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Goat Perception of Human Cues & Reliability of Thermal Imaging in Welfare Research

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Goat Perception of Human Cues & Reliability of Thermal Imaging in Welfare Research

by

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**A thesis submitted in partial fulfilment of the requirements for the degree of
PhD**

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ABSTRACT

Chapter 1 reviews current knowledge on goat cognition, emotions and personality, emphasizing the rich emotional lives of goats, the sophisticated cognitive abilities they possess and inter-individual strategies that emerge as they navigate their complex physical and social environments. As a gregarious species, how goats perceive social cues, including human ones has key implications for welfare. If goats can accurately discriminate among humans, relationships may develop, enabling animals to attribute previous positive and negative interactions with certain people and use these to predict their future behaviour. Our behavioural motivations can also be anticipated using emotional cues which may shape responses to human-goat interactions and the development of these relationships. Using playback experiments **Chapter 2** provides preliminary evidence that goats can combine visual and vocal cues to cross-modally recognize familiar people and **Chapter 3** suggests goats can discriminate emotional valence (happy versus angry) of human voices. However, to understand the significance of sensitivity to human cues from a welfare perspective, we must understand how these affect emotional experiences, requiring indicators to measure such responses. Thermal imaging is a non-invasive technology increasingly used in welfare research, and in **Chapter 4** I examine the reliability of this method for measuring goat peripheral temperatures. Surface temperature measurements in goats were found to be highly repeatable in the short-term (≈ 1 min) but showed poor reproducibility across days. This suggests that although surface temperatures are sensitive to ambient conditions, which should be tightly controlled, thermal imaging may be appropriate for measuring skin temperature changes at the individual-level, for example in response to emotional experiences before and after human handling. This thesis investigates the social cognitive abilities underlying development and maintenance of human-goat relationships, from how they discriminate among us and predict our behavioural motivations to refining indicators enabling future researchers to assess goat emotional responses to human cues.

CONTENTS

ACKNOWLEDGEMENTS	9
 CHAPTER 1: Goat Emotions, Cognition & Personality	 11
1. Introduction	12
2. Emotions	14
2.1. Emotional Indicators	15
2.1.1. <i>Neurophysiological Indicators</i>	<i>15</i>
2.1.1.1. <i>Cardiac Measures</i>	<i>16</i>
2.1.1.2. <i>Thermal Imaging</i>	<i>18</i>
2.1.2. <i>Behavioural Indicators</i>	<i>22</i>
2.1.2.1. <i>Body Posture, Behaviour & Qualitative Behavioural Analysis</i>	<i>22</i>
2.1.2.2. <i>Facial Expressions</i>	<i>25</i>
2.1.2.3. <i>Vocal Expressions</i>	<i>26</i>
2.1.3. <i>Cognitive Indicators</i>	<i>28</i>
2.1.4. <i>Summary</i>	<i>30</i>
2.2. The Social Dimension of Emotion	30
3. Cognition	33
3.1. Physical Cognition	33
3.1.1. <i>Object Discrimination & Categorisation</i>	<i>34</i>
3.1.2. <i>Inferential Reasoning</i>	<i>35</i>
3.1.3. <i>Object Permanence</i>	<i>35</i>
3.1.4. <i>Long-term Memory</i>	<i>36</i>
3.1.5. <i>Behavioural Flexibility</i>	<i>37</i>
3.1.6. <i>Contrafreeloading</i>	<i>38</i>

3.1.7. <i>Summary</i>	39
3.2. Social Cognition	40
3.2.1. <i>Recognition</i>	41
3.2.2. <i>Attributing Attention</i>	42
3.2.3. <i>Interpretation of Human Gestural Communication</i>	44
3.2.4. <i>Use of Social Cues and Social Learning</i>	44
3.2.4.1. <i>Vertical Learning</i>	45
3.2.4.2. <i>Horizontal Learning</i>	46
3.2.4.3. <i>Summary</i>	48
4. Personality	50
4.1. Terminology	50
4.2. Personality and Social Behaviour	51
4.3. Personality and Cognition	53
4.4. Summary	54
5. Linking Emotions, Cognition, Personality and Welfare	56
6. Conclusions and Future Directions	59
7. Thesis Outline and Aims	61
7.1. Summary of Thesis Aims	63
8. References	64
 CHAPTER 2: Goats May Recognise Humans Cross-Modally	 91
1. Introduction	92
2. Materials & Methods	95
2.1. Ethics Statement	95
2.2. Study Site & Sample Population	95

2.3. Stimuli Collection & Preparation	96
2.4. Experimental Enclosure	97
2.5. Habituation Phase	99
2.6. Training Phase	100
2.7. Test Phase	102
2.8. Video Coding	103
2.9. Exclusion Criteria	103
2.10. Data Analysis	104
2.10.1. General Model Parameters	104
2.10.2. Looking Duration	106
2.10.3. Latency to Look	106
2.10.4. Heart Rate	106
2.10.5. Heart Rate Variability	107
3. Results	109
3.1. Looking Duration	109
3.2. Latency to Look	110
3.3. Heart Rate & Heart Rate Variability	111
3.4. Summary	113
4. Discussion	114
5. References	118
 CHAPTER 3: Goat Discrimination of Emotional Valence in the Human Voice	 127
1. Introduction	128
2. Materials & Methods	132
2.1. Study Site & Sample Population	132

2.2. Collection & Preparation of Auditory Stimuli	132
2.3. Playback Procedure	133
2.4. Playback Emotional Valence Validation Experiment	135
2.5. Experimental Enclosure	135
2.6. Ethics Statement	137
2.7. Experimental Preparation & Procedure	137
2.8. Video Coding	138
2.9. Exclusion Criteria	139
2.10. Statistical Analysis	139
2.10.1. General Model Parameters	139
2.10.2. Looking Duration	141
2.10.3. Latency to Look	141
2.10.4. Heart Rate & Heart Rate Variability	142
3. Results	143
3.1. Looking Duration	143
3.2. Latency to Look	145
3.3. Heart Rate and Heart Rate Variability	147
3.4. Summary	149
4. Discussion	150
5. References	156

CHAPTER 4: Thermal Imaging in Goats: Reliability & Precision of Temperature Measurements Taken from Facial Regions	165
1. Introduction	167
2. Materials & Methods	171

2.1. Ethics Statement	171
2.2. Study Site & Sample Population	171
2.3. Experimental Set-up	171
2.4. Experimental Preparation & Testing Procedure	173
2.5. Video Processing & Image Analysis	174
2.6. Statistical Analysis	176
2.6.1. <i>Repeatability of Goat Surface Temperatures Within a Single Measurement Session</i>	176
2.6.2. <i>Precision in Temperature Estimates</i>	178
2.6.3. <i>Reproducibility of Temperature Measures Taken Over Multiple Sessions</i>	179
3. Results	180
3.1. Repeatability of Goat Surface Temperatures Within a Single Measurement Session	180
3.2. Precision in Temperature Estimates	182
3.3. Reproducibility of Temperature Measurements Taken Over Multiple Sessions	183
3.4. Summary	185
4. Discussion	186
4.1. Repeatability of Goat Surface Temperatures Within a Single Measurement Session	186
4.2. Precision in Temperature Estimates	188
4.3. Reproducibility of Temperature Measurements Taken Over Multiple Sessions	189
4.4. Conclusion	192
5. References	194
 CHAPTER 5: General Discussion	 204
1. Overview of Findings	204
1.1. Chapter 2: Goats May Recognise Humans Cross-Modally	206

1.2. Chapter 3: Goat Discrimination of Emotional Valence in the Human Voice	207
1.3. Chapter 4: Thermal Imaging in Goats: Reliability & Precision of Temperature Measurements Taken from Facial Regions	208
2. Influences of Learning & Domestication on Social Cognition in Goats	210
3. Welfare Implications and the Human-Animal Relationship	213
4. A Note on The Study Site	218
5. Future Directions	220
6. Final Remarks & Conclusion	224
7. References	226
 APPENDIX 1: Supplementary Information from Chapter 2	 242
Appendix 1A	242
Appendix 1B	244
Appendix 1C	246
 APPENDIX 2: Supplementary Information from Chapter 3	 247
Appendix 2A	247
Appendix 2B	249
Appendix 2C	252
Appendix 2D	256
 APPENDIX 3: Supplementary Information from Chapter 4	 257

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CHAPTER 1: Goat Emotions, Cognition & Personality¹

Abstract

Positive welfare is a relatively modern concept based on the idea that on the whole, an animal's positive experiences should outweigh their negative ones. Intuitively, we therefore require indicators to measure when animals are experiencing positive and negative emotional states, as well as providing opportunities for animals to create positive experiences. Goats typically live rich social and emotional lives, are naturally inquisitive, and seek cognitive challenges, highlighting the importance of a complex and cognitively stimulating environment for their welfare. However, how goats respond to their environment is not the same for each individual, underlining the shortcomings of a 'one size fits all' approach to provide the best welfare. In sum, to attain positive welfare in goats we must possess a means to monitor their emotional experiences, understand their cognitive abilities and provide sufficient opportunities to apply these, while ensuring welfare measures are tailored at an individual-level. This chapter will therefore focus on potential behavioural, physiological and cognitive indicators used to measure goat emotional states in the short- and long-term; their cognitive abilities in the physical and social domains; and the effect of personality on how goats interact with their social environment and on cognitive abilities.

¹ This introduction section was written as a chapter commissioned by Springer Nature for the book 'Welfare of Goats' for their Animal Welfare series. The content, referencing style and format of this chapter reflects the guidelines provided by Springer.

1. INTRODUCTION

Goats (*Capra hircus*) were one of the first livestock species to be domesticated, around 10,500 years ago (Zeder and Hesse 2000, MacHugh et al. 2017). They have a global population of around 1.3 billion, with most farmed goats living in Africa (43.3%) and Asia (51.4%: FAO 2020). Although still a minority, increasing intensification of production systems in Europe (1.4%) and the USA (0.2%) have moved more goats indoors, strengthening the mismatch between the domestic and natural environment (Zobel et al. 2019). Given the increasing pressure on other nations to compete, and with the growing interest in goat farming as a 'greener' alternative to other livestock production systems, this mismatch is projected to continue (Darcan and Silanikove 2018, Zobel et al. 2019). To ensure welfare standards are still met amidst growing public concern (Alonso et al. 2020), researchers continue to develop indicators for measuring multiple aspects of goat welfare.

A role for emotional states has long been acknowledged as being central to farm animal welfare, but only more recently have positive experiences been explicitly recognized as being important, rather than simply the minimising of negative ones (FAWC 1993). Modern welfare concepts generally promote 'positive welfare,' and key to this is the idea that positive emotional experiences should on the whole outweigh negative ones (Green and Mellor 2011, Mellor and Beausoleil 2015). Therefore, to appraise and improve goat welfare, we clearly require an objective means to assess their positive and negative emotional states, in order to then be able to promote positive experiences.

Goats are naturally inquisitive, motivated to seek cognitive challenges and, as browsers, explore the world through their mouth, using their mobile lips to manipulate and investigate novel objects (Briefer et al. 2014, Berman et al. 2017, Mahdy et al. 2020, Rosenberger et al. 2020). Such tendencies, along with an impressive set of foraging skills evolved in the mountains navigated by their ancestors (Silanikove 2000, Amills et al. 2017, Zobel and Nawroth 2020). However, in the barren indoor environments commonly faced by many goats today, these behavioural tendencies may lead to

boredom and frustration (Franks 2018, Zobel et al. 2019). Furthermore, the altered social conditions on farms (e.g., larger group sizes, higher densities and regrouping of individuals) can pose a challenge for goats from a social cognitive perspective, as they attempt to form social organisations and stable relationships with group-members; this being contingent on their ability to discriminate among them (Miranda-de La Lama and Mattiello 2010, Patt et al. 2012, Stanley and Dunbar 2013). How goats perceive and process information from their physical and social environment is central to their emotional wellbeing, and further, as learning can be inherently rewarding in itself, understanding the cognitive abilities of goats and other livestock is imperative for welfare science (Jensen 1963, Inglis et al. 1997, Franks 2018). However, how individuals respond to their environment varies from goat-to-goat (e.g., Briefer et al. 2015a).

Individual differences in how goats perceive their environment result in individual-level variation in welfare outcomes (Richter and Hintze 2019). Consistent behavioural and physiological variation among goats can be captured through measuring and categorising individuals according to their personality. Accordingly, for the purposes of this chapter we will discuss emotions in goats, while focussing on indicators of emotional responses, as well as their cognition (physical and social) and personality, including how personality feeds into emotional experiences and cognition.

2. EMOTIONS

Emotional responses play a key role in tailoring an animal's behaviour towards environmental information, such as food, predators and mates (Kremer et al. 2020). In psychology, such processes are principally defined either through breaking emotions up into discrete categories (for example, happiness, anger and disgust; Ekman 1992), or as graded responses measured over multiple axes, or dimensions. The most widely-used of the latter, or 'dimensional approaches' splits emotion over two main axes: 'valence', which ranges from positive (e.g., happiness) to negative (e.g., anger/ fear), and 'arousal', which reflects the level of bodily activation (e.g., calm to excited; Russell 1980, Mendl et al. 2010; Figure 1).

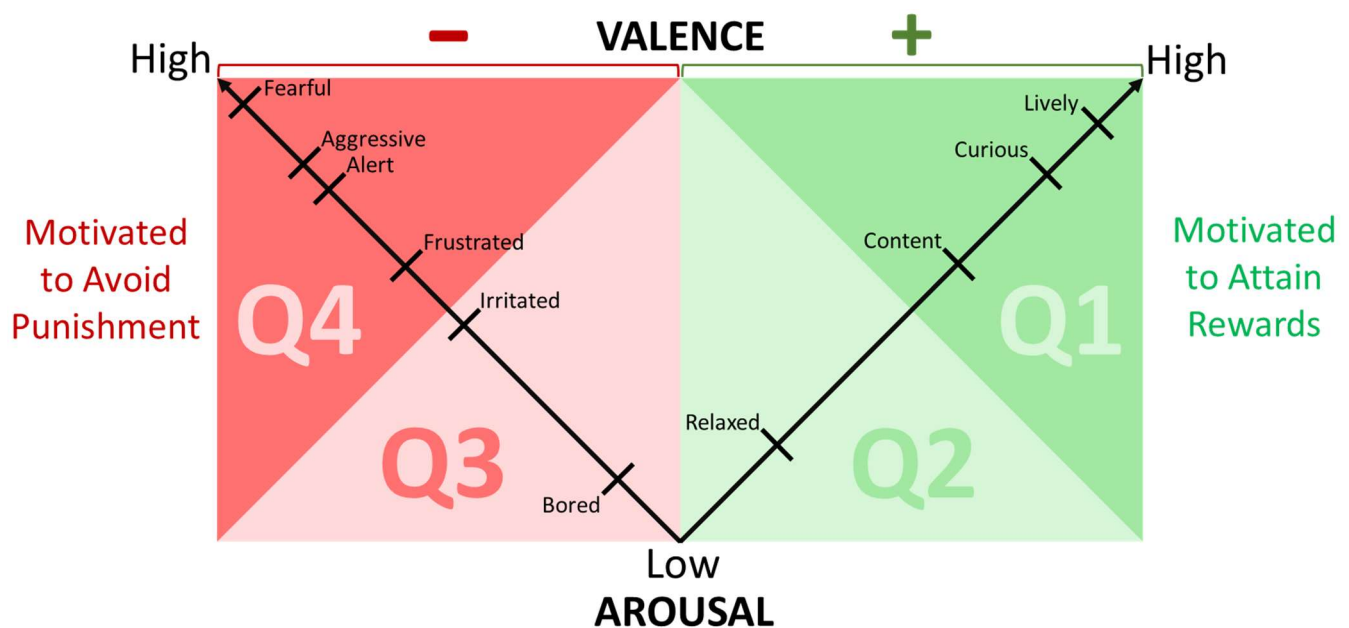


Figure 1. Dimensional model splitting animal emotional state by valence (negative: motivated to avoid punishment and positive: motivated to attain rewards) and arousal (low to high; schematic adapted from Briefer 2020). Examples provided derive from Mattiello et al. (2015) recommended descriptors for goat behaviour. Quadrant 1 (Q1): high arousal, positive emotions; Quadrant 2 (Q2): low arousal, positive emotions; Quadrant 3 (Q3): low arousal, negative emotions; Quadrant 4 (Q4): high arousal, negative emotions.

2.1. Emotional Indicators

We can assess emotional responses according to dimensional criteria, through measuring and combining constituents of an animal's overall emotional response (Mormède et al. 2007). Emotional experiences are the short-lived culmination of cognitive and neurophysiological changes, which may facilitate motor (behavioural) responses, and there may also be a subjective element that supposes a conscious 'feeling' of emotions experienced (Désiré et al. 2002, Špinka 2012). Indeed, although neural structures implicated in emotional processes appear conserved across species, unlike humans who can provide verbal reports, definitive evidence of conscious feelings in non-human animals remains lacking (de Waal 2011, Le Doux 2021). By contrast, emotionally mediated changes in physiological responses and brain activity can be measured using specialised equipment. Behavioural outcomes are directly observable, and cognitive effects can be investigated via certain paradigms (e.g., judgement bias paradigms: Briefer and McElligott 2013, Baciadonna et al. 2016). Measuring emotion provides insight into how animals appraise their environment and as care for goats and other livestock is provided by humans, these conditions are under human control, making emotional indicators indispensable for informing welfare measures.

2.1.1. *Neurophysiological Indicators*

The brain processes environmental information and initiates cascading emotional responses (Machado and da Silva 2019). However, measuring patterns of brain activity linked with emotions often requires animals to be immobilised using anaesthesia or training (Hui et al. 2016, Thompkins et al. 2021). New techniques, such as functional near-infrared spectroscopy (fNIRS) enables remote measurement of brain activity and have been employed in goats using wearable sensors, but these lack the precision of traditional approaches, such as fMRI (Gygax et al. 2013). Neural activity is, in turn,

affected by feedback from all levels of the emotional response, which further modifies the animal's central emotional state (Anderson and Adolphs 2014, Zych and Gogolla 2021).

One prominent level of the emotional response involves the release of hormones (e.g., in goats: Carbonaro et al. 1992a, 1992b). Assessing changes in hormonal profiles is often achieved through blood sampling, but this can exacerbate emotional responses (e.g., stress). Although less invasive methods do exist, such as sampling milk, saliva, urine or faeces, these are often less sensitive and come with their own disadvantages (Mormède et al. 2007). Hormone release can also be a relatively slow process, especially if changes are part of the hypothalamo–pituitary–adrenocortical (HPA) axis response (e.g., corticosteroid release; Mormède et al. 2007). This lag in release can limit its usefulness in assessing an animal's current emotional state, such as their responses to sudden or transient events. Therefore, we will focus below on two relatively rapid and non-invasive physiological measures, cardiac responses and skin temperature changes assessed using thermal imaging.

2.1.1.1. Cardiac Measures

Nervous system activation elicited during emotional responses leads to rapid and predictable changes in cardiac activity, namely in heart rate (HR) and heart rate variability (HRV; Wascher 2021). Relative level of activity between two of the branches of the autonomic nervous system is thought to vary according to emotional state, with the sympathetic nervous system dominating for negative emotions, and parasympathetic for positive ones (Sorinas et al. 2020). HR, primarily quantified as heartbeats per minute is governed by the interaction between the parasympathetic (primarily through the vagal nerves) and sympathetic nervous systems. Specifically, increased parasympathetic nervous activity reduces HR and decreased activity increases HR, perhaps in concert with or independently of increases in sympathetic activity, which often plays a more prominent role in elevating HR (Von Borell et al. 2007). HR increases form part of the initial physiological stress response enabling animals to cope

with challenges imposed by internal and/or external stimuli, and is more generally associated with arousal in a variety of species and emotional contexts (for review, see Wascher 2021).

In goats, increases in HR have been observed in response to positive (feeding and food anticipation) and negative (food frustration) contexts of higher arousal compared to more neutral situations (Briefer et al. 2015b, Baciadonna et al. 2020). HR has also been shown to vary according to social context, with lower HRs observed in goats engaged in affiliative interactions with conspecifics compared to other behaviours, such as agonistic interactions and eating and/or drinking (Briefer et al. 2015a). Intriguingly, HR seems to increase during grooming interactions with humans despite behavioural indications that such interactions were positively received (Baciadonna et al. 2016) and opposite patterns observed in other species experiencing similar interactions with humans (expected to have calming effect, Coulon et al. 2015, Lange et al. 2021). Although HR remains an accurate and widely used measure of arousal, it tells us little about the valence of emotions experienced (Wascher 2021). By contrast, HRV may be a promising tool for contextualising emotional responses according to their valence.

HRV is a measure of the variability in duration between successive heartbeat intervals. Unlike HR, where underlying sympathetic and parasympathetic influences are difficult to disentangle, many researchers consider HRV a reliable indicator of parasympathetic nervous system activity (particularly e.g., RMSSD, de Geus et al. 2019, Thomas et al. 2019). Specifically, increases in vagal nerve activity are associated with increases in HRV (Eckberg 1983, 2003). This association, and by extension with positive emotions, has led some researchers to suggest HRV as a valence indicator, with some investigations finding corroborating increases or decreases in HRV in positive and negative situations respectively (e.g., Reefmann et al. 2009, Kowalik et al. 2017), including in goats (Briefer et al. 2015a, Baciadonna et al. 2019). However, results are not always consistent (e.g., Baciadonna et al. 2020, Lange et al. 2021) and this inference is not universally accepted, particularly in respect to research failing to control for

emotional arousal (e.g., Briefer et al. 2015a, Travain et al. 2016). Where control measures have been implemented (e.g., through comparing situations of opposite valence, but similar arousal), HRV, like HR, more closely reflects changes in arousal, rather than the valence of a situation (Briefer et al. 2015b). Indeed, a non-linear negative relationship exists between HR and HRV, leading some researchers to even propose HRV as a 'surrogate' measure for HR (Monfredi et al. 2014, 2015). Ultimately, it may be safer to preliminarily conclude that HRV, like HR, acts more as an indicator of emotional arousal, with higher HRV measures corresponding to situations where stress decreases (e.g., release from stress, animal relaxing). Further research is needed to examine its value as a valence indicator.

A common means of obtaining cardiac data in goats and other livestock is through belt monitors fitted around the animal's thorax (e.g., Briefer et al. 2015a, 2015b, Baciadonna et al. 2019, 2020). These approaches, while useful, do have several drawbacks. For example, the belt needs to be fitted tightly around the animal, and as these belts are largely designed for humans, they can necessitate a lot of handling to attain an ECG trace before the test and again if it is lost later on (usually through animal movement). Animals, therefore, need to be well-habituated to wearing the belt, otherwise emotional responses can be elicited by the device itself, compromising the validity of emotional measures (for review on cardiac monitoring approaches, see Nie et al. 2020).

2.1.1.2. Thermal Imaging

Thermal imaging is a remote technology increasingly used in animal welfare research to measure the physiological component of emotional responses. Thermal imaging technology captures infrared radiation emitted from objects to generate a thermal profile, enabling users to visualise and measure subtle variations in peripheral temperature (Knížková et al. 2007). When the subject of interest is a living mammal, local variations in blood flow and metabolism create a complex, somewhat fluid topography of temperature zones occurring across the skin's surface (Godyń et al. 2019; e.g., Figure 2). Through

focusing on certain ‘regions of interest,’ (ROIs) typically relatively furless areas (or ‘thermal windows’), such as the eyes and nose, researchers can track changes in skin temperature over time (Tattersall 2016). Importantly, changes in skin temperature are known to be influenced by emotional processes. When stressed, sympathetically-mediated vasoconstriction causes blood (and body heat) to be diverted away from peripheral blood vessels to the core, limiting blood loss from potential injuries and infusing vital organs and tissues important in the pending behavioural response (Travain and Valsecchi 2021).

In goats, current investigations of emotional responses using thermal imaging are limited to negative situations. In both adult and juvenile meat goats, maximum eye temperature, in conjunction with respiration rate, have been shown to increase following a stressful event, i.e., an experimenter guiding animals loudly with exaggerated arm movements to a nearby pen (Bartolomé et al. 2019). As eye temperatures tend to bear a stronger relationship with core temperature relative to other regions (George et al. 2014, de Ruediger et al. 2018, Bleul et al. 2021, Kim and Cho 2021), including in a preliminary study in goats (Marques et al. 2021), we may expect eye and core temperature to increase in tandem with decreases in temperature of other regions, such as the muzzle (e.g., Proctor and Carder 2016). Indeed, given this association with core temperature, as well as its proximity to emotional centres of the brain and rich blood supply, the eyes, and the region around the posterior border of the eyelid and lacrimal caruncle especially, have been proposed as sensitive regions to measure thermal responses to emotional events (Kim and Cho 2021, Travain and Valsecchi 2021; Figure 2).

