014). Bullying is a terrible experience for the victim, and the economic cost to society is astronomical; a survey report from Australia found that the national cost of school bullying could reach AUD 2.3 billion while the children were in school and 20 years after (Alannah and the Madeline Foundation & Pwc, 2018).

Finally, the general role empathy serves in understanding the needs of others must not be underestimated, regardless of whether they are refugees seeking asylum, people living in poverty, or sufferers of addiction or other disorders, even if the other is our neighbour or someone we consider our peer. Empathy is part of what allows us to recognize pain, and can motivate us to help in the real world (Bethlehem et al., 2017). Indeed, empathy may be closely related to helping others or to other kinds of altruistic and prosocial behaviours (Decety et al., 2016; McMahon et al., 2006; Williams et al., 2014).

Empathy and prosociality II: What is empathy and prosociality?

Empathy and prosociality are somewhat related. A laymen's version defines empathy as the ability to understand the feelings, actions and mental state of others (Encyclopaedia Britannica, 2016). One early example of similar usage of this layman's term of empathy in published research is found in Humphrey (1922):

> 'If some one else holds his hand in the flame, I do not experience the sensation of pain, but I do have the feeling of unpleasantness, because the sight of my hand in the fire has in the past been accompanied by feelings of unpleasantness.' (Humphrey, 1922, p. 116)

In his paper, entitled 'The conditioned reflex and elementary social reaction', Humphrey gives a theoretical account of the emergence of sympathetic reactions in humans. As illustrated in the quote above and the title of the paper, the theories in that paper are based on Pavlovian principles of conditioning (Humphrey, 1922). In fact, the author describes it as 'sympathy' in the paper (Humphrey, 1922) but the description in the text is closer to what modern literature defines as empathy rather than sympathy, as a distinction between the two terms mainly relies on sympathy also including care (Decety & Michalska, 2010). Humphrey's term 'sympathy' originates in Adam Smith's *The Theory of Moral Sentiments* in which Smith describes sympathy as a 'fellow-feeling with any passion whatever' (Smith, 1790/2005, p.6) where passion refers to feelings. In other words, to Smith, sympathy is to feel the same as the other person, regardless of what feeling the other person shows. Accordingly, Smith saw sympathy for pain as just one option; sympathy for anger and joy were others. Thus, Smith described a human feeling (i.e. sympathy) that would fit with what is currently termed ‘empathy’, though this term is of more recent origin.

Psychology borrowed empathy from German art aesthetics; the term ‘einfühlung’, used to describe feelings of oneness with aesthetic experience, was translated as ‘empathy’ in the early 1900s by Titchener (Titchener, 1909/2014) and was soon widely adopted in psychology. In the 1940s, empathy was investigated using thematic apperception tests (TAT), in which subjects were shown pictures of people and asked to envision what the depicted characters were thinking and feeling (Dymond, 1948). The TAT tests were based on psychoanalytical “role”-theory of insight: ‘the understanding of the self-other patterns or roles which the individual has incorporated and which form the basis of his expectations of others, his structuring of his life situations and the place he feels he occupies in them.’ (Dymond, 1948, p. 228).

Empathy is used as a shorthand for the cited definition of insight; it is not given a formal definition (Dymond, 1948). This also means that empathy was not used as a descriptor of a specific environment-behaviour contingency, and functionality was never a focus point in early empathy research. Empathy as a measurable and observable concept was largely taken for granted, and psychology instead focused on the degree to which empathy influences, for instance, helping (Aderman & Berkowitz, 1970), and how empathy is expressed (Sagi & Hoffman, 1976; Simner, 1971). Ever since the TAT test (Dymond, 1948) was first used, many studies of empathy relied on responses to questionnaires. This is still the case today, perhaps best exemplified by the empathy quotient (EQ) test developed by Baron-Cohen and Wheelwright (Baron-Cohen & Wheelwright, 2004). Throughout the 1900s, empathy increased in popularity as a research term, and different fields of research treated empathy in their own way. A brief description of the two most relevant examples, social neuroscience and behaviour analysis, is presented below.

In social neuroscience, empathy has been proposed to be made up of several different but related phenomena, and while these phenomena are related, they should not be considered aspects or components of a single, true empathy (Batson, 2009). Instead, Batson (2009) summarised these different phenomena as the answers to two questions: ‘How can one know what another person is thinking and feeling?’(p.3) and ‘What leads one person to respond with sensitivity and care to the suffering of another? (p.3). It is worth noting that the latter of these questions concisely illustrates the connection between empathy and prosociality. However, as social neuroscience gradually branched into animal research, researchers adopted the perception–action model (PAM) proposed by Preston & de Waal (2002). In short, the PAM theory states that observed distress in a target animal causes a similar affect (i.e. distress) in the observer, and this affect motivates behaviour to lessen the target animal's distress (Preston & de Waal, 2002). The PAM theory is considered to be applicable to many different kinds of empathy, such as behaviour in different animals (reviewed in de Waal & Preston, 2017). However, for the PAM theory to be valid, all parts of the definition must be publicly observable. Distress and affect in both the target animal and the observer must be directly measured. Measuring these in non-human animals is not impossible, but the technical hurdles are many, and without an observable definition, determining whether something is empathy will be a matter of speculation.

Empathy has not received much attention in the behaviour analytic tradition, but there are some exceptions. One way to define empathy is to operationalise it within individual papers to describe procedures or experiments therein. For instance, in Argott et al. (2017) and Schrandt et al. (2009), empathic responding is used to describe a correct empathic response to different discriminative stimuli (SD) (i.e. expressions of pain/hurt as SD, and vocal expression of care/concern as a correct response). Operationalising empathy will then serve a good purpose in a study that uses it but generalising it to other studies can be difficult. Another approach to behavioral analytical empathy is found within relational frame theory (RFT) (Vilardaga, 2002). Empathy within RFT is proposed to be somewhat like the usage in other parts of psychology, namely based on perspective taking and separating between speaker and listener. However, while this description of empathy in RFT has been shortened for the current thesis, such a definition demands language. The need for language is problematic in studies of animals, since they do not talk, or of human subjects who do not use language or who have difficulties in speaking. Finally, empathy has been described as a setting event (SE) or an establishing operation (EO); empathy 'refers to a vicarious emotional response signalled by another's emotional cue and responses' (Pelaez, 2001, p.12). However, Pelaez's (2001) paper deals with moral development, and as such is not necessarily applicable to non-human species. Thus, while there are several different variants of empathy within the field of behaviour analysis, there is currently no conceptualisation of empathy that can be extended across species.

Whereas empathy can be traced back to the sympathy described in Smith's *The Theory of Moral Sentiments*, prosociality can be traced back to Auguste Comte and his definition of altruism. Comte described altruism as a moral conduct in which the good of others is the end product (Comte, 1858). In fact, the only thing separating altruism from prosociality is that altruism denotes unselfishness in addition to improving the situation of others (Eisenberg & Miller, 1987). The authors also added notions of voluntary action and intentionality with unknown motivation (Eisenberg & Miller, 1987), and this usage of prosociality is used in current research (Lay & Hoppmann, 2017). It is worth noting that early literature in comparative psychology makes no useful distinctions between altruism and prosocial behaviour. Some use altruism as a term to describe behaviour that helps others (Greene, 1969; Rice & Gainer, 1962), while others refer to altruism and prosocial behaviour synonymously (Rosenhan & White, 1967). Rosen & White (1967) give a concrete definition of prosociality as 'the individual's willingness to give up more than he gains' (p.424).

In summary, mainstream psychology, and to some extent social neuroscience, has studied empathy and prosociality for many years. During this time, many different definitions and uses of empathy have emerged. One probable cause of this plurality is that neither empathy nor prosociality are technical terms, and as such a single definition of either is not to be expected (Harzem, 1984). These terms have their origins in philosophy, as previously described. Earlier research illustrates consequences of a non-technical definition succinctly; a recent conceptual review of empathy identified 43 distinct definitions (Cuff et al., 2016), while a book on social neuroscience and empathy proposed that empathy comprised eight different though related phenomena (Batson, 2009). Finally, empathy has been divided into two versions: one cognitive and one affective (Baron-Cohen et al., 1985). According to the authors, cognitive empathy is the ability to understand the thoughts and mental processes of others, while affective empathy is a direct response to displays of emotions in others (Baron-Cohen et al., 1985). In most research on empathy, however, the behavioural aspect has largely been ignored or ascribed a very minor role. In fact, the mentioned review by Cuff et al. (2016) assimilated the collected definitions of empathy, and their final product did not have behaviour in it. One consequence of this is a negative effect on translational studies with cross-species comparisons; without a measure of behaviour, it is difficult to obtain valid data from organisms that cannot self-report. In other words, investigating empathy in animals is problematic.

Empathy and prosociality III: The relation between empathy and prosociality

The ‘empathy–prosociality’ connection dates back to early social-psychological research which supports empathic motivation for prosociality (Aderman & Berkowitz, 1970; Aronfreed, 1970). The conclusion that empathy can motivate prosociality seems to hold more than a quarter of a century later (e.g. Gini et al., 2007; Stavrinides et al., 2010; Williams et al., 2014). Additionally, as previously mentioned, the relation is indirectly presented as part of the empathy definition within social neuroscience (Batson, 2009). Empathy is frequently researched without prosocial behaviour, but the other way around is not that common (for an empirical exception, see Nowbahari et al., 2009). One reason is that studying prosocial behaviour without underlying motivation easily raises questions about using prosocial as a descriptor at all. For example, if help is being offered purely for monetary gain, then it would not be considered prosocial. The clearest example is in national health systems; it is not considered prosocial that health professionals give advice and treatment to people in need. In studies on humans, motivation behind prosocial action can be assessed by self-reporting; the participant can describe reasons for their action via, for instance, an interview or a questionnaire completed after the experiment. This additional knowledge of motivation enables studies of empathy that use functional magnetic resonance imaging (fMRI) to investigate empathy (e.g. Masten et al., 2011 or Rameson et al., 2012). However, this is not the case in studies of non-human animals or in cases where self-reporting is problematic in humans; without self-reporting, the motivation behind actions becomes somewhat speculative. A related note is the reliability of self-reported motivations. For instance, social desirability bias (SDB) can influence the respondents to answer in ways that seem more positive to others (Edwards, 1953), even if some SDB effects may be overcome (Gordon, 1987). Additionally, even if the researcher takes care to avoid this bias, there is the matter of respondents’ ability to respond truthfully. It is easy to envision a situation in which environmental influences or response-environment relations are replaced by cognitive constructs that may not be relevant.

In summary, while the relation between empathy and prosociality is well established within social psychology, and to some extent within social neuroscience, it is not without caveats, the most important being the reliance on reporting motivation for action, which is not possible in several human patient groups or in animals. An exact definition of motivation is unclear, partly because it is not a technical term (Harzem, 1984). When ‘motivation’ is used to describe the rationale behind experimental design (as in Bartal et al. 2018, about why a rat would release a trapped conspecific), it can be difficult to interpret the results. Moreover, non-technical terms can also lead to circular arguments and category mistakes (Harzem, 1986; Holth, 2001). However, if ‘motivation’ is a set of establishing operations or motivating operations that are clearly defined and measured, it could solve some problems. In that case, ‘motivation’ is simply a catch-all description of influential variables in the organism’s learning history.

Empathy and prosociality IV: Summa summarum

The PAM model of empathy is currently used to describe empathy across species (de Waal & Preston, 2017; Preston & de Waal, 2002). Empathy is described as an affective response (i.e. distress) to perceived distress in conspecifics. With the possible caveat of technical challenges with measuring affect and distress, there is no reason why this model cannot be used to describe empathy across species. However, it lacks a focus on behaviour-environmental contingencies, and the learning history of the organism is not considered. While there are several attempts to both describe and study empathy within behaviour analysis, there is currently no coherent conceptualisation of empathy. For prosociality, while this usually is described as any action that benefits another (Jensen, 2016), this definition also needs to take into account the learning history of the organism. If we do not know what occasions prosocial actions, our understanding of the behaviour is incomplete.

Modelling social behaviour in animals I: Animal model concerns and an excerpt from relevant social behaviour research in rats

Using animals in research has a long history. A classic example is the work of Skinner which demonstrated the effect of reinforcement by establishing the now famous ‘superstitious’ behaviour in pigeons (Skinner, 1948). The important aspect of Skinner’s work (1948) is not that pigeons perform this behaviour, but that the behavioural principles underlying the behaviour can be translated to humans. In other words, the important aspect of behavioural animal research is not the behaviour of the animal itself, but the degree to which the observations can be translated to humans. However, animal models represent a separate part of animal research, and there are several definitions, or criteria, of animal models. McKinney & Bunney (1969) proposed that an animal model for a human condition (i.e. depression) should fulfil several criteria such as objectively observable behaviour and reproduction of the animal model by different researchers. This was followed by several validity criteria proposed to be important for animal models such as face validity and predictive validity (Belzung & Lemoine, 2011; Willner, 1986). For this thesis the recent definition put forth in (Sjoberg, 2017) is a relevant summary. An animal model is:

> ‘an animal sufficiently similar to a human target group in its physiology or behaviour, based on a natural, bred, or experimentally induced characteristic in the animal, and which purpose is to generate knowledge that may be extrapolated to the human target group.’(Sjoberg, 2017, p. 3)

In the present thesis, the animal model proposes the existence of empathically motivated prosocial behaviour in rats (Bartal et al., 2011). This animal model will be referred to as the social release paradigm, as per Hiura et al. (2018). However, prosocial behaviour, empathically motivated or otherwise, has a long research history. A few key examples follow to illustrate relevant precursors to the social release paradigm: early studies of behaviour influenced by social stimuli, altruistic/prosocial behaviour, and transfer of emotional reactions across individuals.

Early comparative research had demonstrated different kinds of social behaviours such as cooperative behaviours in rats (Daniel, 1942, 1943; Tsai 1950, in Smith & Ross, 1952). However, Church (1959) expanded greatly on this by demonstrating how rats respond to distress in other rats. He showed that rats would press a lever to stop distressing sounds from other rats, and that rats would press the lever at a higher rate to stop a distress sound than to stop other sounds (Church, 1959). This indicates that rats respond selectively to sounds of distress in their own species. Shortly thereafter, Rice and Gainer (1962) demonstrated a form of prosocial behaviour which they suggested could operationally be termed altruism, whereby one rat would press a lever to lower a rat suspended by a wire to the ground. In a similar study from the late sixties, rats would press levers to stop foot shocks given to other rats. In that study, the data showed that only rats who had already experienced foot shock would do so (Greene, 1969). This was followed by studies on social facilitation and observational learning; in short, they indicated that rats are not only affected by the presence of conspecifics, but also observe the action of other rats and are influenced by these observations (Levine & Zentall, 1974; Zentall & Levine, 1972).

In other words, much research on the social behaviour of rats existed prior to the development of the social release paradigm (Bartal et al., 2011). Rat research has expanded from early studies of responses to stressful stimuli (Church, 1959) to papers demonstrating altruism/prosocial behaviour (Greene, 1969; Rice & Gainer, 1962) and learning from observing others (Levine & Zentall, 1974; Zentall & Levine, 1972). It should also be mentioned that studies on emotional contagion in mice (i.e. mice freezing while witnessing conspecifics freezing) influenced the development of the social release paradigm (reviewed/summarised in Hernandez-Lallement et al., 2020).

Modelling social behaviour in animals II: The social release paradigm

In the social release paradigm, one rat is trapped inside a cylinder and a conspecific can release the trapped rat from the cylinder. This cylinder is usually made of clear plastic glass and will be referred to as a restrainer in the current thesis. The social release paradigm was designed to investigate whether, in the authors' words: 'rats could use another's distress as motivation for active helping' (Bartal & Mason, 2018, pp.152–153). One key premise is that entrapment causes distress. Studies on restraint stress indicate that entrapment is stressful for rats. Restraint stress affects a wide array of behaviours in rats, such as feeding (Ely et al., 1997; Tu et al., 2019), exploration (Badache et al., 2017) and increased immobility in the forced swim test (Swiergiel et al., 2007). Entrapment also increases the corticosterone response, which is a physiological measure of stress (Kalil et al., 2013). For a more detailed description of the effects of restraint stress, see Buynitsky & Mostofsky (2009) and Glavin et al. (1994). Additionally, rats will exit the restrainer if possible (Bartal & Mason, 2018), but this escape behaviour is hard to interpret as it could just as well be exploration as escape from aversive entrapment. There has also been one recording of negative vocalisations in trapped rats, but the authors did not deem these vocalisations to be the cause for opening (Bartal et al., 2011). It should be noted, however, that emerging evidence suggests that entrapment in the social release paradigm may not be stressful to the trapped rat (Hachiga et al., 2020; Silberberg et al., 2013), due perhaps to procedural differences between earlier research on restraint stress and social release.

Social release in rats seems to qualify as an animal model of empathic prosocial behaviour. In a similar situation, people would feel distressed at seeing a housemate trapped and probably try to free the trapped and distressed person. Surface validity is argued to be relevant for animal models (Belzung & Lemoine, 2011; Willner, 1986). However, several other measures of validity should be considered when evaluating animal models. Of relevance is perhaps mechanistic validity; that cognitive and or biological mechanisms in animals are the same as in humans (Belzung & Lemoine, 2011).

It should be noted that some previous research seems poised to increase the mechanistic validity of social release. These studies employed neuropharmacological treatments to influence behaviour. One study administered anxiolytics, and this did indeed have an effect on social release; less anxious rats are poorer at social release than others, which was argued to be because they did not respond so strongly to perceiving their trapped cagemate (Bartal et al., 2016). Another study used opioids (heroin), and found that a history of opioid usage also negatively affected social release (Tomek et al., 2019). A follow-up study revealed that that such negative effects on social release could be reversed by activating the anterior cingulate cortex in rat brain (Tomek et al., 2020). However, manipulations such as opioid and anxiolytics do not give proper mechanistic validity because both opioids and anxiolytics have a wide array of different effects. In short, these pharmacological treatments do not facilitate understanding of the influences on social release, and failure to understand behaviour cannot be remedied by trying to understand the brain mediating the behaviour (Catania, 2000). Finally, these studies (i.e. Bartal et al., 2016 and Tomek et al., 2018, 2020) did not pinpoint stimuli occasioning opening behaviour. Without knowing whether opening is caused by distress in the trapped rat, it is unknown whether the premise of social release as a model of empathy is true. In other words, there will be no validity unless the premise of distress in the trapped is observed and determined to be necessary for opening to occur.