Temperature changes in positive contexts have yet to be investigated in goats, but in cattle (*Bos taurus*), positive emotions of both low and high arousal can cause a drop in nasal temperatures (Proctor and Carder 2015, 2016). By contrast, nasal and withers temperatures increased in sheep (*Ovis aries*) following brushing, a low arousal, positive experience (Tamioso et al. 2017), while dogs (*Canis familiaris*) showed increases in eye temperature during feeding (high arousal, positive event: Travain et al. 2016). Confusingly, direction of temperature changes within a single ROI can be consistent between both positive and negative contexts (e.g., in cows: Proctor and Carder 2015, 2016), but go in opposite

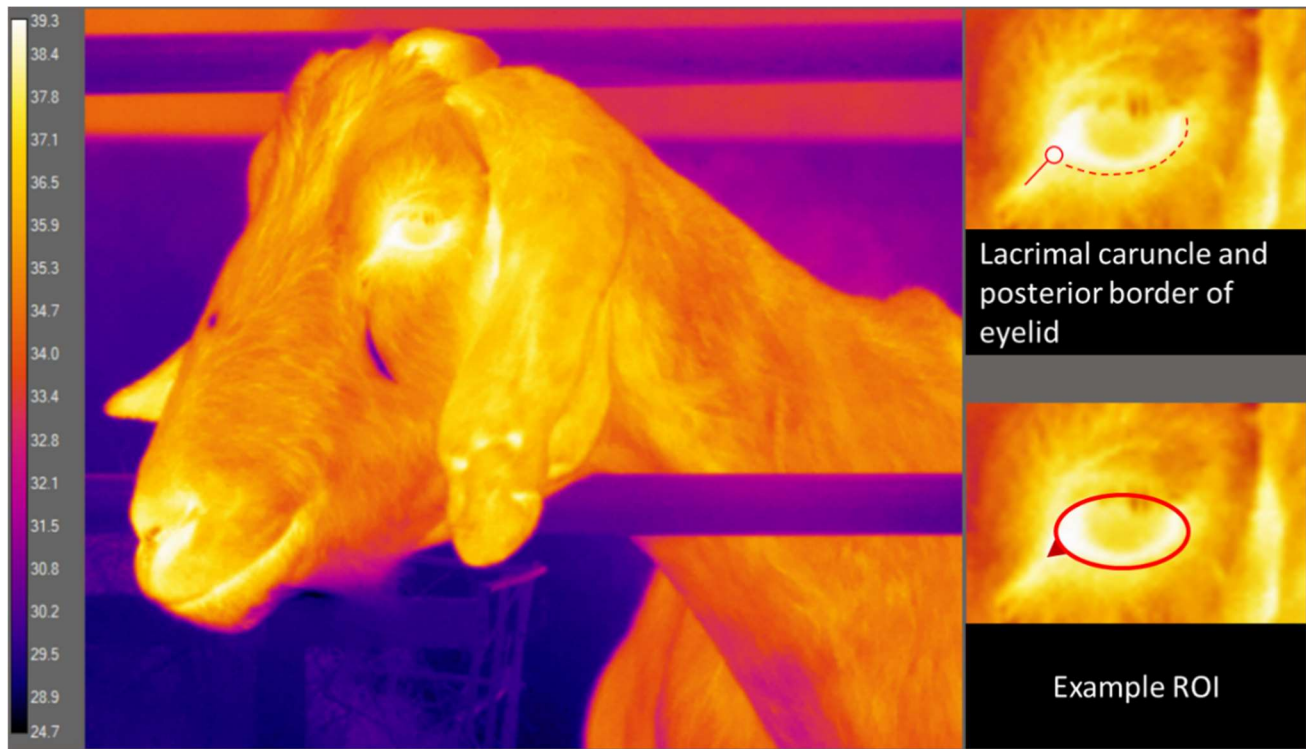


Figure 2. Thermal image of a goat. Magnified version of key ROI, the eye is shown in the panel to the right. Lacrimal caruncle is circled and the posterior border of the eyelid is indicated by a dashed line. An example ROI incorporating both of these sensitive areas is shown below.

directions in situations of the same emotional valence (eye temperature: in goats, Bartolomé et al. 2019, Zebaria et al. 2021; sheep, Stubbsjøn et al. 2009, Cannas et al. 2018; cows, Stewart et al. 2008a, 2008b, Gómez et al. 2018).

Although the direction of emotionally mediated temperature changes is not always uniform and so can be hard to interpret (e.g., Bartolomé et al. 2019, Zebaria et al. 2021), to understand these changes in the context of the dimensional framework, we must consider the intensity of the response and its time course. More arousing emotional events may provoke larger changes in peripheral temperatures and prolonged persistence of temperature changes in the initial (acute) phase of emotional responses, and for very stressful experiences, initial decreases may be accompanied by a delayed temperature increase, exceeding baseline temperatures (chronic phase; Stewart et al. 2007, 2008a, Herborn et al. 2015). Onset of temperature changes has also been shown to vary with valence in cows, with a greater lag in response observed when responding to positive compared with negative

stimuli, despite these contexts being of similar arousal (Proctor and Carder 2016). Since negative emotions are implicated in 'fight-or-flight' responses to threatening stimuli, we might expect quicker mobilisation of physiological responses underlying temperature changes to negative over positive contexts (Chotard et al. 2018). Ultimately, the magnitude and time course of emotionally induced changes in skin temperatures may offer a means to examine emotional responses in relation to arousal, and perhaps even valence.

The main advantage of thermal imaging for investigating emotional responses in goats and other animals lies in the completely non-invasive and remote way in which data can be collected (Tattersall 2016). However, the use of this technology also suffers from several disadvantages that must be carefully considered before it can be effectively applied in practice. For example, skin temperature is affected by numerous endogenous factors, such as individual, breed, sex and physical activity (also affects cardiac measures; Jansson et al. 2021, Travain and Valsecchi 2021), as well as environmental variables, such as ambient temperature, humidity and wind intensity, which influence peripheral temperatures directly and through internal homeostatic processes (Marques et al. 2021, Jansson et al. 2021). Further extraneous variables that affect the accuracy of peripheral temperature readings include distance or angle of the subject to the camera (Tattersall 2016, Ijichi et al. 2020), the ROI chosen, its size and the specific measure used (i.e., maximum, minimum or average temperature; Uddin et al. 2020, Kim and Cho 2021). Indeed, to date there is a marked lack of consensus regarding which combination of region (e.g., eye, nose, rear: Proctor and Carder 2015, 2016, Boileau et al. 2019) and measure should be used when measuring animal emotional responses using thermal imaging. Accordingly, **Chapter 4** will discuss my investigation into reliability and precision of various ROIs and measures to identify suitable candidate combinations in which to assess goat surface temperatures.

2.1.2. Behavioural Indicators

The behavioural component can be considered the final stage and external manifestation of an emotional response (Anderson and Adolphs 2014). Given it is through behaviour that animals directly interact with their environment, it is this component upon which selection most directly operates (Kremer et al. 2020). In an applied setting, behaviour can provide a directly observable indication of an animal's current emotional state (Machado and da Silva 2020).

2.1.2.1. Body Posture, Behaviour & Qualitative Behavioural Analysis

The level of general activity has been suggested as an indicator of emotional arousal, with goats in positive situations of relatively high arousal tending to move around more and show increased head movements, relative to those in less arousing, negative and neutral contexts (Baciadonna et al. 2020). However, to understand the link between activity level and arousal, we must also consider the specific situation and the goat's motivation. For example, although complete social isolation appears to be more stressful than partial isolation (where they could still hear and smell other goats), greater activity has been observed in partially isolated goats, as they attempted to restore contact with their separated group mates (Siebert et al. 2011). Directional responses such as movement towards or away from an object, differentiation in looking behaviours and levels of physical interaction, can be used to judge the level of emotional arousal elicited by a stimulus (e.g., Nawroth et al. 2018, Baciadonna et al. 2019). Particular postures in goats have also been linked to different emotions, with tails expected to be raised more in positive, relative to negative situations (Briefer et al. 2015b). Other valence indicators may include play, which reflects positive emotions (mostly in juveniles: Ahloy-Dallaire et al. 2018), and displacement behaviours, which are assumed to indicate anxiety. Displacement behaviours refer to actions performed that seem irrelevant to an animal's current behavioural context (Breed and Moore 2016) and goats have been shown to engage in displacement activities such as scratching and self-

grooming following conflict (Schino 1998). Interestingly, these behaviours then decrease in receivers of aggression following reconciliation with their aggressor. The behaviours and postures discussed in this section so far can be employed quantitatively to investigate emotions in goats, that is through measuring, for example, the frequency and/ or duration over which they occur. However, sole focus on individual indices can prove problematic, with some behaviours only happening infrequently (e.g., play) and although certain behaviours are relatively simple to interpret in terms of emotional valence (e.g., affiliative behaviours), others are more suggestive of arousal (e.g., activity level; Cooper and Wemelsfelder 2020).

As an alternative to quantitative approaches, qualitative techniques do exist, and require observation of an animal as a 'whole' rather than focussing on specific aspects of its behaviour. Qualitative behavioural assessment (QBA) requires assessors to observe and form impressions of animal behaviour and 'body language' according to a set of pre-defined descriptors (Mattiello et al. 2015, Battini et al. 2016). These descriptors define how goats, or groups of goats interact with their environment (Cooper and Wemelsfelder 2020). Although there appears to be greater coupling of negative emotions with states of higher arousal, as descriptive categories vary in arousal for both positive and negative emotions, QBA can be contextualised using dimensional models (Mattiello et al. 2019; Figure 1). For example, in terms of negative emotions, the AWIN welfare assessment protocol (part of the European Animal Welfare Indicators Project) employ words such as 'fearful' and 'suffering' to describe goats experiencing negative, high arousal states, and 'bored' for those in low arousal, negative states (Mattiello et al. 2015). Conversely, in terms of positive emotions, descriptors such as 'curious' and 'content' are used to denote higher and lower arousal states, respectively. Reassuringly, descriptor use has been shown to vary predictably with husbandry and body condition. Grosso et al. (2016) found that goats with pasture access tended to be described as 'content/ calm' and 'curious/ attentive,' whereas negative descriptors such as 'irritated' or 'suffering' were used more often for indoor-housed goats. Similarly, Battini et al. (2018) found that goats with normal coats were scored as

being more relaxed and sociable than goats with coats in a poorer condition. However, such methods are not without short-comings and most often it is the inherent subjectivity of QBA that brings into question its usefulness for measuring emotion (Spigarelli et al. 2020).

When assessors observe animals, they will be unavoidably aware of the conditions in which animals are kept, and therefore may, to some extent, assign descriptors based on their own presumptions of how animals should be behaving (Spigarelli et al. 2020). Accordingly, Tuytens et al. (2014) found that observers tended to favour descriptors linked to more positive emotions than negative ones, when told hens (*Gallus gallus domesticus*) were from an organic rather than conventional farms, even though they were scoring modified versions of the same video. Strength of biases varied based on observer opinions regarding the relative welfare benefits for hens on organic farms, and additional biases can be introduced for example through differences in professional background and experience (e.g., Grosso et al. 2016) and perhaps even gender (Tallet et al. 2010). However, it seems that such observer biases can be partly overcome with training. Grosso et al. (2016) found that trained observers had a good-level of broad agreement on goat emotional state (i.e., positive or negative), level of arousal and sociability. Finer-grained agreement on specific terms was only possible for some descriptors; however, given the ubiquity of dimensional approaches in modelling animal emotions, this additional refinement may be unnecessary. Furthermore, QBA scores in other livestock species have been shown to vary predictably with other behavioural measures (including in goats: e.g., Miller et al. 2018) and physiological markers of stress (for review see, Fleming et al. 2016). Ultimately, to overcome the subjectivity of qualitative methods, it may be best to employ QBA in tandem with quantitative methods, with QBA in turn complementing and contextualising quantitative approaches at the ‘whole-animal’ level. It must be noted, however, that the majority of QBA research, including the principal AWIN protocol, has been designed around European dairy goats (Mattiello et al. 2015), with no similar developments for meat or fibre goats (Leite et al. 2017).

2.1.2.2. *Facial Expressions*

Humans convey their emotions using a rich array of facial expressions. However, competing demands on facial musculature to facilitate communication and emotional expression may diminish the link between facial expressions and underlying state (Fridlund 1991, Schmidt and Cohn 2001). Outside of humans and other primates, conscious control and complexity of facial musculature is relatively limited, potentially rendering facial expression a more 'honest' indicator of animal internal state (Descovich et al. 2017).

Goats adjust their behavioural responses towards photographs of other goat's faces taken under emotional contexts of opposite valence (Bellegarde et al. 2017), suggesting that emotional experiences create perceivable shifts in their facial expressions. However, what these shifts are, in terms of changes in various facial muscles have not been studied in detail, with the exception of ear position, for which movement is governed by facial muscles (Descovich et al. 2017). In goats, a greater proportion of time spent with their ears pointing forward, relative to the side, is indicative of heightened arousal, whereas time spent with the ears pointed backwards acts as a valence indicator, being more expected in negatively-valenced situations (Briefer et al. 2015b, Bellegarde et al. 2017, Hussein and Hidayet 2019). Additionally, goats in a positive, low arousal emotional state induced through human grooming tend to exhibit ears positioned in a lowered, turned down position (Bellegarde et al. 2017). However, facial expressions are composite emotional responses requiring coordinated action of multiple facial muscles. This focus on a single component may not provide a comprehensive view of how goats may be expressing emotions facially. Techniques such as Facial Action Coding Systems (FACS) which classify facial expressions in relation to the shape and action of the underlying musculature may provide a promising means to analyse facial expressions as a whole (e.g., Wathan et al. 2015), but this method has yet to be applied in goats. Intriguingly, as animals produce distinctive facial expressions when vocalising,

vocal analysis may prove complementary to the measurement of facial expressions and is an area which has been studied to a greater extent in goats (Briefer et al. 2015b, Neethirajan et al. 2021).

2.1.2.3. Vocal Expressions

Goats are highly vocal animals, with calls encoding a variety of information including individual identity, body size, sex, social environment, and moreover, emotional state (Briefer and McElligott 2011a, 2011b, 2012, Briefer et al. 2015b). Similar to facial expressions, diminished conscious control over a vocalisation's structural elements (e.g., frequency) observed in farm animals, compared to humans, results in vocalisations being considered a more 'honest' manifestation of their internal state (Jürgens 2009, Briefer 2012, 2020). Indeed, vocal communication enables state information to be transmitted over longer distances, experiencing less attenuation from intervening objects than visual cues, and shifts in state can be conveyed more rapidly than through chemical communication (Johnstone and Scherer 2000, Laurijs et al. 2021). However, not all emotions elicit vocal responses (e.g., low arousal, negatively valenced depressive states) and like facial expressions, as vocalisations are often inherently communicative in nature, they are rooted in social context (Briefer 2020).

In goats, different calls are favoured in different social situations; for example, bucks produce blubbering vocalisations during courtship, does emit low frequency, affiliative 'murmuring' vocalisations shortly before and after parturition, and alarm snorts are used to alert herd-members to predators (Miranda-de La Lama and Mattiello 2010, Weaver 2021). Social context in gregarious species such as goats often induce predictable shifts in valence and arousal making call-type a useful indicator of animal emotional state, albeit one requiring knowledge of a species-specific communication system (Briefer 2012, 2020). Nevertheless, vocalisations produced in multiple emotional situations are considered particularly useful for assessing animal emotional state as they enable better comparison of acoustic features across contexts (Briefer 2012, 2020). The principal form of vocalisation emitted by goats are

contact calls, comprising closed- and open-mouthed bleats, which are generally thought to be produced to maintain social cohesion over shorter to longer distances respectively (Briefer and McElligott 2011a, O'Bryan et al. 2019). Closed-mouthed bleats may also play an additional role in “auto-communication,” produced to self-regulate an individual’s emotional state (Siebert et al. 2011), but moreover, both call-types vary predictably with emotional arousal and valence (Briefer et al. 2015b).

The source-filter theory posits that mammal vocalisations are initiated via vibrations of the vocal folds (the source, which determines fundamental frequency or pitch, F0), before being filtered through the vocal tract (Taylor and Reby 2010). This filtering process modulates the vocalisation’s energy distribution, dampening certain frequencies and amplifying others, giving rise to ‘formants.’ In goats, like in other taxa, both source- and filter-related components of vocalisations have been shown to vary somewhat predictably with emotional arousal (Briefer 2012, 2020). Briefer et al. (2015b) found that goats in highly arousing situations called more, and the calls they produced had a higher overall frequency, as well as a higher F0. Furthermore, goats in positive situations produced calls with a lower and more stable F0 relative to negative situations. Thus, as well as which call-type is favoured (e.g., blubbering, snorting; Briefer 2012, 2020), some characteristics of F0 may act as a useful valence indicator (Briefer et al. 2015b).

Given consistent correlates of emotions present in goat vocalisations (Briefer et al. 2015b), there is obvious scope for automated bioacoustic techniques for monitoring their welfare, as have already been investigated in pigs (*Sus scrofa domesticus*), cows and chickens (*Gallus gallus domesticus*; for review, see Mcloughlin et al. 2019). Indeed, vocalisations provide a long-range, instantaneous signal of animal emotional state, which in the context of precision livestock farming, can provide a highly informative, remote means to assess welfare in real-time (Briefer 2020). A single microphone mounted in a goats’ indoor environment would be sufficient to determine emotional state at a group-level (e.g., Herborn et al. 2020). To achieve a finer-grained analysis, the use of specialised microphones, or several

microphones in conjunction with sound triangulation techniques (Matthews et al. 2016, Laurijs et al. 2021) or even wearable audio-recorders fitted to collars would be necessary (O'Bryan et al. 2019).

Until now we have focused on methods to measure short-term emotional experiences in goats provoked by specific events. In the next section, we discuss how these link to longer-term emotional states and how these can be measured.

2.1.3. Cognitive Indicators

Although emotions can be considered as short-lived shifts in affective state prompted by a specific stimulus or event, they can have cumulative and lasting impacts on an animal's overall 'mood' (Russell 2003, Kremer et al. 2020). This in turn affects cognitive processes, influencing how goats and other animals attend to, learn, memorise and appraise stimuli in general (Baciadonna and McElligott 2015). Specifically, the cognitive component of an animal's emotional experience can cause attention biases, resulting in individuals in negative states, like those experiencing anxiety, being more conscious of or attentive to negative or novel stimuli (for review see, Crump et al. 2018). Similarly, long-term emotional states can induce memory biases, with stimuli or events in line with the animal's state being easier to recall; for example, depression in humans is linked to selective retention of negative memories (e.g., Dillon and Pizzagalli 2018). However, given the greater focus and support for the use of judgement bias tests compared to attention or memory biases in non-human animals (Lagisz et al. 2020), we will concentrate on this test for the current section.

To investigate the presence of judgement biases, animals are first trained to make an active choice between two alternatives (e.g., left or right lever; go/go task), or to approach a rewarded cue and suppress approach to an unrewarded or aversive cue (e.g., air puff; go/no-go; Lagisz et al. 2020). Once a set learning criterion has been reached, animals are then presented with intermediate cues that give an ambiguous outcome. The expectation is that animal decision making will be in line with their current

emotional state, with individuals in a positive state behaving optimistically, so will predict positive outcomes when appraising ambiguous cues, compared to those in negative states which are expected to behave pessimistically (Harding et al. 2004; Baciadonna and McElligott 2015). Changes in judgement biases have been shown in relation to for example, housing and enrichment in hamsters (*Mesocricetus auratus*) and horses (*Equus caballus*; Bethell and Koyama 2015, Henry et al. 2017), pair-housing in cows (Bučková et al. 2019), and dominance rank and pro-active-reactive personality traits in pigs (Horback and Parsons 2019, Asher et al. 2016).

In goats trained in a go/no-go task to approach a rewarded, but not an unrewarded location, contrary to predictions, short-term positive handling and prior poor welfare did not induce an optimistic or pessimistic bias, respectively, when exploring ambiguous locations (Briefer and McElligott 2013, Baciadonna et al. 2016). Despite evidence that human grooming was positively perceived, given goats at the study site received regular positive contact with humans and were generally well-cared for, short-term handling appeared to be insufficient for producing measurable shifts in judgement biases (Baciadonna et al. 2016). Indeed, another investigation carried out at the same site suggested that female goats subject to past mistreatment tended to inspect ambiguous locations faster, indicating that these individuals were more optimistic than control females, while previously mistreated males expressed similar levels of optimism to control males (Briefer and McElligott 2013). However, judgement bias tasks and especially those involving training, such as the go/no-go task used for the above experiments, are not without criticism (Lagisz et al. 2020). Repeated presentations of ambiguous stimuli over multiple trials could cause reduction in response towards these unrewarded locations based on learning, rather than a pessimistic tendency (Perdue 2017). Ultimately however, although further refinement of the methodology may be warranted, the use of judgement bias tasks has so far provided a promising means to assess the positive impacts of good welfare on goat rehabilitation and long-term emotional state.

2.1.4. Summary

Indicators have been developed to measure goat emotions at multiple levels, from changes in physiology such as HR and skin temperature, to behaviour like facial expressions and vocal responses, and finally, in the long-term, observing how emotional experiences affect decision-making (e.g., Briefer et al. 2015b, Bartolomé et al. 2019, Briefer and McElligott 2013). In light of increasing concern for animal welfare, research has moved away from simply trying to minimise negative experiences, such as pain and suffering, towards providing opportunities for animals to experience positive emotions as well (Green and Mellor 2011, Mellor and Beausoleil 2015). The ability to identify when goats and other livestock experience positive and negative emotions is, therefore, central to providing good welfare. When considering these emotional indicators in relation to dimensional frameworks, physiological indicators, such as HR, are generally more readily quantifiable and accurate proxies of arousal, but tell us little about emotional valence (Briefer 2020, Wascher 2021). Through integrating physiological, behavioural and cognitive measures, we can investigate animal emotions in terms of valence and arousal, both in the short- and long-term. Emotional indicators and particularly, the overt and transient nature of facial and vocal expressions establishes them as powerful tools to appraise an animal's current emotional state, both in the context of welfare assessment and, moreover emotional communication (e.g., Shariff and Tracy 2011).

2.2. The Social Dimension of Emotion

For gregarious species like goats, reading another individual's emotions can be highly informative, enabling them to anticipate a signaller's changing motivations and tailor their own behaviour accordingly (Schmidt and Cohn 2001, Seyfarth and Cheney 2003). When presented with facial photographs of another goat taken under situations of opposing valence, goats spent more time with their ears pointed forward in response to conspecifics conveying negative (in discomfort) relative to

positive emotions (being groomed), which was interpreted as them expressing greater interest in the former (Bellegarde et al. 2017). This difference suggests not only that goats register differences in valence of conspecific facial expressions, but that negatively valenced facial expressions may have greater perceived relevance, as they could indicate potential threats, so have clearer implications for survival and fitness. Similarly, having habituated to contact calls conveying one valence (e.g., negative), goats renewed behavioural responses (or dishabituated) when calls expressing the opposite valence were presented (e.g., positive; Baciadonna et al. 2019). This suggests that they can perceive differences in emotional content in the vocalisations of other goats. In addition, shifts in valence seemed to be accompanied by changes at physiological levels, with HRV being higher when experiencing positive calls in the first and last of three playback phases. These increases in HRV suggest greater parasympathetic influences on cardiac activity (implicated in rest and digest states), which could indicate that positive calls were less emotionally arousing to goats than negative ones. However, these changes occurred in the absence of shifts in HR, a (probably) more sensitive measure of emotional arousal (Baciadonna et al. 2020). In sum, it appears goats can discriminate between, and show perceptual biases towards, conspecific facial and vocal emotional cues based on valence.

For animals living closely with another species, as goats do with humans, emotional cues from members of another species may be almost as relevant as those of conspecifics. Although throughout their domestic history, goats generally have not possessed a close working relationship with humans in the same way as horses (but see pack goats, Sutliff 2019), nor are household companions like cats (*Felis catus*) and dogs, they still rely on us for food, shelter and protection from predators (Jardat and Lansade 2021). Given this shared history with us, goats might be expected to develop a suite of social cognitive abilities to discriminate between and interpret our cues as well as their own (e.g., Hare et al. 2005). As the outcome of interactions with humans and their predictability can have substantial consequences for animal welfare and productivity (Zulkifli 2013, Rault et al. 2020), human emotional cues may be salient for goats, which might use them to anticipate our behaviour. Indeed, goats discriminate human facial

expressions of opposing valence, and display inherent preferences for happy over angry facial expressions (Nawroth et al. 2018). Given the likelihood of happy facial expressions being paired with positive interactions and angry with negative, such biases towards human emotional cues are perhaps to be expected. However, goats themselves have less developed facial muscles restricting their ability to produce complex emotive facial expressions. Although, goats do seem to discriminate conspecific facial expressions (Bellegarde et al. 2017), vocalisations may provide a richer medium to assess emotions of other individuals. Indeed, both human and goat vocalisations vary with emotional arousal and valence which can potentially be interpreted across communication systems (Scheumann et al. 2014; Briefer et al. 2015b). Accordingly, **Chapter 3** will discuss my findings regarding whether goats can discriminate emotional valence conveyed in the human voice.

Ultimately, the ability to interpret the emotions of others, most likely from other goats, but perhaps even from humans as has been seen in dogs (e.g., Katayama et al. 2019), provides an avenue for emotions to be transmitted between individuals. This phenomenon is known as emotional contagion (yet to be clearly demonstrated in goats, Briefer 2018, Döpjan et al. 2020, Pérez-Manrique and Gomila 2022). Discriminating social cues, including emotional ones can be defined under the umbrella of social cognition.

3. COGNITION

Cognition can be defined as the process through which animals collect, process, retain and respond to environmental information (e.g., perception, memory, learning and decision-making: Shettleworth 2010). These are often split into two broad domains, those concerning an animal's mental adaptations to their physical environment, i.e., physical cognition, and to their social one, i.e., social cognition.

3.1. Physical Cognition

Physical cognition concerns an animal's understanding of the physical properties of objects found in their environment and of an object's causal and spatial relationships with other objects and/or events (Auersperg et al. 2017, Nawroth et al. 2019). The simplest means by which animals can establish these causal links is through associative learning, for example if an animal repeatedly experiences *a*-stimulus with *b*-event, it will learn *a* predicts *b* (Auersperg et al. 2017). Now say *c* and *d* share properties with *a* and also predict *b*, animals may be expected to generalize their responses to *a* to *c*, *d* and other similar objects adding a further level of sophistication. However, to establish existence of 'complex' cognitive abilities in goats and other species, we must move beyond these learnt contingencies and generalisations to evaluating their understanding of more abstract causal relationships which apply across a greater range of situations (Auersperg et al. 2017). Therefore, in addition to examining object discrimination and categorisation in goats (generalisation), we will discuss evidence for 'higher order' reasoning, specifically inferential reasoning and object permanence, as well as long-term memory and behavioural flexibility (important for coping with environmental change: Coppens et al. 2010). Because cognitive challenges are not always perceived by animals as purely an obstacle to attaining resources, but can in themselves be inherently rewarding (Inglis et al. 1997), we will also be discussing evidence of contrafreeloading.

3.1.1. Object Discrimination & Categorisation

Discrimination refers to the ability to differentiate between objects, while categorisation is the capacity to perceptually group objects based on their shared properties (Shettleworth 2010). Domestic goats, when given the opportunity, tend to have a diet richer in browse than their feral or wild counterparts (Landau and Provenza 2020). Higher browse consumption means greater exposure to plant secondary compounds such as tannins, which can reduce food intake, and cause liver damage. Being able to discriminate between and categorise plant species is therefore a crucial skill for goats, enabling them to avoid plants containing higher concentrations of these compounds (e.g., Provenza et al. 1994), and/or consume a more optimal mix of plant species to enhance feed intake (Estell 2010). In an experimental setting, goat proficiency for grouping foraging resources extend to categorising artificial symbols (e.g., Meyer et al. 2012).

Goats can be readily trained to discriminate between artificial symbols presented using an automated learning device. Use of this paradigm has shown that goats can generalise responses between symbols, forming open-ended categories based on shared visual properties (Meyer et al. 2012), and even transfer knowledge of the task itself to learn new problems, in other words 'learning to learn' (Langbein et al. 2007). Specifically, goats having been trained to select one out of four symbols showed increases in learning performance after being presented with further sets of symbols, suggesting they had developed a 'learning set.' Similar investigations have shown that some goats can learn the 'oddity concept', selecting the odd symbol out of three other uniform symbols (Roitberg and Franz 2004). The ability of goats to discriminate between and categorise objects may partially underlie their impressive ability to adapt and colonize novel environments (Chynoweth et al. 2013).

3.1.2. Inferential Reasoning

Inferential reasoning refers to the capacity to integrate indirect information regarding an event or stimulus to form inferences, enabling animals to better cope with novel challenges (Heimbauer et al. 2019). Solutions must be reached without explicit learning and are assumed to be particularly advantageous in unstable, but predictable physical or social environments (Völter and Call 2017, Nawroth et al. 2019). Nawroth et al. (2014) demonstrated that both goats and sheep could select a rewarded over an unrewarded cup when given direct information (sight of food), but most goats (8/11), and no sheep were able to infer the presence of food from indirect information (absence of food under the unrewarded cup). Support for inferential reasoning in goats, but not sheep, can be interpreted as reflecting differences in feeding ecology between these two related species; goats, as browsers, are more selective in what they eat, compared to sheep, which are grazers. As a result, goats but not sheep flexibly learn for example, to avoid high fibre foods when lower fibre preferred foods become available (Hosoi et al. 1995). For the wild ancestors of domestic goats inhabiting mountainous terrain, and contemporary free-ranging domestic and feral populations in harsh environments, foraging resources are often patchily distributed and can require substantial effort to navigate between (e.g., Negi et al. 1993, Shrader et al. 2012). Therefore, reaching informed decisions based on both direct and indirect information may be extremely valuable to locate and prioritise foraging patches (Nawroth et al. 2014).

3.1.3. Object Permanence

Object permanence refers to the understanding that an object continues to exist even when it is no longer visible to the observer (Piaget 1954). Such a capacity enables animals to predict the location and trajectory of a hidden physical or social object and can have key implications for an animal's fitness (Jaakkola 2014). For example, it can help animals to keep track of the relative locations of group-members, allowing them to maintain group cohesion in dense vegetation or even follow the movements

of a hidden predator (Noë and Laporte 2014). Goats have been shown to express a relatively sophisticated ability for object permanence, being capable of tracking the movement of a reward hidden under an opaque cup as it switched positions with an adjacent cup (Nawroth et al. 2015a). Especially when colour and shape of the cups differed, goats were able to select the rewarded cup with a moderate to high level of success (3/9 goats performance exceeded chance levels). The ability to infer the location of out of view objects can substantially increase how predictable a goat perceives its environment to be.

3.1.4. Long-term Memory

Goats have demonstrated a high propensity to discriminate and learn in physical cognitive challenges (e.g., Langbein et al. 2007), and to retain the solutions of these tasks in the long-term. For example, goats have an excellent memory for spatial and visual cues, remembering the solutions to a Y-maze three months after it had been learned (Langbein 2012). Similarly, Langbein et al. (2008) trained goats to learn a rewarded symbol for each of 10 different sets of four symbols presented consecutively. When presented these tasks concurrently, goats were able to solve the task immediately in at least half of cases, even for tasks learnt several weeks before, and others were re-learned at a faster rate than it took originally. However, one of the best examples of long-term memory in goats has been demonstrated by their performance in a two-step foraging task (Briefer et al. 2014). Goats were first trained to extract food from a box through pulling out a lever and lifting it upwards. Not only were nine out of 12 goats able to learn this highly novel foraging task in a relatively small number of trials (8-22), but they also retained the knowledge in the long-term, exhibiting no decrease in performance even 10 months after the task had been learnt (and anecdotally over seven years).

3.1.5. Behavioural Flexibility

Behavioural flexibility, i.e., the degree to which an animal's behaviour can be shaped by external parameters, is a key determinant in their ability to adapt and survive in changing environments (Coppens et al. 2010). We have already described goat proficiency for flexible object categorisation, learning and decision making (e.g., Meyer et al. 2012, Langbein et al. 2007, Nawroth et al. 2014). However, behavioural flexibility is more commonly inferred from how well animals can inhibit or control a behaviour of interest or through their performance in reversal learning tasks (Nawroth et al. 2016a, Raoult et al. 2021), both of which have been explored in a variety of contexts in goats.

Inhibitory control of behaviour can be defined as an animal's capacity to suppress a more direct, impulsive response in favour of an action more appropriate for a given situation (Diamond 2013). For example, after training goats to obtain a reward from an opaque cylinder, Langbein (2018) substituted the cylinder for a transparent one, requiring animals to avoid direct attempts to retrieve the reward through the cylinder, and instead detour around its side. Goats were shown to perform this feat at a comparable level or better than a variety of bird and mammal species (average accuracy = 63%). However, despite the wide use of this task, given performance can vary according to an individual animal's experience with or understanding of artificial, transparent barriers, its ecological validity is questionable (van Horik et al. 2018). In an arguably more ecologically valid task, goats (but not all sheep) were shown to immediately detour around a physical barrier to retrieve food, despite momentarily increasing the distance between itself and the reward (Nawroth et al. 2016a, Raoult et al. 2021).

In addition to testing detour performance, Raoult et al. (2021) investigated reversal learning, by moving the gap in the barrier that animals could use to reach the reward to the opposite side following training. Reversal learning paradigms first reinforce a particular behaviour, such as selecting a specific rewarded location, before the reinforced behaviour is switched with a previously unrewarded pattern of response. More flexible goats are expected to be quicker in adjusting behaviours in line with task

parameters, and therefore show less persistence in performing the previously reinforced behaviour, otherwise known as perseveration, or A-not-B errors. In Raoult et al. (2021), when the gap was switched to the opposite side of the barrier, goats were much quicker than sheep to adjust behaviour and detour around the correct side to reach the reward (also see, Nawroth et al. 2016a). Given the relatively close phylogenetic relatedness, similarities in social structure and domestic history between goats and sheep, this difference in behavioural flexibility was again thought to be due to differences in their feeding ecology. Goats as browsers, unlike sheep, exploit more patchily distributed, ephemeral food resources and thus probably benefit more from expressing a flexible foraging strategy. Accordingly, when presented with a T-maze in which both arms contained a food reward, goats and sheep tended to repeatedly return to the same arm over multiple trials (Hosoi et al. 1995). However, when the quality of the food patch in one of the arms was lowered, goats, but not sheep, responded by increasing the frequency of switching between the food patches. Intriguingly, differences in behavioural flexibility have also been found between goat breeds, in that although dairy and dwarf goats performed similarly in an initial visual discrimination task, dairy goats were slower to learn in a subsequent reversal task (Nawroth et al. 2022). This was interpreted as reflecting a trade-off between behavioural flexibility and production traits in dairy goats, and may mean they are slower to adapt to new environments and/or husbandry conditions.

3.1.6. Contrafreeloading

Goats appear to be motivated to use their impressive suite of physical cognitive abilities to solve tasks (Briefer et al. 2014, Zobel and Nawroth 2020). Contrafreeloading refers to the phenomenon where animals continue to work for a resource when an identical one is freely available (Jensen 1963, Inglis et al. 1997). For example, goats trained in a visual discrimination task to receive water, continued to direct a third of their interactions towards the learning device (and as many as 90%), despite having free

access to a water dispenser (Langbein et al. 2009). Similarly, goats trained to slide open a door to access food, continued to do so even when an identical food resource was provided through a nearby open door (Rosenberger et al. 2020). Goat HR has been shown to decrease with increasing competence in a discrimination task; however, when the challenge was removed (all choices rewarded), the subjects HR increased once again (Langbein et al. 2004). Engagement in contrafreeloading coupled with shifts in response at autonomic levels, suggests that mastery of cognitive tasks induces positive emotions in goats, which extend beyond acquisition of the reward alone (Langbein et al. 2009). Indeed, cognitive tasks have been suggested to provide goats with an opportunity to manipulate their environment, with success increasing their perceived control over their surroundings, which, in turn, motivates them to continue engaging with the task (White 1959, Rosenberger et al. 2020). Ultimately, the indicators of advanced cognition and contrafreeloading in goats highlight the importance of cognitive challenges for their welfare.

3.1.7. Summary

Goats possess a relatively advanced understanding of their physical environment, from discriminating between and categorising objects to inferential reasoning, object permanence, and the capacity to memorise solutions to complex challenges in the long-term (e.g., Meyer et al. 2012, Nawroth et al. 2014, 2015a, Briefer et al. 2014). Advanced physical cognitive abilities and behavioural flexibility in particular (e.g., Pérez-Barbería and Gordon 2005, Amici et al. 2008, Nawroth et al. 2016a, 2022, Raoult et al. 2021), have been proposed to have evolved to cope with the demands of increasing complexity of social systems (van Horik and Emery 2011). Goats live in sophisticated fission-fusion societies (Calhim et al. 2006), built on individual recognition (Briefer et al. 2012, Pitcher et al. 2017), perhaps predisposing them towards more advanced cognitive capabilities. However, sheep exhibit similar social systems, and although their performance is comparable to goats in some aspects of physical cognition (see Raoult et

al. 2021), they diverge in others (e.g., Nawroth et al. 2014, Raoult et al. 2021), highlighting a potential role for foraging ecology on the evolution of goat cognition. Performance also varies substantially among individual goats (e.g., Roitberg and Franz 2004; Briefer et al. 2014), but the extent to which differences can equate to, for example, sex or breed is little understood. Indeed, preliminary evidence suggests goat breeds selected more or less intensely for productivity have similar cognitive abilities in some respects (visual discrimination and propensity to engage in contrafreeloading: Nawroth et al. 2022, Rosenberger et al. 2020), but differ in others (behavioural flexibility: Nawroth et al. 2022).

Another important consideration is how far domestication has shaped these abilities in goats as a whole. Human intervention has diminished the link between performance of a behaviour and the fitness advantage gained in a natural setting (e.g., finding food, shelter and predator avoidance). This, in turn, relaxes selection on the cognitive mechanisms underlying these behaviours in goats and other domesticated animals (particularly for physical cognition: Frank 1980, Price 1984). Indeed, goats possess approximately 85% of the brain volume (corrected for body size) of their wild progenitor, the bezoar goat (*Capra aegagrus*; Balcarcel et al. 2021), but how the physical cognitive abilities of bezoar compare against their domesticated cousins has yet to be addressed. Regardless, given what is known about cognition in domestic goats, and particularly of their behavioural flexibility (Sol et al. 2008), goats appear well-equipped to deal with novel environmental challenges, as demonstrated by how readily they become feral and thrive in new and often harsh environments (Chynoweth et al. 2013).

3.2. Social Cognition

Goats navigate a complex social world featuring relatively stable, near-linear dominance hierarchies (Barroso et al. 2000, Saunders et al. 2005, Aschwanden et al. 2008), and aggregations of individuals that form based on sex, social bonds, and kinship, but fluctuate in composition hourly as groups fuse, and/or separate (fission; Calhim et al. 2006, Stanley and Dunbar 2013). Although goats

incur the costs of group-living through increased aggression and resource competition (e.g., Shi and Dunbar 2006), the effects of negative interactions can be counteracted with positive ones, which help reduce stress and mend damaged social bonds (Schino 1998, Briefer et al. 2015a). Goats further show sensitivity to their wider social environment, intervening in conflicts between other goats (Keil and Sambras 1998), and to the orientation and motion of fellow foragers. Motion of certain group-members can initiate collective movement, allowing foraging parties to exploit new resources (Sankey et al. 2021). Indeed, by paying attention to where group-members are and what they are interacting with, goats can gain valuable information regarding foraging resources and threats (e.g., Shrader et al. 2007, Kaminski et al. 2005).

Goats have developed a suite of cognitive abilities to cope with challenges imposed by the social environment, from discriminating between group-members, to interpreting their attentional state and motivations, to using social learning to determine where foraging resources are, and which ones are best to exploit. However, in the domestic environment, it is not only conspecific social cues that are relevant. The interdependent relationship between humans and domesticated animals spanning thousands of generations has provided a unique setting for goats and other livestock to develop more sophisticated forms of interspecific communication and perception of human cues (Avarguès-Weber et al. 2013). Accordingly, we will discuss goat ability to recognize, attribute attention to and learn socially from both other goats and humans and their interpretation of human gestural cues.

3.2.1. Recognition

Through social recognition, animals can attribute outcomes of previous interactions to particular individuals (individual recognition), or groups of individuals (class-based recognition, e.g., sex, familiar versus unfamiliar) and use these to anticipate future behaviour (Yorzinski 2017). Discriminating among group-members may, for example, enable goats to keep track of dominance relationships, (Miranda-de

La Lama and Mattiello 2010), and avoid costs of misdirected parental or affiliative behaviours (Yorzinski 2017). In the mother-offspring context, initial recognition and social bonding is facilitated through olfactory cues (Poindron et al. 2007). However, individualised vocal signatures develop quickly in kids (before 5-9 days old) and although these become further emphasised with age, mothers and offspring appear capable of discriminating each other vocally from other familiar kids and females respectively by this stage (Briefer and McElligott 2011a). This recognition persists at least to 13 months post-weaning in mothers (Briefer et al. 2012). Visual cues also play a role, with pelage colour being important for kids in identifying their mother (Ruiz-Miranda 1993). However, head-cues appear to be non-essential for social recognition, with goats able to discriminate group-members from unfamiliar individuals even when the head is hidden (Keil et al. 2012). Goats can even combine cues in different sensory modalities, using visual and vocal cues to cross-modally recognize preferred conspecific social partners (Pitcher et al. 2017). Such a capacity suggests goats can develop cognitive templates for familiar individuals, which can be used to compare against available cues; this being a pre-requisite for individual recognition (Proops et al. 2009). However, despite the research exploring how goats recognize each other, curiously no current research has tested if and how they recognize their next most important social partners, humans. To address this knowledge gap, **Chapter 2** will discuss my investigation into social recognition of humans by goats, specifically using visual-vocal cross-modal recognition.

3.2.2. Attributing Attention

Direction and level of attention conveyed by conspecifics and humans provide important cues for gregarious livestock, such as goats as it increases the predictability of social interactions (Nawroth et al. 2019). Goats are sensitive to human attentional cues, with body orientation (Nawroth et al. 2015b, 2016b, Nawroth and McElligott 2017), and to a lesser extent head orientation (observed in: Nawroth et al. 2015b, 2016b, but not: Nawroth and McElligott 2017), and whether the eyes are open or closed (in:

Nawroth and McElligott 2017, but not: Nawroth et al. 2016b) allowing them to appraise the level of attention they receive from humans. Goats appear to use these attentional cues to adjust investment in human-directed communication. When faced with a task that they were unable to solve independently, goats looked faster and for longer, and moreover performed more gaze alternations between experimenter and the task, when an experimenter faced towards them rather than away (Nawroth et al. 2016c).

Referential communication refers to the transfer of signals that encode information about external stimuli or events (Evans 1997). Gaze alternations can be interpreted as a form of referential communication, with goats attempting to draw the experimenter's attention to an external stimulus, such as a task they cannot solve, in a bid to solicit help (Nawroth et al. 2016c). However, perhaps unsurprisingly, given the mixed evidence of the use of head orientation to attribute attention to humans, goats do not appear to follow human gaze (Kaminski et al. 2005, Nawroth et al. 2015b, 2020), but have been shown to use conspecific gaze referentially, to locate hidden food (Kaminski et al. 2005). This ability is not only important for locating foraging resources, but also to detect predators over distance, which is crucial in prey-species like goats (Nawroth et al. 2015b, Kaminski 2017). Gaze-following may be an example of an innate behaviour, or one achieved through learning (e.g., cue learning, stimulus enhancement). Kaminski et al. (2006) found that subordinate goats that had received aggression were more likely to consume a piece of food that was not visible to the dominant aggressor, whereas, subjects that had not received aggression consumed visible pieces as well. This suggests that subordinate goats possessed an understanding of the perceptual experience of their dominant social partner, adjusting their own behaviour accordingly to reduce costs of receiving aggression. Sensitivity to the perspective of others may underlie the presence of gaze-following behaviour in goats (Kaminski et al. 2005, 2017).

3.2.3. Interpretation of Human Gestural Communication

Comprehension of human pointing gestures has been investigated in a variety of species, from our closest living relatives, the great apes, to domesticated (dogs especially) and non-domesticated species, such as seals and bats (for review, see Krause et al. 2018). For goats, pointing gestures are uniquely human signals and, although they were largely domesticated for products rather than behavioural cooperation (e.g., dogs and horses; MacHugh and Bradley 2001), their domestic background *per se* may have sensitised goats to human behaviour (Hare et al. 2005). In line with this argument, goats have been shown to use human pointing and tapping gestures to infer the location of a food reward hidden under one of two cups (Kaminski et al. 2005, Nawroth et al. 2015b). Nawroth et al. (2020) investigated the extent to which goats understand the referential intent of these cues by examining their ability to follow an array of different pointing gestures to locate a reward placed in one of two buckets. Goats successfully used proximal (nearest arm pointed towards bucket) and crossed pointing gestures (arm crossed across body), where the distance between the experimenter's index finger and rewarded bucket was lower, but not asymmetrical pointing cues, where the experimenter's body was closer to the unrewarded bucket. This suggests that although goats can use a variety of pointing gestures, they do not understand their referential motivations and rely on simpler mechanisms, such as local or stimulus enhancement. Given performance did not improve over time (eight trials per gesture), it appears that no learning took place.

3.2.4. Use of Social Cues and Social Learning

Animals need to make frequent decisions, such as *where should I forage?*, *with whom should I mate?* and *where should I live?* (Valone and Templeton 2002). To select a more optimal behaviour for any given situation, they must gather information about their environment, either through trial-and-error (hereafter personal information) or by observing the behaviour of others facing similar challenges

(social information; Danchin et al. 2004). The value of information in decision-making will depend on the degree to which it reduces uncertainty about environmental conditions, offset against the cost of acquiring it (e.g., time, energy and predation risk: Dall et al. 2005, Aguiñaga et al. 2021). The net value will, in turn, vary according to sampling technique used, with personal information often assumed to be more costly but more accurate, and social learning a cheaper but error-prone alternative (Laland 2004). As a herd-living species, goats are well-positioned to acquire social information (Shrader et al. 2007), but whether they should rely on it will depend on whether the costs of obtaining personal information are high (e.g., time, energy, lost opportunity, predation risk), and whether personal information is unreliable or outdated (van Bergen et al. 2004, Rieucou and Giraldeau 2011). In addition, to decide when to use social information, animals must also decide whom to acquire it from, with several strategies having been proposed; including adopting the majority's behaviour, learning from more successful (e.g., more dominant) individuals, from older, more experienced individuals, or from kin (Laland 2004). Indeed, the most prominent early-life role model for many species, including goats, is the mother (e.g., Glasser et al. 2009).

3.2.4.1. Vertical Learning

Mothers provide a wealth of social information for their offspring, from shaping species-specific social behaviours, including mating preferences (i.e., sexual imprinting: Kendrick et al. 1998, 2001), to influencing what plants kids will forage on in later life (Landau and Provenza 2020). These feeding preferences can be initially formed through passive learning *in-utero*, via exposure to flavour molecules in the amniotic fluid (Hai et al. 2014), and later through the mother's milk and microbiome transfer through saliva and social contact (Nolte and Provenza 1992, Landau and Provenza 2020). Later, passive learning mechanisms are combined pre-weaning and replaced post-weaning with active learning from mothers. For example, Mamber and Damascus breeds differ in their propensity to consume tannin-rich

lentisk (*Pistacia lentiscus*), but when Mamber kids are fostered by Damascus mothers and vice versa, differences in kid preference for lentisk most closely reflect that of their foster-mother than their own breed (Glasser et al. 2009). This suggests that breed-specific feeding preferences are largely actively, and/or passively learned from mothers rather than being genetically pre-determined.

Processes underlying vertical learning may include a mixture of “local enhancement” and “production imitation” (Landau and Provenza 2020). Specifically, kids may learn through local enhancement when the mother’s presence or actions draws their attention to a particular location, such that they are more likely to visit or interact with stimuli at that location (Hoppitt and Laland 2013). This process is generally considered to be relatively simple and can occur with or without learning. By contrast, production imitation requires performance of a novel action, or sequence of actions after observing a demonstrator (the mother) performing the same behaviour. Feeding preferences in a Martinique population of criollo goats reflect matrilineal lineage, but also year of birth (Biquand and Biquand-Guyot 1992). This convergence in feeding preferences within age cohorts suggests a role both for independent environmental sampling and social transmission of feeding preferences among peers.

3.2.4.2. Horizontal Learning

Goats that are able to observe the foraging decisions of their peers have been shown to be more likely to select the highest quality foraging patch first, compared to those that did not which distributed themselves equally among three patches (Shrader et al. 2007). Through observing others, goats located foraging patches probably through local enhancement caused by the presence and/or inadvertent actions of foragers, and used ‘public information’ of their foraging success to assess patch quality (Valone 1989, Hoppitt and Laland 2013). In contrast, Baciadonna et al. (2013) found that naïve observers that had watched conspecific demonstrators select a food patch placed at the end of one of the arms of a T-maze did not show a preference for the side the demonstrators chose. Furthermore, when goats

possessed personal information conflicting with that of the demonstrator, they tended to rely on the former. Similarly, goats able to observe demonstrators solve a two-step foraging task were shown to depend more on trial-and-error, being no faster to learn the task than goats that received no demonstration (Briefer et al. 2014). However, this lack of social learning may be unsurprising given the technical difficulty of the task, as well as the observed sequence of actions perhaps being less ecologically-relevant to receivers (e.g., lifting a lever: Nawroth et al. 2016a). Comparing the results of Baciadonna et al. (2013) and Shrader et al. (2007), it could be that goats needed to rely on subtly different learning processes. Goats may be attracted to a foraging location by local enhancement through the simple presence of a conspecific demonstrator or immediately after their removal, due to a social aggregation tendency, with little or no learning (Hoppitt and Laland 2013). By contrast, 'delayed local enhancement' is a form of stimulus enhancement requiring goats to recall and be attracted to the previous location of the demonstrator (Hoppitt and Laland 2008). In both experiments, demonstrators were removed before a goat was tested, and this interval between demonstration and trial was (probably) greater for Baciadonna et al. (2013), perhaps increasing task difficulty (also applies to Briefer et al. 2014). Moreover, in Shrader et al. (2007), goats observed an initial 15-minute demonstration of the patch use of two conspecifics before having visual access to the foraging decisions of all goats tested before them. By contrast, in Baciadonna et al. (2013), goats observed a short demonstration from a single group-member. Feeding by multiple demonstrators not only provides more conspicuous social information, but may allow individuals to reach more informed decisions regarding patch quality (Aguiñaga et al. 2021). In addition, sustained patch use by multiple foragers suggests patches have not been depleted by previous users. Nevertheless, it appears that although goats use simpler social learning mechanisms, such as local enhancement and perhaps delayed enhancement, support for more complex peer learning in adult goats is limited and they seem to prioritise personal over social information. It has been suggested that goats lack sophisticated forms of social learning, as simple forms may be sufficient to effectively exploit the patchily distributed resources wild and free-ranging goat

populations often encounter (Shrader et al. 2012, Baciadonna et al. 2013, Briefer et al. 2014).

Alternatively, it could be a by-product of domestication, caused by relaxed reliance on conspecifics (suggested in dogs: Range and Virányi 2014) and increased sensitivity towards human cues (Udell et al. 2010).

Through monitoring human and conspecific behaviour, goats gain valuable information regarding foraging and other resources, but unlike other goats, humans provision but do not compete for resources and thus provide a unique source of social information in the domestic environment (Avarguès-Weber et al. 2013). Indeed, goats faced with a detour task where they had to navigate around a V-shaped hurdle, performed better when they could watch a human complete this task before they attempted it independently (Nawroth et al. 2016a). As the demonstrator's actions actively maintained goat attention throughout their demonstration (shaking the box containing food), goats could have improved task performance using local or stimulus enhancement, where the demonstrator's behaviour drew goat attention to the box or its location. However, given most goats receiving the demonstration took the same route as the demonstrator on their first trial, there is a possibility that goats used imitation to replicate human behaviour.

3.2.4.3. Summary

Goats mostly show evidence of simple social learning processes, such as local enhancement, but definitive support for more sophisticated abilities, particularly in adult goats, remains lacking. Indeed, during the sensitive developmental period, kids are expected to be more reliant on social information acquired from older and more experienced individuals (Laland 2004), such as their mother (e.g., Glasser et al. 2009). However, although thought to involve local enhancement and imitation (Landau and Provenza 2020), little has been conclusively proven about the mechanistic basis of social learning in developing goats. When considering adults, given the impressive repertoire of cognitive abilities goats

have demonstrated in the physical domain (e.g., Raoult et al. 2021), it may make sense for them to prioritise personal over social information (Baciadonna et al. 2013, Briefer et al. 2014). Indeed, in rapidly changing environments, lags between acquiring and using social information can lead to a mismatch between the information obtained and current environmental conditions, potentially leading to maladaptive decision-making which can spread to group levels through copying (informational cascades: Laland and Williams 1998, Rieucou and Giraldeau 2011). However, in Baciadonna et al. (2013) and Briefer et al. (2014), which suggested goats favour independent over social learning, as goats were well-fed and kept in predator free environments, costs of asocial learning were minimal, which is a context expected to favour such a strategy (Laland 2004). Over their extensive worldwide range, feral and free-ranging domestic goats frequently encounter situations where costs of asocial learning are high; for example, when food is scarce (e.g., in winter), when individuals are at risk of being left behind by the group (Kendal et al. 2004, Shrader et al. 2012), and in high predation risk environments (Shrader et al. 2008). In sum, although it may be concluded that when costs of asocial learning are low, goats favour personal over social information, through testing other populations or manipulating costs of asocial learning (e.g., Shrader et al. 2008, Cox et al. 2012), we can investigate whether this holds true across ecological contexts.

4. PERSONALITY

Variation is the substrate of natural selection, and one that might be expected to erode over time as traits conferring the highest fitness become fixed in a population (Darwin 1859, Endler 1986, Wilson 1998). However, one continuous source of behavioural variation retained across a diverse range of taxa is personality (Wolf and McNamara 2012, Wilson et al. 2019). Personality refers to behavioural (and physiological) differences between individuals that are consistent over time and across contexts (Réale et al. 2010, Finkemeier et al. 2018). Resulting variation in behaviour is expected to lead to differences in costs and benefits accrued based on personality. For example, bolder individuals that control resources through aggression may be expected to have greater reproductive success, but also to bear costs (e.g., injury) reducing their longevity relative to shyer individuals (Smith and Blumstein 2008). Variation in payoff across contexts and in the short- and long-term, coupled with frequency-dependent selection (fitness of one personality depends on the proportion of the population with the same personality) is expected to allow personality differences to become entrenched in animal populations (Wolf and McNamara 2012, Lichtenstein and Pruitt 2015). In an applied setting, given that personality can predict how individual animals respond to their environment, the importance of personality research is being increasingly recognized from an animal welfare perspective (Richter and Hintze 2019, Vaz et al. 2022). With this in mind, here we discuss evidence for personality in goats, with focus on the effects of personality on how goats interact with their social environment and how far personality can explain differences in cognition among individuals.