In short, much work remains before social release becomes a fully valid animal model of empathic prosocial release. Validity of social release as a model of empathy rests on the premise of distress caused by entrapment. While this distress is found and measured in studies of restraint stress, it has yet to be measured in the social release paradigm, apart from the observation that a trapped rat will exit the restrainer. Exiting the restrainer, however, can be caused by many things other than distress during entrapment. Distress calls have been measured as well, but these have not been found to be the reason for opening. Attempts have been made to obtain mechanistic validity in the social release paradigm, but since no studies have shown that opening is caused by stimuli indicating distress in the trapped rat, any claim of mechanistic validity seems dubious. Furthermore, studies are emerging that indicate the opposite; that is, that entrapment may not be distressing in the social release paradigm.

Ire manu in manu: Theory and practice in improving experimental design and apparatus

During this PhD project, piloting the experimental apparatus and design led to improving the conceptualisation and the theoretical rationale (presented in study 1) as well as the experimental design (used in studies 2 and 4). In the pilot study, we wanted to stay as close as possible to the original experimental design used in Bartal et al. (2011) to demonstrate the ability to replicate the findings in our own laboratory. Additionally, it was decided to partially replicate the experiments on familiarity from Bartal et al. (2014). In Bartal et al. (2011), a rat is trapped within a restrainer. This restrainer has a door which can be opened from the outside. The restrainer is housed centrally within a small arena, like an open field, measuring 0.5*0.5m. A cagemate is then inserted, and freely moves around for a set amount of time. This is repeated over several days, and within six to eight days, the free rat releases the trapped rat. Following this initial occurrence, the latency before opening occurs drops drastically (Bartal et al., 2011). The experimental studies (studies 2 and 4) in the present thesis used the same kind of restrainer, location and arena size as in Bartal et al. (2011). See Figure 1 for a sketch showing the most relevant parts of the experimental apparatus used in the pilot for study 2.

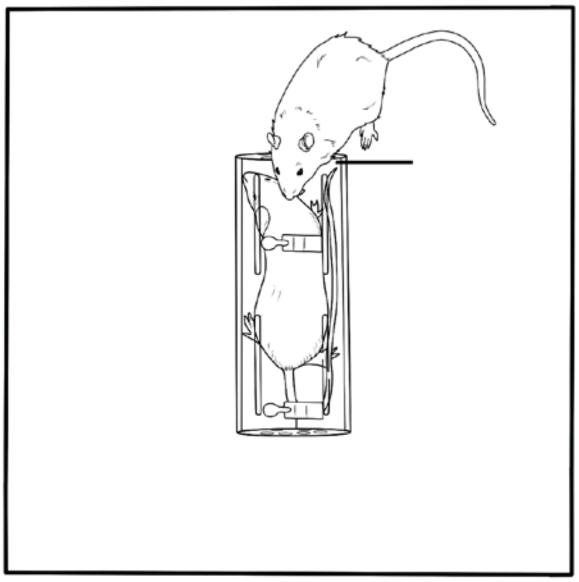


Figure 1. The restrainer is in the center of the arena. A simple black lever protrudes from the side, which will tip the door open if pressed down. The door cannot be opened from the outside.

Additionally, a high-frequency microphone was installed in the corner to record ultrasonic vocalisations (USVs) during the experiment. During the pilot, USV collection was only tested for proper functioning and was therefore not included in the analysis. USVs have only briefly been investigated in studies of social release (Bartal et al., 2011) , but are thought to be relevant for communication of emotions in rats (Brudzynski, 2013). Finally, a counterweight was attached to the restrainer door (missing from Figure 1 but visible in the left part of Figure 2) to tip the door open once the lever was pushed.

Results from this replication produced the same general findings as the experiments in Bartal et al. (2011,2014); the free rat would open the restrainer door to release a trapped a cagemate, but if the cagemate was replaced with an unknown rat, the latency before social release increased (Blystad et al., 2016). However, the pilot study clarified important procedural weaknesses in the original design that were improved before running the group study. First, the pilot illustrated problems with the shaping phase of the experiment. In Bartal et al. (2011), and in their follow-up studies (i.e. Bartal et al., 2014, 2016), restrainer door-opening was not shaped. Bartal et al. (2016) describe door-opening with no prior response shaping as *natural*, and argue that this *natural* behaviour is easier to interpret because the rat has no learning history of shaping or door-opening producing food/water reinforcers that could have affected the behaviour (Bartal & Mason, 2018).

It should be noted that the term ‘natural’ to describe behaviour is not a technical term. It does not describe a behaviour–environment relationship. In other words, the term ‘natural’ does not contain information regarding what stimuli in the environment affect the behaviour. Thus, describing behaviour as natural can lead to several different problems when interpreting the results. Some examples are circular arguments or category mistakes where ‘natural’ describes both behaviour and cause for the behaviour (Holth, 2001; Ryle, 2009)and smuggled connotations (Harzem, 1984) (see study 1 for a detailed discussion). A consequence of not shaping restrainer door-opening is a long and undocumented learning history of the free rat as it explores the arena across several days. In other words, it is not known why the first opening occurs. In study 2, restrainer door-opening was shaped according to the method of successive approximations using food reinforcers and was observed to be in the rat’s behavioural repertoire before testing with a cagemate in the restrainer. Thus, the process of learning restrainer door-opening was controlled by the experimenter and not left to be an ‘accidental’ side-effect of exploration. Second, and related to the first point of not shaping the restrainer door-opening, the choice in the original study not to include shaping of restrainer door-opening also meant that no baseline data were collected prior to the first restrainer door-opening. Originally, the social release paradigm has a within-group design (e.g. Bartal et al., 2011, 2014), and in a within-group design one or more subject(s) are exposed to multiple conditions and comparisons are made across these conditions (Charness et al., 2012). A concrete example from the social release paradigm is that latency to open the restrainer has been measured when the restrainer contained either a familiar or an unfamiliar rat (Bartal et al., 2014). However, the original study (Bartal et al., 2011) and its follow-up studies (Bartal et al., 2014, 2016) did not include baseline recordings of restrainer door-opening rates or latency when the restrainer was empty. The claim that a rat opened the door to free its cagemate is severely weakened if baseline recordings show that rats also open the door to an empty restrainer or that latency in opening an empty restrainer is the same as for a restrainer containing a cagemate. Baseline recordings, where restrainer door-opening produces different stimuli such as food or other non-social reinforcers, are essential for demonstrating how restrainer content controls door-opening. Baseline recordings of restrainer door-opening for food or water also give information regarding the strength (reinforcer value) of different content (e.g.

cagemate versus food). Finally, a practical concern was that the restrainer door could be opened by accident. This lack of experimental control can be problematic for analysing why behaviour occurs in the first place, but also for analysing later openings, as these could be a result of exploration as well as of restrainer content. For those reasons, part of the opening mechanism was separated from the rest of the arena. The lever was partly walled in, and the counterweight was hidden within a hollow semi-arch (Figure 2).

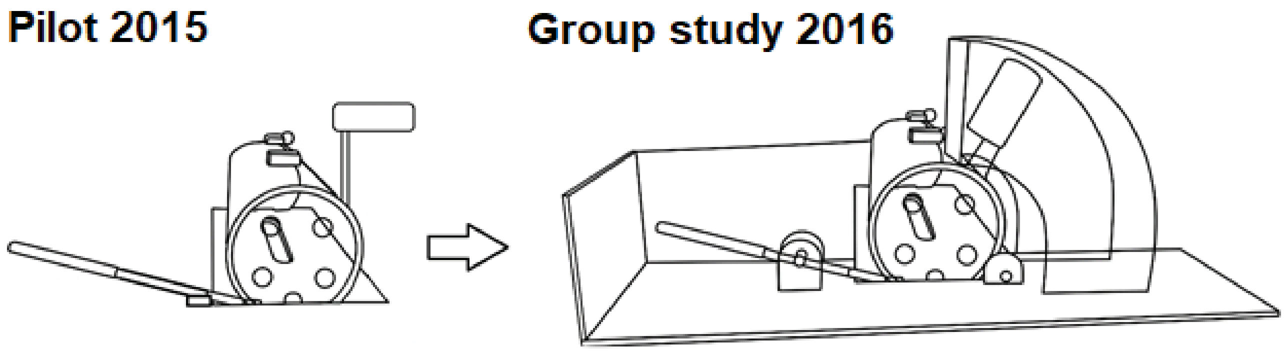


Figure 2. Modifications to experimental design between the pilot and study 2. The illustration on the left shows the design in the pilot study of 2015. Before conducting study 2, a new opening mechanism was manufactured; the lever was partly walled in in a plexiglass corner, and the counterweight was concealed within a hollow semi-arch. The lever and counterweight are made of metal, all other parts are made of transparent plastic glass. Figure 2, right, is adapted from Figure 1 in Blystad et al. (2019).

Even with the modifications described above, the experimental apparatus and response topography required to open the restrainer door were like those in Bartal et al. (2011). Both designs required physical interaction with the door in order to open it (see Figure 3) as opposed to studies with other response requirements (Hiura et al., 2018; Silberberg et al., 2013).

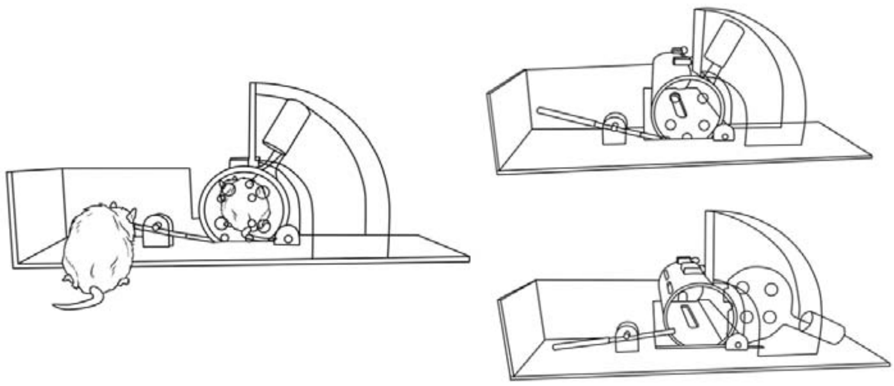


Figure 3 Door-opening mechanism. The illustration above shows the opening mechanism in the experimental apparatus improved after the pilot study. The lever could be pressed down to tip open the door to the restrainer. A counterweight would then pull the door all the way open. Figure 3 is adapted from Figure 1 in Blystad et al. (2019).

A detailed top-down view of the final experimental apparatus and setup used in studies 2 and 4 is shown in Figure 4. The restrainer was purchased from Panlab Instruments and then attached to the door-opening mechanism.

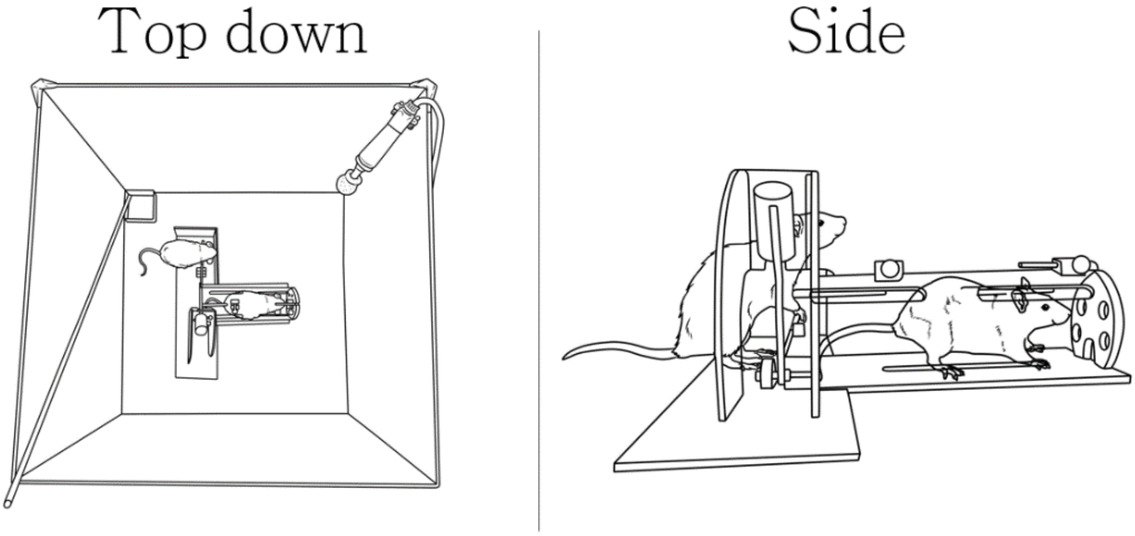


Figure 4 Detailed overview of arena with rat trapped in restrainer. Right, a metal pipe extends into the arena, ending in a 5*5cm metal box. This pipe was used to administer food pellets during shaping with successive approximations. The restrainer with a trapped rat can be seen in centrally in the arena. In the top left-hand corner, a microphone is mounted extending into the arena to record ultrasonic vocalisations (USVs). Figure 4, left, is adapted from Figure 2 in Blystad et al. (2019).

Purpose of this thesis and its development

To improve the understanding of the social release paradigm via changes to experimental design and new conceptualisations of empathy.

In order to improve the understanding of social release in rats, the current thesis adapted a two-pronged approach:

1. Theoretically address:

a. The need to integrate research findings to map environmental variables and social stimuli of importance for interpreting observations in the social release paradigm, and to identify areas for future collaborative research. It is suggested that prior research be systematised using a three-term contingency analysis (study 1).

b. The lack of a behavioural conceptualisation of empathy that allows for integration of previous research with recent research in animal modelling (study 3).

2. Increase experimental control and investigate possible environmental variables that could influence the observations. This work is presented study 2 and study 4. Study 2 is a replication of Bartal et al. (2011) that includes shaping and training of behaviour and makes a preliminary investigation of illumination effects. Illumination was studied because this environmental variable is known to affect rat behaviour relevant for the social release paradigm, such as open-field exploration (Igarashi & Takeshita, 1995; Valle, 1970; Williams, 1971). Study 4 investigates the effect of restrainer aversion by measuring restrainer entries and positive USVs. Restrainer aversion is a necessary premise for social release to be considered empathic, but few papers (e.g. Hachiga et al., 2020 and, partly, Silberberg et al., 2013) have investigated restrainer aversion. Additionally, neither Silberberg et al. (2013) nor Hachiga et al. (2020) investigated restrainer aversion in a design where both the free and the previously trapped rat could re-enter the restrainer. Positive USVs have not been investigated in the social release paradigm.

Articles included in the thesis

Four studies are included in this thesis, two of which are theoretical (studies 1 and 3) and two are experimental (2 and 4). In study 3 the term ‘empathetic’ is used instead of ‘empathic’, which is used elsewhere in this thesis, but these terms are interchangeable and used synonymously (Merriam-Webster.com, 2019). ‘Empathetic’ was chosen in study 3 for aesthetic preferences by the co-author of study 3 to which the PhD candidate did not object.

Ethical concerns

This thesis contains two theoretical studies (1 and 3) and two experimental studies (2 and 4). Ethical concerns regarding the rights and concerns of subjects are irrelevant for the theoretical studies (1 and 3) as these contain no collected data. The subjects in studies 2 and 4 were the same group of rats, and a total of 30 subjects were included in those studies. Additionally, two pilot studies preceded the data collection in studies 2 and 4, with a total of six subjects for the first pilot and four subjects in the last pilot. The last pilot did not collect data for analysis but was necessary to test new equipment. Both the pilots and the experiments were conducted in the animal facility at the Institute of Biosciences, University of Oslo. All research on rodents in Norway requires authorisation from the Norwegian Food Safety Authority (Mattilsynet) and that the main researcher in the application holds FELASA C certification. The application for the pilots and studies 2 and 4 was approved prior to the first pilot in 2015, and was given the FOTS-ID 7966, with the title 'Pro-social behaviour in rats / Prososial atferd i rotter'. The PhD candidate had acquired the FELASA C qualification during his preceding master education.

All pilots and experiments in studies 2 and 4 were administered and conducted with the PhD candidate as the lead researcher. Bachelor students from the psychology programme at OsloMet assisted in the first pilot and in studies 2 and 4. These students were continuously supervised by the PhD candidate to maintain proper data collection and other relevant laboratory routines.

Aside from general handling, rats used in all pilots and studies underwent the same two main stressors: food deprivation during parts of the experimental design and entrapment in a restrainer for half of the rats. Several measures were taken to limit exposure to these two stressors. During the food deprivation phase, all animals were subjected to daily weighing to make sure no rat lost more than 15% of its weight. To limit the time in captivity during the experiments, data from the pilot studies indicated that shorter entrapment time still yielded good data. This allowed for using shorter captivity time during the larger experimental study (studies 2 and 4), and presumably alleviates distress in the animals. Additionally, the animals were routinely inspected by the animal facility and veterinary staff. Finally, all rats were euthanised with CO2 gas by the FELASA C certified PhD Candidate in the animal facility. Euthanisation via CO2 was chosen because it is an accepted and correct method of euthanising adult rats according to relevant judicial regulations in Norway (i.e. regulations concerning the use of animals in experiments (*Forskrift om bruk av dyr i forsøk*), section 16, second paragraph and Annex C).

Overview of studies

Study 1: A critical review of the rodent social release paradigm: empathy or social reinforcement

Blystad, M.H.

Status: Published, 2019. *Mexican Journal Of Behavior Analysis*, 45(2), 199–222. doi: 10.5514/rmac.v45.i2.75563

Studies that use the social release paradigm with rats have largely been divided into two main camps. The original authors claim in their seminal study and follow-ups that the behaviour should be called prosocial and is empathically motivated (Bartal et al., 2011, 2014, 2016; Shan et al., 2016) and their empathy claim is echoed by other researchers (Quinn et al., 2018; Tomek et al., 2019, 2020). This claim, however, is challenged by authors who argue that neophobia, a fear of novel objects and locations (Silberberg et al., 2013) and social reinforcement (Hachiga et al., 2018; Hiura et al., 2018; Silberberg et al., 2013) represent a more parsimonious explanation of cagemate release. It has also been claimed that prosocial behaviour could exist without any sharing or perception of emotions (Vasconcelos et al., 2012), as demonstrated in studies of helping behaviour in ants (Nowbahari et al., 2009). Study 1 in the present thesis describes a unifying and theoretically neutral approach that can systematise data from both empathy and social reinforcement research using a behaviour analytic three-term contingency analyses. This systematisation shows that in the social release paradigm, very little is known about how the different social and physical stimuli affect the observed behaviour. While the social reinforcement position claims release is reinforced and maintained by social reinforcement, as demonstrated in Hiura et al. (2018), an empathy interpretation requires more. Cognitive aspects of empathy (i.e. the free rat *cares* for the trapped rat, or the free rat *wants* to release the trapped rat) cannot readily be observed or measured in rats. Thus, for social release to be empathically motivated, opening must be occasioned by stressful stimuli from the trapped rat. One example of such a stressful stimulus could be USV that signalize distress in the trapped rat.