4.1. Terminology

In goats, as for many species, several related terms have been used to define inter-individual differences in behaviour. For example, temperament can refer to heritable, early-emerging behavioural tendencies that persist over time, and is considered to serve as a foundation for personality (Gosling

2001, Finkemeier et al. 2018, e.g., Lyons et al. 1988, Kannan et al. 2022). By contrast, identity profiles describe consistent social strategies adopted by certain individuals (i.e., aggressive, affiliative, passive and evasive), combined with the behavioural and morphological characteristics that often accompany their expression (Miranda-de la Lama et al. 2011, Pascual-Alonso et al. 2013). Finally, coping styles refer to how animals respond to and mitigate the effects of aversive stimuli (Wechsler 1995, e.g., Toinon et al. 2021). However, as terminology has been inconsistently defined and is often used synonymously, for example to avoid anthropomorphism through ascribing non-human animals with a personality (MacKay and Haskell 2015), for the sake of simplicity, we will employ the umbrella term “personality” to incorporate all related terminology.

4.2. Personality and Social Behaviour

The social environment is often synonymous with conflict, as individuals compete with conspecifics to gain resources such as mates, food and space (Bergmüller and Taborsky 2010). For goats, effects of social conflict can become further exacerbated on farms as space is more limited, opportunities for social assortment (based on, e.g., social preferences and rank) are reduced, and resources are often clumped (e.g., food troughs), enabling dominant individuals to monopolise their access (e.g., Jørgensen et al. 2007, Stanley and Dunbar 2013). In the face of such costs, divergences in behaviour that reduce the scope for conflict among competitors will be favoured (Bergmüller and Taborsky 2010). Given that consistency in inter-individual behavioural differences is expected to increase with rising costs of conflict, shifts in behaviour may manifest as differences in personality, which can translate into asocial contexts as well.

Neave and Zobel (2020) measured personality in female dairy goats based on their behaviour towards novel objects, a novel environment and startling (opening umbrella) and threatening stimuli (a dog). In a competitive feeding context, “bolder” goats tended to aggressively control resource access,

fearful goats were less aggressive and spent less time feeding, and exploratory goats fed more from elevated than ground level feeders (the latter being subject to higher levels of competition).

Although the proximate and ultimate explanations underlying their association with personality remain poorly understood, changes in physiology underpin shifts in behaviour and *vice versa* (Finkemeier et al. 2018, Wilson et al. 2019, McMahon and Cavigelli 2021). More social goats have been found to have a more stable HR than less social goats, with the latter expressing greater HR reactivity according to behavioural context (e.g., greater decrease in HR when engaged in affiliative behaviours; more elevated HR during eat/drink: Briefer et al. 2015a). A concurrent investigation found that shyer and/or more active goats expressed a sympathetic bias in nervous system activity at rest (higher SDNN, a measure of HRV: Finkemeier et al. 2019). This, coupled with greater HR reactivity, likely predisposes shy (and more active) goats to mobilise and adapt more quickly to physical and social challenges than those with other personality types. Importantly, the literature discussed used a mix of breeds and ways to define and test goat personality, making comparison between investigations more difficult.

In addition to production traits, goat breeds are well-known to be associated with certain behavioural dispositions. For example, Nubians are tame and affectionate, British Saanen are less aggressive to group-members and Old English goats tend to be more active and vigilant (Weaver 2021). These differences in behavioural tendencies may translate into differences in how personality is expressed across breeds. Through observing the behaviour of dairy and angora (fibre) goats, Miranda-de la Lama et al. (2011) and Pascual-Alonso et al. (2013) respectively, found four personality traits associated with behavioural and morphological characteristics. Aggressive individuals were larger, more dominant and better able to monopolise feed, while affiliative goats were of middling rank and gained resource access through prosocial interactions, rather than aggression. Both passive and evasive goats were lower ranked, but passive individuals were less active and showed little avoidance of agonistic interactions, whereas evasive goats actively avoided conflict, which in dairy goats extended to avoiding

affiliative interactions as well. Indeed, although there were subtle differences in expression of these personalities between goats of different breeds, it is interesting that the same personality types emerge. Furthermore, personality in angora goats appears to relate to cognitive ability.

4.3. Personality and Cognition

Like personality, cognitive ability can vary substantially among members of a population (Nawroth et al. 2015a), and how far these differences equate to differences in personality has been becoming of increasing interest to empirical researchers over the last decade or so (Dougherty and Guillette 2018). The mechanisms driving such covariation have been suggested to, for example, result from pleiotropic effects of a shared neuroendocrinological system acting on both personality and cognitive development (e.g., stress hormones), and/or from personality traits causing differences in opportunity to access and learn about environmental stimuli (Griffin et al. 2015, Wilson et al. 2019). For example, bolder, and/or more exploratory individuals may be expected to approach novel tasks faster, or be more attentive to changes in their environment, to retain information more quickly, and/or form and memorize associations between environmental stimuli more easily (Wilson et al. 2019). Conversely, more aggressive goats (associated with boldness: e.g., Neave and Zobel 2020) have been shown to be slower to solve and learn the solution to a T-maze than those with other personality types (Pascual-Alonso et al. 2013). Less dominant goats, and especially those with a passive personality, were the quickest to solve the T-maze on both their first and second exposure to the task. As lower-ranking goats regularly receive aggression from higher ranking individuals, they may have acquired greater sensitivity to food-related cues, such as the feeding-related sounds used to direct goats to the rewarded location (e.g., rattling of feed pellets) to locate food before they can be displaced. Similarly, goats that were more or less social and exploratory were found to express distinct differences in performance of cognitive tasks accordingly (Nawroth et al. 2017).

In a transposition task (used to test object permanence), less exploratory goats were shown to track movements of a hidden reward better than more exploratory individuals (Nawroth et al. 2017). Rather than suggesting a cognitive impairment, this was interpreted as reflecting, for example, the former being less distracted by external cues, or the latter being less motivated by the food reward. Conversely, performance on a visual discrimination task was not affected by goat exploratory tendencies, but by their sociability, with social goats being slower to learn than less social individuals, perhaps due to relatively greater levels of stress experienced by the former at being separated from conspecifics. Alternatively, as less social goats were also shown to preferentially rely on a container's colour and shape over its spatial position when locating hidden food, it could be social goats are more attentive to other cues. In sum, although personality affects cognition, there is little evidence that goats with different personalities diverge in 'general cognitive ability' with variation in performance appearing to be more task-specific, based on motivation and/or differences in how goats learn and process particular cues.

4.4. Summary

Personality is an important and predictable source of variation in behaviour, explaining inter-individual differences in how goats interact with their physical and social environment and how effectively they respond to environmental challenges. An array of personality traits has been investigated in goats, from their boldness to fearfulness, aggressiveness to affiliativeness, exploratory to evasive tendencies, and their general sociability and levels of activity (Miranda-de la Lama et al. 2011, Pascual-Alonso et al. 2013, Briefer et al. 2015a, Finkemeier et al. 2019, Neave and Zobel 2020). Due to the range of ways in which personality has been identified and studied, comparisons between studies can be difficult, but personality appears to be strongly associated with dominance in goats, and as such can be accompanied by related morphological differences (e.g., size; Miranda-de la Lama et al. 2011,

Pascual-Alonso et al. 2013). Personality expression also varies based on for example, breed and group composition.

Personality interacts with environmental conditions, creating differences in opportunity to experience positive and negative emotions. For example, shy, more subordinate goats may have more difficulties accessing food, more social goats may react more negatively to separation from group-members, and more reactive individuals may respond more strongly to husbandry routines (e.g., Miranda-de la Lama et al. 2011, Briefer et al. 2015a, Kannan et al. 2022). Ultimately, personality research in goats and other livestock has underlined the need to move past 'one size fits all' interventions (at group- or species-levels), and towards a more tailored approach to ensure opportunities to experience positive welfare are provided for every individual (Green and Mellor 2011, Mellor and Beausoleil 2015, Richter and Hintze 2019, Vaz et al. 2022).

5. LINKING EMOTIONS, COGNITION, PERSONALITY AND WELFARE

As emotional experiences are a key component of goat welfare, approaches that enable us to objectively measure emotion have strong value as welfare indicators (Désiré et al. 2002). The indicators discussed over the course of this chapter have assessed multiple levels of the composite emotional response, from internal neurophysiological changes (e.g., thermal imaging and cardiac responses), to behaviour (e.g., postural and vocal expression) and moreover, cognitive processes (Briefer et al. 2015b, Bartolomé et al. 2019, Baciadonna et al. 2020). Indeed, how environmental information is processed, retained and acted upon are all guided by an animal's emotional state; with the cumulative effect of emotional experience on creating cognitive biases, and on decision-making in particular (judgement biases) being the best investigated (Briefer and McElligott 2013, Baciadonna et al. 2016). Cognitive biases provide a further means to measure welfare and long-term 'mood' states in particular; however, the relationship between emotions and cognition is not unidirectional (Russell 2003, Kremer et al. 2020).

A goat's ability to discriminate, learn and form expectations about its environment can have substantial implications for its emotional state and welfare. For example, interpretation of social or physical cues enables goats to anticipate positive and negative events (Kaminski et al. 2006, Baciadonna et al. 2020). Furthermore, in the case of positive predictors, emotional changes can extend beyond the rewarding properties of the event itself, and towards the process of building the association, i.e., learning. Learning seems to have inherent value to goats and drives them to seek cognitive challenges (Langbein et al. 2009, Rosenberger et al. 2020). When considered from a social perspective, the ability to, for example, learn the identities of group-members and humans can serve as a foundation for social bonding, acting to promote prosocial behaviours in goats, which can alleviate stress and create opportunities to experience positive emotions (Schino 1998, Stanley and Dunbar 2013, Briefer et al. 2015a, Baciadonna et al. 2016, Pitcher et al. 2017). Indeed, goats have demonstrated a sophisticated

suite of cognitive abilities both in the social (e.g., cross-modal recognition and perspective taking) and physical domains, including evidence for abstract thinking (e.g., inferential reasoning and object permanence; Kaminski et al. 2006, Nawroth et al. 2014, 2015a, Pitcher et al. 2017). The general problem-solving ability established in this species, and behavioural flexibility in particular may, for example, enable goats to adapt more quickly to changes in husbandry regime and their environment, but also predispose them towards boredom and anhedonia (Coppens et al. 2010, Briefer et al. 2014, Franks 2018, Raoult et al. 2021). Ultimately, accumulating evidence of the emotional lives and cognitive sophistication, or sentience of goats and other animals under our care, not only helps us assess how far their cognitive needs are being met, but often our perceived level of obligation in ensuring their welfare (Broom 2010, Franks 2018). Indeed, the recognized importance of learning and cognition on animal welfare is particularly evident in the wide-spread use of environmental and cognitive enrichment to create cognitively stimulating environments for captive animals (Oesterwind et al. 2016, Clark 2017, Zobel and Nawroth 2020). However, given that both cognitive ability and propensity to seek cognitive challenges appear to vary among individual goats (Langbein et al. 2009, Nawroth et al. 2015a), the importance of cognitive stimulation on welfare will not be the same for every individual.

Differences in personality can be used to predict consistent differences in how goats process and respond behaviourally and emotionally to environmental cues, underlining the fact that species- or group-level welfare interventions can be insufficient for ensuring welfare needs are met for every goat (Nawroth et al. 2017, Briefer et al. 2015a, Finkemeier et al. 2019, Richter and Hintze 2019, Vaz et al. 2022). In this chapter, we have focused solely on the top-down effects of personality on cognition and emotions. Although beyond the scope of our review, it is clear early-life emotional experiences such as maternal deprivation, hand-rearing (Lyons et al. 1988, Toinon et al. 2021), and problem-solving opportunities (Oesterwind et al. 2016), can create long-term differences in behaviour among goats. Notwithstanding genetic influences, particularly if these experiences occur during ‘sensitive windows’ of heightened developmental plasticity (largely occurring during ontogeny), they can potentially create

persistent or even irreversible changes in an adult animal's personality (Wilson et al. 2019). Ultimately, personality affects how goats emotionally respond to, process and deal with environmental challenges. However, both emotional experiences (particularly those associated with the HPA axis) and problem-solving opportunities can interact in complex ways during development to affect personality.

6. CONCLUSIONS AND FUTURE DIRECTIONS

Over the last decade or so, a growing body of research has illustrated the rich emotional lives goats lead, as well as the sophisticated cognitive adaptations and inter-individual differences they express when navigating their challenging physical and social environments. Indeed, a suite of indicators has been developed to assess goat emotional states, both in the short- and long-term (Briefer and McElligott 2013, Mattiello et al. 2015, Briefer et al. 2015b). Given the majority of these indicators more reliably relate to either arousal (particularly physiological variables: e.g., cardiac measures and thermal imaging) or valence (e.g., certain ear postures and judgement biases), assessing emotions according to dimensional criteria necessitates integration of multiple indices of a goat's overall response. There is a growing interest in monitoring livestock emotions in precision livestock farming, especially in the field of bioacoustics (Mcloughlin et al. 2019). Given what is known about emotional signatures present in goat vocalisations (Siebert et al. 2011, Briefer et al. 2015b) there is obvious scope for implementation of automated emotional monitoring techniques as, for example has been used to classify kid calls according to individual, age and group membership (Favaro et al. 2014). Goats not only exhibit a sophisticated set of physical and social cognitive abilities, but actively seek opportunities to apply them to solve tasks (e.g., Briefer et al. 2014, Pitcher et al. 2017, Rosenberger et al. 2020); with these attributes underscoring the significance of cognitive challenges for goat welfare (see Zobel and Nawroth 2020 for review on how this can inform species-specific enrichment). However, many questions remain unanswered, including whether goat preference for asocial over social learning holds up across ecological contexts (i.e., when costs of asocial learning are high), and whether more sophisticated forms of social learning exist in goats, particularly over the developmental period (Glasser et al. 2009, Baciadonna et al. 2013, Briefer et al. 2014). Also, how domestication shaped goat cognitive abilities, specifically in respect to differences in cognitive performance among breeds (e.g., those bred for higher or lower productivity) and how these differ from their wild progenitors has been little investigated. Individual differences between goats have also been shown to manifest on a finer scale, with differences in behaviour,

cognitive performance and emotional responses to an extent being predicted by a goat's personality (Briefer et al. 2015a, Nawroth et al. 2017, Neave and Zobel 2020). Ultimately, to achieve positive welfare in goats (Green and Mellor 2011, Mellor and Beausoleil 2015), we must monitor their emotional, as well as physical wellbeing, give opportunities for them to apply their impressive cognitive skills and to recognize the importance of individual-level strategies to provide good welfare for every goat.

7. THESIS OUTLINE AND AIMS

Goats, a species largely domesticated for meat, hair and dairy products (MacHugh and Bradley 2001), have been shown to read a variety of human cues. However, literature to date has focused on their capacity to perceive general cues common to all humans, i.e., pointing gestures, facial expressions and attentional states (Kaminski et al. 2005, Nawroth et al. 2015b, 2016b, 2016c, 2018, 2020, Nawroth and McElligott 2017). Indeed, no previous investigations have evaluated how and whether goats can discriminate more individual-specific human cues and how this could affect their behaviour. Accordingly, in **Chapter 2** I investigated their ability to combine visual and vocal cues to recognize familiar people. If goats are indeed capable of cross-modal recognition, it would suggest they can form mental representations for familiar people, a key requisite for individual recognition (Proops et al. 2009). With the ability to discriminate, goats would be better able to use a history of positive and negative interactions with certain people to predict that individual's future behaviour (Tibbetts and Dale 2007, Hemsworth and Coleman 2010, Rault et al. 2020). In a more immediate sense, perceiving human emotional cues may provide goats with an indication of a person's current behavioural motivations (Schmidt and Cohn 2001). In **Chapter 3** I examined whether class-level recognition (e.g., familiar versus unfamiliar) affected goat ability to discriminate emotional valence in human voices. Given the recognized importance of the human-animal relationship on animal emotional experiences and welfare (e.g., Rault et al. 2020), understanding cues which goats may use to anticipate human behaviour are important from a welfare perspective. I assessed goat ability to discriminate between familiar people and human emotional cues of opposing valence through measuring their behavioural and physiological responses, specifically heart rate and HRV. Another physiological indicator becoming increasingly used in the welfare literature is skin temperature, which can be measured remotely using thermal imaging.

Thermal imaging has already been used to investigate animal emotional responses to a variety of human cues, from positive interactions such as stroking and grooming (e.g., Proctor and Carder 2015,

Tamioso et al. 2017), to negative ones, like husbandry procedures (Stewart et al. 2008b, Herborn et al. 2015), including in goats (Bartolomé et al. 2019). However, at least compared to species like horses and cows (reviews: Soroko and Howell 2018, Mota-Rojas et al. 2021), this technology remains a relatively underexploited resource in goat welfare and veterinary research. Accordingly, in **Chapter 4** I investigated the reliability of surface temperatures taken in various body regions (eyes and nose) and using different measures (mean, maximum and minimum temperatures). In doing so, I aimed to identify suitable combinations of ROI and measure to allow future researchers to effectively track differences in goat surface temperatures in relation to for example, time courses of emotional responses to human cues, among other stimuli and for veterinary applications. Reliability is defined here according to two of its principal subcategories: repeatability and reproducibility. Repeatability and reproducibility refer to the degree of similarity between repeated measures taken under the same and under variable conditions respectively (Bartlett and Frost 2008; Fernández-Cuevas et al. 2015). So specifically, I investigated the precision and repeatability of measurements taken within a single session (so under consistent conditions) and reproducibility of goat surface temperatures over five consecutive days (under different environmental conditions). Lastly, **Chapter 5** discussed my findings presented in **Chapters 2-4** together in the context of the human-animal relationship and their implications for welfare, with recommendations for future research in measuring goat emotions and social cognition.

7.1. Summary of Thesis Aims:

- **Chapter 2:** To investigate whether goats can combine visual and vocal cues to recognize familiar people cross-modally.
- **Chapter 3:** To examine whether goats can discriminate between positive and negative emotional valence conveyed in the human voice, and if familiarity with the voice presented affects their ability to discriminate.
- **Chapter 4:** To evaluate the repeatability and reproducibility of goat mean, maximum and minimum surface temperatures measured in the eye and nasal regions in the short- (measured in a single session) and longer-term (measured over five consecutive days), respectively.

Chapters 1-4 have been written as self-contained articles with publication in mind.

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CHAPTER 2: Goats May Recognise Humans Cross-Modally

Abstract

Recognition plays a key role in the social lives of gregarious species, enabling animals to distinguish among social partners and to tailor their own behaviour accordingly. As domesticated animals regularly interact with humans, as well as members of their own species, we might expect mechanisms that they use to discriminate between conspecifics to also apply to humans. Given goats can combine visual and vocal cues to recognize one another, we investigated whether this cross-modal recognition extends to discriminating among familiar humans. We presented 28 goats with facial photographs of familiar people and two repeated playbacks of a voice, which was either congruent (from the same person) or incongruent (from a different person) with that photograph. When cues presented were incongruent, which is predicted to violate their expectations, we expected goats would respond faster and for longer after playbacks, as well as showing increases in physiological arousal (increased heart rate and/ or decreased heart rate variability). We found that although goats took longer to respond to voices as the playback series progressed, this increase in latency was greater when the human face and voice presented were incongruent. As differences were not as predicted and were observed in only one of the responses measured, our evidence should be considered preliminary, but as we did find changes in behaviour based on congruency, this could suggest that goat cross-modal recognition extends to humans. If so, this would infer the presence of an internal cognitive representation of familiar people, a prerequisite for individual recognition. Given the importance of human-animal relationships for welfare, understanding how and how well goats and other livestock distinguish between humans is crucial as it affects the extent to which they can attribute the outcomes of previous positive and negative interactions to individual people.

1. INTRODUCTION

Recognition forms a foundation for complex social behaviour, enabling animals to discriminate among social partners and tailor their behaviour accordingly (Tibbetts & Dale, 2007; Wiley, 2013; Yorzinski, 2017). For domesticated animals, close-contact husbandry tasks (e.g., feeding, cleaning and health-checks) and repeated interactions (a prerequisite for recognition) with humans are a frequent occurrence. Through these interactions, dyadic social relationships can develop, requiring participants to recall outcomes of previous interactions to anticipate the other party's future behaviour (Hemsworth & Coleman, 2010). This proximity to humans over thousands of generations has made the domestic environment a unique setting for the development of interspecific communication, potentially fostering more cognitively demanding forms of perception of human cues (Avarguès-Weber et al., 2013; MacHugh et al., 2017).

Several companion species have been found to integrate cues in two sensory modalities not only to recognize members of the same species, but also familiar humans (Adachi et al., 2007; Proops et al., 2009; Proops & McComb, 2012; Taylor et al., 2011; Takagi et al., 2019). Known as cross-modal recognition, such an ability infers the existence of a mental representation, for a conspecific or person which can be used to compare against available cues (a pre-requisite of individual recognition: Proops et al., 2009). Dogs (*Canis lupus familiaris*), cats (*Felis catus*) and horses (*Equus caballus*) combine visual and vocal cues to recognize familiar people (Adachi et al., 2007; Proops & McComb, 2012; Takagi et al., 2019). These discriminatory abilities may enable these companion species to categorize human identity cues with greater accuracy, which would be especially advantageous when cues in particular modalities are attenuated or unavailable (e.g., visual features at low light intensities or over distance; Ratcliffe et al., 2016). Comparatively little is known about complex recognition of humans in livestock, although cross-modal recognition has been demonstrated in the intraspecific context (in goats, *Capra hircus*: Pitcher et al., 2017).

Unlike species domesticated for companionship or as working animals, livestock occupy a niche more exclusively centred around their products, but likewise rely on us for food, shelter and protection from predators (MacHugh et al., 2017; Jardat & Lansade, 2021). Although livestock may be expected to be under weaker selection to interpret our cues and communicate with us, they have already demonstrated an impressive repertoire of social cognitive abilities in this respect (for review, see Jardat & Lansade, 2021). Goats were among the first livestock species to be domesticated, approximately 10,500 years ago (Zeder & Hesse, 2000; MacHugh & Bradley, 2001; MacHugh et al., 2017). At least compared to horses and other companion animals like dogs and cats, goats generally do not possess a close 'working' relationship with humans, being primarily domesticated for meat, milk and hair products (MacHugh & Bradley, 2001; but see pack goats: Sutliff, 2019). However, they have been shown to read a variety of human cues, such as attentional cues (Nawroth et al., 2015; 2016a; 2016b; Nawroth & McElligott, 2017), facial expressions of opposing valence (frowning from smiling: Nawroth et al., 2018) and communicative gestures (pointing and tapping: Kaminski et al., 2005; Nawroth et al., 2015; 2020).

Goats recognize each other using a variety of cues, including in combination. Pitcher et al. (2017) investigated whether goats can match vocal playback to the original caller out of a pair of conspecifics. They could make this association only when comparing between a pen-mate and a less familiar herd-member, but not between two less familiar individuals. Besides cross-modal recognition, goats are capable of long-term vocal discrimination, with dams preferentially responding to their own kid's calls over those of another familiar kid up to 13 months post-weaning (Briefer et al., 2012). Vocal characteristics and coat colour appear important for kids to recognize their mothers (Ruiz-Miranda, 1993; Briefer & McElligott, 2011) and goats are capable of discriminating group-members from non-group-members even when the head of the target animal is hidden (Keil et al., 2012). Despite the extensive research into how goats recognize conspecifics, no investigation to date has explored cues that they might use to recognize their next most important social partners, humans.

We used a congruency paradigm to investigate whether goats can recognize familiar humans cross-modally using visual and vocal cues. Goats were presented with a facial photograph and a voice which was either congruent or incongruent with that photograph's subject. Following work in other species (e.g., Adachi et al., 2007; Takagi et al., 2019), we predicted that if goats can recognize humans cross-modally, their responsiveness would increase when visual and vocal cues are incongruent, reflecting a violation of their expectations. Specifically, following presentation of a voice incongruent with visual cues, goats were predicted to respond faster and for longer, as well as exhibiting a higher heart rate and lower heart rate variability (associated with heightened physiological arousal: Briefer et al., 2015a; Baciadonna et al., 2020). In conducting this research, we aimed to see whether goat ability to develop cognitive representations for known individuals, a building block of individual recognition, extends beyond their own species.

2. MATERIALS & METHODS

2.1. Ethics Statement

All animal care and experimental procedures were approved by the University of Roehampton Life Sciences Ethics Committee (Ref. LSC 19/ 280) and were in line with ASAB guidelines for the use of animals in research (Bee et al., 2020). All tests were non-invasive and lasted a maximum of seven minutes per subject for each trial. A sample consent form signed by staff and volunteers providing photographs and voice samples for the current experiment is shown in the appendix (Appendix 1A)

2.2. Study Site & Sample Population

We conducted experiments between 8th September - 19th October 2020 and 19th May – 16th July 2021 at Buttercups Sanctuary for Goats in Kent, UK (51°13'15.7"N 0°33'05.1"E). During these periods, the sanctuary was open to visitors. Goats had daily access to a large outdoor area and were kept individually or in small groups within a large stable complex at night (mean pen size = 3.5m²). Throughout the day, animals had *ad libitum* access to hay, grass and water, and were supplemented with commercial concentrate according to age and condition. Our final sample comprised 28 adult goats (17 castrated males and 11 intact females) of various breeds (five Anglo Nubians, one British Alpine, one Golden Guernsey, one Old English Feral, 11 Pygmy goats, two Saanens, three Toggenburgs and four mixed breeds) and ages (mean age \pm SD: 9.42 \pm 3.581 years), which had resided at the sanctuary for over eight months (for detailed subject information, see Appendix 1B). Subjects were well-habituated to human presence and had been described by a particular caretaker, volunteer or frequent visitor (from whom stimuli was collected for the current experiment) as being particularly responsive to them. The reported preferential attention given to a particular person (hereafter known as a preferred person) we assumed would indicate goats were more familiar with their individual characteristics.

2.3. Stimuli Collection & Preparation

Goats were always tested with stimuli from one preferred person and one gender-matched caretaker to avoid potential reliance on gender as a cue and in the aim of ensuring subjects were familiar with all human stimuli presented. In 2020, we collected photographs and voice samples from two male and three female caretakers. Photographs and voice samples for each person were collected in a single session at a 2m distance, outdoors (as stimuli would normally be experienced by goats) and at the same location and time of day. This ensured better consistency in lighting and auditory environment between photographs and recordings which subjects were to experience in various combinations over their experimental trials. In 2021, we collected stimuli from five additional volunteers and frequent visitors to the sanctuary and one familiar staff member not involved with carrying out husbandry procedures (five females and one male) who had developed bonds with individual goats. For these, we took photographs and voice samples based on availability, meaning similarity in time of day could not be maintained, and location was sometimes shifted based on prevailing light conditions (otherwise conditions were as described above). Goats tested in 2020 were subject to stimuli gathered from caretakers only, whereas in 2021 we also tested goats using samples from people not involved in carrying out negatively perceived husbandry procedures. This could have affected the nuance of the relationship with their preferred person for goats tested in 2020 compared to those tested in 2021.

To collect visual stimuli, we asked each person to maintain a neutral expression and face the camera (Panasonic Lumix DMC-FZ45) before several photographs of their head and shoulders were taken against a white background. Photographs were later cropped so only the head and neck was visible, processed to improve clarity and brightness before being blown up to A3 landscape size (slightly larger than natural head-size). We used images instead of their real-life counterparts to avoid unintentional cuing of subjects (Samhita & Gross, 2013) and to restrict available cues to the visual

modality. Goats have previously been shown to be capable of discriminating details presented in both black and white (Nawroth et al., 2018) and moreover, colour photographs (Bellegarde et al., 2017).

For collection of voice stimuli, each person was then asked to say the phrase: “Hey, look over here,” several times in a manner they would normally use to address goats. We avoided using goat’s names and other potentially salient words, (e.g., food-related vocabulary) to test whether potential vocal recognition can be generalised based on vocal features, rather than being restricted to specific familiar words or phrases (Kriengwatana et al., 2015). Voice samples were recorded using a Sennheiser MKH 416 P48 directional microphone and a Marantz PMD-661 digital recorder (sampling rate: 48kHz, with an amplitude resolution of 16 bits in WAV format). We selected the clearest recording with the lowest background noise (mean recording length \pm SD: 1.276s \pm 0.350) and shifted the mean amplitude to 70dB to ensure consistency between playbacks and compiled these into a playback sequence using Praat v.6.1 (Boersma & Weenink, 2019). Playback sequences comprised five seconds of silence before the first voice sample, followed by 10s of silence, a repeat of that sample, and 30s of silence. We measured goat responses in the 10s of silence immediately following each voice sample (hereafter known as the response period).

2.4. Experimental Enclosure

The test enclosure was constructed out of opaque metal agricultural fencing and barred metal hurdles in a large outdoor paddock that goats had ready access to throughout the day. In 2020, we constructed this away from areas experiencing greater visitor traffic to reduce disturbance. However, due to this location also being further away from areas more commonly frequented by goats, in 2021 we constructed the enclosure to similar dimensions, but moved it to ease subject transit to the experimental arena. The enclosure was divided into five sections (Figure 1). Goats entered through the preparation pen where we equipped them for experiments. Trials took place in the experimental arena.

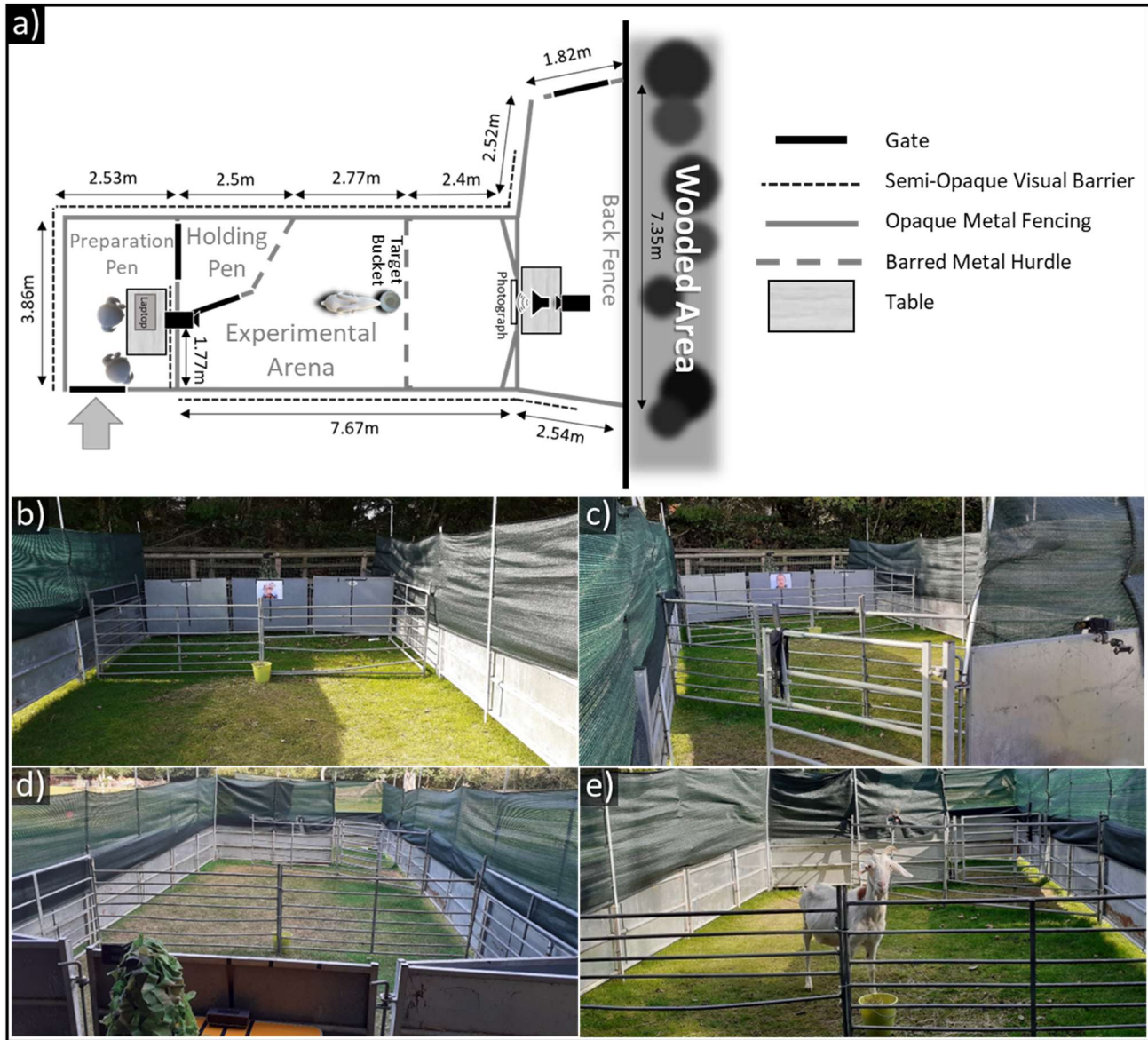


Figure 1. a) A schematic of the experimental enclosure used in 2020. Goats entered the enclosure through the preparation pen where they were fitted with a heart rate monitor, before being moved into the experimental arena for training and experimental trials. b) A photograph showing the view of the front of the arena in 2020. The target bucket used to manoeuvre goats into a suitable position for stimuli presentation was placed directly in front of the photograph and speaker behind the front separator. c) A view of the front of the arena in 2020, including the holding pen and video camera positions. d) A view of the back of the arena, including the video camera (hidden under camouflage netting) and speaker position. e) This photograph shows a subject in an ideal position for stimuli presentation.

A corner of the arena (the holding pen) was sectioned off with hurdles and used both for training (see section 2.6.) and to prevent subjects from having visual access to experimenters during trials. We erected a semi-opaque green barrier around the fencing's edge to prevent subjects from being able to see inside the preparation pen and outside the arena to reduce distractions and unintentional cuing

from experimenters, visitors and other goats. Two Sony CX240E video cameras (frame rate = 25 FPS) were positioned at the front and back of the arena. The camera at the front was hidden under camouflage netting to prevent subjects attributing it as the sound source. We placed a target bucket filled with compressed hay next to the hurdle barrier, directly in front of the stimuli array. Subjects were encouraged to approach and inspect this bucket as from this position they would have a clear view of the photograph, unimpeded by this barrier.

During experiments, the appropriate photograph was affixed to a pre-determined position at the front of the arena (top edge of image was 93.5cm off the ground). This position ensured that the speaker (a Bose Soundlink Mini Bluetooth Speaker II), which was placed directly behind the image was at approximately mouth level (70cm off the ground). The speaker used to broadcast playbacks in the current experiment has been verified to faithfully reproduce the human voice (Ben-Aderet et al., 2017). The relative positioning of the speaker and photograph was aimed to direct subject attention towards the photograph and increase likelihood of goats perceptually coupling visual and vocal stimuli presented. We separated off the front of the arena using hurdles imposing a distance between the subject and stimuli-set of a minimum of 2.4m. This stopped goats from damaging photographs and was aimed to prevent them from localizing the speaker as the sound source. Furthermore, based on evidence in sheep (*Ovis aries*), it is likely goats most effectively differentiate visual stimuli at mid-long distances (approximately $\geq 1\text{m}$ away from the head) with closer objects being perceived with reduced acuity (Piggins & Phillips, 1996). This enforced distance therefore aimed to enable animals to better distinguish photographic features.

2.5. Habituation Phase

We habituated subjects to staying in the experimental arena alone over extended periods of time over three, four-minute sessions which took place prior to testing, and occurred between a

minimum of three hours and a maximum of eight days apart (mean \pm SD = 2 days 6 hrs \pm 1 day 21 hrs). The variation in interval between successive habituation sessions was necessary as goats were not always willing to be led to the experimental apparatus or were displaced by more dominant individuals en route. Before starting each habituation session, goats were equipped with a Zephyr™ BioHarness 3.0, which in conjunction with AcqKnowledge v.4.4.2 software (BIOPAC System Inc.) was used to transmit live cardiac data to a laptop (HP ProBook 650 G4) via Bluetooth during experimental trials. If goats exhibited signs of stress or aggression while this device was being fitted, we stopped and restricted future measurements taken during such trials to behaviour (collected cardiac data from 16 out of 28 goats; for further details, see Appendix 1B).

For the first habituation session, an experimenter sat still with their head down at the front of the arena where the photograph would be placed during experimental trials. As initially goats were not completely isolated, we aimed for this to reduce neophobia and encourage subjects to investigate their surroundings. For the following two habituation sessions subjects were kept alone in the arena. We occasionally repeated sessions when previous ones were halted due to adverse conditions such as rain, or when a long period of time had elapsed since the goat's third habituation session (approximately seven days). For all three habituation sessions, we ensured animals had access to water and small food rewards (dry pasta), the latter of which were placed in and around the target bucket to encourage them to investigate and spend more time at the front of the arena. The habituation phase proceeded the test phase by a minimum of three hours and 15 minutes and a maximum of eight days (mean \pm SD = 1 day 19 hrs \pm 2 days 2 hrs).

2.6. Training Phase

The training phase took place directly before each experimental trial and aimed to incentivise goats to approach and investigate the target bucket during the test phase. Initially, goats entered the

apparatus through the preparation pen where they were fitted with the BioHarness, which subjects had become accustomed to wearing during habituation sessions. To attain a clearer ECG trace, we clipped a patch of fur around the left shoulder blade at least one day prior to testing, over which the BioHarness module would be positioned. ECG gel was applied liberally to sensors on the BioHarness belt before it was placed around the subject's thorax to improve conductance to the skin. Once a clear ECG trace had been secured, we led goats into the holding pen to begin training.

For training trial 1, Experimenter 1 and the subject were positioned inside the holding pen. Experimenter 2 held a piece of pasta (or cracker if they were not sufficiently motivated by pasta) near the subject's head and, once they had noticed it, walked slowly backwards towards the bucket while actively maintaining their attention. They then slowly and overtly placed two pieces of pasta inside, before crouching by the bucket and looking at it. Experimenter 1 then released the subject from the holding pen and stood aside, allowing the goat to pass and retrieve the pasta. The subject consumed both pieces of pasta before being led back into the holding pen. Training trial 2 proceeded similarly to the first, but instead of crouching down by the bucket, Experimenter 2 released the goat from the holding pen and stood aside to allow them to retrieve the reward. For training trials 3 and 4, Experimenter 2 gained the subject's attention from the bucket, before baiting it and releasing them from the holding pen. Goats passed a trial if they successfully reached the bucket within 30s after release and needed to pass all four trials consecutively to proceed to the test phase. If a subject failed to pass a trial, the training process was repeated from the beginning and if they were not sufficiently motivated to participate in training, they were released, and the experimental trial was carried out on a different occasion.

2.7. Test Phase

Goats experienced four experimental trials each (between 3-14 days apart, mean = 7 days). Two trials were congruent (face and voice were from the same person) and two incongruent (from different people), with subjects experiencing all combinations of photograph and voice samples from a preferred person and a caretaker in a randomised order.

Once training had been completed, we led subjects back into the preparation pen and following checks to ensure the ECG signal had been maintained, they were distracted while the photograph was positioned. The goat was then led back into the arena and the holding pen shut behind them. Experimenters 1 and 2 quietly hid behind the visual barrier in the preparation pen and monitored subject movements in a nearby video camera's LCD monitor (Figure 1). We expected goats to approach and inspect the bucket (no pasta or water available during test phase) and when they were positioned close to and facing the front, we initiated playbacks (maximum amplitude: mean \pm SD = 76dB \pm 2 measured 1m away under field conditions using a CEMTM DT-8851 sound-level meter). If a subject moved away within the five seconds of silence preceding the first playback, where possible the playback sequence was aborted, and we re-initiated it when they were in a good position. If goats failed to be in a suitable position for six minutes following trial initiation (n = 11 trials), the trial was suspended, and they were released. We placed an event marker in the ECG trace to indicate occurrence of each playback for later analysis of cardiac measures. Goats that had been subject to both playbacks were released 30s after the final playback (duration in arena: mean \pm SD = 1 min \pm 53 s \pm 1 min 20s). Of the 33 subjects tested, we excluded one from further testing due to health concerns, one for repeatedly failing to be in a suitable position for stimuli presentation, and a further subject and two trials from another were excluded due to lack of training motivation.

2.8. Video Coding

We coded behavioural data using BORIS v.7.8.2 (Friard & Gamba, 2016), with goat latency to look towards the photograph and looking duration in the 10s response periods following each playback defined to the nearest frame (0.04s). Behavioural measures were extracted from footage captured from the front and back of the arena, before being compared and combined. Measurements taken from the front were often clearer and without a blind spot, so these took precedence for quantifying behaviour. This was not always possible, as technical issues in the front camera for three trials and the back camera for two prevented experiments from being successfully captured by both, so in these cases we coded behaviours from the footage available. Under such circumstances, when goats went into the camera's blind spot ($n = 1$ trial), only behaviours that could be coded with certainty were recorded, with others defined as missing.

Although we ultimately analysed behavioural data coded by a single observer, two further observers scored independent sets of videos comprising 37.9% and 42.1% of trials respectively (80% in total) to evaluate the accuracy of our data set. Inter-observer reliability proved relatively high for duration (intra-class correlation analysis assuming Poisson distribution: $R \pm \text{s.e.} = 0.806 \pm 0.029$, $p < 0.0001$, $n = 1000$ bootstraps; rptR R package: Stoffel et al., 2017) and latency measures (proportional distribution assumed: $R \pm \text{s.e.} = 0.929 \pm 0.038$, $p < 0.0001$, $n = 1000$ bootstraps).

2.9 Exclusion Criteria

We applied two exclusion criteria when determining which trials should be considered for analysis. Firstly, if goats failed to look towards the stimuli array during both response periods in the playback sequence, the trial was excluded as subjects were interpreted as not being sufficiently attentive to human cues to notice incongruencies between them ($n = 22$ trials). Secondly, once the first exclusion criteria had been applied, we also excluded goats that did not look for at least one congruent

and one incongruent trial as these prohibited within-subjects comparison ($n = 2$ subjects excluded).

Ultimately, we analysed 95 trials from 28 subjects, nine of which experienced stimuli from men and 19 from women.

2.10. Data Analysis

2.10.1. General Model Parameters

We avoided automated model selection approaches for two reasons. Firstly, stepwise selection methods are well-known to lead to inflated type 1 errors and direction of selection (forwards or backwards) can have key implications for which variables get fitted into analytical models (Mundry & Nunn, 2009). Secondly, even the currently favoured information criterion approaches (e.g., Akaike's and Bayesian) may not perform substantially better (Bishop, 2006; Mundry, 2011; Forstmeier et al., 2017). Instead, as in addition to congruency, there were various factors which could have profound effects for goat behavioural and physiological responses we used a full model approach, as recommended by, for example, Forstmeier & Schielzeth (2011).

Our primary variable of interest for all models was congruency, i.e., whether the face and voice presented were from the same person (were congruent), or from different people (were incongruent). We also investigated whether goat responses changed over the playback series (playbacks 1 and 2), as could happen owing to, for example, habituation. In addition, we explored the interaction between congruency and playback number as there may be a lag before goats register and respond to incongruencies between stimuli presented. This interaction term was included in all models to begin with but removed if its effect was not significant (only retained in models predicting latency to look) to allow us to interpret the effects of playback number and congruency separately (as recommended by Engqvist, 2005). In addition, as the experimental enclosure was erected at different locations in 2020 and 2021 and the pool of human stimuli collected was expanded in 2021, we investigated the effect of

year on goat responses. The sex of the subject and gender of the person whose identity cues were presented was also considered. This is because several studies have found sex-specific differences in responses to social stimuli (Proverbio, 2017; Bognár et al., 2018), including in the context of cross-modal recognition (Proops & McComb, 2012) and based on whether animals were experiencing stimuli from men or women (McComb et al., 2014; Shih et al., 2020; Li et al., 2020). Furthermore, we considered the identity of the photograph and voice, specifically whether or not they were derived from the preferred person, as this could have affected level of familiarity with cues presented. The interval between the experimenters leaving the arena (trial beginning) and the onset of playbacks (preliminary duration) was included as a covariate. Goats experiencing an extended time in the experimental enclosure may have had longer to habituate or become more aroused due to prolonged isolation from conspecifics, which may have affected their behavioural and emotional responses (e.g., Siebert et al., 2011; Briefer et al., 2015a). Finally, we also fitted the covariate ‘measurement period’ to all models predicting cardiac responses. Noise present in the ECG trace meant heart rate and heart rate variability (HRV) often could not be calculated over the entire response period. Measurement period therefore refers to the total time over which it was possible to calculate these responses. Given shorter measurement periods were likely the result of reduced ECG signal quality, this factor potentially represented an important control variable (e.g., Reefmann et al., 2009; Briefer et al., 2015b). As for random effects, trial number (1-4) was nested within subject identity to control for repeated measurements taken for each goat both within and between trials, as well as the unique identifier given to the photograph and playback used for an experimental trial (the same stimuli were used over multiple trials).

These variables were used to model the two behavioural and two physiological responses of interest: looking duration and latency to look at the stimuli array following playbacks, as well as heart rate and HRV. All statistical analyses were conducted using R (version 4.1.1.: R Core Team, 2021).

2.10.2. Looking Duration

As looking duration was restricted within the bounds of 0-10s and model residuals did not fit a normal error structure, we considered approaches more typically applied to count data. Data was overdispersed and zero-inflated (verified using the DHARMA package: Hartig, 2021), therefore using the package glmmTMB, we compared fit of multiple models assuming different error distributions (Poisson, zero inflated-Poisson and negative binomial: Brooks et al., 2017). According to Akaike's Information Criterion (AIC) we found that the best fit model had a zero-inflated negative binomial type 1 error structure (assumes variance increases linearly with the mean: Brooks et al., 2017). Such an approach generates both a conditional and a zero-inflated model, with the former predicting duration values greater than zero seconds and the latter, the probability of a zero observation (goats did not look) using a logit link. Preliminary duration and the random effect voice identity were removed due to issues with model convergence.

2.10.3. Latency to Look

Due to the bimodal nature of latency responses, with peaks at 0s (subjects were looking at onset of the response period) and 10s (subjects failed to look throughout the response period), we analysed this variable using a binomial generalised linear mixed model (GLMM; glmer function, lme4 package: Bates et al., 2015). Post hoc tests were conducted using the emmeans package with Tukey's corrections to account for multiple comparisons (Lenth, 2021).

2.10.4. Heart Rate

We calculated heart rate (beats per minute) over the 10s response periods following playbacks 1 and 2, and a baseline heart rate, which was calculated within the 10s before playbacks. Trials began

when both experimenters had left the arena and to reduce the effect of human manipulation on heart rate measures, baseline heart rate was only calculated following this, which for some observations ($n = 13$ trials) meant the measurement period was less than 10s. When noise present in the ECG trace restricted this period to less than five seconds, where possible (preliminary duration before onset of playbacks greater than 10s), we expanded the time frame for calculating baseline up to 30s prior to the first playback until a measurement period of 10s could be achieved ($n = 7$ trials).

Specifically, we examined the difference in heart rate calculated in the response periods following playbacks 1 and 2 compared to the baseline period ($\Delta HR = HR_{pb1} - HR_{baseline}$ or $\Delta HR = HR_{pb2} - HR_{baseline}$). This measure was used as variation in baseline heart rate meant relative changes in heart rate measured over a single trial were more meaningful than absolute differences in heart rate between individuals and trials (baseline BPM: mean \pm SD = 115.15 ± 16.97). Model residuals conformed to an approximately normal error structure with homogenous variance, so we fitted a linear mixed model (LMM) to goat heart rate responses (lmer function, lme4 package: Bates et al., 2015).

2.10.5. Heart Rate Variability

HRV was calculated as the root mean square of successive differences between heartbeats multiplied by 1000 (RMSSD). HRV was again calculated over the baseline period (using guidelines outlined above for heart rate), and the response periods following playback 1 and playback 2. ΔHRV ($HRV_{pb1} - HRV_{baseline}$ or $HRV_{pb2} - HRV_{baseline}$) was used instead of comparing absolute differences in HRV between trials, again to account for basal variability between subjects and trials (baseline RMSSD: mean \pm SD = 22.42 ± 25.57).

Having fitted a LMM and visualised its residual variance, plots indicated presence of extreme values. As these outliers had the potential to have a disproportionate effect when estimating model parameters, steps were taken to identify and exclude such observations. Using a z-score method, we

identified HRV values falling outside the 95% quantiles. After excluding these observations ($n = 8$), LMM assumptions were met so we used this approach to model shifts in HRV relative to congruency accordingly (lme4 package: Bates et al., 2015).

3. RESULTS

3.1. Looking Duration

There was no effect of congruency between human facial and vocal identity cues on how likely goats were to look following playbacks (zero-inflated model: $\beta \pm \text{s.e.} = -0.030 \pm 0.419$, $Z = -0.07$, $p = 0.943$) or how long subjects looked when they did so (conditional model: $\beta \pm \text{s.e.} = 0.149 \pm 0.107$, $Z = 1.39$, $p = 0.165$)(Table 1; Figure 2a & 2b). However, goats were marginally less likely to look after playback 2 than playback 1 (zero-inflated GLMM: $\beta \pm \text{s.e.} = 0.760 \pm 0.423$, $Z = 1.80$, $p = 0.072$). The year goats were tested, their sex, the gender of the person providing stimuli and whether the face and voice belonged to the goat's preferred person or not had no effect on the probability or duration over which they responded to playbacks (Table 1).

Table 1. Predictors of goat looking duration (conditional model) and likelihood of not looking (zero-inflated model) at the photograph following voice playbacks. Parameter estimates come from a zero-inflated negative binomial type 1 model.

Explanatory Variable	Looking Duration (conditional model)				Likelihood of Not Looking (zero-inflated model)			
	β	S.E.	z-value	p-value	β	S.E.	z-value	p-value
Intercept	8.170	0.170			-2.219	0.606		
Congruency (I)^a	0.149	0.107	1.39	0.165	-0.030	0.419	-0.07	0.943
Playback No. (2) ^b	-0.100	0.097	-1.03	0.305	0.760	0.423	1.80	0.072
Year (2021) ^c	-0.070	0.131	-0.53	0.597	0.374	0.437	0.86	0.392
Subject Sex (M) ^d	0.165	0.133	1.24	0.216	-0.176	0.435	-0.41	0.685
Human Gender (M) ^d	0.091	0.137	0.66	0.509	0.163	0.444	0.37	0.714
Photograph ID (P) ^e	-0.088	0.107	-0.82	0.413	0.106	0.417	0.25	0.799
Voice ID (P) ^e	-0.080	0.106	-0.75	0.453	-0.244	0.417	-0.59	0.558

Results concerning the primary effect of interest, congruency are shown in bold. Key: I = Incongruent; M = Male; P = Preferred Person. Reference Categories: a = Congruent; b = Playback Number 1; c = 2020; d = Female; e = Non-Preferred Person.

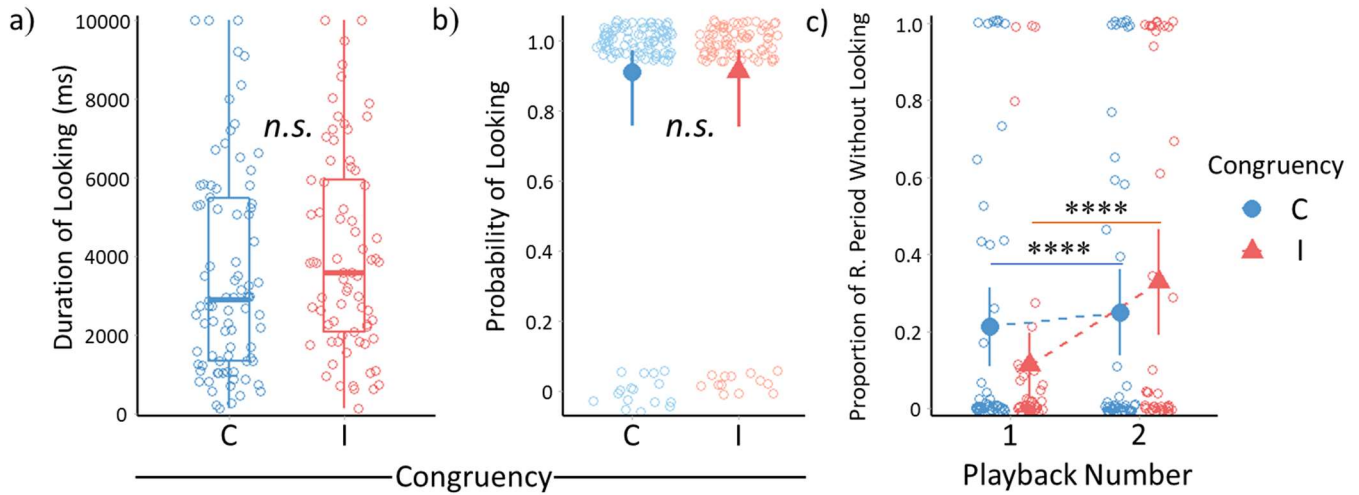


Figure 2. Effect of congruency between human facial and vocal cues on goat looking behaviours. a) Median and interquartile range (IQR) for looking duration values greater than zero as a function of congruency. Boxplot whiskers extend to the maximum and minimum value less than 1.5 times above or below the IQR respectively. b) Predicted probability and 95% confidence intervals of goats looking in the congruent and incongruent conditions for each playback. c) The mean and confidence intervals for the effect of congruency and playback number on the proportion of the 10s response period that passed before goats looked. R. Period = Response period; C = Congruent; I = Incongruent. *n.s.* = non-significant; **** $p < 0.0001$

3.2. Latency to Look

The time goats took to look towards photographs following playbacks was affected by the congruency between the person's face and voice in combination with playback number (Table 2). Post-hoc tests revealed that although goats in both the congruent and incongruent conditions took longer to respond for playback 2 than playback 1 (congruent playback 1 vs congruent playback 2: $\beta \pm \text{s.e.} = -0.311 \pm 0.006$, $Z\text{-ratio} = -53.68$, $p < 0.0001$; incongruent playback 1 vs incongruent playback 2: $\beta \pm \text{s.e.} = -2.073 \pm 0.007$, $Z\text{-ratio} = -277.31$, $p < 0.0001$), this increase in latency was greater in goats experiencing incongruent human cues (congruency x playback number: $\beta \pm \text{s.e.} = 1.76 \pm 0.009$, $Z\text{-value} = 186.13$, $p < 0.0001$) (Table 2; Figure 2c; see Appendix 1C for further post-hoc comparisons). Additionally, preliminary duration had a small, but significant effect on latency, with goats spending a longer time in the arena before playbacks were initiated tending to respond more quickly ($\beta \pm \text{s.e.} = -0.031 \pm 0.008$, $Z = -3.69$, $p = 0.0002$). Goats also took a marginally longer time to respond to men's versus women's voices and in 2021 versus 2020 (human gender: $\beta \pm \text{s.e.} = 2.586 \pm 1.469$, $Z = 1.76$, $p = 0.078$; year tested: $\beta \pm$

s.e.= 2.662 ± 1.365 , $Z = 1.95$, $p = 0.051$)(Table 2). However, sex, and whether the photograph and the voice presented were from a preferred person did not affect the time it took for goats to look.