Study 1 further describes several different approaches to investigate how social stimuli influence behaviour in the social release paradigm. These are divided into visually perceived behaviour, odours, and auditory communications. From other research (Brudzynski, 2013; Marquez et al., 2015; Wesson, 2013), it is known that rats use all these three sensory modalities to communicate. The study concludes that much work remains before it is known what occasions opening behaviour in the social release paradigm of rats, but a three-term contingency systematisation can serve as a way to illustrate what further work needs to be done. When this further research is added to the systematisation in study 1, it will be apparent how different stimuli affects opening behaviour and whether opening should be called empathic or not.

Study 2: Female rats release a trapped cagemate following shaping of the door opening response: Opening latency when the restrainer was baited with food, was empty, or contained a cagemate

Blystad, M. H., Andersen, D., & Johansen, E. B.

Status: Published, 2019. *PLOS ONE*, 14(10), e0223039. doi: 10.1371/journal.pone.0223039

In the first experimental study on social release in rats, the authors discovered what they claimed to be prosocial behaviour motivated by empathic distress (Bartal et al., 2011). The main result supporting the empathy-based conclusion was that the rats would release a cagemate from a restrainer even when socialisation was not possible afterwards (Bartal et al., 2011). Additionally, over 50% of female rats tended to release a cagemate to share chocolate treats rather than eat all the treats themselves. However, that paper, and follow-up studies (Bartal et al., 2014; Bartal et al., 2016), had several critical design weaknesses: namely the lack of a baseline, and related to this, insufficient experimental control of how door opening was acquired (i.e. the learning process). The current study included a baseline with both food in the restrainer, and an empty restrainer, before testing with a trapped cagemate. Moreover, the experimental apparatus was altered so that accidental opening of the restrainer would be reduced. In addition, a shaping procedure was included in the beginning of the experimental procedure to ensure door opening was in the rats' behavioural repertoire before further testing. Lastly, study 2 included a preliminary test of illumination as an environmental stressor.

The absence of a baseline is problematic because without it, it is unknown whether the first opening that occurs is under the control of the restrainer content. This lack of experimental control affects the comparisons of different conditions (i.e. restrainer content). To solve this problem, this study used a design with three steps:

1. Rats are food-deprived and demonstrate restrainer door-opening with a food reward, which serves as a baseline.
2. Rats are exposed to a restrainer without any content to prove that opening was due to the food in the restrainer in step 1.
3. The cagemate is put into the restrainer.

The latencies in found in the study showed that that opening for food occurred significantly faster than opening to release a cagemate or opening the restrainer when the restrainer was empty. However, opening to release a cagemate had lower latency than when the restrainer was empty. This seem at odds with findings from Bartal et al. (2011) were rats would share a chocolate treat. Though, in Bartal et al. (2011) rats were given a choice between opening to release a cagemate and share a chocolate treat or eat the treat without sharing. Choosing between cagemate and chocolate is different from comparing latency for food in one condition and a cagemate in another as in the present study. This illustrates the importance of what kind of measurement of behaviour is employed, choice vs latency, and procedural differences (e.g. food deprivation). Thus, study 2 supports the main experimental findings of Bartal et al. (2011). Moreover, the rats in Blystad et al. (2019) had lower latencies than Bartal et al. (2011), probably due to difference in shaping, and the baseline measurements in Blystad et al. (2019). Furthermore, first-time release occurred sooner in study 2 (i.e. first trial versus after one week) than in Bartal et al. (2011).

Finally, study 2 made preliminary investigations into the effects of illumination on restrainer door-opening. Changes in illumination were chosen for their known effect on many different behaviours in rats (Igarashi & Takeshita, 1995; Valle, 1970; Walker & Davis, 2002; Williams, 1971). The changes in illumination in study 2 did not reveal any significant effects on latency in releasing a cagemate. Still, the comparison was preliminary, and a proper group design with one group in the dark and one in the light was not employed. Future research should perform a proper study of this variable to properly determine whether illumination affects social release.

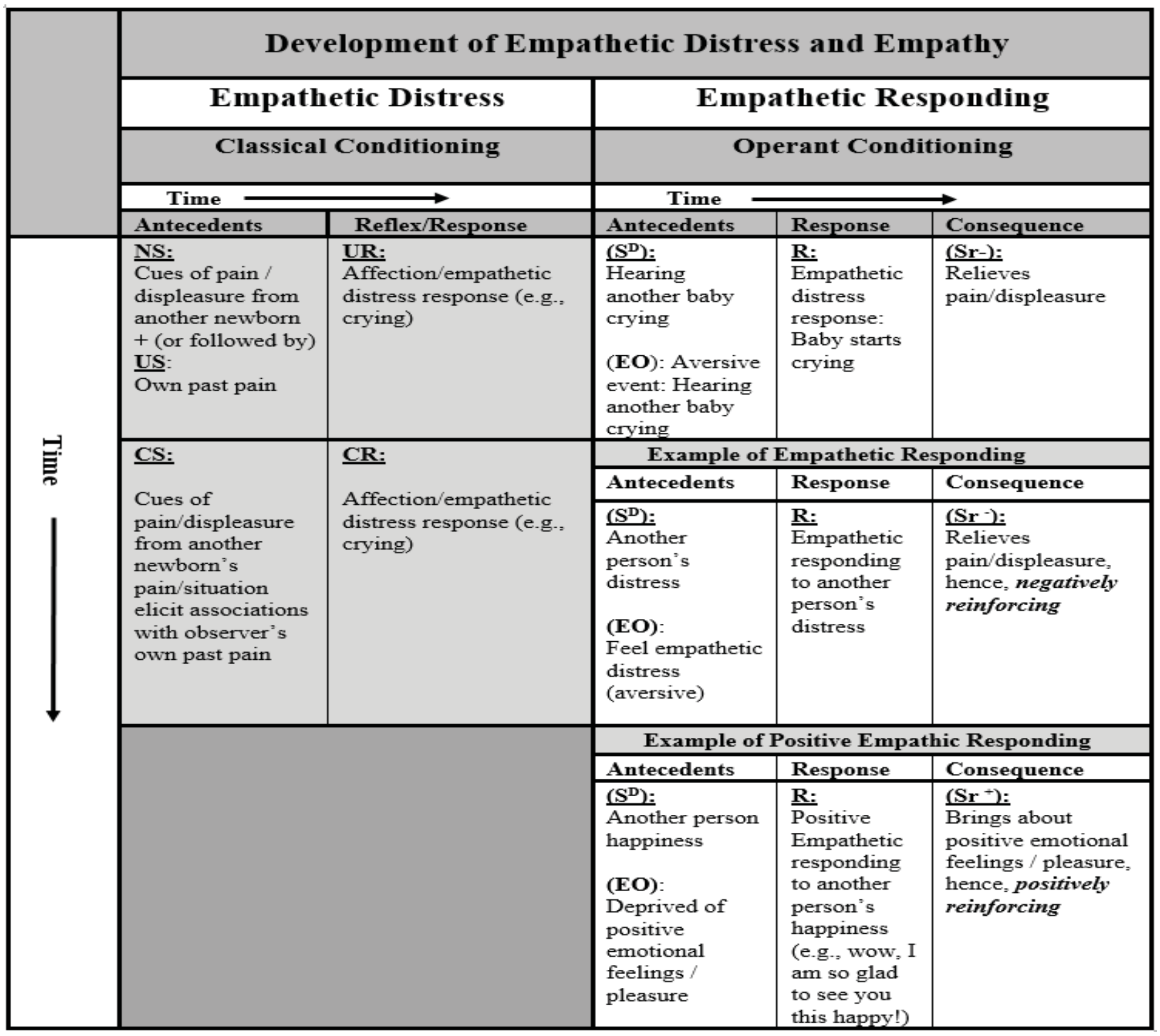
Study 3: Empathy or not empathy, that's the question: A pragmatic behaviour analytical approach

Blystad, M. H. & Hansen, S.

Status: Submitted, 2020. *Behavior Analysis Research and Practice*

To this thesis, it was necessary to develop a conceptualisation of empathy that could serve as theoretical background for translational behavioural research. This is the aim of study 3. Study 3 establishes a new conceptualisation of empathy as an alternative to the plethora of existing definitions of empathy used in psychology and related fields. This novel conceptualisation was borne out of the lack of a behavioural component in most modern definitions of empathy (Cuff et al., 2016). The novel conceptualisation bears a close resemblance to those used in applied studies within the field of behavioural analysis (Argott et al., 2017; Schrandt et al., 2009), and to those described in Peláez (2001), but none of those studies describe a full conceptualisation of empathy based on basic principles of behaviour. As such, the conceptualisation of empathy in those studies is difficult to apply in different kinds of research, which in turn greatly affects the ability to translate findings from of animal studies to humans. However, inability to generalise will occur across different human subjects as well, since only subjects with the ability to self-report will be able to provide the motivation for their behaviour.

In study 3, a brief description of the origins of empathy in psychological research is given before empathetic responding is described as a process that begins with an empathetic distress response. This response is observed in new-borns who cry more when they hear the cries of other new-borns than when they hear other, similar sounds (Missana et al., 2017; Sagi & Hoffman, 1976; Simner, 1971). Such crying in infants is proposed to be an innate reflex. In short, this distress response begins with a neutral stimulus (NS), for instance cues of pain/displeasure from other new-borns paired with an unconditioned stimulus (US) such as associations of own past pain or distress. To begin with, the responses to these NS/US are unconditioned reflex-like unconditioned responses (UR). However, through time and exposure the NS/US gives way to a conditioned stimulus CS (i.e. social cues, expressions of pain in others) and a conditioned response (CR). After this early development and exposure to classical conditioning, operant conditioning is suggested to maintain this developed empathetic distress response and to generalise it into empathic responding. See Figure 5 below for a flowchart of the empathic development (adapted from study 3).



<table>
<tr><td rowspan="5"></td><td colspan="5">Development of Empathetic Distress and Empathy</td></tr>
<tr><td colspan="2">Empathetic Distress</td><td colspan="3">Empathetic Responding</td></tr>
<tr><td colspan="2">Classical Conditioning</td><td colspan="3">Operant Conditioning</td></tr>
<tr><td colspan="2">Time →</td><td colspan="3">Time →</td></tr>
<tr><td>Antecedents</td><td>Reflex/Response</td><td>Antecedents</td><td>Response</td><td>Consequence</td></tr>
<tr><td rowspan="9">Time ↓</td><td><u>NS:</u>
Cues of pain / displeasure from another newborn + (or followed by)
<u>US</u>:
Own past pain</td><td><u>UR:</u>
Affection/empathetic distress response (e.g., crying)</td><td><u>(S^D):</u>
Hearing another baby crying
(EO): Aversive event: Hearing another baby crying</td><td><u>R:</u>
Empathetic distress response: Baby starts crying</td><td><u>(Sr-):</u>
Relieves pain/displeasure</td></tr>
<tr><td rowspan="3"><u>CS:</u>
Cues of pain/displeasure from another newborn's pain/situation elicit associations with observer's own past pain</td><td rowspan="3"><u>CR:</u>
Affection/empathetic distress response (e.g., crying)</td><td colspan="3">Example of Empathetic Responding</td></tr>
<tr><td>Antecedents</td><td>Response</td><td>Consequence</td></tr>
<tr><td><u>(S^D):</u>
Another person's distress
(EO):
Feel empathetic distress (aversive)</td><td><u>R:</u>
Empathetic responding to another person's distress</td><td><u>(Sr^{-}):</u>
Relieves pain/displeasure, hence, <i>negatively reinforcing</i></td></tr>
<tr><td rowspan="3" colspan="2"></td><td colspan="3">Example of Positive Empathic Responding</td></tr>
<tr><td>Antecedents</td><td>Response</td><td>Consequence</td></tr>
<tr><td><u>(S^D):</u>
Another person happiness
(EO):
Deprived of positive emotional feelings / pleasure</td><td><u>R:</u>
Positive Empathetic responding to another person's happiness (e.g., wow, I am so glad to see you this happy!)</td><td><u>(Sr^{+}):</u>
Brings about positive emotional feelings / pleasure, hence, <i>positively reinforcing</i></td></tr>
</table>

Figure 5 Flowchart of suggested origins of empathetic distress and development of empathetic responding.

Empathetic responding is maintained by the effects of both positive and negative reinforcement in a manner described in Figure 6 below (adapted from study 3).

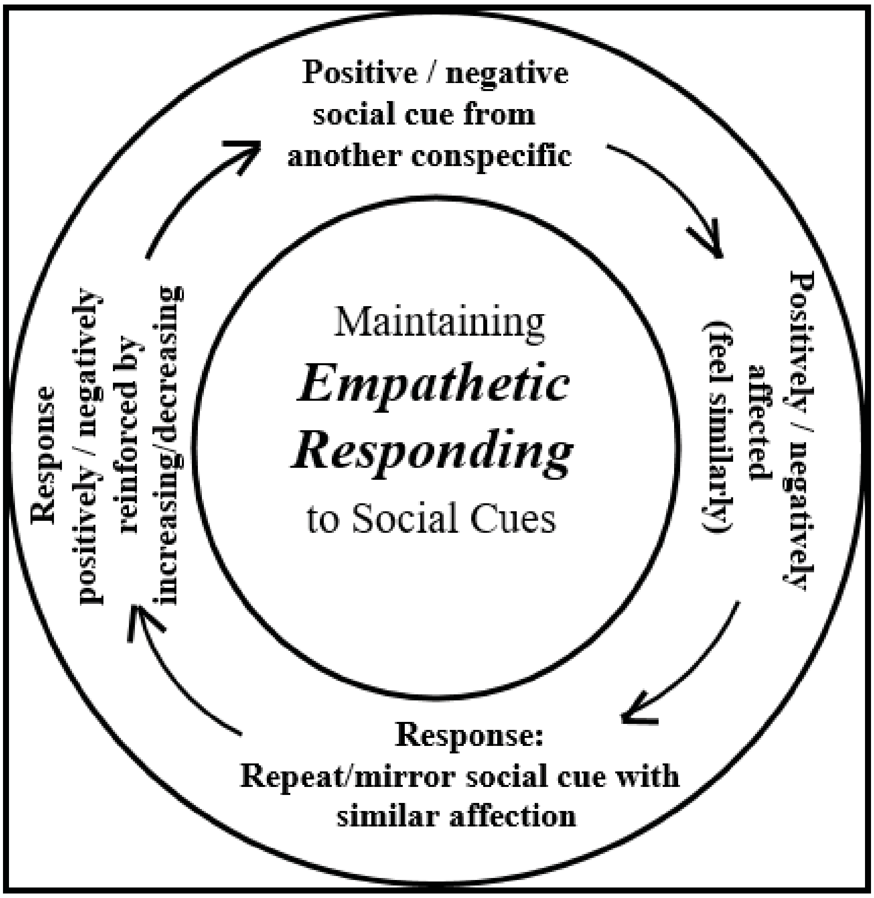


Figure 6 The arrows within the circle show how positive/negative social cues from another conspecific can lead to a positive or negative affect. This affect leads to a response with a mirrored social cue, which is either positively or negatively reinforced by either an increase or decrease in the social cue.

Study 4: The social release paradigm: Investigating restrainer aversion by restrainer entries and positive ultrasonic vocalizations

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The fourth and final study expands on the findings in study 1 by investigating restrainer aversion measured by restrainer entries after release and positive ultrasonic vocalisations. If entrapment is aversive, then the trapped rat should stay away from the restrainer after release due to place avoidance. Positive ultrasonic vocalizations occur in situations such as social play, and as such these are expected to mostly occur after the cagemate release have occurred. Positive USVs prior to release are incompatible with restrainer distress in the trapped rat or emotional contagion in the free rat. Restrainer aversion is a premise for an empathy explanation of social release, because if entrapment is not aversive, then release from entrapment is not prosocial. Social release cannot be empathic in that case either, since if the restrainer is not aversive, then the trapped rat is not distressed.

There are several categories of ultrasonic vocalisations (USVs), but the two main categories are those used to communicate positive or negative affect (Brudzynski, 2013). One of these, the category labelled 22 kHz and associated with negative affect, has briefly been investigated in relation to social release. The 22 kHz USVs were collected by Bartal et al. (2011), but the authors concluded that such USVs had no effect on social release. However, this claim not been replicated. On the other hand, *positive* ultrasonic vocalisations have not been studied at all in any investigation in prior studies of rodent prosocial behaviour (Bartal et al., 2011, 2014, 2016; Sato et al., 2015; Shan et al., 2016; Tomek et al., 2018, 2020) nor in replications investigating social reinforcement (Hachiga et al., 2018; Schwartz et al., 2017; Silberberg et al., 2013, Hiura et al., 2018). In study 4, positive USVs were collected and compared before and after social release for the pair of rats. We were unable to say which of the rats emitted the USVs, thus, the data concerning positive USVs in study 4 constitute preliminary results which future research could build upon. In sum the data showed that most positive USVs were made prior to opening, which indicate that entrapment is not aversive. If the positive USV was made by the trapped rat then this would not indicate distress, and if they were made by the free rat then that would not indicate any form of emotional contagion with a trapped and distressed rat.

Silberberg et al. (2013) briefly investigated if being in the restrainer or entering the restrainer could be reinforcing. However, due to the experimental design, only the previously trapped rat could enter the restrainer after opening. Hachiga et al. (2020) conducted a full investigation of restrainer aversion, but while that study demonstrated that being in the restrainer can be reinforcing, the experiments only used one rat. In study 4, both rats could enter the restrainer after opening, and while this can lead to confounding variables (i.e. one rat following the other or other social interactions), it is still a design that remains truer to Bartal et al. (2011).

Data from the restrainer entries showed that both rats enter the restrainer after release, and both have more partial restrainer entries than full. There was no significant difference in full entries between the rats. However, rats with a history of entrapment had more partial than full restrainer entries compared to the free rat. It cannot be ruled out that this difference in partial entrances could indicate caution in the previously trapped rat, but such an interpretation is at odds with the rest of the data; there was no statistically differences in the free and formerly restrained rat when comparing total number of restrainer entries, or full restrainer entries.

Overall, the data from both positive USVs and restrainer entries support the conclusions of Hachiga et al. (2020) and Silberberg et al. (2013), which is that rats in the social release paradigm are not distressed by entrapment. If being in the restrainer does not cause distress in the trapped rat, then being released from the restrainer cannot be considered prosocial or empathic. Additionally, study 4 also illustrates the importance of understanding exactly what influences behaviour and investigating specific stimuli in the social release paradigm.