Table 2. Predictors of time taken for goats to look at the photograph following playbacks of a familiar person's voice (binomial GLMM).

Explanatory Variable	β	S.E.	z-value	p-value
Intercept	-5.786	1.607		
Congruency (I) ^a	-0.719	1.227	-0.59	0.558
Playback No. (2) ^b	0.311	0.006	53.68	<0.0001****
Congruency (I)^a x Playback No. (2)^b	1.761	0.009	186.13	<0.0001****
Year (2021) ^c	2.662	1.365	1.95	0.051
Subject Sex (M) ^d	-1.071	1.413	-0.76	0.449
Human Gender (M) ^d	2.586	1.469	1.76	0.078
Photograph ID (P) ^e	-0.865	1.217	-0.71	0.477
Voice ID (P) ^e	0.598	1.206	0.50	0.620
Preliminary Duration	-0.031	0.008	-3.69	0.0002***

Results concerning the primary effect of interest, congruency x playback number interaction is shown in bold. Key: I = Incongruent; M = Male; P = Preferred Person. Reference Categories: a = Congruent; b = Playback Number 1; c = 2020; d = Female; e = Non-preferred Person. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; **** $p < 0.0001$

3.3. Heart Rate & Heart Rate Variability

Congruency between human identity cues did not affect goat heart rate ($\beta \pm \text{s.e.} = -1.147 \pm 3.112$, $F_{(1,35.32)} = 0.14$, $p = 0.715$)(Table 3; Figure 3a), or HRV relative to baseline values ($\beta \pm \text{s.e.} = -3.083 \pm 2.415$, $F_{(1, 27.98)} = 1.63$, $p = 0.212$)(Figure 3b). However, goats did show a decrease in heart rate between playbacks 1 and 2 ($\beta \pm \text{s.e.} = -5.220 \pm 1.113$, $F_{(1,48.69)} = 22.01$, $p < 0.0001$) and had a lower HRV when there was a longer measurement period available for calculating this response ($\beta \pm \text{s.e.} = -1.907 \pm 0.936$, $F_{(1,48.80)} = 4.15$, $p = 0.047$)(Table 3). There was no effect of playback number on HRV, or measurement

period on heart rate, nor was there an effect of year the goat was tested, their sex, or the gender of the human stimuli experienced, whether these came from a preferred person, or the preliminary duration before onset of playbacks on heart rate or HRV (Table 3).

Table 3. Predictors of goat heart rate and HRV, relative to baseline values (measured before onset of playbacks) in the response periods following presentation of a familiar human voice (LMM).

Explanatory Variable	Heart Rate (BPM)				Heart Rate Variability (RMSSD)			
	β	S.E.	F-value	p-value	β	S.E.	F-value	p-value
Intercept	-4.255	8.268			22.135	9.539		
Congruency (I)^a	-1.147	3.112	(-)0.14	0.715	-3.083	2.415	(-)1.63	0.212
Playback No. (2) ^b	-5.220	1.113	(-)22.01	<0.0001****	1.116	2.010	0.31	0.582
Year (2021) ^c	4.531	3.842	1.39	0.263	-4.567	3.708	(-)1.52	0.248
Subject Sex (M) ^d	-1.519	3.979	(-)0.15	0.710	-1.202	3.767	(-)0.10	0.757
Human Gender (M) ^d	-2.698	3.930	(-)0.47	0.507	2.775	3.988	0.48	0.518
Photograph ID (P) ^e	3.527	3.102	1.29	0.263	1.479	2.506	0.35	0.580
Voice ID (P) ^e	-3.205	3.118	(-)1.06	0.311	-0.013	2.561	(-)0.00	0.996
Preliminary Duration	0.010	0.024	0.19	0.667	-0.013	0.020	(-)0.44	0.512
Measurement Period	0.242	0.766	0.10	0.752	-1.907	0.936	(-)4.15	0.047 *

Results concerning the primary effect of interest, congruency are shown in bold. Key: I = Incongruent; M = Male; P = Preferred Person. Reference Categories: a = Congruent; b = Playback Number 1; c = 2020; d = Female; e = Non-Preferred Person. *p*-values calculated using Satterthwaite's degrees of freedom method, but direction of relationship of predictor on heart rate or HRV shown in brackets. **p*<0.05; ***p*<0.01; ****p*<0.001; *****p*<0.0001

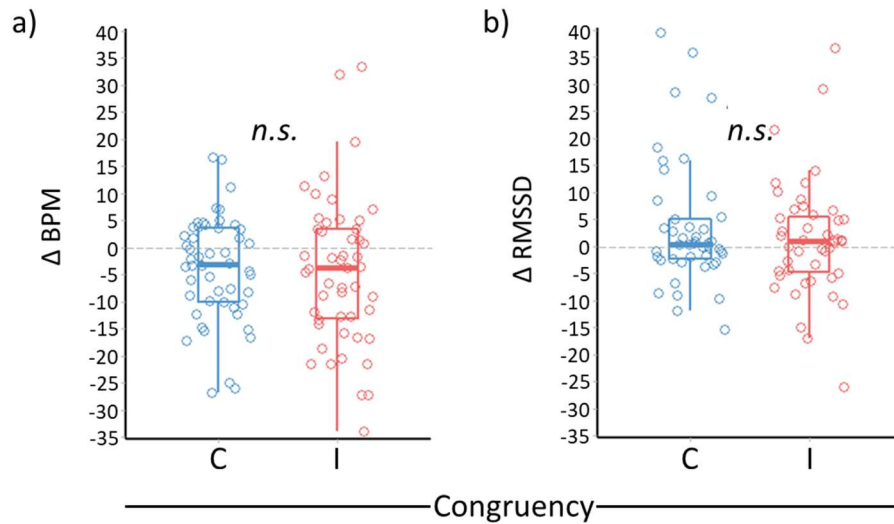


Figure 3. Effect of congruency between human visual and vocal identity cues on a) shifts in goat heart rate and b) HRV from baseline values (measured before onset of playbacks). Boxplots feature median and IQR. Whiskers extend to the maximum and minimum value less than 1.5 times above or below the IQR respectively. Baseline values are indicated by the dashed grey line. BPM = Beats per minute; C = Congruent; I = Incongruent. *n.s.* = non-significant

3.4. Summary

To summarize, goat looking duration and cardiac responses were not affected by whether the human face and voice presented were from the same or different people. However, although time taken for them to look at the photograph following playbacks increased between playbacks 1 and 2 in both conditions, this increase was significantly greater when they were experiencing incongruent human identity cues.

4. DISCUSSION

We used a congruency paradigm to investigate whether goats can combine visual and vocal cues to recognize familiar people. Goats were presented with a photograph of a familiar person and a voice that either matched (was congruent with) or did not match (was incongruent with) that photograph's subject. If they could recognize the familiar person cross-modally, goats were predicted to respond faster and longer when there were incongruencies between stimuli presented, reflecting a violation of their expectations (e.g., Adachi et al., 2007; Takagi et al., 2019). Contrary to predictions, whether the photograph and voice were taken from the same or different people had little effect on how long or how likely goats were to look at the photograph, or on their cardiac responses (heart rate and HRV) following playbacks. However, congruency between human facial and vocal cues did affect the time it took for goats to look. Although not as predicted, as we did observe changes in behaviour between conditions, it could suggest that goats had successfully perceived differences in congruency between the human visual and vocal information presented. These results give a first indication that the ability to use complex cross-modal recognition systems to discriminate human, as well as conspecific identity cues may not be limited to primates or species bred for work or companionship (Adachi et al., 2007; Sliwa et al., 2011; Proops & McComb, 2012; Takagi et al., 2019).

Evidence that goats recognize humans using visual and vocal cues would contribute to a growing body of literature emphasising the flexibility of complex recognition systems to create mental representations for members of a highly dissimilar species (Ratcliffe et al., 2016). Within a species, recognition mechanisms are expected to co-evolve with signalling systems to facilitate communication between, for example mates, kin, group members and competitors (e.g., Miller et al., 2020; Tibbetts et al., 2020). However, for domesticated species like goats, humans represent a salient feature in their environment both within and between generations. Given behaviour can vary consistently among people, based on for example their attitudes, gender, skills and/ or experience (Hemsworth et al., 2000;

Hemsworth & Coleman, 2010; Ceballos et al., 2018; Celozzi et al., 2022), animals which discriminate may be favoured. Indeed, possession of recognition systems that enable animals to categorize human identity cues with greater accuracy may increase predictability in outcome when interacting with certain people (Hemsworth et al., 1987; Hemsworth & Coleman, 2010; Brajon et al., 2015; Yorzinski, 2017).

Anticipating positive or negative events as a result of human-animal interactions may affect animal emotional experiences, and ultimately have important implications for welfare (Davis et al., 1998; Sankey et al., 2010; Green & Mellor, 2011; Mellor & Beausoleil, 2015; Somavilla et al., 2016). For instance, if animals are motivated to seek contact with a preferred person, this will create opportunities for them to experience positive emotions and may provide a buffer for stressful situations (e.g., husbandry procedures; for review see, Rault et al., 2020). Conversely, contact with people associated with a history of negative interactions may evoke fear, and have negative implications for animal welfare. The specificity of recognition that goats express will affect whether these experiences are attributed to individuals (individual recognition), people sharing similar features (class-level recognition, e.g., vets versus regular caretakers) or even to humans in general (although recognition and generalisation are not mutually exclusive: Brajon et al., 2015; Yorzinski et al., 2017).

As goats in the current study were required to discriminate cues from a single pair of familiar humans, we did not explicitly test whether cues they employed were at the individual (goats recognized both parties), or at the class-level (e.g., level of familiarity: Proops et al., 2009; Pitcher et al., 2017). However, the evidence that goats registered incongruencies between human stimuli presented in different modalities could suggest the presence of an internal representation for familiar people; a foundation of individual recognition (Proops et al., 2009). Given the acknowledged importance of the human-animal relationship on welfare (Mota-Rojas et al., 2020; Rault et al., 2020), understanding recognition is important from such a perspective, as it affects the overall structure and complexity such

relationships may take. However, further research is needed to more fully understand the specificity and mechanisms that goats use to discriminate among people.

Similar congruency paradigms to the one used here have found a range of species tend to look quicker and/ or for longer when presented with incongruent conspecific cues (e.g., Proops et al., 2009; Gilfillan et al., 2016; Baciadonna et al., 2021) and, moreover, human identity cues in divergent modalities (e.g., Adachi et al., 2007; Takagi et al., 2019; Lampe & Andre, 2012). Conversely, goats in our experiment took longer to look as the playback series progressed when human facial and vocal cues were incongruent. Although, this could indicate goats were quicker to respond (but not significantly so), but also habituated more quickly (again not significantly) to these abnormal stimuli combinations, the mechanistic basis underlying the observed changes in response remains elusive. Ultimately, goats in our experiment did not show the expected differences in behaviour in relation to stimuli congruency, or any evidence of differences in physiological responses between conditions.

We believe the lack of support for our key predictions may be due to two main factors. Firstly, in order to register incongruencies, animals need to have developed an internal template for known individuals (Proops et al., 2009; Ratcliffe et al., 2016). Not all goats in our investigation may have possessed such a template for both people they were experiencing cues from, either through lack of cognitive ability or familiarity with their individual-specific cues. Secondly, we used photographs as visual stimuli instead of the live people they depict (thus excluding possible use of other cues e.g., olfactory and body cues: Poindron et al., 2007; Keil et al., 2012). To register incongruencies, goats would not only have to recognize the photograph's subject, but treat it as a representation of that subject (Fagot & Parron, 2010). This, in conjunction with the relatively limited visual information available (e.g., loss of depth, perspective and motion cues) and modification of colour can make interpreting photographs difficult for non-human animals (Hill et al., 1997; Fagot & Parron, 2010; Lansade et al.,

2020). Furthermore, the static, unresponsive nature of images can mean they are less salient and more rapidly habituated to than live stimuli (Vandenheede & Bouissou, 1994; Bovet & Vauclair, 2000).

In summary, our research provides evidence that goats may combine visual and vocal cues to recognize familiar humans, just as they can do with conspecifics (Pitcher et al., 2017). By extension, it suggests that goats may be able to form internal representations of heterospecifics, adding to a growing body of literature documenting the adaptability of complex cross-modal recognition systems to discriminate individuals of other, even phylogenetically very distant species (e.g., Adachi et al., 2007; Proops & McComb, 2012). Overall, these findings may not only be important in furthering our basic knowledge of social cognition in human-animal relationships, but could have critical applied implications for better understanding, and ultimately improving the welfare of domesticated animals.

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CHAPTER 3: Goat Discrimination of Emotional Valence in the Human Voice

Abstract

Reading another individual's emotional state can enable receivers to anticipate their behavioural motivations, important in guiding interactions with that individual. For species living closely alongside us, the emotional cues we express can be almost as informative as those of members of the same species. Given goats can discriminate conspecific calls based on their emotional valence, we investigated whether this ability extends to discriminating analogous cues in human speech. We presented goats with a habituation-dishabituation-rehabilitation paradigm, where they experienced multiple playbacks of a familiar or unfamiliar human voice conveying a single emotional valence (e.g., angry; habituation phase), before the valence of the voice changed (e.g., happy; dishabituation phase) and then reversed again in-line with the habituation phase (e.g., angry; rehabilitation phase). Over the habituation phase, we found goats became less likely to look towards the sound source, took longer to do so and responded for a shorter time with increasing playback number, suggesting they had habituated to the playback stimuli presented. Following a change in emotional valence (dishabituation phase), goats were less likely to respond, but significantly goats which did, looked for longer, suggesting these goats could perceive this change. Conversely, no changes in physiological arousal (heart rate or HRV) were detected in relation to playback valence. These findings contribute to the limited literature available indicating livestock, like companion animals, are sensitive to human emotional cues, raising questions about the effect of domestication, individual experience and learning, among other factors in interspecific emotional communication.

1. INTRODUCTION

Emotional processes help tailor behaviour adaptively towards internal/ and or environmental cues (Kremer et al., 2020). Specifically, they can motivate approach towards fitness-enhancing stimuli such as mates and foraging resources, and avoidance of fitness-threatening ones, like predators. Such responses are multicomponent, incorporating neural, physiological, cognitive, (sometimes) subjective and behavioural elements (Špinka, 2012). The behavioural component is often overt and somewhat ritualised, leading many researchers to conclude that while emotional displays generally serve a direct adaptive function (e.g., moving away from danger), in social species they may perform an additional role in communication (e.g., Shariff & Tracy, 2011). Indeed, another individual's emotional state can be used referentially, with receivers benefitting from the ability to assess signaller motivations, important in guiding future interactions with that individual (Schmidt & Cohn, 2001).

Widely used 'dimensional approaches' principally model emotion as graded responses across two axes, usually valence (positive or negative, e.g., happiness to sadness) and arousal (the intensity of the emotion experienced, e.g., calm to excited; Mendl et al., 2010), both of which mediate perceivable changes in animal vocalisations. Although vocal signals are rooted in social context and functional relevance (e.g., chronic versus acute emotional stimulation and predator presence), greater emotional arousal is often associated with predictable increases in call rate, frequency and loudness (Briefer, 2012; 2020). Conversely, shifts in vocal features relative to valence appear more species-specific, with different types of call being favoured in different social and emotional contexts (Briefer, 2012; 2020). For example, laughter and crying in humans tend to be linked to positive and negative emotions respectively. However, it has been suggested positive vocalisations tend to be shorter, with a lower and less variable fundamental frequency (relates to pitch), than negative ones (Briefer, 2020).

Vocalisations are considered to match emotional state more closely in non-human animals than in humans, with this relationship becoming more complicated in our own species owing to the greater

conscious control we exhibit over our vocal apparatus (Jürgens, 2009; Briefer, 2012). However, the link between emotional state and vocal communication has not been entirely eradicated, with emotional cues remaining clearly evident in our non-verbal utterances (e.g., crying and laughter) and speech (Ackermann et al., 2014; Bryant, 2018; 2021). Similarities in how emotion is conveyed across taxa may to an extent enable animals to apply rules from their own emotional communication systems to discriminate analogous heterospecific cues (Faragó et al., 2014; Filippi et al., 2017; Bryant, 2021), with accuracy of such distinctions potentially being further tailored through experience (Kitchen et al., 2010; Merola et al., 2014; Scheumann et al., 2014; Barber et al., 2016). Accurate perception of heterospecific emotional cues is particularly important when animals live closely with another species.

Emotional cues can act as salient predictors of human behaviour, which if perceived, can be used to anticipate positive and negative events as a result of interacting with certain people (Schmidt & Cohn, 2001). If sensitive to these cues, it may affect the emotional experiences and welfare of animals living alongside us (Green & Mellor, 2011; Mellor & Beausoleil, 2015; Baciadonna et al., 2020). Companion animals have been shown to perceive human emotional cues in multiple sensory modalities, including in combination (e.g., Albuquerque et al., 2016; Nakamura et al., 2018; Quaranta et al., 2020). However, far less is known about these abilities in livestock. Unlike species domesticated for companionship or work, livestock have been bred largely for their products, so may be expected to be under weaker selection to interpret our communicative cues, including emotional ones (MacHugh et al., 2017; Jardat & Lansade, 2021). Despite this, livestock have been shown to read a variety of human cues sometimes showing comparable levels of performance to companion animals. For example, pigs (*Sus scrofa domesticus*), like horses (*Equus caballus*) respond differently to human voices based on their emotional valence (Maigrot et al., 2022) and cows (*Bos taurus*) can discriminate chemical cues, preferentially interacting with sweat odours from humans in neutral, but not in stressful situations (Destrez et al., 2021). Similarly, sheep (*Ovis aries*) and goats (*Capra hircus*) presented with photographs of an unfamiliar human exhibiting

facial expressions of opposing emotional valence, preferentially approached and interacted with the happy, relative to angry faces (Tate et al., 2006; Nawroth et al., 2018).

Goats, a species primarily domesticated for milk, meat and hair products (MacHugh & Bradley, 2001; but see pack goats, Sutliff, 2019) are sensitive to a variety of human cues. For example, when confronted with an unsolvable task, goats altered their human-directed gazing behaviour in relation to the perceived level of attention they received (Nawroth et al., 2016a). This indicates not only that goats discriminate our attentional cues, but these gaze alternation behaviours have been interpreted as attempts at human-directed communication. Goats can also use our gestural cues to solve tasks (pointing/ tapping: Kaminski et al., 2005; Nawroth et al., 2015; 2020) and even learn socially from humans (Nawroth et al., 2016b). Moreover, they are sensitive to emotional cues, discriminating between human, as well as conspecific positive and negative facial expressions (Bellegarde et al., 2017; Nawroth et al., 2018). That being said, the ability of goats and other ungulate livestock themselves to produce complex, emotive facial expressions is constrained by their relatively limited facial musculature and the morphology of these expressions appear poorly conserved across taxa (Waller & Micheletta, 2013).

Goats are a highly vocal species, with calls encoding a range of information, including the caller's age, body size, sex, social environment, individual identity (Briefer & McElligott 2011a; 2011b; 2012) and importantly, their emotional state (Briefer et al., 2015a). Such variability provides ample substrate for making related distinctions and indeed, goats have been shown to discriminate identity information (Briefer & McElligott, 2011a; Briefer et al., 2012; Pitcher et al., 2017) and moreover, emotional valence conveyed in conspecific calls (Baciadonna et al., 2019). To test whether they can discriminate analogous emotional cues in the human voice, we presented goats with a playback paradigm to investigate whether subjects could perceive shifts in valence, specifically, anger versus happiness conveyed in human speech.

Goats experienced a series of nine voice playbacks expressing either a positive (happy) or a negative (angry) valence (habituation phase), before the valence of playbacks was changed (e.g., from positive to negative: dishabituation phase) and then reversed in-line with that of the habituation phase (based on Charlton et al., 2007; 2011; 2012; Baciadonna et al., 2019). We predicted that if goats could discriminate emotional content conveyed in the human voice, they would dishabituate, looking faster and for longer towards the source of the sound following the first shift in valence. We also expected potential changes at physiological levels with heart rate increasing and heart rate variability (HRV) decreasing after a shift in valence, indicating an increase in arousal (Briefer et al., 2015a; Baciadonna et al., 2020). Alternatively, goats may also express differences in arousal based on the valence that the voice conveyed (Baciadonna et al., 2019). In dogs (*Canis lupus familiaris*) and horses, familiarity with the individual conveying the emotional cues appears to facilitate their discrimination (e.g., Merola et al., 2014; Briefer et al., 2017), and thus subject responses were investigated in relation to whether voice playbacks were taken from familiar or unfamiliar people.

2. MATERIALS & METHODS

2.1. Study Site & Sample Population

Experiments took place at Buttercups Sanctuary for Goats (<http://www.buttercups.org.uk/>) in Kent, UK (51°13'15.7"N 0°33'05.1"E) between 6th August and 2nd October 2019. The sanctuary was open to visitors and features a large outdoor paddock which goats could access throughout the day, and at night they were kept either individually or in small groups (average pen size 3.5m²). Animals had *ad libitum* hay, grass and water available and provided with commercial concentrate in relation to age and condition. Our final sample size for this study was 27 subjects (13 castrated males and 14 intact females) of various breeds and ages (for further information, see Appendix 2A) which had resided at the sanctuary for over a year and were well-habituated to human handling.

2.2. Collection & Preparation of Auditory Stimuli

We collected human voice samples using a Sennheiser MKH 416 P48 directional microphone in combination with a Marantz PMD-661 digital recorder (sampling rate: 48kHz, with an amplitude resolution of 16 bits in WAV format). Recordings were taken from eight speakers for which English was their first language, four of whom were familiar to subjects and four unfamiliar (two male and two female speakers in each group). Those familiar to subjects had worked or volunteered in a husbandry-related capacity at the sanctuary for at least one year. Recording sessions took place in enclosed, quiet areas to minimise background noise, although a common location in which all recordings could be collected was not possible. While recording, we held the microphone close to the speaker's face (approximately 20cm away) and they were asked to say the phrase "hey, look over here" multiple times, first using a happy voice (positive valence) and then an angry voice (negative valence). The same phrase was used so responses would depend on the emotional content of the voice sample rather than the specific words used (Schamberg et al., 2018).

Recording quality and efficacy in which emotional valence was expressed was evaluated for each voice sample by a single listener. If recordings were not deemed to be of sufficient quality, the recording session was repeated. Only voice samples taken from a single recording session were used in playbacks to ensure auditory environment in which samples were recorded was consistent across the entire playback. We used the three clearest samples most strongly expressing the desired emotional valence for both positive and negatively-valenced samples to construct playbacks (giving six voice samples per speaker in total). Voice samples had a mean length \pm SD of 1.43s \pm 0.373, with length not differing significantly according to the emotional valence conveyed (linear mixed model, LMM: $\beta \pm$ s.e. = 0.102 \pm 0.085, $t_{(39)} = 1.20$, $p = 0.238$).

We assembled playback stimuli using Praat v.6.1. (Boersma & Weenink, 2019), with these comprising a series of voice samples from a single speaker, with each of the 13 samples followed by 20s of silence, in which time (hereafter known as the response period), behavioural and cardiac responses were measured. Mean amplitude of recordings was scaled digitally to 70dB, but when measured under field conditions, there was a small, but significant difference in average maximum amplitude between positively- and negatively-valenced voice samples (positive: 74.18dB \pm 3.026; negative: 75.41 dB \pm 3.289; LMM: $\beta \pm$ s.e.= 1.137 \pm 0.456, $t = 2.49$, $p = 0.014$; measured at a one meter distance using a CEMTM DT-8851 sound-level meter). Overall, playback sequences had a mean length (\pm SD) of 4 minutes 38s \pm 4s.

2.3. Playback Procedure

To investigate goat ability to discriminate emotional cues in the human voice, we used a habituation-dishabituation-rehabilitation paradigm, similar to that of Baciadonna et al. (2019), which investigated their discrimination of valence in conspecific calls. In each phase, voice recordings conveyed a single emotional valence, the valence being the same in the habituation and rehabilitation phases, but different in the dishabituation phase (so e.g., if valence was positive in the habituation and

rehabilitation phases, it will be negative in the dishabituation phase). In the habituation phase three different recordings were repeated three times and combined in a random order (so nine recordings in total). Through repeated exposure to auditory stimuli sharing similar properties, we expected goats to lose interest, or habituate and consequently reduce responsiveness to playbacks over the course of the habituation phase. Furthermore, as different voice samples from the same speaker were used, goats were anticipated to habituate to the valence content of the samples, rather than to individual recordings (Charlton et al., 2011). The subsequent dishabituation phase consisted of three different recordings conveying the opposite valence to that of the habituation phase, with recordings again combined in a random order. If a goat perceives the shift in valence, we expected them to dishabituate, or renew responsiveness towards the playbacks presented. A randomly selected single recording from the habituation phase comprised the rehabilitation phase. We predicted responsiveness would again decrease during this phase if shifts in behavioural and physiological measures observed during the dishabituation phase are robust and not an artefact of for example, a chance renewal in attention (Charlton et al., 2007; 2011; 2012).