Discussion

History and current climate

The question of whether animals, specifically rodents, are empathic has been raised many times. Early studies claimed that rats would behave altruistically; that is, behave in such a way as to relieve another animal of distress (Church, 1959; Greene, 1969; Rice & Gainer, 1962). For instance, rats would press levers in order to stop stressful vocalisations made by other rats (Church, 1959). However, these studies did not describe any empathic motivation behind the altruism. Empathy as motivation for altruism, or prosociality, is claimed in recent studies (Bartal et al., 2011). Bartal and colleagues showed that rats would open a small plastic tube, a restrainer, to free a trapped rat, and that many rats chose to free a trapped rat rather than to access chocolate (Bartal et al., 2011). The rats would also continue to release their cagemate even if direct physical interactions were not possible, which was taken as evidence that the rats were not motivated by socialisation alone. Taken together, these findings were argued to be caused by empathic motivations; namely that the free rat acted to end the perceived distress of the trapped rat (Bartal et al., 2011). Responses from critical voices argued that helping behaviour could exist without the sharing of emotions; in other words, that 'helping' could occur without empathic motivations (Vasconcelos et al., 2012). For instance, helping without any sharing of emotions has been observed in ants, a species considered not to have emotional capacities (Nowbahari et al., 2009).

Additionally, Silberberg et al. (2013) claimed that social reinforcement could explain why free rats would release other rats from entrapment, and that neophobia in the trapped rat would explain why it would escape the restrainer. In other words, the free rat approached the restrainer out of interest in the trapped rat, and the trapped rat left the restrainer because the restrainer instilled a novelty fear in the trapped rat. In response to Silberberg et al. (2013), the original authors showed that rats treated with anxiolytics had higher latency to release a trapped cagemate; summarised, anxiolytic-treated rats that showed a weaker affective response to the trapped cagemate did not open the restrainer (Bartal et al., 2016). Bartal et al. (2016) meant that this proved that an affective response was not only necessary for opening the restrainer to free a trapped cagemate; it was also evidence of empathic motivations in the free rat. However, no comment was made on the potential relevance of neophobia to the trapped rat escaping the restrainer. After Silberberg et al. (2013), more research followed that indicated a role for social reinforcement in rodent social release (Hachiga et al., 2018; Hiura et al., 2018; Schwartz et al., 2017). It was also demonstrated that residing in the restrainer could in itself be rewarding (Hachiga et al., 2020), and albeit in mice, interest in the restrainer itself was shown to be the most important factor for social release (Ueno et al., 2019). More importantly, while Bartal et al. (2016) had attempted to respond to the critique in Silberberg et al. (2013), they made no attempt to measure what kind of stimuli might occasion social release. Without knowing what kind of stimuli occasions social release, it is hard to fully understand it or determine whether it should be labelled prosocial and empathic.

As the debate stands today, there is no agreement on what controls the release of a trapped rat cagemate from a restraining device. However, to fully understand the behaviour in rodent social release, it is necessary to look at all available data and conduct a thorough analysis of the behaviour and its controlling variables. If opening is a social behaviour, then it must be controlled by social stimuli (Skinner, 1953). One approach is presented in the present thesis. This study outlines a systemisation of experimental findings using a three-term contingency analysis; all research can then be integrated to yield a better/more complete picture of how different stimuli in the experimental situation influence rodent social release (Blystad, 2019). Most likely, such an approach requires collaborative effort, as it necessitates measurements of all relevant social stimuli for the rats. Rodent social stimuli include at least stimuli in the auditory, visual and odorous categories (Blystad, 2019).

A premise for empathy in social release: Aversion to entrapment

Opening the restrainer door to release a trapped cagemate can only be considered prosocial and empathically motivated if entrapment is aversive. This underlying premise was the key motivation for study 4, which represents an expansion of both Silberberg et al. (2013) and Hachiga et al. (2020), who investigate restrainer aversion in rodent social release. This study measured restrainer entries in two categories (partial and full), for both the free and the trapped rat. The key differences between study 4 and the previous studies (Hachiga et al., 2020; Silberberg et al., 2013) are that the experimental setting in study 4 uses a single arena with a centrally located restrainer and where the rats can socialise after opening. This design is therefore closer to that of Bartal et al. (2011), since neither Hachiga et al. (2020) nor Silberberg et al. (2013) had a design where both rats could freely explore the restrainer after opening. Study 4 also records positive USVs before and after restrainer door-opening, one of the possible relevant social stimuli in rodent release (Blystad, 2019). These kinds of USVs have not been systematically studied in the social release paradigm, so their role remains unknown. Study 4 has a few shortcomings, mainly concerning the degree of experimental control and level of detail in the observed behaviour. In short, we were unable to determine which of the rats made the USVs, the exact time at which the USVs were made, and what kind of positive USVs were made, as several subcategories of these USVs exist (Brudzynski, 2013, 2015). Additionally, noise pollution hindered collection of negative USVs around 22 kHz, which also could influence opening. Nevertheless, the data show that more positive USVs were made prior to opening, which supports previous research (i.e. Hachiga et al., 2020; Silberberg et al., 2013) and the conclusion that entrapment in the restrainer is not aversive in the social release paradigm. While studies of restraint stress certainly show negative effects of restraint on both behaviour and physiology (reviewed in Buynitsky & Mostofsky, 2009), the social release paradigm uses different procedures and experimental settings, which may perhaps explain the difference. Any negative effects of being trapped in a restrainer is perhaps ameliorated by the social situation in the arena, or by a reduction in neophobia across trials as theorised by Silberberg et al. (2013). Future studies should replicate Bartal et al. (2011), but with USV recordings that allow for collecting and sorting USVs not only into the positive and negative main USV categories, but also into the existing subcategories of USVs (as described in, for instance, Brudzynski, 2013, 2015). Additionally, it is necessary to know which animal produced the USVs and when.

The findings on restrainer entries in study 4 also support previous research concluding that restrainer entrapment does not cause aversive effects. The findings of study 4 show that after the free rat had released the trapped rat, both rats entered the restrainer several times. The trapped rat would not be expected to re-enter after release if restraining was aversive, but data in study 4 show that this is not the case. Furthermore, that study showed that the number of entries was comparable to that of the free rat, even though the free rat had no history of entrapment.

Taken together however, the findings of study 4 do not support the assumption that entrapment in the restrainer is an aversive experience for the trapped rat in the social release paradigm. Therefore, our findings question the assumption of restrainer aversion underlying the explanation of restrainer door-opening in the social release paradigm with reference to empathy. Instead, study 4 supports the social reinforcement explanation, but perhaps most of all highlights the importance of measuring all relevant social stimuli in the social release paradigm before labelling or explaining the observed behaviour.

The term ‘empathy’ in studies of rodent social release

Using the term ‘empathy’ to explain why one rat would release a trapped cagemate from a restrainer can also be quite confusing and problematic. Several different versions of empathy exist and are used in many fields of research. Research examples are found in brain imaging studies (Fan et al., 2011), applied behaviour analysis (Schrandt et al., 2009) and of course in animal research such as dogs (Sanford et al., 2018), rats (Bartal et al., 2011) and primates (de Waal, 2012), to name a few. However, a version that places empathy solely within the realm of behaviour has not been used in any studies of rodent social release. On the contrary, the definition of empathy employed in much rodent social release (e.g. Bartal et al. 2011, 2014, 2016) contained cognitive constructs that could not be reliably measured in rats. Cognitive constructs include caring for the trapped cagemate or wanting to relieve the trapped cagemate of distress. This concern has been raised before, and it has been suggested that rats could release a trapped cagemate without any sharing of emotion (Vasconcelos et al., 2012); that is, without empathy. The need to explain behaviour, including restrainer door-opening to release a cagemate, in terms of observable events is emphasised in study 3. Here, a novel conceptualisation of empathy is presented, which is based on previous experiments from applied behaviour analysis (Argott et al., 2017; Schrandt et al., 2009), studies of infant responses to distress (Missana et al., 2017; Sagi & Hoffman, 1976; Simner, 1971) and basic principles of behaviour. This conceptualisation puts behaviour back into empathy, after a recent review found behaviour not to be a necessary component; Cuff et al (2016) surveyed previous research that used empathy as a concept and attempted to assimilate these empathy conceptualizations into one definition. That assimilated definition of empathy did not contain behaviour, or behavioural measures (Cuff et al., 2016). Study 3 goes on to show how classical and operant conditioning could work together in the development and maintenance of empathetic responding. In short, it proposes that empathetic responding begins with a social cue that triggers affect. Affect then leads to a response with a mirrored social cue, which is either positively or negatively reinforced by either an increase or decrease in the social cue. With a measure of affect, either physiological, such as stress hormones, or behavioural, one advantage of this conceptualisation is that it can be used across different species. However, the main difference between the conceptualisation of empathy in study 3 and previous definitions of empathy, such as the perception–action model (Preston & de Waal, 2002), is not the responses to social cues or mirroring of affect, but rather the underlying behaviour analytic theory of empathy's development and continued maintenance. In short, study 3 presents a framework for how empathy can be developed and maintained using behaviour analytic terms. It is not presumed that this conceptualisation will be heavily adopted, but perhaps it can be of use to those who try to distance themselves from mentalism and cognitive constructs.

Problems with a ‘natural’ approach to behaviour in social release

Another problematic topic in the original study (Bartal et al., 2011) and in subsequent replications by the same author (Bartal et al., 2014, 2016) concerns the experimental design. More precisely, the lack of a baseline usually established during habituation/training prior to experimentation (see descriptions in, for instance, Hiura et al., 2018). None of the three papers by Bartal et al. (i.e. Bartal et al., 2011, 2014, 2016) demonstrate restrainer door-opening as a part of the rat’s behavioural repertoire before experimentation. Instead, the free rat is inserted into the arena with the cagemate already inside the restrainer. Opening to release a cagemate is described as a natural behaviour (Bartal et al., 2016) and that rats ‘teach themselves’ this opening behaviour (Bartal & Mason, 2018). The argument for this approach is that standardised operant conditioning procedures rely on reinforcers such as food, and the authors did not want the rat to associate the restrainer with a previous reinforcer (Bartal & Mason, 2018). It is also worth mentioning that this lack of conditioning during training is employed by others (i.e. Tomek et al., 2018, 2020). However, there are at least two potential problems with such an approach; one concerns the term ‘natural’ itself, and the other is how the lack of a baseline affects experimental control.

Natural behaviour is not a scientific or technical term to describe why a certain behaviour occurs, but rather invokes ecological validity. Ecological validity describes the kind of validity found in experiments where the setting is close to real-world situations (American Psychological Association, 2020; Schmuckler, 2001). However, ecological validity simply implies what is meant by natural in this matter. Study 1 looks to existing theories concerning the use of laymen and technical terms in psychology (e.g. Harzem, 1984, 1986; Ryle, 2009) and illustrates several issues using a non-technical term (i.e. natural) to describe the behaviours observed in the social release paradigm. Put briefly, the key issues as proposed in study 1 are: (1) risk of smuggling other descriptors (e.g. normal or robust), (2) risk of introducing claims not warranted by data or observations, (3) risk of committing a category mistake. In this instance, a category mistake could lead to natural behaviour becoming evidence for phylogenetical empathy while directly reinforced behaviour is caused by the organism's learning history (Blystad, 2019). Altogether, it seems unlikely that describing the behaviour in the social release paradigm as natural has any scientific value and should thus be avoided.

Lack of baseline is the other concern. Establishing a baseline enables an important comparison for later observations and proves that the necessary behaviour exists in the subject's behavioural repertoire. If the rat has not demonstrated restrainer door-opening, then reasons why opening occurs for the first time will not be known. Study 2 illustrates how baseline data can be collected in the social release paradigm, while also showing how to avoid the problem of the rat 'associating'[1] the food with the restrainer (Bartal & Mason, 2018). In brief, the baseline established with food in the restrainer is followed by a condition with an empty restrainer. This condition with an empty restrainer serves both to extinguish the opening behaviour and to demonstrate that opening was occasioned by the restrainer content. Directly following a condition with an empty restrainer, the cagemate conditions begin (Blystad et al., 2019). While concerns have been raised that the rats open the restrainer due to a previous learning history with food inside (Bartal & Mason, 2018), this may be responded to by looking at data presented in study 3. Rats opened fastest for a food reward, slowest with an empty restrainer, and intermediate when the restrainer contained a cagemate (Blystad et al., 2019). In summary, this pattern of fast, slow, and intermediate latencies does not indicate that the rats remember the food reward or that previous food reward controls opening. It is therefore suggested that future research using the social release paradigm employ a similar experimental design with baseline recordings before extinction and then testing in with a trapped cagemate.

The scientific discourse of rodent social release

The controversy surrounding the social release paradigm is sadly not reflected well in the current literature. For instance, a very recent paper attempted to disentangle factors that influence social release in rats shows some support for social reinforcement (Silva et al., 2020). However, the authors did not collect and measure all relevant social stimuli, and only cited two previous

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[1] After all, it is the researcher who associates the food with the restrainer, not the rat (Skinner, 1977).

papers critical of the empathy explanation of rodent social release; this severely understates the status of the current debate, as many authors remain unconvinced of the empathy explanation in rodent social release (Blystad et al., 2019; Hachiga et al., 2018; Hiura et al., 2018; Schwartz et al., 2017; Silberberg et al., 2013; Vasconcelos et al., 2012). This pattern of not referring to studies critical of empathic motivations is seen not only in Silva et al. (2020) but also in several other experimental studies (e.g. Quinn et al., 2018; Shan et al., 2016; Shinozuka et al., 2019; Tomek et al., 2018, 2020), a current review of animal models of empathy (Uysal et al., 2020), a recent study on the bystander effect in rats (Havlik et al., 2020), and a commentary on the promise of a novel empathy model in rodents (Venniro & Golden, 2020). This non-scientific practice gives the impression that the empathy explanation of social release in rats is much stronger than it is. In turn, this impression has consequences for novel research using the social release paradigm and for the strength of the findings in these studies. Shinozuka et al. (2019) is perhaps the most problematic of these examples, as it is a biomedical paper reporting on a rat stroke model, where effects of social modulation on stroke rat behaviour and physiology are described. In Shinozuka et al. (2019), the paper by Bartal et al. (2011) is uncritically used as evidence of rodent empathy, in blatant disregard of the scientific controversy that currently exists. Results will then be much harder to interpret, and conclusions weaker, considering how one of the premises for the paper (i.e. rat empathy) is not fully understood.

A brief point worth mentioning while discussing civilised referencing is the unfortunate practice of publishing one interpretation or perspective in one journal and a critical perspective in another. None of the papers by the original authors (i.e. Bartal et al., 2011, 2014, 2016) are published in the same journal as the critical responses (e.g. Blystad et al., 2019; Hachiga et al., 2018, 2020; Hiura et al., 2018; Schwartz et al., 2017; Silberberg et al., 2013; Vasconcelos et al., 2012). This may give a false impression of the current state of knowledge in a research area and lead to instances like the paper by Tomek et al. (2020). In Tomek et al. (2020) the researchers used social release to investigate effects of opioids and relevant brain areas, but only Bartal et al. (2011, 2014, 2016) were cited. However, considering the ubiquity of the modern internet, it should be possible to avoid this problem altogether. Additionally, reviews such as study 1 are invaluable for critically evaluating published findings, where research from both the empathy and the social reinforcement points of view are presented and discussed. Other reviews of rodent social behaviour exist, but these do not present the controversies concerning rodent social release (see for instance Keum & Shin, 2016 and Sivaselvachandran et al., 2016).

Limitations

In study 4 there were problems with the recordings of ultrasonic vocalisations. Before the study was planned, several recordings were made to ensure that the full sound spectrum necessary to collect both negative (22 kHz) and positive (50 kHz) sounds were obtainable. However, as the study began in earnest, a source of noise was detected on the recordings. This noise was in the ultra-high frequency band and the source could not be located. The noise made it impossible to identify negative USVs, which is why study 4 does not include them. While some preliminary findings have failed to find an effect of these negative USVs on social release (Bartal et al., 2011), collecting and analysing all USVs in the social release paradigm is needed to understand the behaviour. This should be remedied in future research, as both positive and negative USVs are potentially relevant influencers of social release in rats (Blystad, 2019). Our USV analyses were also limited by the lack of ability to identify which of the two rats made the USV and the exact moment when the USV was made. However, to the authors' knowledge, no research on social release in rats has investigated the positive USV. For that reason, the data in study 4 are still relevant and can serve as a starting point for future research.

In study 2, illumination was briefly investigated, and is given a few preliminary comments. As an environmental variable capable of influencing behaviour (Igarashi & Takeshita, 1995; Valle, 1970; Walker & Davis, 1997; Williams, 1971), illumination should be given proper attention. Study 2 does not do that but can hopefully inspire future studies to run a group design where one group is tested in the dark and one in the light, to properly measure effects of illumination on social release.

Additionally, in study 2, total trial length across conditions differs (five minutes for food, and empty vs 10 minutes for the other conditions with a trapped cagemate). This means that theoretically, even if most openings occurred within five minutes, there could be an effect on latency caused by difference in trial length. Future research should use the same maximum time across all conditions to control for such effects.

Finally, during the review process of study 2, it was pointed out that studies on social release should also account for the biological effects of hormones, both those relevant for the female oestrous cycle and stress hormones. This was not an option due to the lack of technical equipment in the animal facility, but it is an important point that should be given proper attention. This shortcoming is also found in the papers on which this thesis is based and in more recent studies of rodent social release (e.g. Bartal et al., 2011, 2014, 2016; Sato et al., 2015; Tomek et al., 2018).

Conclusion

When a new animal model is developed and demonstrated, much work is required to ensure validity and reliability, as many biases plague animal model research (Sjoberg, 2017). The exact path towards a valid animal model is not unanimously agreed upon. However, it is suggested that developing an animal model begins with a hypothesis about brain–behaviour relationships before subjecting it to testing and replication, followed by scientific and ethical evaluation (van der Staay et al., 2009). The current work presents several necessary steps to ensure validity and reliability of the rodent social release model first presented in Bartal et al. (2011). These steps include changes to experimental procedures in order to obtain more parsimonious results (study 2), development of novel conceptualisations to translate terms across species (study 3), systemisation of previous research that can be used to integrate all studies regardless of causal explanation (study 1), and preliminary findings regarding two possible influencers, positive USV and restrainer aversion, in the rodent social release paradigm (study 4).

In other words, the present thesis identifies areas for improvement and delineates how rodent social release research can move forward in such a way to allow us to better understand this phenomenon and how the brain serves this behaviour. Moreover, it seems that a similar approach could be taken in many existing animal models, especially those of social behaviour. Thus, generally speaking, this thesis attempts to answer the call for improving animal models in social neuroscience (Keysers & Gazzola, 2016, 2018) such that measurements of neural correlates can be obtained in a valid manner. It is impossible to understand the brain without first understanding the behaviour (Catania, 2000).