For each of the eight people providing voice samples, two playback sequences were produced: one comprising voice samples expressing a positive valence during the habituation and rehabilitation phases (i.e., Happy-Angry-Happy) and one a negative valence in these phases (i.e., Angry-Happy-Angry). This produced 16 playbacks in total, eight from familiar and eight from unfamiliar people. Each goat experienced at least two trials, one using a playback of a familiar voice and one using an unfamiliar voice. The speaker's gender and valence expressed during the habituation phase was the same across both trials. Sanctuary staff and volunteers were asked which goats appeared especially responsive to them, and therefore likely to be more familiar with their voice. When tested, these goats were subject to playbacks derived from these staff members voices and the rest were assigned playback stimuli semi-randomly, while ensuring half of subjects experienced playbacks of male voices, and half from females.

2.4. Playback Emotional Valence Validation Experiment

To verify whether the voice samples used effectively conveyed the desired emotional valence, after carrying out the playback experiments in goats, we asked a convenience sample of ten volunteers with fluency in English (five males and five females) to score all recordings according to their emotional valence (angry or happy). Participants listened to all 48 voice samples used in our experiment, which had been combined in a random order and split into three playback sequences (of 16 recordings each). Following each voice sample, participants were given five seconds of silence in which to score its emotional valence.

Participants correctly scored an average of 46.4 ± 1.27 out of 48 voice samples. 87.5% of mistakes occurred in the first playback sequence, and so it is likely this error rate is at least partially inflated as participants adapted to the experimental protocol. For most playbacks which participants had scored incorrectly, only one or two of the ten participants had made mistakes, suggesting valence had overall been effectively conveyed. There was however, one recording where only 40% of participants correctly scored valence suggesting it was ambiguous, but this voice sample only featured in four out of 42 experimental trials.

2.5. Experimental Enclosure

We constructed the experimental enclosure from opaque metal agricultural fencing placed within the large outdoor paddock that subjects could readily access throughout the day. The enclosure was divided into three sections (Figure 1). Subjects initially entered through the preparation pen, before being led into the experimental arena where trials took place. The equipment section was separated from the experimental arena by a gate comprising horizontal metal bars. A Sony CX240E video camera and speaker were positioned in this section 2.65m away from the front of the experimental arena. The Bose Soundlink Mini Bluetooth Speaker II we used to broadcast playbacks during trials has been verified

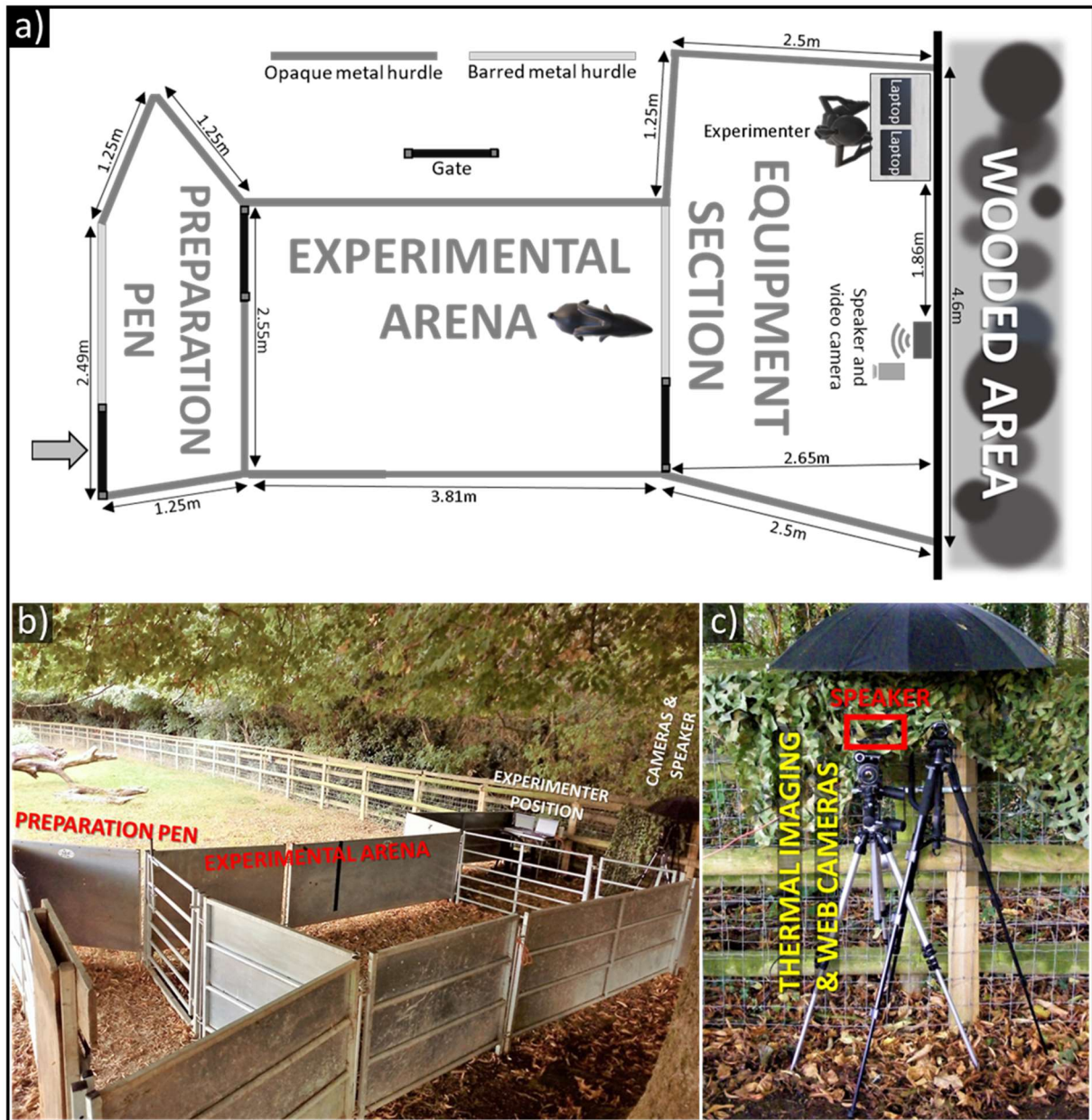


Figure 1. a) Schematic of the experimental enclosure. Goats entered through the preparation pen where they were fitted with a heart rate monitor. Trials took place in the experimental arena. The speaker was positioned 2.65m away from the front of the experimental arena. b) Photograph showing the view of the experimental enclosure indicating the relative locations of the preparation pen, the experimental arena, as well where the experimenter, speakers and video camera would have been positioned. c) The set-up of the speaker, video camera and back up web camera. We initially planned to collect thermal imaging data, however, attempts to get thermal images of sufficient quantity and quality were ultimately unsuccessful.

as effective in reproducing the human voice by another study (Ben-Aderet et al., 2017). We covered the camera and speaker in camouflage netting to reduce the likelihood of subjects locating the sound source. The experimenter was positioned within this section during experimental trials, with their back turned away from the goat being tested to avoid unintentionally cuing them.

2.6. Ethics Statement

All animal care and experimental procedures were conducted in line with ASAB guidelines for the use of animals in research (Vitale et al., 2019). Procedures were further subject to approval by the University of Roehampton's Life Sciences Ethics Committee (Ref. LSC 19/ 280). All methods were non-invasive, and trials were a maximum of 8 mins 5s in duration. The valence validation experiment carried out on human volunteers was approved through an amendment made to the original ethics application (Amendment 06.20). Sample consent forms, both for participants providing voice samples for the original playback experiment and for those taking part in the valence validation experiment are provided in Appendix 2B and 2C respectively.

2.7. Experimental Preparation & Procedure

We habituated goats to the experimental arena over two five-minute sessions taking place over consecutive days, with the final session taking place a minimum of 1 hr 50 mins prior to the onset of experimental trials (maximum = 7 days). This variation in interval between habituation trials and experiments was necessary as goats were not always willing to be led to the experimental enclosure or were displaced by a more dominant individual during transit. Trials themselves took place on weekdays between 11:00 am and 4:00 pm.

Subjects were first gently led to the experimental enclosure and upon entering the preparation pen, we fitted them with a Zephyr™ BioHarness 3.0 affixed to a belt. During trials this device was used to transmit live cardiac data via Bluetooth to a laptop (HP ProBook 650 G4). To improve conductance of the BioHarness to the skin, we clipped fur over the left shoulder blade (across which the BioHarness module was to be positioned) at least one week prior to onset of experiments and liberal amounts of ECG gel were applied to sensors before the belt was placed around the goat's thorax. Once we found a clear ECG trace, the goat was led into the experimental arena.

One minute after the subject had entered the arena, we initiated data logging in the heart rate monitor and recording using the video camera. If the ECG trace had been maintained, goats were kept in the arena for a further two minutes before playbacks were initiated to habituate without human interference, but if it had been lost, the trial was paused and the BioHarness re-positioned. Following initiation of the playback sequence, we marked an event in the cardiac data at the end of each recording to indicate onset of the 20s response period. This process was repeated until the end of the playback sequence, after which time we led the subject back into the preparation pen where the BioHarness was removed before they were freed. The two trials of any given subject, one of which played voice samples from a familiar, and one trial where samples were from an unfamiliar person were separated by a minimum of seven days (mean \pm SD = 9.38 days \pm 3.21).

We scored videos for levels of visitor disturbance, and repeated corresponding trials when this was deemed to be too great. The repeated trial took place a minimum of 17 days after the second trial (maximum = 48 days). 14 out of the 30 goats tested had to have a trial repeated, with four of these subjects requiring both trials to be repeated.

2.8. Video Coding

We coded all experimental trials on a frame-by-frame basis using BORIS v.7.8.2. (Friard & Gamba, 2016). The majority of these were captured at a frame rate of 25 FPS, but for two trials, technical issues prevented reliable footage being taken, so behavioural data was coded from back-up footage captured by a webcam at a much slower rate of five FPS. We specifically scored how long goats looked towards the speaker (defined as when their snout was pointed within approximately 45 degrees of the speaker), and how long it took them to look in the response period following each of the 13 playbacks.

Data used in analysis was extracted by a single observer, but a second blind observer coded all trials included in analysis to assess the reliability of the behavioural data set. This observer was not informed of experimental hypotheses, and ignorance of the playback paradigm was maintained through coding videos in absence of auditory and trial information. There was high fidelity in looking duration values measured by these two observers (intra-class correlation analysis; Poisson distribution assumed: $R \pm s.e = 0.83 \pm 0.013$, $p < 0.0001$, $n = 1000$ bootstraps; R package, rptR: Stoffel et al., 2017).

2.9. Exclusion Criteria

Initially, we excluded one male and one female from further analysis, due to expression of abnormal behaviour and successful escape from the experimental arena respectively. Based on criteria employed by Baciadonna et al. (2019), further trials were also excluded if they satisfied the following: 1) goats failed to respond to the first recording (i.e., did not look towards the speaker), and/ or 2) subjects did not habituate to playbacks, which was interpreted as when the looking duration after the habituation phase's final playback exceeded that observed in the response period following the first by more than two times. In addition, trials in which goats did not look at the speaker for more than 10 seconds in total over the entire playback sequence were excluded as these subjects were considered not attentive enough to playbacks for their discriminatory abilities to be effectively assessed. We excluded a total of 18 trials, which included all records collected from three subjects. Ultimately, observations from 27 goats participating in 42 trials (familiar speaker = 20; unfamiliar = 22) were included in analysis.

2.10. Statistical Analysis

2.10.1. General Model Parameters

We fitted mixed models to the response variables looking duration, latency to look, heart rate and HRV all measured over in the 20s response periods following each of the 13 playbacks, using R

version 4.1.1. (R core team, 2021). To begin with, we investigated changes in each of these behavioural and physiological responses over the habituation phase (H1-H9) to examine the likelihood of habituation having taken place. Following this, we conducted pairwise comparisons to evaluate changes in relation to shifts in valence, by comparing goat responses to the last playback of the habituation phase and the first of the dishabituation phase (H9 v. D10), as well as towards the last playback of the dishabituation phase and the rehabilitation phase (D12 v. R13). To avoid overfitting models, we used the Akaike's information criterion (AIC) to identify and remove parameters which proved poor predictors of looking duration, i.e., goat sex and speaker gender to arrive at a single set of parameters for all analytical models.

Our primary variable of interest was playback number, as we wanted to examine how responses changed over the course of the habituation phase and between playback phases. Given familiarity with the individual expressing the emotional cues is of known importance for discriminating valence in other species (e.g., Merola et al., 2014; Briefer et al., 2017), the effect of voice familiarity (familiar v. unfamiliar) on goat responses was also investigated. Accordingly, we explored the interaction between playback number and familiarity to explicitly test whether voice familiarity affected goat ability to discriminate human emotional cues. For models where this interaction was non-significant, we removed this term to enable interpretation of the effects of playback number and familiarity independently (as recommended by Engqvist, 2005). This interaction term was ultimately only retained in models predicting the time it took for goats to look. In addition, we investigated the effect of playback order on goat responses, with this variable denoting the order in which valence is presented over the habituation, dishabituation and rehabilitation phases, i.e., angry-happy-angry or happy-angry-happy. As for cardiac responses, noise present in the ECG trace sometimes prevented heart rate and HRV being measured across the entire response period. The period over which it was possible to calculate these responses was therefore referred to as the measurement period (mean = 18.10s; range = 5.96-19.46s). As longer measurement periods provide more information, this covariate can have important implications for the

accuracy of cardiac measures, so was fitted to all relevant models (Reefmann et al., 2009; Briefer et al., 2015b). Finally, we nested trial number within goat identity and added this as a random effect to control for repeated measurements taken from each individual both within and between trials, as was playback code (a unique identifier for each playback sequence) to control for the same playbacks being used over multiple trials.

2.10.2. Looking Duration

As looking duration was restricted between zero and 20s, and model residuals failed to conform to a normal error structure, we considered statistical approaches more typically applied to count data. As data was both zero-inflated and overdispersed (verified using the DHARMA package: Hartig, 2021), we used AIC to test the fit of multiple error structures (Poisson, zero-inflated negative binomial; glmmTMB package: Brooks et al., 2017), finding a zero-inflated negative binomial type II model to be most appropriate for our data. This approach produces both a conditional model, which was used to predict duration values greater than zero seconds, and a zero-inflated model which predicted the probability of a zero second observation (the goat did not look) using a logit link. The random factor, playback code caused model convergence issues for the dishabituation-rehabilitation phase comparison so was removed accordingly. The removal of the latter random effect may make the D12-R13 comparison less robust compared to the other analyses.

2.10.3. Latency to Look

Latency conformed to an approximately bimodal distribution with peak abundances at zero seconds (the goat was looking from the outset of the response period) and 20s (subjects did not look throughout the response period), so this response was analysed using a binomial generalised linear mixed model (GLMM; glmer function, lme4 package: Bates et al., 2015). Post hoc comparisons for the

interaction between playback number and familiarity were carried out using the emmeans package with Tukey's corrections to control for multiple comparisons (Lenth, 2021).

2.10.4. Heart Rate & Heart Rate Variability

We measured heart rate as heartbeats per minute and HRV, as the root mean square of successive differences between heartbeats (RMSSD) measured in the 20s response periods following playbacks. Before cardiac data was extracted, we visually inspected the ECG trace for artefacts, which were excluded from subsequent heart rate and HRV calculations. Although RMSSD especially is not typically considered count data, as resulting residuals from modelling cardiac responses failed to conform to a gaussian distribution and were restricted to positive values, Poisson error structures were adopted to model both responses (lme4 package: Bates et al., 2015). Models were formally tested for dispersion using the DHARMA package (Hartig, 2021) and we fitted all models predicting goat cardiac responses with an observation-level random effect accordingly. Upon fitting models and plotting their error structures, we noticed the presence of influential observations in heart rate measured during the habituation phase. Using the outlierTest function (car package: Fox & Weisberg, 2019), we identified and removed the most extreme outlier from habituation phase analyses to avoid it having a disproportionate effect on resulting model parameters.

3. RESULTS

3.1. Looking Duration

Goats looked for an increasingly shorter period of time and were less likely to look towards the sound source with increasing playback number over the habituation phase (conditional model: $\beta \pm \text{s.e.} = -0.075 \pm 0.016$, $Z = -4.76$, $p < 0.0001$; zero-inflated model: $\beta \pm \text{s.e.} = 0.136 \pm 0.052$, $Z = 2.63$, $p = 0.009$, respectively)(Table 1; Figure 2). In addition, subjects were marginally less likely to look when experiencing human voices conveying a negative over a positive valence in this phase ($\beta \pm \text{s.e.} = -0.860 \pm 0.486$, $Z = -1.77$, $p = 0.077$). In contrast, familiarity with the voice presented had no effect on how likely or how long goats looked over this phase.

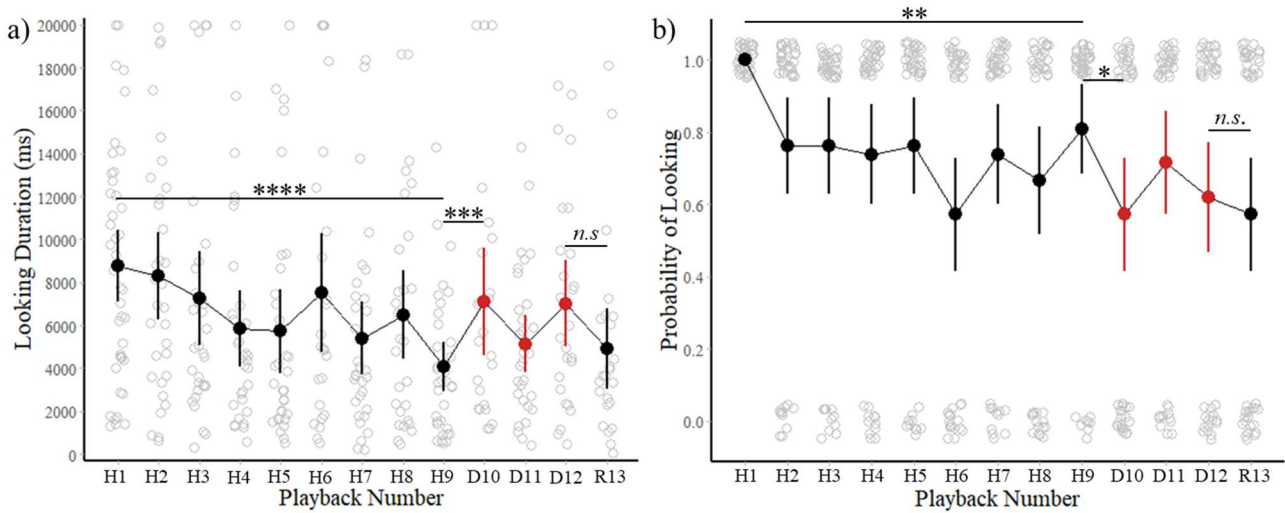


Figure 2. Effect of playback number on goat looking behaviours in the 20s following playbacks. Mean and 95% confidence intervals shown for a) goat looking duration values greater than zero b) the likelihood that goats looked, as a function of playback number. Goat responses towards the dishabituation phase playbacks are shown in red. Comparisons are shown above and significance indicated. *n.s.* = non-significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; **** $p < 0.0001$

Goats were less likely to look immediately following a change in emotional valence after the first playback of the dishabituation phase (D10), compared to the last of the habituation phase (H9)(zero-inflated model: $\beta \pm \text{s.e.} = 1.427 \pm 0.597$, $Z = 2.39$, $p = 0.017$)(Table 1; Figure 2). However, goats that looked, did so for longer (conditional model: $\beta \pm \text{s.e.} = 0.558 \pm 0.154$, $Z = 3.62$, $p = 0.0003$). When

Table 1. Predictors of time goats spent looking (conditional model) and likelihood that they did not look (zero-inflated model) towards the sound source following each human voice playback of the habituation phase (H1-H9), after the shift in emotional valence between the habituation and dishabituation phase (H9 v. D10) and finally, between the dishabituation and rehabituation phases (D12 v. R13). Parameter estimates come from zero-inflated type II model.

Explanatory Variable	Looking Duration (conditional model)				Likelihood of Not Looking (zero-inflated model)			
	β	S.E.	z-value	p-value	β	S.E.	z-value	p-value
H1-H9								
Intercept	9.059	0.167			-1.634	0.464		
Playback no.	-0.075	0.016	-4.76	<0.0001****	0.136	0.052	2.63	0.009 **
Familiarity (U) ^a	0.021	0.155	0.14	0.891	-0.012	0.320	-0.04	0.971
Playback Order (HAH) ^b	-0.152	0.176	-0.87	0.386	-0.860	0.486	-1.77	0.077
H9 v. D10								
Intercept	7.802	0.235			-1.333	0.657		
Playback no. (D10)^c	0.558	0.154	3.62	0.0003***	1.427	0.597	2.39	0.017 *
Familiarity (U)^a	0.550	0.256	2.15	0.032*	0.036	0.567	0.06	0.950
Playback Order (HAH) ^b	-0.042	0.257	-0.17	0.869	-0.876	0.697	-1.26	0.209
D12 v. R13								
Intercept	9.003	0.264			-0.559	0.698		
Playback no. (R13) ^d	-0.399	0.230	-1.74	0.082	0.283	0.534	0.53	0.597
Familiarity (U) ^a	-0.154	0.232	-0.66	0.507	-0.244	0.591	-0.41	0.680
Playback Order (HAH) ^b	-0.243	0.290	-0.84	0.401	0.224	0.801	0.28	0.780

Significant results are shown in bold. Key: U= Unfamiliar; HAH = Happy-Angry-Happy Playback Order. Reference Categories: a = Familiar; b = Angry-Happy-Angry playback sequence; c = H9; d = D12. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; **** $p < 0.0001$

visualising the relationship between looking duration and playback number, the presence of three goats that looked for the entire 20s response period after D10 were noted (Figure 2a). As these observations could have had a disproportionate influence on parameter estimates in the conditional model (measuring looking duration for goats that looked), we removed data from these goats but found the effect of playback number on looking duration remained significant ($\beta \pm \text{s.e.} = 0.403 \pm 0.191$, $Z = 2.11$, $p = 0.035$). Familiarity with voices presented also affected looking behaviours, with goats played unfamiliar voices looking for longer than those experiencing familiar voices over the H9 versus D10 comparison ($\beta \pm$

s.e. = 0.550 ± 0.256 , $Z = 2.15$, $p = 0.032$). Between the end of the dishabituation (D12) and start of the rehabilitation phases (R13), the probability that goats looked remained unaffected, although subjects tended to look for a shorter time after R13 ($\beta \pm \text{s.e.} = -0.399 \pm 0.230$, $Z = -1.74$, $p = 0.082$)(Table 1; Figure 2). In contrast, playback order (angry-happy-angry or happy-angry-happy) had no effect on how long or how likely goats were to look after the dishabituation phase and neither familiarity nor playback order had an effect on their responses following the rehabilitation phase.

3.2. Latency to Look

Goats became slower and slower to respond to playbacks as the habituation phase progressed, with time taken to look increasing at a faster rate when they were experiencing unfamiliar, compared to familiar voices (playback number x familiarity interaction: $\beta \pm \text{s.e.} = 0.059 \pm 0.001$, $Z = 81.85$, $p < 0.0001$)(Table 2). However, it appears that voice familiarity only had a weak (and possibly negligible) effect on goat responses, as suggested by the low effect size and lack of obvious trend when visualising this relationship (Figure 3). The valence that the voice conveyed had no effect on how long it took goats to respond to playbacks over the habituation phase.

Goats were slower to look at the speaker following a change in valence between the habituation and dishabituation phase (H9 v. D10 comparison; playback number x familiarity interaction: $\beta \pm \text{s.e.} = 1.968 \pm 0.010$, $Z = 195.17$, $p < 0.0001$), with how long they took to respond affected by goat familiarity with the human voice presented (Table 2; Figure 3). To expand, the increase in time taken to look after D10, compared to H9 was greater when goats were experiencing unfamiliar (25.67% increase; $\beta \pm \text{s.e.} = -2.435 \pm 0.008$, $z\text{-ratio} = -291.68$, $p < 0.0001$), compared to familiar voices (8.39% increase; $\beta \pm \text{s.e.} = -0.467 \pm 0.006$, $z\text{-ratio} = -82.58$, $p < 0.0001$)(see Appendix 2D for further post hoc comparisons). When considering responses to H9 alone, goats were faster to look when the voice presented was unfamiliar (EMM $\pm \text{s.e.} = 3.48\% \pm 4.85$ into response period), than when it was familiar (EMM $\pm \text{s.e.} = 72.03\% \pm$

29.85; $\beta \pm \text{s.e.} = 4.269 \pm 1.499$, $z\text{-ratio} = 2.85$, $p = 0.023$), with no differences in time taken to respond to D10 between familiar and unfamiliar voices.

Table 2. Predictors of time goats took to respond after each playback over the habituation phase (H1-H9), following the valence change between the last playback of the habituation and first of the dishabituation phase (H9 v. D10) and to the last playback of the dishabituation phase and to the rehabilitation phase (D12 v. R13)(binomial GLMM).