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A CRITICAL REVIEW OF THE RODENT SOCIAL RELEASE PARADIGM: EMPATHY OR SOCIAL REINFORCEMENT

UNA REVISION CRÍTICA DEL PARADIGMA DE LIBERACIÓN SOCIAL EN ROEDORES: EMPATÍA O REFORZAMIENTO SOCIAL

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Abstract

Research on social animal behavior is growing within social neuroscience. Basic research on behavioral processes in animals has always been the forte of behavior analysis, but the collaboration and crossover between the fields are minimal. This is illustrated with the well-established rodent social-release paradigm, which features two conflicting explanations: empathic motivations from social neuroscience, and social reinforcement from a behaviorist point of view. A three-term contingency analysis identifies areas within the studies of social release where more research is needed, and which is neutral regarding explanatory causes. This analysis allows for

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the integration of data from both the empathy and the social reinforcement point of view. This neutrality opens the way for collaborations and invites joint efforts to study and increase understanding of different variables in the rodent social-release paradigm.

Keywords: Social Neuroscience, three-term contingency, prosociality, animal models, rats

Resumen

La investigación sobre conducta social animal está creciendo dentro de la neurociencia social. La investigación básica sobre procesos conductuales en animales ha sido siempre el fuerte del análisis de la conducta pero la colaboración y traslape entre ambos campos es mínima. Esto puede ilustrarse con el bien establecido paradigma de liberación social, que involucra dos explicaciones en conflicto: motivaciones empáticas desde de la neurociencia social y reforzamiento social desde un punto de vista conductual. Un análisis basado en la contigencia de tres términos identifica areas dentro de los estudios de liberación social donde hace falta más investigación y que es neutral respecto a las causas en las explicaciones. Este análisis permite la integración de datos desde los puntos de vista de la empatía y el reforzamiento social. Este neutralidad abre el camino para colaboraciones e invita esfuerzos conjuntos para estudiar y aumentar la comprensión de las variables involucradas en el paradigma de liberación social.

Palabras clave: Neurociencia social, contingencia de tres términos, prosocial, modelos animales, ratas

Social behavior arises because one organism is useful to another as part of its environment. A first step, therefore, is an analysis of the social environment and any special features it may possess (Skinner, 1953, p. 298). The topic of this article is how the behavior-analytic three-term contingency could systematize studies and findings of animal models of social behavior. Additionally, the three-term contingency analysis reveals important areas for future research.

Modelling social behavior in animals is a topic of growing interest, especially in social neuroscience, the subfield of neuroscience focusing on the neural correlates of social behavior (Cacioppo & Berntson, 1992; Matusall, Kaufmann, & Christen, 2011). As a field of research, social neuroscience is marked by a multilevel integrative analysis of social, behavioral and cognitive data, but it does not seek to replace either behavior or social science (Decety & Cacioppo, 2010). This subfield of neuroscience traditionally has worked mainly with humans, but investigators acknowledge that data from animal studies should validate findings from humans (Decety & Christen, 2014), and that they are necessary when using the more invasive techniques that are needed to better understand topics such as empathy (Keysers & Gazzola, 2016). Not all social behavior can be modeled in animals (i.e., behavior reliant on language, or with human-specific features). However, several classes of behavior relevant to the field of social neuroscience (e.g., empathy, pro-sociality) show degrees of evolutionary conservation (de Waal, 2012; Decety, Bartal, Uzefovsky, & Knafo-Noam, 2016; Decety, Norman, Berntson, & Cacioppo, 2012; Pérez-Manrique & Gomila, 2018), inviting investigation in nonhuman animals. While prosocial is defined as "actions that are intended to benefit another" in both the most relevant experimental paper on social release (Bartal, Decety, & Mason, 2011, p. 1427) and in recent conceptual work (Jensen, 2016), empathy is more broadly used. As many as eight different phenomena have been identified as empathy in social-neuroscience, but a conceptual discussion of the term is beyond the scope of this review. Readers are advised to see Cuff, Brown, Taylor, & Howat (2016) or Pérez-Manrique & Gomila (2018) for further discussion. The most relevant use of empathy is in the first social-release paper, which used empathic concern described as "an other-oriented emotional response elicited by and congruent with the perceived welfare of an individual in distress" (Bartal et al., 2011, p. 1427).

Within social neuroscience, behavioral animal studies are the point of origin, and once the behavior is adequately understood, the social neuroscientist moves on to investigating neural correlates of the behavior. For instance, mutual reward preference in rats was demonstrated (Hernandez-Lallement, van Wingerden, Marx, Srejic, & Kalenscher, 2014) before neural correlates were investigated (Hernandez-Lallement, van Wingerden, Schäble, & Kalenscher, 2016). However, the step from behavior to neural correlates can be problematic.

Whereas a molecular level of understanding of both behavior and influencing factors is necessary to avoid causal mistakes in neuroscience (Krakauer, Ghazanfar, Gomez-Marin, MacIver, & Poeppel, 2017), behavior is often a neglected part of modern neuroscience that has focused more on technological than conceptual advancement (Le Moal & Swendsen, 2015). This present review elucidates that problem with a selected literature review of a specific animal model using the behavior analytic three-term contingency. This approach continues the implementation of behavior analysis into neuroscience and vice versa. Such implementation is important to properly understand behavior (Moore, 2002; Skinner, 1974), and some even argue that both fields are subfields of biology with a logical fitness (Donahoe, 1996, 2002, 2017). That is not to say it is unproblematic. As Schaal (2005) stated, some of the concerns about neuroscience are with studies that retain mentalistic explanations, disregard the learning history of the organism being studied, and how the past necessarily has shaped the brain. However, the current critical review uses the three-term contingency to systematize selected studies and findings with a recent animal model, and thus will avoid mentalism that otherwise could prove problematic.

The exemplar animal model that is the subject of this review is one suggested for prosocial behavior: the rodent social-release paradigm (Bartal et al., 2011); however, the approach should prove useful with any behavioral animal model. Prosociality, with its related topic of empathy, has not been studied much within behavior analysis (however, for a presentation see Schlinger, 1995), but is important and relevant within social neuroscience (Batson, 2009; Decety & Lamm, 2006). Using rats instead of humans to investigate social behavior allows a broader range of neuroscientific tools, and even if the animal subjects cannot self-report, rats do exhibit specific responses to social situations with conspecifics. Two examples are social facilitation (i.e., the mere presence of conspecific influences responses; Weiss, Segev, & Eilam, 2014) and emotional contagion (i.e., an emotional, behavioral reaction that occurs on perceiving the emotion of others, as when witnessing conspecifics in pain; Carrillo et al., 2015). Additionally, rats communicate positive and negative affect via ultrasonic vocalizations (USVs) (Kim, Kim, Covey, & Kim, 2010; Willadsen, Seffer, Schwarting, & Wöhr, 2014), reviewed by Brudzynski (2013). They also use odor-based communications (Debiec & Sullivan, 2014).

In addition to investigating important topics within social neuroscience, the social- release paradigm was chosen as it has been subjected to critical replication from a behavioral perspective (Hachiga et al., 2018; Hiura, Tan, & Hackenberg, 2018; Schwartz, Silberberg, Casey, Kearns, & Slotnick, 2017; Silberberg et al., 2013), which offered an alternative explanation of social release based on social reinforcement. The present review offers a framework for integrating all previous research, regardless of causal explanations (empathy vs social reinforcement). This review makes a similar claim to that of earlier researchers that to understand the brain it is necessary to understand behavior (Catania, 2000; Krakauer et al., 2017; Le Moal & Swendsen, 2015). Before presenting and discussing the three-term contingency analysis, however, it is necessary to describe the social-release paradigm in detail.

Animal Models of Social Behavior: The Social-Release Paradigm

The social-release paradigm features a pair of cage mates, where one rat is trapped inside a clear plastic tube (Bartal et al., 2011) known as a restrainer. Being thus trapped causes both behavioral and physiological stress-like effects in rats (Ely et al., 1997; Paré & Glavin, 1986). The restrainer can be opened from the outside either by manual interaction with the door (e.g., tipping it open with the head and/or forelimbs) or by leaning on a counterweight extending from the top of the door. One rat is trapped in the restrainer, and the trial begins once the second rat is put into the experimental space. The dependent variable is latency to door opening. The free rat is removed if door opening does not occur within a predetermined time. In the original experiment, 60 min max time was allowed before removing the rat if it did not open the restrainer door (Bartal et al., 2011), but our research with a different habituation and training design indicates that a much lower (<10 min) max time can be used (Blystad, Andersen, & Johansen, 2019). A latency analysis showed that (1) after first opening the door the latency goes down and remains short throughout the remainder of the trials, (2) latency goes down and remains short even if the released cage mate cannot physically interact with the free rat after being released (Bartal et al., 2011). The main interpretation of the latency results has been empathic concern; perceiving the trapped cage mate motivated prosocial door opening. A role of social stimuli is indicated by the result showing that the number of rats that opened increased when the restrainer contained a cage mate when compared to an empty restrainer. Independent variables in this procedure are different manipulations of the experimental environment such as social learning history (Bartal et al., 2014), drugs (Tomek, Stegmann, & Olive, 2018) or stress (Sato, Tan, Tate, & Okada, 2015).

In a second variant of the social-release paradigm, the experimental arrangement described above was slightly modified. Sato et al. (2015) trapped and soaked one cage mate in a water-filled area and separated the soaked cage mate from a free rat with a transparent plastic wall. The wall contained a door that could only be opened from the free rat's side. The side of the trapped rat contained water, from which the trapped rat would try to escape. Again, the free rat could approach the door to open and release the trapped rat, thus creating a similar design to that of Bartal et al. (2011). Sato et al.'s results were consistent with Bartal et al. (2011) in that the free rat opened the door, releasing the soaked cage mate. Claims of rodent empathy by Sato et al. (2015) and Bartal et al. (2011), however, have not gone uncontested. In a commentary on Bartal et al. (2011), Vasconcelos, Hollis, Nowbahari, & Kacelnik (2012) suggested that prosocial behavior could be described without including elements of empathy; namely without any sharing of emotions. This was the case for explaining similar helping behavior in ants. In that study, ants released a tied down ant from the same colony (Nowbahari, Scohier, Durand, & Hollis, 2009). Furthermore, in a replication of Bartal et al. (2011), Silberberg et al. (2013) suggested that social contact and time-dependent degradation of neophobia, a fear of new objects, could explain the observed release of the cage mate. Similarly, in a replication of Sato et al. (2015), Schwartz et al. (2017) found that the helping behavior also could be explained by the reinforcing property of proximity to water in addition to the effects of social reinforcement.

This criticism has spurred another approach to the social-release paradigm spearheaded by behaviorists. Focusing on social contact and social reinforcement, Hiura et al. (2018) used the social-release paradigm to investigate social reinforcement. They set out to do an "… analysis of social contact as a reinforcer, measured in multiple ways, relative to food reinforcers, and as a function of price and motivational variables" (p. 5). To this, they added that empathy-based explanations would be made superfluous if the behavior could be explained in terms of social reinforcement (Hiura et al., 2018). Thus, Hiura et al. echoed Silberberg et al.'s (2013) assertion that social contact after the trapped conspecific was released was a necessity for such releasing to occur.

Empathic concern vs. social reinforcement

Terminology and design have differed greatly between social-release experiments rooted in behaviorism (Hiura et al., 2018) or social neuroscience (Bartal et al., 2011; Sato et al., 2015; Tomek et al., 2018). Although reviews of rodent models of empathy exist (e.g., Sivaselvachandran, Acland, Abdallah, & Martin, 2016), no attempts have been made to integrate and review both social reinforcement and empathy-based studies of rodent social release. Research from either field contributes little to the other. The criticism of the empathy explanation might be addressed briefly before being discarded (Tomek et al., 2018) or not even mentioned at all (Shan, Bartal, & Mason, 2016). Thus, the three-term contingency will be used to analyze and systematize selected data from the social-release paradigm. With the three-term contingency, these two main approaches to the problem can be included in a manner that remains neutral regarding causality, but which elucidates what has been investigated and what is lacking.

A Three-Term Contingency Systematization

The traditional three-term contingency consists of behavior antecedents (stimulus, A), behavior (the response occasioned by a stimulus, B) and consequences (reinforcement, C) (Skinner, 1953). However, research on the social-release model also focuses on previous conditions of the organism itself. To add this level of analysis, an organism (O) is included in Table 1, which summarizes the social-release research. From a neuroscience perspective, the O is where future neural manipulations will occur (such as in Hernandez-Lallement et al., 2016); however, for the behavior analyst the O could perhaps be removed in that antecedents encompass the organism's learning history (i.e., neural manipulations or neuroactive drugs).

The O term also encompasses the motivating operations (MO) concept. In fact, the MO began as an expansion of the three-term contingency, originating within Skinner's radical behaviorism (Nosik & Carr, 2015). The MO concept has been expanded considerably in recent years. According to Laraway, Snycerski, Olson, Becker, & Poling (2014. pp. 3) MOs "…(a) influence the capacity of operant consequences (reinforcers and punishers) to alter the strength of future behavior (the value altering effect) and (b) change the current strength of behaviors related to the consequences affected by the MO (the behavior altering effect)." As an aside, there is also the related concept of setting events, which too is used to describe variables outside of the three-term contingency. However, although setting events could be relevant as a more complex version of the MO or establishing operations (EO) (Danforth, 2013), setting events are not functionally defined (Nosik & Carr, 2015). Lack of a functional definition can serve to confuse, and for that reason, the MO concept serves a better purpose in the present analysis. This is not to say that others will not find a purpose for setting events in research on social animal models. It is simply beyond the scope of the current paper.

Table 1. Three-term contingency analysis applied to social-release paradigm research

Research papers	**O: Organism level manipulations**	**A: Antecedent recordings/Sd**	**B: Behavioral recordings**	**C: Consequence**
Bartal et al., 2011a	No manipulation	23kHz USV (L=), Undefined stimuli emitted by trapped rat (L–)	Latency to open and release, Choice between release of cage mate and chocolate	Socialization after release (L–), Release without socialization (L–), Access to chocolate treats (L=)
Silberberg et al., 2013b	Group based learning histories. Group 1: Learning to open without trapped cage mate, Group 2: Learning to open with trapped cage mate	Undefined stimuli emitted by trapped rat (L–)	Latency to open and release	Socialization after release (L–), No socialization after opening for more time, (L+). Group 1 did not learn to open.
Bartal et al., 2014a	Social Learning History (L + / L–)	Undefined stimuli emitted by trapped rat (L–)	Latency to open and release	Socialization with: Familiar trapped rat (L–), Unfamiliar trapped rat (L+)
Sato et al., 2015a	No manipulation	Undefined stimuli emitted by stressed, soaked, trapped rat (L–)	Latency to open and release	Socialization after release (L–)
Bartal et al., 2016a	Anxiolytics (L+)	Undefined stimuli emitted by trapped rat (L–)	Latency to open and release	Socialization after release (L–)
Schwartz et al., 2017b	No manipulation	Undefined stimuli emitted by stressed, soaked, trapped rat (L–)	Choice between different boxes (empty, water filled, trapped rat)	Access to content in box (water, empty area, rat)
Hiura et al., 2018b	No manipulation	Undefined stimuli emitted by trapped rat (L–)	Lever press for access to socialization	Socialization after release (L–) with schedules for social reinforcement
Tomek et al., 2018a	Heroin (L+)	Undefined stimuli emitted by trapped rat (L+)	Latency to open and release	Socialization after release (L–)

L+ : Increase in latency
L– : Decrease in latency
L= : No effect

[a] Empathy as cause
[b] Social Reinforcement as cause

Table 1 organizes data from experiments using the social release paradigm into a three-term contingency, with the added O to specify organism level manipulations.

Table 1 shows that the focus of previous investigations using the social-release paradigm has been on the consequences of opening, with additional investigations into effects of organism-based manipulations (i.e., social learning history, anxiolytics and opioids). Only Bartal et al. (2011) have investigated specific antecedent stimuli, and in that case only in terms of the role of stress-induced 23kHz ultrasonic vocalizations. However, considering that no control experiments were performed in either their experiment or in subsequent replications, it is uncertain whether 23kHz USVs have a central role or not. In other words, little is currently known about discriminative stimuli for opening behavior in the social-release paradigm, which is necessary for investigating the relevant parts of the central nervous system. This bridge between social behavior and neural activity is not only the concern of social neuroscience (Cacioppo & Berntson, 1992; Matusall et al., 2011) but also the behaviorist seeking to more fully understand behavior-environment relations (Moore, 2002; Skinner, 1974). Without knowing which stimuli serve as SDs for social release, moving on to neural investigations is troublesome, as the behavioral observations lack necessary detail (Krakauer et al., 2017) ;"If we fail to understand the behavior, we will probably also fail to understand how the brain serves it" (Catania, 2000).

The following sections explore how to increase knowledge about antecedent stimuli missing from Table 1, which is where special features of the social environment relevant to the organism will be found (Skinner, 1953). Based on these explorations, suggestions are made on how to improve measurements via technical equipment and design. Following this, other terms in the three-term contingency are given the same treatment. Necessary, or relevant, parts of each of these terms will be suggested for both empathy and social reinforcement explanation of social release. For the sake of clarity, antecedent social stimuli are divided into three categories; auditory, visual and olfactory.

Antecedents to Social Release: USV

Although separated by the restrainer, rats still can communicate via different categories of USVs. These USVs are especially interesting for social neuroscience as they seem to have different points of origin within the rat brain depending on whether they are emitted in appetitive or aversive situations (Sadananda, Wöhr, &

Schwarting, 2008). This makes them prime targets for neural manipulation. These USVs have been investigated in one experiment. Those in the category of 23kHz were recorded in the original experiment (Bartal et al., 2011). These 23kHz USVs are expressed in stressful and aversive situations (Brudzynski, 2013), and primarily occur when rats have conspecifics nearby (Kim et al., 2010). Although Bartal et al. (2011) claimed that they did not record enough USVs to influence opening behavior (i.e., that the rats acted to stop these sounds), a control experiment was not performed (e.g., playing back the recorded sound to measure increase or decrease in latency to prosocial action). Furthermore, USV recording was not included in any of the replications (Bartal et al., 2014; Bartal et al., 2016; Silberberg et al., 2013; Tomek et al., 2018). The aversive 23kHz vocalization is one of many sonic and ultrasonic modes of vocal communication in rats. Another category of USVs is in the range of 50kHz, and these sounds are associated with different social behavior than those in the 23kHz range (Seffer, Rippberger, Schwarting, & Wöhr, 2015; Willadsen et al., 2014). These occur primarily in positive situations (Brudzynski, 2013). Although it would be speculative to assign one category of USV importance over the other in social-release paradigms, the existence of multiple categories should not be subjected to negligence as the degree to which they are involved in the measured behavior remains unknown. Control experiments with animals' incapable of making USVs are one way to control for the influence of these social stimuli (e.g., via surgical devocalization, or optogenetic interventions to turn the brain areas responsible for vocalization on and off). Another way would be to undertake playback experiments. Playing back USVs could either begin or stop after prosocial action to assess whether USVs act as positive reinforcers (prosocial action produces appetitive USVs and thereby becomes more probable) or negative reinforcers (prosocial action terminates aversive USVs and thereby becomes more probable) for prosocial behavior. Optimally, these playback experiments allow for measuring USVs in the previously mentioned categories, as these categories may have different roles in the social-release paradigm.

Antecedents to Social Release: Odorants

Odors as social stimuli are common in rats and serve many different social functions such as searching for a mate (Ferkin, 2018), discriminating between conspecifics (Carr, Yee, Gable, & Marasco, 1976), and communicating fear (Debiec & Sullivan, 2014). The behavior that brings rats in contact with odorants, sniffing, functions to communicate the rat's role in the social hierarchy (Wesson, 2013). Additionally, albeit in mice, odor alone recently was reported to induce hypersensitivity to pain (Smith, Hostetler, Heinricher, & Ryabinin, 2016).

Although it is technically challenging to experimentally control and measure, the significance of odorants for prosocial behavior invites investigation. For example, the experimental arrangement could involve giving the conspecific time in the restrainer and then removing it before testing the free rat for opening behavior. The restrainer would then be empty but retain odorants from the previously trapped rat. Another approach would be to block the sense of smell entirely via surgical interventions, similar to what recently was shown in mice to impact health and obesity (Riera et al., 2017). No investigation of the possible role of odor has been undertaken in the social-release paradigm. For that reason, whether odor is an antecedent or a consequence and can influence social release, remains an empirical question.

Antecedents to Social Release: Visible Behavior

While USVs and odorants are stimuli that require advanced technical equipment to manipulate, measure, and analyze, visible behavior is more readily accessible for experimental manipulation and recording. It is also the only social stimulus that has been experimentally shown to affect prosocial behavior: displayed behavior in one rat is known to influence behavior in the experiments on prosocial reward sharing (Marquez, Rennie, Costa, & Moita, 2015). That observed behavior influences actions in the observer rat is described in the research literature: emotional contagion in rats (Atsak et al., 2011; Carrillo et al., 2015), social fear learning (reviewed in Debiec & Olsson, 2017) and other behavior learned via observation (Galef, 1982). This leads to the conclusion that the displayed behavior, perhaps especially of the recipient of prosocial action, should be monitored closely.

Antecedents to Social Release Summarized

It is currently not known which social stimuli have the most significant influence on prosocial or empathy-like behavior. Possibly, it is not one single stimulus but a combination of them that controls or influences prosocial behavior. The reviewed literature on USVs, odorants and visible behavior shows the potential importance of these stimuli for social and possibly also prosocial behavior. Thus, these stimuli should be investigated in future experiments and added to Table 1 to make a more comprehensive understanding of the controlling variables of social release. These improvements are necessary because of the proclaimed goal in social neuroscience of understanding neural correlates of social behavior (Cacioppo & Berntson, 1992; Matusall et al., 2011).

In order for an empathy explanation of the behavior to hold in the social-release paradigm, the relevant antecedents will be those that communicate negative emotions (i.e. distress) from the trapped rat. A theoretical experiment could make use of trapped rats that are unable to communicate via one or two modalities (i.e. USVs, odors). If no known emotional communication is relevant for social release, then that would severely discredit the interpretation of empathic concern made by Bartal et al. (2011). In fact, an empathic concern account with the three terms would need an SD such as aversive USV or visible behavioral distress, without which social release does not occur. If the trapped rat does not emit any stimuli that would indicate aversiveness towards entrapment, then releasing it could hardly be described as either prosocial or empathic. Such a description is not found in any research that appeals to an empathy account of social release (Bartal et al., 2011, 2014, 2016; Sato et al., 2015; Tomek et al., 2018).

Social reinforcement, however, does not require the discriminative stimulus for social release to be indications of aversiveness towards entrapment from the trapped rat; the consequence (i.e. social interaction) is what matters. Nonetheless, the existence of social reinforcement in rats (demonstrated in Hachiga et al., 2018, Schwartz et al., 2017 and Silberberg et al., 2013), does not exclude empathic distress. However, the empathy account currently remains the least causally proven one.

Behavioral Recordings in Studies of Social Release in Rats

Table 1 does not list considerable variation in behavioral recordings of the responses in the social-release paradigm. Although different experiments used slightly different response requirements from opening by tipping over a door (Bartal et al., 2011; Sato et al., 2015) to door opening upon activation of a sensor bar (Silberberg et al., 2013), these different topographies have not themselves been investigated. Some behavior will be more similar to existing behavior in the animal's repertoire (tipping open a door by using claws or head versus activating a sensor bar). Although the function of the response is the same–opening the restrainer – the difference in topography could affect latency and other measures of behavior. The importance of requirements is illustrated by Blystad et al. (2019). Even if the rats had lever pressed for door opening before testing with food inside the restrainer, they manually interacted with the door to open it and access the food (Blystad et al., 2019). The reinforced response was subjected to topographical drift in which the function remains the same, but the response topography changes (Breland & Breland, 1961). When the food was replaced with a cage mate, the animals persisted in the manual interaction topography instead of lever pressing (Blystad et al., 2019). Summarizing, no comparisons are made thus far, and so any effect of different topographies is unknown.

A related issue is that the baseline response latency needs to be established before testing for social release. Establishing the baseline, and even the existence of a response topography within the behavioral repertoire, often is found in the procedure section where descriptions of magazine training or habituation are made. Following response shaping or training, the animal demonstrates the operant response (examples can be found in Hiura et al., 2018; Tan & Hackenberg, 2015; and Vandbakk, Olaff, & Holth, 2018). Although door opening was shown to be in the behavioral repertoire in the soaked-rat model before testing prosocial action (Sato et al., 2015), this was not the case in Bartal et al. (2011). The latter found that the rats opened to release a cage mate after several days (±7), even if the rats had not been subject to any prior conditioning. Door opening was not trained in the follow-up experiments of Bartal and colleagues either (Bartal et al., 2014; Bartal et al., 2016). In one instance, the finding that rats open to release a trapped cage mate is referred to as *natural behavior* (Bartal et al., 2016, abstract). Whether or not laboratory experiments have much ecological validity has been debated (e.g., Schmuckler, 2001), and as such the term *natural behavior* is perhaps not fitting. Using a lay term like *natural behavior* also bears the risk of falling into the language trap, because the description of *natural behavior* is an unempirical language construction (Harzem,1986). In other words; the term "natural" is merely an artifact of language, it does not exist in a measurable or objective manner. A consequence of using "natural" can be that other descriptors are smuggled along with it, such as normal, or robust, as no word from ordinary languages has a singular meaning (Harzem, 1986). Additionally, such operationism of lay words run the risk of introducing claims not warranted by the data or observations themselves (Harzem, 1984). Category mistakes may also occur, where *natural* behavior is caused by other reasons than behavior that is not *natural* when it belongs to the same logical category (Ryle & Tanney, 2009). For instance, opening the restrainer with a directly reinforced behavior (Blystad et al., 2019), may not belong to a different category than *natural* opening after repeated exposure to the restrainer with a trapped cage mate (Bartal et al., 2011). A consequence is the category mistake where *natural* behavior becomes evidence for a phylogenetic empathy, while directly reinforced behavior is caused by the organisms learning history. Additionally, the *natural* description can be used to justify not measuring environmental variables, which lowers experimental control and predictability. Furthermore, the term "natural" holds little explanatory power (Hempel & Oppenheim, 1948). Describing behavior as "natural" does not contribute to understanding why the observed behavior happens. The term "natural" lacks the focus of the pragmatic selectionism inherent in behavior analysis, as pragmatic selectionism guides the researchers in answering "how things comes to be"-questions (Moxley, 2003). Pragmatic selectionism then circumvents the need to describe the occurring behavior as natural; accounts of experiments will be technical and observable descriptions of the environment (i.e., social stimuli) and the behavior.

Consequences

The experiment by Hiura et al. (2018) on the effects of social reinforcement is one of the most thorough with respect to design and terminology. One useful detail in their design is the use of schedules of reinforcement (Hiura et al., 2018). Different schedules of reinforcement generate different response rates and patterns (Ferster & Skinner, 1957). The study of social behavior by using schedules of reinforcement allows for investigating the strength of the social reinforcement by comparing one kind of reinforcement with another in the same schedule (Hiura et al., 2018) such as alcohol and narcotics (Caine & Koob, 1994; Spoelder et al., 2015). Table 1 illustrates that differences in the consequence of opening has been investigated, but aside from Hiura et al. (2018) the choices have been binary (i.e., another rat or an empty restrainer). Implementing different schedules of reinforcement could provide more information regarding the reinforcing value of the consequence. No social-release experiment with an empathy explanation has investigated reinforcement strength of the claimed empathic response. The closest is perhaps an experiment in Bartal et al. (2011) in which the rats could open the door to a restrainer with a cage mate or open a second door to access chocolate chips. More than half of the female rats opened the restrainer with the cage mate first, and chocolate chips second (Bartal et al., 2011). However, binary choices combined with a latency measure are poorly suited for measuring reinforcement strength. A social-release experiment to investigate reinforcement strength properly would require a response rate measure; single responses (such as those in Bartal et al., 2011, 2014, 2016; Sato et al., 2015) are less than optimal. Topographies could be restricted so that only multiple lever presses will open the restrainer door (i.e. using an intermittent reinforcement schedule). The rate of the door opening could be compared between changes in restrainer content (i.e. cage mate, empty or food). This resonates with Hiura et al. (2018), who showed that food had a stronger reinforcement value than social contact, but that the reinforcement strength of social contact increased with social deprivation. Additionally, latency to open for food in food deprived rats is also lower than for a cage mate (Blystad et al., 2019). If social release is governed by reinforcement in the same way as behavior in general is controlled by other reinforcers (e.g. food, water), then it follows that patterns of social release responses during different schedules of reinforcement (e.g. continuous, intermittent) should be lawful as well and follow the same regularity as observed for food or water reinforcers. Finding the same regularity support the interpretation that social release is controlled and maintained by social consequences (e.g. social contact). However, if the same regularity is *not* found, then two options present themselves. Either the reinforcer in the social-release paradigm is incorrectly identified, or the behavior is not controlled by reinforcers in the same manner as with traditional reinforcers such as food or water. Regardless of outcome, this would be a valuable contribution to the research field.

Summary of the Three Terms and Strategies for Further Experiments

The social reinforcement and empathy approaches both attempt to explain observations in the social-release paradigm. A three-term contingency analysis systematizes requirements for these two approaches. Antecedents in the social reinforcement approach do not have to be social, but the consequences do. Additionally, prior social deprivation is expected to increase social reinforcement preference. Indeed, this has been shown by Hiura et al. (2018). In that experiment, involving rats pressing levers for social reinforcement, there was a higher production of social reinforcement during social deprivation. Social reinforcement, however, does not exclude an empathy interpretation since the social interactions are not incompatible with prosocial behavior.

An empathy account of social release predicts that the SD is a stimulus that communicate distress of the trapped rat (e.g. stressful USVs, visually observable behavior, odors). Visual and auditory stimuli of distress affect rat behavior (Brudzynski & Chiu, 1995; Carrillo et al., 2015), but whether these stimuli function as SDs for social release remains unclear. That the trapped rat emits stressful 23kHz USVs has been shown (Bartal et al., 2011), but it has not been shown that this specific stimulus is necessary for social release. On a related note, there has been no attempt to record positive USVs. An empathy account of social release further predicts that positive USVs should not serve as SDs for opening since they are not expressing distress, but appetitive situations (Brudzynski, 2013).

The consequence must be fewer distressing stimuli (i.e., the previously trapped rat stops expressing 23kHz USVs or showing visible behavior/emitting odors indicating stress, after it has been released). In other words, empathy in social release is negative reinforcement, where the reinforcer is removal of distress. A stronger account of empathy would have additional requirements regarding how the free rat perceives the trapped rat, which is a part of the empathic concern definition used in Bartal et al. (2011). This is closer to the cognitive variant of empathy that uses the theory of mind (ToM) concept of visualizing the point of view of others (Baron-Cohen, Leslie, & Frith, 1985). However, ToM is not investigated, or measured in any way, during research on social release. In other words, the cognitive aspects of empathy in social release should probably be discarded, but the version of empathy similar to negative reinforcement can be preserved.

One prediction of an empathy interpretation, without cognitive aspects, is less distress stimuli post release. This could easily be tested with an experiment in which release causes more distress stimuli than entrapment (e.g., the release activates electrical grids which shocks the trapped rat). Under such circumstances, being trapped might be “preferable”, and empathic concern could not explain opening. No such experiment has been conducted. From a social reinforcement approach, while it would seem likely that the free rat would continue to release the trapped rat for social interactions, this may not be so because of shock effects on the released rat (i.e. freezing or in other ways displaying discomfort). In other words, social interaction with a rat that has just been shocked may not be positive reinforcement, and failure to open seem possible.

Conclusions

A framework for systematizing and integrating previous research on social release, regardless of causal explanations (empathy vs social reinforcement), has been presented. Social reinforcement is relevant for social release (Hachiga et al., 2018; Hiura et al., 2018; Silberberg et al., 2013), but this relevance does not exclude a possible effect of empathy. An empathy account would predict that the SD for social release are stimuli indicating distress in the trapped rat and that this distress ends upon release. Thus, an empathy account, without cognitive constructs, for opening behavior in the social-release procedure is negative reinforcement. However, when prior research was analyzed within a three-term contingency framework, it was suggested that little is known regarding antecedent stimuli, social or otherwise. A full survey of relevant antecedent stimuli (i.e. stimuli related to distress) seems to be needed. This systematization with a three-term contingency also could be used on other animal models, perhaps especially those subjected to different theoretical and experimental approaches. In brief, the presented three-term contingency approach allows for behavior- analytical contributions to the field of social neuroscience to improve both existing and new animal models.

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Study 2:

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RESEARCH ARTICLE

Female rats release a trapped cagemate following shaping of the door opening response: Opening latency when the restrainer was baited with food, was empty, or contained a cagemate

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Abstract

Research on pro-social rat behaviour is growing within the fields of comparative psychology and social neuroscience. However, much work remains on mapping important variables influencing this behaviour, and there is even disagreement on whether this behaviour is empathetically motivated and correctly labelled pro-social, or whether the behaviour is motivated by social contact. The present study used the helping behaviour paradigm where a rat can release a familiar cagemate from a restrainer. Prior to testing with a trapped cagemate, restrainer door opening was trained and baseline opening latencies when the restrainer was empty or baited with food were established. The findings show that the first-time release occurred sooner than in previous research and that rats used a previously demonstrated response to release the trapped cagemate. Further, rats opened the restrainer door more often and with shorter latencies when the restrainer contained a cagemate than when the restrainer was empty, but less often and with longer latencies than when the restrainer contained food. The test of whether illumination levels affect door-opening included in the study showed no effects.

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Introduction

The importance of empathy is made most salient by its absence or dysfunction as evidenced in disorders like autism [1,2], schizophrenia [3,4] and psychopathy [5,6]. Additionally, empathy dysfunction is found in several other psychopathologies [7]. For non-clinical settings, studies on school bullying indicate that a lack of empathy, or low levels of empathy, is a contributing factor [8,9]. Moreover, the relationship between empathy and bullying might be reciprocal [10]. The term empathy originates from a description of feeling at one with aesthetic experience and was proposed to denote the feeling/understanding of the thoughts and behaviour of others [11]. Psychology has a long tradition of experimentally studying empathy (for instance [12,13]), but the emergence of social neuroscience in the nineties [14] offered novel methods and opened for new lines of research. However, there is no single definition of empathy. Researchers in these fields have operationalised empathy in many different ways [15]. In an attempt to distil operationalizations into a single definition, Brown and colleagues arrived at a definition without a behavioural measure which was unfortunate as behavioural measures are paramount for animal studies [15]. Animal research, on the other hand, has identified some possible behavioural measures, specifically pro-social behaviour, which mirrors studies on pro-social behaviour and empathy in humans [16,17]. Animal studies of pro-social behaviour allow for the employment of neuroscientific techniques necessary for understanding the neurobiological bases of empathy and the aetiology of previously mentioned empathy-affecting disorders [18].

Many species engage in pro-social or helping-behaviour, e.g., dolphins [19], ants [20], rats [21], and a wide array of primates [22]. Neural correlates of different empathy responses in rodents indicate common mechanisms in the central nervous system [23]. Brain imaging studies in humans also support the existence of specific neural structures involved in empathy [24]. Taken together, these different findings on animal helping behaviour and neural correlates of empathy support conserved evolutionary mechanisms of empathically motivated helping-behaviour [25]. However, the findings above do not mean that empathy is expressed to the same degree or in the same manner across species. Indeed, species differing in social and cognitive abilities will most likely display different empathic abilities [26] which are in line with theories regarding empathy as having an evolutionary basis [7] (see a comprehensive review of comparative studies of empathy and sympathy in [27]). Animals that are living in social groups, such as rats, would then be expected to show a higher degree of empathic reactions than solitary species.

Early studies indicated that rats selectively react to the distress of cagemates [28] and also show forms of altruism [29] (but see [30] for early discussions and critique). Studies have shown emotional contagion in rats, where one rat responded with freezing behaviour upon observing another rat exhibiting freezing [31,32]. Social communications have also been observed in rats; they express socially relevant information transmitted through ultrasonic vocalizations (USV) [33] (reviewed in [34]). Rats also acted instrumentally to benefit other rats by sharing food, as long as they experienced no cost themselves [35] and the recipient showed food-seeking behaviour [36].

Helping-behaviour was observed in the experiments of Bartal, Decety & Mason [21] where a free rat released a trapped rat from a Plexiglas tube restrainer. They claimed not only that the rats showed helping behaviour, but that it was motivated by a form of empathy [21]. In follow-up studies to Bartal and colleagues seminal paper, researchers have demonstrated the influence of social learning history, anxiolytics and opioids on the helping behaviour of rats [37–39]. However, rigorous experimental control and detailed knowledge about influencing variables are needed to draw firm conclusions regarding the observations (i.e., empathic motivations and pro-social intentions). This point has been accentuated theoretically by researchers [40] and experimental findings [41–43], and it is now debated whether restrainer opening door to release a cagemate is empathically motivated or is motivated by social contact.

The current study used a slightly modified version of the procedure described by Bartal et al. (2011) and was not to designed to separate between possible empathic motivations or social contact. In fact, in accordance with this uncertainty, we will in the following use the neutral and purely descriptive term “door opening” for restrainer door opening resulting in the release of a trapped cagemate. This neutral term avoids labelling behaviour according to assumed controlling or motivating factors (e.g. prosocial door opening, helping).

The present study aims to control for potential confounding variables overlooked in previous studies, and is based on the procedure developed by Bartal et al. with the following additions/modifications:

1. Rats were required to demonstrate opening for a food reward to ensure that door opening was in the rats' behavioural repertoire before testing with a trapped cagemate.
2. After exhibiting door-opening with a food-baited restrainer, rats were tested for door-opening with an empty restrainer to show that opening and latency was controlled by the content of the restrainer.
3. Only after completion of key points 1 & 2 were the rats tested with a trapped cagemate.

The inclusion of these procedural steps served three related purposes. First, by shaping responding and demonstrating that door-opening is in the rats' behavioural repertoire prior to testing door opening with a trapped cagemate, the learning of door-openings is not left to "accidental" side effect of exploration. Second, testing for door-opening latency when the restrainer is baited (food) or empty provides essential baseline comparisons for interpreting door-opening latency with a trapped cagemate. Interpreting door opening to release the trapped cagemate as pro-social behaviour is problematic if the latency is the same when the restrainer is empty as when a cagemate is trapped inside. Third, the comparison of door-opening latency when the restrainer contains a cagemate with latency when the restrainer contains food reinforcers offers information about the relative strength (reinforcer value) of the two stimuli (cagemate/food) in controlling behaviour.

Additionally, we did a preliminary investigation of the effect of a change in illumination on door openings. Rats are nocturnal animals, and bright light has been described as anxiogenic inducing a fear response [44] and increasing the fear-related startle reflex [45]. Other rat behaviour is also affected by illumination, e.g. maze exploration [46] and social play [47] in addition to physiological measures [48]. Level of illumination also influences rat behaviour in an open-field test [49–51], which is a larger version of the experimental setup in the current study. Effects of illumination have not previously been investigated in the helping behaviour paradigm, and as no measures of stress are included in the study, the test is only preliminary. Hopefully, it can serve as inspiration for studies that investigate this experimental variable more systematically on a more granular level and with the necessary additional measures of stress.

Materials and methods

Subjects and housing

Thirty female Sprague-Dawley rats, 100 days old and weighing 150-200g, were purchased from Janvier, France. The animals were randomly divided into 15 couples and housed in transparent cages (412 x 25 x 25). Cohabitation for 14 days began upon arrival at the animal facility in order to establish cagemate relations between the randomly coupled rats. After the cohabitation period in a single home cage, the rats were housed in separate cages, and one rat from each couple was food-deprived during behavioural training. Food deprivation lasted for a total of 10 days, and daily weighing ensured that no rat lost more than 15% of its free-feeding weight. Rats that were food deprived were given smaller rations of standard chow and housed in adjacent cages to maintain social bonds during food deprivation and the separated living phase. This housing situation avoided depriving both animals of food, but enabled the animals to maintain social vocalization, transmission of odours, and observation of behaviour. Additionally, the rats were given 1 hour per day to socialize in a neutral cage except during the weekend. Following food deprivation, the animals were housed together and given food and water ad lib. One couple was removed from the study due to deviant behaviour caused by incorrect deprivation during the shaping procedure. The study was approved by the Norwegian Animal Research Committee (ID# 7966). All procedures for housing and euthanasia were performed at the Department of Biosciences at the University of Oslo (https://www.mn.uio.no/ibv/english/). Daily inspections by the main author, in addition to the in-house animal technicians and veterinarian ensured the animal welfare. All animals were euthanized with carbon dioxide gas.

Experimental apparatus and technical equipment

The experiment was run in a 0.5*0.5m plastic-glass box, with 0.5m high walls. Matte black duct tape covered all walls to prevent mirror-like reflections. A small metal pipe, extending from the leftmost wall out of the arena and connected to a 5*5cm square metal box positioned in the leftmost corner, was used to administer reinforcers (i.e., food pellets) during magazine training and subsequent behavioural shaping. The experimenters inserted a modified restrainer (Panlab, Harvard Apparatus, Holliston, MS, USA), which is a clear plastic tube with doors on both sides, into the arena during shaping. See Fig 1 for details.

Illumination of the experimental room was measured with a light meter (TES-1337 Digital wd1Light Meter, TES Corporation, Taiwan). Fluorescent ceiling lights were turned on during habituation, the two sessions when the restrainer contained a trapped cagemate (sessions 12 and 13), and during the light phase when testing effects of illumination (sessions 14 and 15). The average and median illuminations were 385 and 407 lux with lights on, and 1 lux with lights off, respectively. These lux values will be referred to as “light” and “dark” through the remainder of the paper. A vertically mounted digital video-camera (Panasonic HC-V160, Panasonic Corporation, Japan) recorded behaviour during testing.

Procedure

The rats underwent habituation to the arena, magazine training, and three phases of hand shaping using the method of successive approximations:

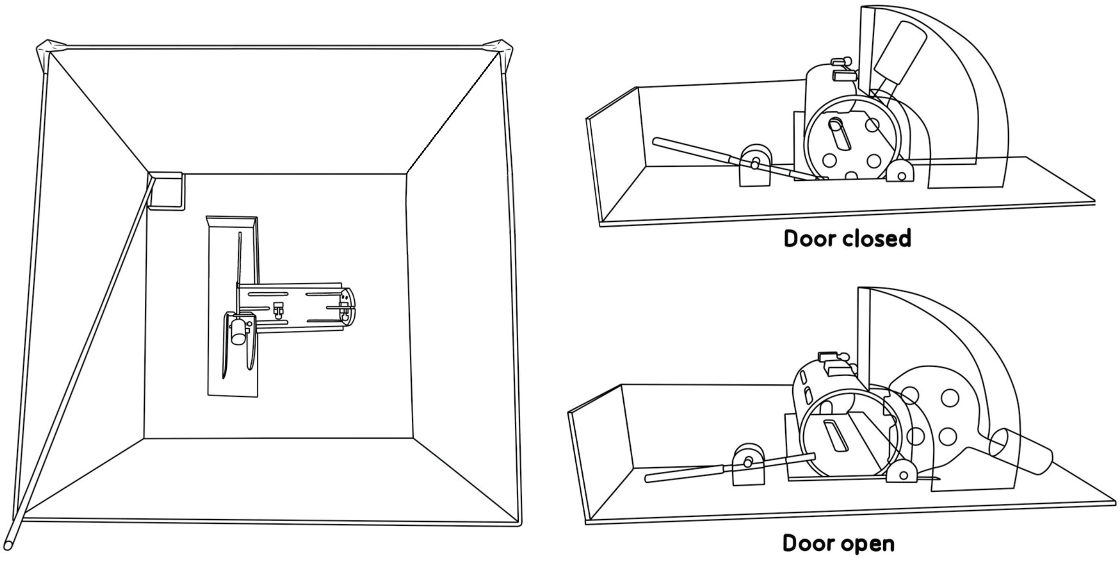

Fig 1. Arena with restrainer. The metal pipe for administration of food reinforcement extended out of the arena on the leftmost side. Right: The door opening mechanism of the restrainer; a lever can be pushed down to tip open a door attached to a counterweight.

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1. The first phase consisted of location shaping; food was administered when the rats ventured into the quadrant of the arena with the opening mechanism, door and food box.
2. The second phase consisted of more precisely based location shaping; food was administered when the rats spent time by the door opening mechanism.
3. The third phase consisted of presenting food rewards for engagement with the lever, pressing or pushing it down, causing the door to open.

The rats transitioned gradually at individual paces through the three phases. All animals acquired the lever pressing response before proceeding to the next condition testing with food in the restrainer. Both restrainer doors were open for exploration in the first day of shaping. In condition Food through DL, one door was always closed while the other could be opened from the outside using either a lever-press, tipping the door open with paws/head, or tipping over a counterweight. If a trapped rat escaped, a plastic cap was fitted inside the restrainer to prevent access to the door, similar to Bartal et al. (2011). Then, the rat was re-inserted before restarting the trial.

No animals were tested on Saturdays or Sundays. Lights in the animal facilities were on between 7 am to 7 pm. During each session of testing, four trials were run. Training and test-conditions up to session 15 were performed in the light phase of the rats' ultradian rhythm, as their day-and-night cycle was not inverted in the animal facilities where the animals were kept when not tested. The 15 experimental sessions took place over 15 days, see Table 1 below for an overview of the experimental conditions.

Eight students assisted in the experiments, and each of the rat-couples was assigned one set of handlers for the entirety of the experiment; two student laboratory assistants and the primary author. To minimize noise in the data, a detailed experimental protocol was developed, and all students underwent a training program in animal handling and experimental testing under the auspices of the main author. The laboratory assistants were continuously supervised by the main author to ensure that protocols for laboratory conduct and experimental procedures were followed. The following measures were taken to reduce effects of single housing

Table 1. Overview of experimental conditions across sessions.

Session	Condition	Restrainer content	Description
1	Magazine Training	No restrainer	Habituation to the arena. Response-independent food delivery. Food deprivation, average bodyweight decline was 1.4% (range 0–2%)
7-Feb	Three shaping phases	Empty	Shaping of location in the arena and opening of restrainer door. Food deprivation: average bodyweight decline was 7.8% (range 6–12.7%)
8–10	Food[a]	Food pellets	Food placed inside the restrainer. Food deprivation: average bodyweight decline was 10.6% (range 7.5–14.3%)
11	Empty	Empty	Restrainer empty. No food deprivation, average bodyweight fully recovered[c] (range 0–1.5%)
12–13	Trapped cagemate Day 1 & 2[b] (CM1,CM2)	Cagemate	Test for opening restrainer door. No food deprivation, average bodyweight fully recovered[c] (range 0–2.2%)
14	Light to dark (L-D)	Cagemate	First trial light, then dark-dark-light. No food deprivation, average bodyweight fully recovered[c] (range 0–0.7%)
15	Dark to light (D-L)	Cagemate	First trial dark, then light-light-dark. No food deprivation, average bodyweight fully recovered[c] (range 0–3%)

[a] The last three trials of the Food and Empty condition were used for analysis.

[b] Three rats did not increase latency to open when the restrainer was empty. These three were tested with an empty restrainer for one additional day and did not complete Trapped cagemate Day 2 (session 13).

[c] Same weight as at age 114 days.

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and food deprivation when proceeding to subsequent conditions: 1) The rats were allowed to play and socialize for 1 h each day in a separate cage and were housed in adjacent cages to maintain social bonds, and, 2) 60 h of co-habitation and food *ad lib* took place before proceeding to the next condition.

Measures

To assess the effects of shaping, video-recordings of behaviour during session one, four and seven of were analysed using the Ethovision XT software package (Noldus, Netherlands). Heat maps (Fig 2) show how behaviour gradually changed following the shaping procedure. The first day, the rats explored the arena and spent most time close to the walls, the corners, and around the restrainer. By day four of behavioural shaping, the movement had become more restricted to the area where food pellets were delivered. On the seventh day of shaping, the rats spent most of the time in the top left corner of the arena.

We measured latency to open the restrainer door, opening topography (technique), and occurrence of aggressive behaviour after opening. All measures were obtained by manually inspecting the video recordings with VLC media player (VLC Mediaplayer, VideoLAN) on a Microsoft Windows computer.

Latency was defined as the time from the rat was inserted into the arena, with no part of the experimenter visible on the video-screen, until the opening of the restrainer door. In all conditions, there was limited time available for restrainer door opening before the trial was terminated. The time limit (maximum latency) was 5 min during the Food and Empty conditions (sessions 8–11), and 10 min in the other conditions (sessions 12–15). In case no door opening occurred within the time limit, latency was set to maximum (i.e., 5 min) to enable quantitative comparisons across conditions. Max latency was higher during pro-social testing to give ample time for cage mate release to occur, as this was the main focus of the study. Although we used different max latencies across conditions, a latency score of 300 has a comparable meaning in all conditions; no opening took place during the first 5 minutes. Still, the different max latencies across conditions introduces a possible ambivalence in interpreting the results because the consequence of not opening was different across conditions (i.e. the animal was left in arena for 5 or 10 min).

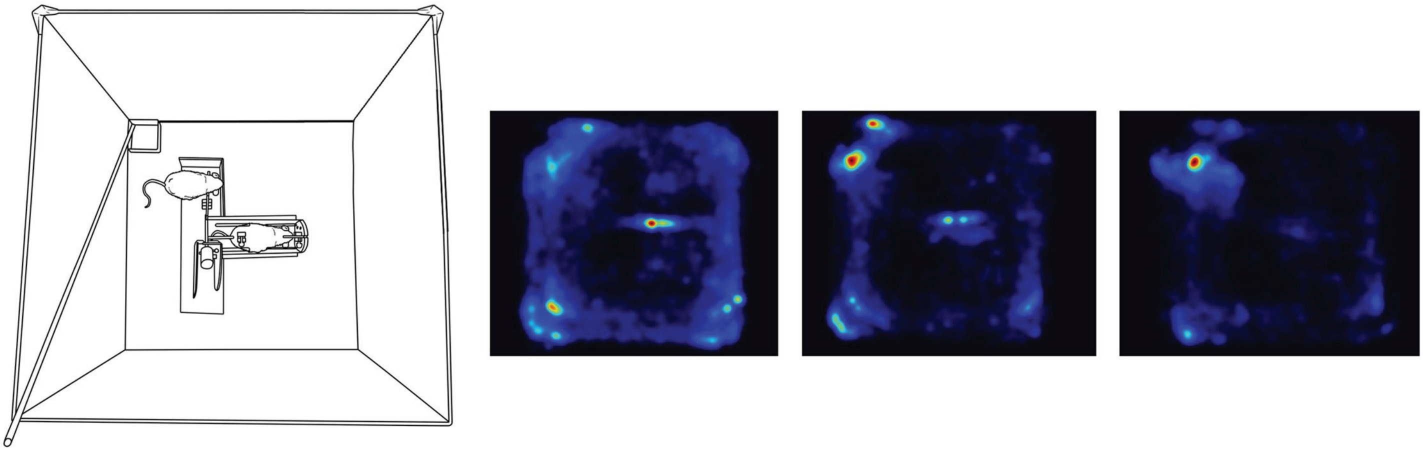

Fig 2. From left to right: Overview of the arena, day 1, day 4 and the last day (7) of shaping. Rats were given food reinforcement for spending time in the quadrant (top left corner) of the box containing the opening mechanism, door, and food box. Red/bright blue areas indicate areas where the rats spent the most time during the trials.

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The rats could use one of three response topographies (door-opening techniques) to open the restrainer door: Pressing the lever, tipping the door open with paws/head, or tipping over the counterweight. In the shaping procedure, only lever pressing was reinforced. However, in the following condition when the restrainer was baited with food, the rats started to tip the door open using their paws or head. Although this response topography was not reinforced during the shaping procedure, it served the same function as lever presses and consequently belong to the same operant class [52]. Due to the change in response topography prior to testing with a trapped cagemate, the opening topography used by the animals in the Food condition termed "Food-reinforced openings" was used for scoring correspondence with opening topography in the subsequent conditions with a trapped cagemate.

Aggressive behaviours were defined as instances of biting or pinning, during the interplay between the rats following the release of the trapped cagemate.

Statistical analyses

The study employed a within-subjects design, in which all rats underwent the experimental procedure in the same order (Table 1) with a few exceptions. Three rats were exposed to one additional Empty session due to short latencies during the first Empty session. These short latencies could perhaps be explained by prolonged food deprivation effects even though the weight was regained at this point (Table 1). For these rats, this additional session was used in the analyses, and they also did not complete Trapped cage mate Day 2 where imputations were made (below). Analyses of these three rats separately showed latencies that did not contribute differently than the other rats in any condition. Therefore, all animals were included in the following statistical analyses.

Each session included four trials. The first trial was excluded from the statistical analyses for two reasons: 1) Prior to testing, the animals were moved from the sleeping quarters to the experimental room. During transport, they were exposed to sounds and smell in addition to shaking and movement that was suspected to affect test results, and 2) During some conditions (e.g. empty, the first with trapped cage mate), the first trial was the first time the animals came in contact with the new contingencies; the consequence of door opening would have had no previous opportunity to affect behaviour.

Average door opening latencies across the conditions were analysed with a non-parametric Friedman test, followed by multiple pairwise comparisons using Nemenyi's procedure / Two-tailed test. Wilcoxon signed-rank test / Two-tailed test was used to compare door opening latencies in the dark vs light conditions. An alpha level of 0.05 was used for all statistical tests, and all statistical analyses were performed with Xlstat (Addinsoft, 2019).

Imputations and outliers

In order to run the Friedman test, 18 (7.1%) missing trial data points were replaced by imputations. For three rats in the Trapped cagemate Day 2 condition, missing data from nine incomplete trials were replaced. Additionally, mechanical failure led to loss of one data point in Trapped cagemate Day 2, five in condition L-D and three in condition D-L.

Visual inspection indicated one or two outliers in some of the conditions in the dataset. To investigate this, we ran double Grubbs test. The double Grubbs test revealed one outlier in condition Food, Trapped cagemate Day 1, Trapped cagemate Day 2, and DL, respectively. These outliers were removed and imputed. All trial and average imputations were made with the MD Imputation function in Statistica (Statsoft Inc., 2014) which uses the k-nearest neighbour algorithm.

Results

Number of trials to the first door opening, topography, and behaviour following door opening

In the present study, door opening was first shaped and then reinforced by food to ensure that the behaviour was in the animal's repertoire before testing with a trapped cagemate. The first occurrence of door opening to release a cagemate was observed in 12 out of 14 (85%) subjects in trial one during day 1, and 13 out of 14 (≈93%) rats opened in at least one out of the three trials.

The rats employed the food-reinforced opening topography 77.9% of the time across all conditions with a trapped cagemate. Inter-observer agreement for opening topography was 95% across the conditions Food, Trapped cagemate Day 1 & 2, L-D and D-L.

Visual observations of the recorded interplay between the rats following the release of the trapped cagemate revealed no instances of biting, pinning or other aggressive behaviours in any sessions and will not be discussed further.

Door opening latency across conditions

Door opening latency was shortest under the Food condition, longest during the Empty condition, and of intermediate duration in the remainder conditions (Fig 3).

The comparisons of conditions were done with was done with a non-parametric Friedman test. The Friedman test rendered a Chi square value of 42.122, which was significant (p>0.0001). Multiple pairwise comparisons using Nemenyi's procedure / Two-tailed test was run after the significant Friedman test to investigate which conditions were different from each other. The Nemenyi's procedure showed that the Food condition was statistically significantly different from all other conditions except the DL illumination condition where the *p*-value was just shy of significance ($p = 0.056$); the Empty condition was statistically significantly different from all other conditions except the CM2 condition; and none of the four conditions with a trapped cagemate were statistically significantly different from each other (see Table 2).

Door-opening occurred in 100% of the trials except when the restrainer was empty where opening occurred in only 71.4% of the trials. (Fig 3, solid line). The cumulative incident plot (Fig 4) illustrates the different opening latencies with individual door openings represented as steps in the lines.

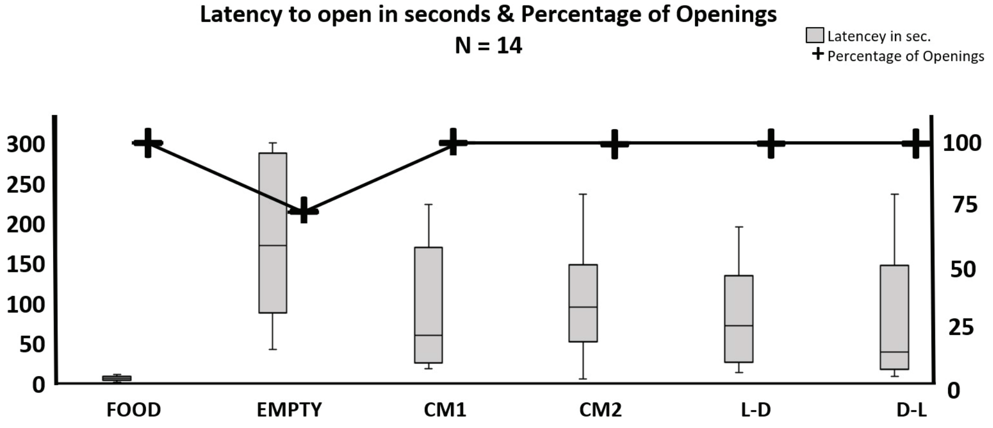

Fig 3. Door opening (boxplot) and percentage of openings (solid line) across the experimental conditions (left and right ordinate, respectively). Door opening latency based on mean of three trials was shorter when the restrainer contained a trapped cagemate than when it was empty but longer than when the restrainer contained food. The box whiskers extend to the most extreme data points lying within 1.5 interquartile range. The percentage of openings were calculated by number of subjects that opened the restrainer door at least once during the condition, divided by total number of subjects.

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Table 2. Nemenyi's comparisons of condition.

	FOOD	EMPTY	CM1	CM2	LD	DL
FOOD	0	**-4.500**	**-2.357**	**-2.857**	**-2.429**	-2.000
	$p = 1$	**$p < 0.0001$**	**$p = 0.0013$**	**$p = 0.001$**	**$p = 0.009$**	$p = 0.056$
EMPTY	**4.500**	0	**2.143**	1.643	**2.071**	**2.500**
	$p < 0.0001$	$p = 1$	**$p = 0.032$**	$p = 0.189$	**$p = 0.043$**	**$p = 0.006$**
CM1	**2.357**	**-2.143**	0	0.500	0.071	0.357
	$p = 0.013$	**$p = 0.032$**	$p = 1$	$p = 0.981$	$p = 1.000$	$p = 0.996$
CM2	**2.857**	-1.643	0.500	0	0.429	0.857
	$p = 0.001$	$p = 0.189$	$p = 0.981$	$p = 1$	$p = 0.991$	$p = 0.831$
LD	**2.429**	**-2.071**	0.071	0.429	0	0.429
	$p = 0.009$	**$p = 0.043$**	$p = 1.000$	$p = 0.991$	$p = 1$	$p = 0.991$
DL	2.000	**-2.500**	0.357	0.857	0.429	0
	$p = 0.056$	**$p = 0.006$**	$p = 0.996$	$p = 0.831$	$p = 0.991$	$p = 1$

Critical difference: 2.0314

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In order to visualize possible differences on a trial-by-trial level, the average score for each trial within each condition was graphed. Food showed a stable low latency, Empty showed a rising high latency, and all condition with a trapped cagemate had semi-stable, intermediate latency scores (see Fig 5).

Illumination: No significant effects

Light and dark sessions were compared in order to investigate effects of illumination. The average latencies were 89.9 s for dark, and 82.7 s for light. A non-parametric Wilcoxon signed-rank test / Two-tailed test did not reveal any significant differences between sessions in the light vs in the dark ($p>0.05$).

Discussion

The present experiment studied door opening to release a trapped cagemate using a modified procedure developed by Bartal et al. (2011) which included demonstration of door opening

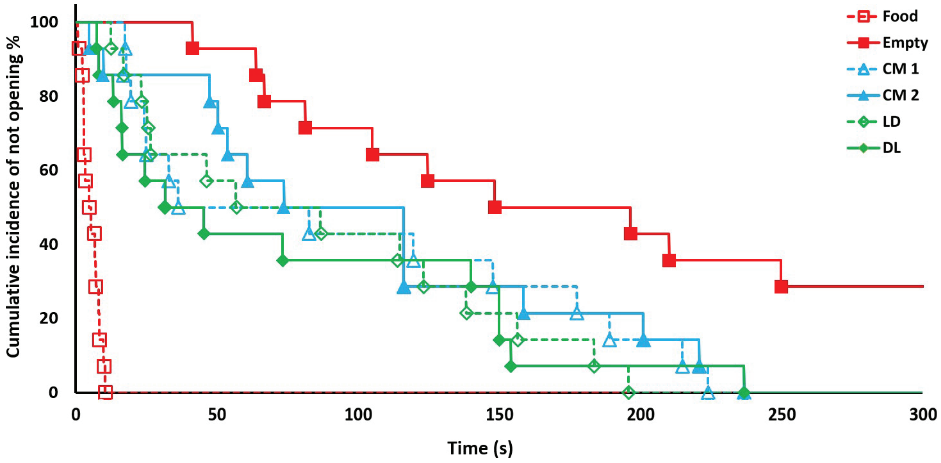

Fig 4. Cumulative incident plot showing percentage of not opening across time. All conditions with a trapped cagemate (CM1 through DL) show a decline with a steepness in-between the Food and Empty conditions. Each step down represents rat(s) opening the restrainer in the different conditions and are based on subject mean latency of the three trials in each condition.

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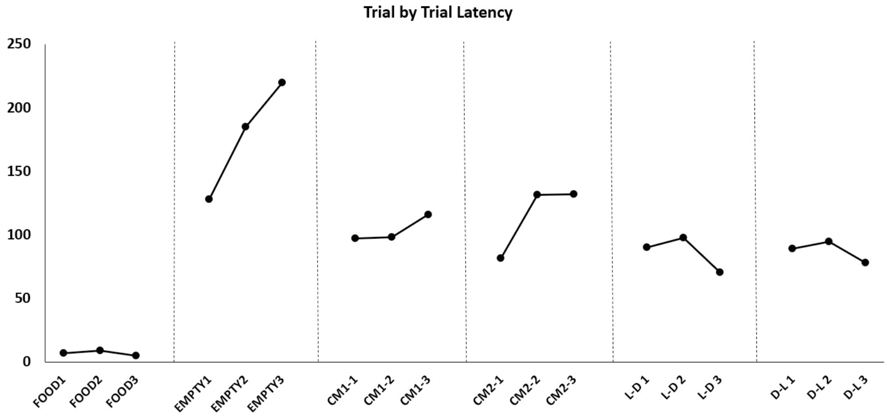

Fig 5. Average data illustrated in Figs 3 and 4 broken down into individual trials. The Food condition had the lowest and most stable latency, the Empty condition had a rising latency across trials, and the conditions where the restrainer contained a cagemate had a semi-stable pattern with an intermediate latency compared to Food and Empty.

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and baseline recordings before testing with a trapped cagemate. Additionally, the effects of illumination on door opening were examined. The findings show that door opening topography to release a cagemate was largely the same as when the restrainer was baited with food. The first occurrence of restrainer door opening to release a trapped cagemate took place during the first few trials. Door opening latency was shortest when the restrainer contained food, intermediate when the restrainer contained a cagemate and longest when the restrainer was empty (see Figs 3–5). Door openings occurred in 100% of the trials when the restrainer contained food or a cagemate, and in 71.4% of the trials when the restrainer was empty (Fig 3, solid line). Finally, door opening latencies to release a cagemate was not different across the two levels of illumination when all trials were analysed.

Door opening—Shaping, first occurrence, and topography

In the present study, door openings were shaped before door opening latencies when the restrainer was empty or contained food were examined. This procedure served three main functions. First, by explicitly training door-opening, the acquisition of this behaviour was not left to chance but was controlled by the experimenter. In previous studies, no shaping procedure was in effect [21,41]. Thus, the occurrence of the first door-opening in these experiments was not experimenter-controlled, but spontaneously emitted by the rat as it roamed around freely and explored the arena. Second, the inclusion of the two control conditions where the restrainer was either empty or contained food provided essential baseline comparisons for interpreting latencies during later testing with a trapped cagemate. Third, latency comparisons across these conditions reveal the degree and relative strength to which the restrainer content control door opening.

In the present study, food was used to train door opening in all rats before testing with a cagemate. Sato et al. (2015) reported that the stimulus used to shape door opening in rats (food or helping a soaked cage-mate) affected subsequent choice. They found a higher proportion of pro-social behaviour in the group trained to open the door for a soaked cage-mate compared to the group trained to open for food reinforcers. However, when the two groups were presented with the choice between opening one door leading to food and another door letting the soaked cage mate out of the pool area, they found that first-choice latency was not different in the two groups. The implication for the present study is that learning door opening in the context of a trapped cagemate may be different from learning door opening through a shaping procedure with food reinforcers, thus, type of reinforcer used during the shaping procedure may affect the data.

Across the seven days of shaping, the rats spent more time in the area containing the lever opening the door, around the door itself, and by the food delivery box (Fig 2). Subsequent shaping, all rats demonstrated proficiency to open the door to obtain food and did so on 100% of the trials with short opening latencies. However, during this condition, a shift in response topography was observed. Lever pressing, reinforced during the shaping procedure, was replaced by tipping the door open by the paws or head. This change in response topography may have occurred because some response topographies are more similar to natural behaviour than other responses [53]. If some responses are easier to learn and maintain than others, this may also affect response rates or latencies used to assess effects of variables and conditions and have implications for the experimenter's choice of response to release the trapped rat in experimental studies (e.g. lever press, nose poke) and for comparisons of data (i.e. latencies) across studies. It also emphasizes the importance of including a training procedure to ensure that the response is in the rat's repertoire prior to testing with a trapped cagemate. In the present study, the response topography to access food in the restrainer was the same as when opening the door to release the cagemate (77.9% correspondence). In the present study where door openings were shaped, the first occurrence of restrainer door opening to release a trapped cagemate took place during the first few trials. In Bartal's study, where no shaping procedure was included, one week of testing was needed before door opening was observed (Bartal et al., 2011). This difference is likely due to the pre-training procedure used in the present study. Without pre-training, the first occurrence of door opening is not controlled by the experimenter but emitted by the animal as part of exploration or general locomotion. Thus, responses not frequently found in the behavioural repertoire may take many trials to spontaneously occur. In Bartal's study [21], this introduced a long and uncontrolled learning history, both for the trapped as well as the free rat, that may have affected the data. This could have been avoided if a pre-training procedure had been included but had the advantage that the response was learned in a social context, which may be of importance (Sato et al. 2015).

Opening latency and percentage openings across conditions

The comparisons across conditions of door opening latencies and percentage of trials containing door-openings showed that restrainer content affected both measures (Fig 3). The latency was shorter, and a higher percentage of trials contained door-openings when the restrainer contained a cage-mate as compared to when the restrainer was empty. This difference indicates that some aspect(s) of freeing the trapped rat acted as a reinforcer(s) for the free rat's door-opening. Previous findings suggest that several stimuli in the experimental setting may reinforce door openings, e.g. social contact or water [41,54]. The reinforcing stimuli in the present experiment could be several of these, but the present study was not designed to isolate and identify these reinforcers.

It may be argued that the data can be explained in terms of an extinction process or as a "transferred situation even when the outcomes are different". Extinction is by definition the discontinuation of the reinforcement of a response, e.g. door opening; in the present study defining all trials following the Food condition. Studies show that during extinction, rate of previously reinforced responses returns to operant level, i.e. the level observed before responses were reinforced. General findings show that the extinction curve is a gradual decline in responding but may also initially include an extinction burst (the organism "tries harder" for a period) before rate of responding declines. The pattern of decreasing and then increasing latencies found for the conditions following food reinforcement in the present study does not conform to known extinction curves and runs counter to extinction as an explanation of the findings. Further, the suggestion of "transferred situation" implies a similarity between the reinforcement condition (Food) and subsequent conditions (Empty, cagemate) and that some situations are more similar that others causing differences in results across conditions. Across the conditions in our study, most preceding stimuli are the same although we cannot rule out the possibility of smell- (food, trapped cagemate) and sound-differences (vocalizations by trapped cagemate) across conditions that may have influenced behaviour. However, this possibility disagrees with the suggestion of similarities between situations. The consequences for opening the restrainer door obviously differ across conditions. It is conceivable that when the restrainer contains a cagemate, this consequence is more similar to when the restrainer contains food than when it is empty, and that this similarity causes the rats to open the restrainer door with shorter latencies than when the restrainer is empty. This suggestion implies that door openings are maintained during all cagemate trials by similarity to the Food condition and not by some aspect of freeing the cagemate acting as a reinforcer. If this explanation were to be true, one would expect that the rats learn to discriminate between the two consequences (food, cagemate) and stop responding towards the last cagemate-trials (Figs 3 and 5). After all, the rats are obviously able to discriminate between when the restrainer contains food and when it is empty (Figs 3 and 5), and quickly learn to do so. The stable pattern of latencies observed across trials in our study (Fig 5) suggests that the data is not explained by similarity between situations.

The food-condition produced shorter latencies than when testing with a trapped cagemate. Reinforcer value is not a unitary concept, and there are several accepted measures of reinforcement value in the literature [55]. However, given that latency reflects reinforcer value, our results indicate that food has a higher reinforcer value than freeing a cage-mate. These results are at odds with Bartal et al.'s (2011) findings of similar latencies to open the restrainer door for chocolate chips and to free a cage-mate, and who concluded that reinforcer value for accessing chocolate chips and freeing a cage-mate was the same. Additionally, a key point in Sato et al. (2015) is the usage of a setup with a soaked cagemate, and in their study they found that opening to release a cagemate was the first choice more often than opening to access food. This seems to be at odds with our finding that the latency to open was much faster in the food condition than in three out of the four conditions with a trapped cagemate (CM1, DL and LD). However, crucially for food to serve as a reinforcer for behaviour is hunger, and unlike this study, the rats in Sato et al. (2015) did not undergo food deprivation. This seems to be the likely reason why the rats in our study showed a lower latency for food than for most of the conditions with a trapped cagemate and illustrates the importance of investigating factors that influence reinforcer strength.

Several procedural differences between the studies may explain the inconsistent findings. Of particular importance is that both the Bartal et al. (2011) and Sato et al. (2015) studies used chocolate chips as reinforcers for responding in undeprived rats, whereas we in the present study used standard rat food for responding in rats weighing no less than 85% of free-feeding weight. Reinforcer values are not fixed but depend on past and immediate learning history including satiation and deprivation (as discussed in [56]). It is likely or possible that the motivating operation of food deprivation used in the present study increased the reinforcer value of food up and above the value of freeing a cage-mate or the value of chocolate chips in undeprived rats. Thus, the conflicting findings in the three studies may illustrate limitations to external validity—i.e., that findings are limited to the specific experimental manipulations used, including reinforcer type (food, chocolate chips, water), reinforcer amount, and deprivation level.

Illumination was briefly investigated in this study but did not yield any significant effects. Neither light, nor dark, settings were associated with positive or negative effect on helping behaviour. However, this study used a setup where rats were habituated and tested in the brightest setting, and additionally the rats were tested during the light-phase of their day/night cycle. Due to these limitations, we cannot dismiss that a study with a larger group, and with a design that controls for light cycle and illumination during habituation, can discover effects of illumination on door opening for cagemate release. Preferably, this should be replicated with a between-group design in which one group is tested in the dark and the other in the light. This replication should also include behavioural and biological measures of stress.

Summary and conclusion

The presents study investigated restrainer door opening in rats using the helping paradigm developed and described by Bartal et al. (2011), but with a few changes to the experimental procedure used in the original study. First, a shaping procedure was included to ensure that the door-opening response was in the rats' behavioural repertoire prior to pro-social testing. Additionally, the rats were tested when the restrainer was empty or food-baited to establish essential baseline comparisons for interpreting percentage of openings and opening latency during pro-social testing.

In the present study, the first occurrence of pro-social door-openings was observed during the first few trials of testing with a trapped cagemate. In Bartal's study (2011), it took approximately one week of testing before door opening was observed. This is likely due to differences in training and habituation procedures in our (shaping with food reward) and Bartal's (2011) (always trapped rat, no direct shaping) studies.

Our data shows that the rats opened the restrainer door with shorter latencies to release a cagemate than when the restrainer was empty, but with longer latencies than when the restrainer contained food (Fig 3). This suggests that food is a more potent reinforcer to a food-deprived rat than releasing a cagemate is to a rat not deprived of food. The food deprivation procedure used in the present study is the probable explanation for the shortest opening latency found when the restrainer was baited with food, a finding that is somewhat at odds with Bartal's findings (2011). A future study should investigate the effect of deprivation and choice between opening for a cagemate and opening for food. Choosing between food and releasing a cagemate when the rat is hungry would also give more indication regarding the reinforcing value of releasing a trapped cagemate.

Illumination was briefly investigated in this study but did not yield any significant effects. We suggest a proper between-group experiment with one group habituated and tested in the dark vs one group habituated and tested in the light to properly address this environmental variable. This should also include proper measures of stress, both biological and behavioural.

Trial-by-trial latencies indicate that stable state was not reached in all conditions, and this should be addressed in future research. Stable state behaviour has not been a point of focus in prior research either, with some papers only recording one response per day [21,41]. If a stable state was reached, this could possibly yield clearer results between Empty and other conditions in the present study, as the behaviour in Empty shows an increase in latency throughout trials (Fig 4).

There is a difference in total trial length across conditions, with 5 minutes for Food and Empty vs 10 minutes for the other conditions with a trapped cagemate. Even if the results show that most openings occurred within 5 minutes during conditions with a trapped cagemate (see for instance Fig 5), a theoretical possibility remains that this difference in trial length could affect the results. For that reason, we suggest retaining the same maximum time for future studies.

Oestrous cycle and possible associations between ovarian hormones and door opening latencies were not measured in our study. This is a limitation of the present and previous studies (e.g. [21,41,54]) of cage mate release, as hormone level is known to affect both social -, operant -, and open field behaviour in rats [57,58]. Future studies should include oestrous cycle and hormone level measurements to test how hormones affect cage mate release and for the generalizability of findings.

In conclusion, the main findings in the present study replicate and extend the findings in Bartal et al. (2011). Rats pre-trained to open the restrainer door for food will also open the door to release a cagemate, though with longer opening latencies than for food. Whether this opening behaviour is best conceptualized as empathically motivated, pro-social behaviour, or is motivated and controlled by social contact is debated and has yet to be resolved.

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Study 3:

Empathy or not empathy, that’s the question - a pragmatic behavior analytical approach.

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[Article is not attached due to it being under review]

Study 4:

The social release paradigm: Investigating restrainer aversion by restrainer entries and positive ultrasonic vocalizations. Blystad, M. H., Asare, P., Andersen, D., & Johansen, E. B. Submitted, 2020. *Journal of Comparative Psychology*

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