Explanatory Variable	β	S.E.	z-value	p-value
H1-H9				
Intercept	-1.884	0.852		
Playback no.	0.151	0.001	294.86	<0.0001****
Playback no. x Familiarity (U)^a	0.059	0.001	81.85	<0.0001****
Familiarity (U) ^a	-1.244	0.838	-1.49	0.138
Playback Order (HAH) ^b	-0.791	1.279	-0.62	0.536
H9 v. D10				
Intercept	3.024	1.988		
Playback no. (D10)^c	0.467	0.006	82.58	<0.0001****
Playback no. (D10)^c x Familiarity (U)^a	1.968	0.010	195.17	<0.0001****
Familiarity (U)^a	-4.269	1.499	-2.85	0.004**
Playback Order (HAH) ^b	-4.156	2.574	-1.62	0.106
D12 v. R13				
Intercept	0.925	2.549		
Playback no. (R13)^d	2.405	0.008	283.10	<0.0001****
Playback no. (R13)^d x Familiarity (U)^a	-3.322	0.011	297.82	<0.0001****
Familiarity (U) ^a	-0.456	2.101	-0.22	0.828
Playback Order (HAH) ^b	2.203	3.335	0.66	0.509

Significant results are shown in bold. Key: U= Unfamiliar; HAH = Happy-Angry-Happy Playback Order. Reference Categories: a = Familiar; b = Angry-Happy-Angry playback sequence; c = H9; d = D12. ** $p < 0.01$; *** $p < 0.001$; **** $p < 0.0001$

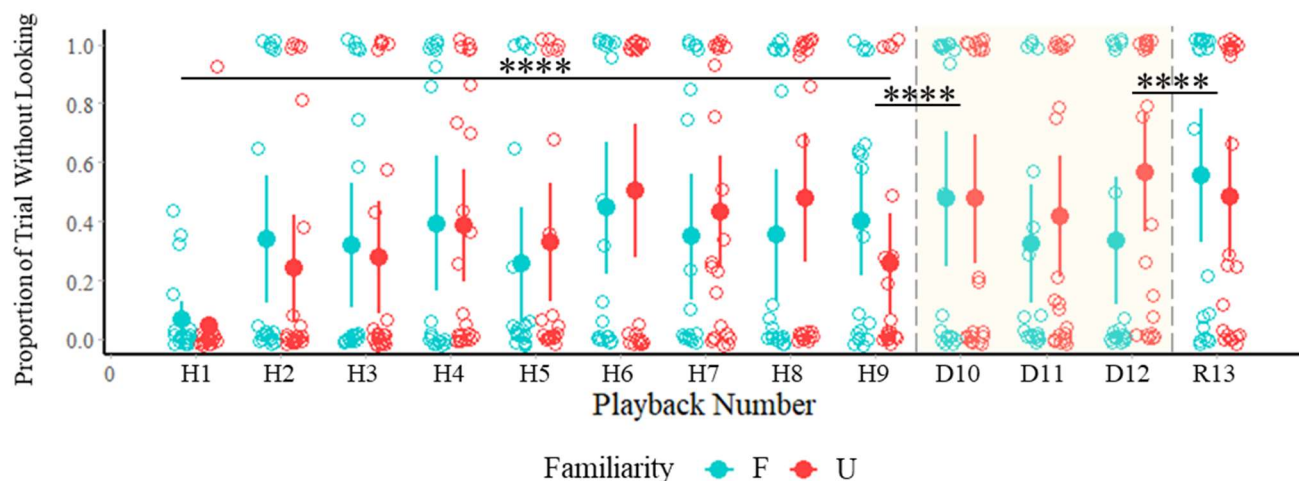


Figure 3. Mean and 95% confidence intervals shown for the effect of playback number and familiarity on goat latency to look following presentation of human voice samples. Playbacks comprising the dishabituation phase (D10-D12) are highlighted and significance of interaction between playback number and familiarity is indicated above. **** $p < 0.0001$

Goats showed differences in time taken to look between the dishabituation and rehabilitation phases, with the direction of this change affected by their familiarity with the voice presented (playback number \times familiarity: $\beta \pm \text{s.e.} = -3.322 \pm 0.011$, $Z = -297.82$, $p < 0.0001$) (Table 2; Figure 3). Specifically, goats were slower to look after R13, relative to D12 when the voice was familiar ($\beta \pm \text{s.e.} = -2.405 \pm 0.009$, $z\text{-ratio} = -283.10$, $p < 0.0001$), but when the voice was unfamiliar, they were slightly faster to respond to R13 ($\beta \pm \text{s.e.} = 0.916 \pm 0.007$, $z\text{-ratio} = 126.82$, $p < 0.0001$) (Appendix 2D). By contrast, the order in which valence was presented over the habituation, dishabituation and rehabilitation phases had no effect on how long it took goats to respond after D12, or R13.

3.3. Heart Rate and Heart Rate Variability

Overall, goat heart rate remained constant over the course of the habituation phase, whereas, HRV may have decreased with increasing playback number over this phase, although this effect was small, and only marginally significant ($\beta \pm \text{s.e.} = -0.016 \pm 0.008$, $Z = -1.93$, $p = 0.054$) (Table 3). In addition, heart rate was lower when there was a greater measurement period available for calculating this

response over the habituation phase ($\beta \pm \text{s.e.} = -0.007 \pm 0.003$, $Z = -2.82$, $p = 0.005$). No further changes in heart rate or HRV were observed in relation to changes in valence of voice recordings during the dishabituation phase or when it reversed during the rehabilitation phase.

Table 3. Predictors of goat heart rate and HRV measured in the 20s response periods following each playback of the habituation phase (H1-H9), following shifts in emotional valence between the habituation and dishabituation phase (H9 v. D10) and the dishabituation and rehabilitation phases (D12 v. R13)(Poisson GLMM).

Explanatory Variable	Heart Rate				Heart Rate Variability			
	B	S.E.	z-value	p-value	β	S.E.	z-value	p-value
H1-H9								
Intercept	11.638	0.067			10.036	0.399		
Playback no.	-0.001	0.001	-0.60	0.551	-0.016	0.008	-1.93	0.054
Familiarity (U) ^a	-0.055	0.034	-1.61	0.107	0.375	0.239	1.57	0.116
Playback Order (HAH) ^b	-0.072	0.060	-1.22	0.224	-0.071	0.254	-0.28	0.781
Measurement Period	-0.007	0.003	-2.82	0.005**	-0.007	0.018	-0.38	0.706
H9 v. D10								
Intercept	11.645	0.131			9.888	0.809		
Playback no. (D10) ^c	-0.010	0.010	-1.01	0.314	-0.017	0.064	-0.26	0.792
Familiarity (U) ^a	-0.046	0.037	-1.24	0.214	0.219	0.291	0.75	0.452
Playback Order (HAH) ^b	-0.079	0.061	-1.29	0.198	0.049	0.297	0.17	0.868
Measurement Period	-0.008	0.007	-1.25	0.212	-0.001	0.043	-0.03	0.974
D12 v. R13								
Intercept	11.521	0.152			11.122	1.034		
Playback no. (R13) ^d	-0.001	0.010	-0.06	0.956	0.003	0.082	0.04	0.970
Familiarity (U) ^a	-0.035	0.036	-0.98	0.329	0.291	0.296	0.98	0.325
Playback Order (HAH) ^b	-0.067	0.059	-1.12	0.261	-0.020	0.284	-0.07	0.944
Measurement Period	-0.003	0.008	-0.42	0.677	-0.073	0.055	-1.34	0.182

Significant results are shown in bold. Key: U = Unfamiliar; HAH = Happy-Angry-Happy playback order. Reference Categories: a = Familiar; b = Angry-Happy-Angry playback sequence; c = H9; d = D12. ** $p < 0.01$

3.4. Summary

As the habituation phase progressed, goats became increasingly less likely to look, took longer to do so and looked for a shorter length of time. After a shift in emotional valence during the dishabituation phase, the likelihood that goats looked decreased further, however subjects that did look, looked for longer. Finally, goats tended to look for a shorter time when the valence was reversed during the rehabilitation phase. Voice familiarity also had a significant effect, with time taken to respond to playbacks increasing at a faster rate over the habituation phase, and again after a change in valence (dishabituation phase) when goats were experiencing unfamiliar voices. Goats also took longer to respond when the valence reversed during the rehabilitation phase, but only when the voice was familiar; when it was unfamiliar, they were slightly faster to look.

4. DISCUSSION

We investigated goat ability to discriminate emotional valence of human speech using a habituation-dishabituation-rehabilitation paradigm. When repeatedly presented with a human voice conveying a single emotional valence (during the habituation phase), goats showed robust evidence of habituation, becoming less likely to look, looking for a shorter time and taking longer to look with an increasing number of presentations. Following a change in valence (dishabituation phase), goats were less likely to look, but significantly, those that looked, looked for longer, suggesting these goats had perceived this change. After a subsequent reversal of valence to match that of the habituation phase (the rehabilitation phase), goats that looked tended to do so for a shorter time than they did after the final playback of the dishabituation phase. Familiarity with the voice presented also seemed to affect goat behavioural responses in complex ways, perhaps indicating a role for familiarity in emotional discrimination, as has been observed in other species (Merola et al., 2014; Briefer et al., 2017). In contrast, changes in goat behaviour with emotional valence, did not seem to be accompanied by shifts in physiological arousal (heart rate and HRV). Perception of human emotion has largely been investigated in companion animals, but work in goats is starting to bridge this gap, suggesting such cues are important for animals living alongside us, regardless of the specificities of their domestic history (Nawroth et al., 2018; Jardat & Lansade, 2021).

Emotions affect vocalisations in similar ways across diverse vertebrate taxa (Briefer, 2020) and resulting similarities in how it is conveyed may predispose animals with the ability to interpret emotional content of heterospecific vocalisations (Filippi & Gingras, 2018). This is especially the case for emotional arousal, with for instance Filippi et al. (2017) finding human participants could recognize differences in arousal in the vocalisations of nine different species, representing all classes of terrestrial vertebrate. However, goats in our study were required to discriminate human voices based on their valence. Although cross-species evidence for vocal indicators of emotional valence do exist (call duration, fundamental frequency and its variability), these do not appear to apply to the human voice

and expression of valence can differ substantially even among closely related species (Briefer, 2012; 2020). Moreover, the relevance of heterospecific emotional cues will vary according to the species in question (Avarguès-Weber et al., 2013).

Whether domesticated for companionship or, like goats, largely for their products, all domesticated animals rely on humans for their habitat, food and protection from predators (MacHugh & Bradley, 2001; Jardat & Lansade, 2021). Through multiple generations of this inter-dependent relationship, domesticated species have undoubtedly become well-adapted to occupying this anthropogenic niche. For example, pigs, but not wild boar (*Sus scrofa*) behave differently to human voices based on the valence they express (Maigrot et al., 2022). Like goats and pigs, companion animals can discriminate between human emotional cues of opposing valence (Siniscalchi et al., 2018; Smith et al., 2018), but have also been shown to use these referentially, offering clues as to how animals may benefit from doing so. For example, horses can remember human emotional cues in the long-term, with a single presentation of a photograph expressing a positive or negative facial expression being sufficient to cause changes in their behaviour upon encountering the photograph's subject 3-6 hours later (Proops et al., 2018). Dogs, cats (*Felis catus*) and horses use of emotional cues is not limited to guiding behaviour towards the person expressing them, with these species showing differences in behaviour towards an object based on whether a familiar person had expressed positive or negative emotions towards it (Merola et al., 2014; 2015; Schrimpf et al., 2020). These social cognitive abilities may not solely be the product of domestic heritage though, with evidence in companion species suggesting emotional recognition can be further developed over an animal's lifetime (e.g., Merola et al., 2014; Briefer et al., 2017).

Because goats were overall less likely to respond following a change in emotional valence of human vocal cues, it could suggest there were differences among individuals in ability to perceive this change. Goats at the study site came from a variety of backgrounds, and their individual experiences with human voices of differing valence and their past association with positive or negative events may

have affected the salience of, and/ or their ability to discriminate between such cues. Indeed, horses and pigs can readily form associations between human vocal cues and positive and negative events, either experienced directly (horses: d'Ingeo et al., 2019) or indirectly, based on maternal experiences during gestation (pigs: Tallet et al., 2016). In dogs, human emotions appear easier to discriminate if they are more relevant to their daily lives (happiness over fear), if expressed by an owner over those of a stranger (Merola et al., 2014) and even when shown by individuals of the same gender as their owner (Nagasawa et al., 2011). Similarly, we investigated the effect of familiarity with the speaker and discrimination of their emotional cues.

Goats were slower to respond following a change in valence (dishabituation phase), but importantly this change in looking behaviour was more pronounced in those experiencing unfamiliar voices. The relative stability in time taken to respond could suggest attention was retained to a greater extent in goats listening to familiar voices. Subjects also tended to spend less time looking following a reversal of valence (rehabilitation phase), suggesting a drop in behavioural arousal. According to Charlton et al. (2007; 2011; 2012), this would suggest that the observed increase in looking duration at the start of the dishabituation phase was robust and not due to a chance renewal in attention. Although this decrease in time spent looking after the rehabilitation phase was only marginal, taken together with changes in latency to respond, it could indicate a role for familiarity for the ease in which goats can discriminate human emotional cues. Specifically, goats experiencing familiar voices were slower to respond following the rehabilitation phase which is consistent with the expected decline in behavioural arousal. Comparatively, goats were actually quicker to respond to unfamiliar voices after a reversal of emotional valence. In sum, as time taken to respond was more stable before and after a change in valence and was longer following a subsequent reversal of valence in goats experiencing familiar voices, this could suggest they were better able to discriminate emotional valence in familiar compared to unfamiliar human voices.

Goats took an increasingly longer time to respond as the habituation phase progressed, with this rate of increase being greater when the voice presented was unfamiliar, which could indicate familiar voices were harder to habituate to. However, voice familiarity only weakly affected goat responses over this phase, and when the voice was unfamiliar, goats looked for longer after the end of the habituation and start of the dishabituation phases and were quicker to respond to the former than when the voice was familiar. Dogs and cats have been shown to monitor emotional displays produced by their owner for longer than those of a stranger, with this difference speculated to have an effect on the relative ease with which animals could interpret their owner's emotional cues (Merola et al., 2014; Galvan & Vonk, 2016). However, goats in the current investigation did not show robust evidence of being more attentive to familiar over unfamiliar voices. Alternatively, familiarity with a person and by extension, how they express emotions may ease discrimination of these cues, enabling goats to distinguish even more subtle emotional signals (Preston & De Waal, 2002; Briefer et al., 2017). Ultimately though, goats took longer to respond following a change in valence both when the voice was familiar and unfamiliar, which goes against the predicted renewal of attention should they have perceived this change (Charlton et al., 2007; 2011; 2012). Familiarity may facilitate the ability to discriminate valence of human voices, but for the current investigation it appears familiarity affects goat behaviour in complex ways which are difficult to interpret.

Further explanations as to why some goats responded for longer and some not at all following a change in voice valence may include variation in social cognitive abilities among goats to perceive human emotional cues. Goats may have also needed to maintain a certain level of attention to the playback sequence to discriminate its emotional content. Alternatively, variation in goat behavioural responses could at least in part be an artefact of the playback composition itself. Emotional arousal, as well as the clarity and intensity in which valence was portrayed will have varied among the eight speakers, and between voice samples taken from the same speaker. Although a valence validation test was performed in human participants who were largely able to correctly score emotional valence in

voice samples used for testing goats, the ability of these participants to detect differences in valence would have been far more refined than that of a goat. It is therefore possible that valence portrayed in the voice samples was not always clear enough for goats to effectively discriminate.

The human voice is a major auditory signal perceived by goats, and other livestock, during daily management practices (e.g., feeding and cleaning), but its implications for animal welfare remain poorly understood (Tallet et al., 2018). Voices conveying negative valence (e.g., shouting, use of a stern tone and growling) have been shown to produce fear and vigilance-related responses in domesticated animals (Waynert et al., 1999; Merckies et al., 2013; Smith et al., 2018), whereas soothing voices may be calming (Lange et al., 2020). Furthermore, positive human emotional cues have been linked to approach, including in goats (Nawroth et al., 2018), so may facilitate human-animal bonding. Although goats in the current investigation did not show clear changes in physiological arousal linked to emotional valence of human voices, we only looked at cardiac responses and did not see how these changed with valence over playback phases (e.g., habituation phase). It is therefore still possible an emotional response took place, which may have been detectable using a different behavioural or physiological measure. Further research is needed to understand the importance of the human voice on the emotional lives and welfare of goats and other domesticated species.

We present here the first evidence that goats can discriminate between cues expressed in the human voice, namely, emotional valence. These findings contribute to the limited literature available indicating livestock, like companion animals, are sensitive to human emotional cues. In doing so, we raise a number of interesting questions, not limited to those regarding the role of domestication on the development of such social cognitive abilities. Indeed, the observed differences in goat responses to human emotional cues, may indicate the importance of individual experiences and learning in particular on interspecific emotional communication. Moreover, although vocal cues are a common means through which humans and domesticated animals interact, the importance of the voice, and the

emotional cues it conveys for animal welfare remains little understood and is a potentially fruitful area for future research.

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CHAPTER 4: Thermal Imaging in Goats: Reliability & Precision of Temperature Measurements Taken from Facial Regions

Abstract

Thermal imaging has become increasingly popular in animal health and welfare research, but there remains a lack of consensus of how it should be best applied, including which body regions and measures should be favoured for quantifying animal peripheral temperatures. Reliability of temperature estimates can be assessed through examining the degree of similarity between repeated measurements. Our objective was to investigate short-term repeatability (measurements taken in the same session) and reproducibility (over multiple sessions), two subcategories of reliability, as well as the precision of goat surface temperature measures, assessed in two facial regions. 20 goats were imaged over five measurement sessions taking place on consecutive days. During each session, five frames were collected from approximately one-minute-long videos, and from each, we extracted the mean, maximum and minimum surface temperatures from the left eye, right eye and nose tip. To calculate repeatability, we compared variation in temperature attributed to differences between goats against total variation in surface temperatures measured in a single session. We defined precision as the temperature deviation within which the average temperature measured from one to five thermal images were expected to fall in relation to the average of five image replicates 95% of the time. Reproducibility was investigated through comparing variation attributed to differences in temperature between measurement sessions, against total variation in goat surface temperatures. We found repeatability and precision of mean and maximum temperatures across five repeated measurements was high for all body regions, with between 93.50% and 99.81% of total temperature variation attributable to the individual goat tested. Conversely, minimum temperatures were more variable, less repeatable and less precise. For reproducibility, measurement session accounted for a high proportion of variation in nasal temperatures especially (74.61-85.85%), and a lower, but substantial proportion of eye temperature variation (49.59-67.01%). Our results indicate that mean and maximum measures

show promise for quantifying goat nasal and eye temperatures in the short-term (especially if replicate images are taken). However, surface temperature measured across several days were not readily comparable, highlighting the importance of ambient conditions in thermal imaging research.

1. INTRODUCTION

Thermal imaging is an approach increasing in prominence within the fields of animal welfare and veterinary research. Applications of this technique are based on the principle that all terrestrial objects with an absolute temperature exceeding zero generate radiant heat in the infrared region of the electromagnetic spectrum (Knížková et al., 2007; Speakman & Ward, 1998). Levels of infrared radiation emitted by objects can be detected via thermal imaging, and used to generate a visual representation, allowing users to observe and quantify even minute spatial and temporal disruptions in an object's surface temperature (Knížková et al., 2007). When the object of interest is an endothermic animal, local fluctuations in blood flow, metabolic activity, tissue conductivity and environmental heat exchange create a dynamic network of graded temperature zones occurring across the periphery of the skin (McCafferty et al., 2015; Godyń et al., 2019). By concentrating measurements to particular regions of interest (ROIs), generally areas where fur is thinner or absent, such as the eyes or nose it is possible to investigate differences in skin temperature both between- and within-individuals, over time (Tattersall, 2016).

As an animal's peripheral body temperature responds to a variety of internal and external processes, the value of thermal imaging has been investigated across a wide range of applications. For instance, diversion of blood away from peripheral blood vessels caused by stress, not only acts to limit blood loss and infuse core muscles and organs required in 'fight or flight' responses, but redistributes heat causing a drop in peripheral temperature (Travain & Valsecchi, 2021). Interestingly, this redistribution of body heat during emotional experiences has been demonstrated in positive (Proctor & Carder, 2015; 2016; Tamioso et al., 2017), as well as negative contexts (Stewart et al., 2008a; 2008b; Herborn et al., 2015; 2018). Similarly, skin temperature changes caused by local increases in metabolism and blood flow can be indicative of inflammation in underlying tissues, and temperature shifts in the urogenital region especially, of differences in reproductive receptivity, both of which have been

investigated using thermal imaging (Kominsky et al., 2010; Byrne et al., 2019; LokeshBabu et al., 2018; Façanha et al., 2018; Mota-Rojas et al., 2021).

The primary advantage of thermal imaging to investigate animal physiological responses is that measurement can be carried out entirely remotely (Tattersall, 2016). However, the sensitivity of peripheral temperature, as well as thermal imaging itself to a suite of different factors can make this technology difficult to apply in practice. As well as any variable of interest, animal surface temperatures are affected by endogenous factors, such as individual, breed, sex, age, level of physical activity, as well as skin and coat characteristics (thickness and colour; Bartolomé et al., 2013; Rizzo et al., 2017; Jørgensen et al., 2020; Jansson et al., 2021; Mota-Rojas et al., 2021). Environmental conditions, such as ambient temperature, humidity and wind speed also affect peripheral temperatures, either directly, or via internal, homeostatic mechanisms (Church et al., 2014; Jansson et al., 2021). Further extraneous factors affecting accuracy of temperature readings include distance, or angle of the subject in relation to the camera, the camera model, the ROI used, it's size and the particular measure chosen, i.e., mean, maximum or minimum temperature (Church et al., 2014; Howell et al., 2020; Ijichi et al., 2020; Playà-Montmany & Tattersall, 2021; Uddin et al., 2020; Kim & Cho, 2021). Indeed, taking the literature applying thermal imaging to measure animal emotional responses as an example, there is a distinct lack of consistency between investigations in terms of ROIs chosen and specific temperature measures favoured. These have included, mean and minimum nasal temperatures (Proctor & Carder, 2015; 2016; Kano et al., 2016; Brügger et al., 2021), maximum eye temperatures (Stewart et al., 2008a; 2008b; Bartolomé et al., 2019), temperatures in specific eye regions (e.g., lacrimal caruncle: Dai et al., 2015) and other regions, such as maximum temperatures of a chicken's comb and wattle (*Gallus gallus domesticus*; Herborn et al., 2015) and a pig's rear (*Sus scrofa domesticus*; Boileau et al., 2019).

To assess reliability of various combinations of descriptive measure and ROI in measuring animal surface temperature, we must determine the degree of similarity between repeated measures taken

from the same ROI and subject (Bartlett & Frost, 2008; Fernández-Cuevas et al., 2015). High levels of repeatability (repeated measurements taken under identical conditions) and reproducibility (measurements taken in variable conditions), two subcategories of reliability (Bartlett & Frost, 2008) have been found in a medical setting with human patients (Ammer, 2008; Petrova et al., 2018). By comparison, on a farm, or similar setting ambient conditions are more variable, and non-human subjects less compliant, making obtaining accurate measurements using thermal imaging more of a challenge. Investigations into the reliability of thermal imaging have been conducted in cows (*Bos taurus*; Byrne et al., 2017; Scoley et al., 2019), sheep (*Ovis aries*; Byrne et al., 2019) and horses (*Equus caballus*; Howell et al., 2020), but to our knowledge no similar efforts have been made in goats (*Capra hircus*). Indeed, although applications of this technology have been explored across a few contexts in goats (e.g., Façanha et al., 2018; Bartolomé et al., 2019; Giannetto et al., 2020), at least compared to other domesticated species (e.g., horses and cattle: reviews by, Soroko & Howell, 2018; Mota-Rojas et al., 2021, respectively) thermal imaging remains a relatively untapped resource in goat welfare and veterinary research. Therefore, the current investigation aims to identify suitable candidate regions and measures to reliably quantify surface temperature from thermal imaging videos in goats.

Video analysis, although less commonly employed, offers numerous advantages over extracting temperature data from a series of stills collected manually using a handheld device (Wijffels et al., 2021; McManus et al., 2022). For example, the quantity of measurement frames that researchers can collect in a short time-frame is substantially increased, not only enhancing precision in animal surface temperature estimates (Byrne et al., 2017; Scoley et al., 2019; McManus et al., 2022), but also enabling finer-grained analysis of skin temperature changes over time (e.g., for measuring respiration rate: Stewart et al., 2017; Jorquera-Chavez et al., 2019; and time courses of emotional responses: Stewart et al., 2008a; 2008b; Herborn et al., 2015). Furthermore, given footage can be taken from fixed positions, for example next to objects animals regularly interact with, such as feeders and automated milking systems (Hoffmann et al., 2013), it minimises the need for human proximity. This latter point is

important as presence of experimenters may affect animal physiological responses (emotional experiences), perhaps undermining validity and generality of results obtained (Moe et al., 2017; Cannas et al., 2018). However, attempts to assess reliability and other practical aspects of this method of data collection remain limited (Hoffmann et al., 2013; Cuthbertson et al., 2019; Jorquera-Chavez et al., 2019). Therefore, the objective of the current investigation was to evaluate short-term repeatability (measurements taken within a single session) and precision, as well as reproducibility (over five consecutive days) of goat mean, maximum and minimum temperature measured in the eyes and nasal region, extracted from thermal imaging videos.

2. MATERIALS & METHODS

2.1. Ethics Statement

All animal care and testing protocols were in line with ASAB guidelines for the use of animals in research (Bee et al., 2021). Further approval was granted through an ethical amendment (03.21) made to the PhD project 'goat perception of human cues' (Ref. LSC 19/ 280) by the University of Roehampton's Life Sciences Ethics Committee. All procedures were non-invasive, goats were kept unrestrained and tested in groups to avoid social isolation, showing no obvious signs of stress during experimental trials.

2.2. Study Site & Sample Population

Experiments were carried out between 5th - 23rd July 2021 at Buttercups Sanctuary for Goats in Kent, UK (51°13'15.7"N 0°33'05.1"E; <http://www.buttercups.org.uk/>). During this period, the sanctuary was open to the public and featured a large outdoor paddock to which goats had access to during the daytime, before being housed individually or in small groups within a large stable complex at night (mean pen size = 3.5m²). Goats had hay, grass and water available ad libitum throughout the day, and supplemented with commercial concentrate in relation to age and condition. We selected subjects based on their ease of handling and, as goats were tested in groups of three, on whether they showed evidence of affiliative relationships with two other goats as indicated by staff at the sanctuary (to minimise instances of aggression). Our final sample size comprised 20 goats (10 intact females and 10 castrated males) of various breeds and ages (see Appendix 3 for further details).

2.3. Experimental Set-up

Experiments were carried out within a familiar stable that goats could freely access during the day. We kept windows closed to minimise drafts, and to avoid direct sunlight falling on subjects both the

windows and two skylights directly above pens A, B and C were covered (Figure 1). To improve consistency in imaging conditions between subjects and over repeated measures, trials mainly took place within pen B, with other members of the subject's group being placed in adjacent pens A and C. This was not always possible, and for two groups, some group members were placed in pen D to prevent agonistic interactions with the subject. Distractions from surrounding objects also meant two subjects were imaged in pen A so that their attention could be successfully directed towards the camera. Pens featured a hayrack to encourage subjects to spend time at the front of the pen (hay availability shown to elicit minimal emotional arousal in goats at the same study site: Briefer et al., 2015). Water was available in pens A, C and D, but not in B to reduce the potential effect of presence of moisture on the muzzle on goat nasal temperatures.

The thermal imaging camera, a FLIR A655sc (with a 25° lens) was mounted on a tripod and placed directly in front of the subject in pen B, with its height adjusted according to that of the subject's head. This mid- to high-end camera has a spectral range of between 7.5–14 μm , a resolution of 640 \times 480 pixels, a $< 0.03^\circ\text{C}$ thermal sensitivity and $\pm 2^\circ\text{C}$ accuracy. During trials, the camera worked in tandem with the software FLIR ResearchIR Max v. 4.40.9.30 to record thermal imaging videos and save them to an external laptop (HP ProBook 650 G4) connected via a USB and ethernet cable. Goats tended to spend more time near the front of their pen, and the camera was placed at a distance 2.06m away from the front of pen B. This subject-camera distance of approximately 2m is outside the recommended range for thermal imaging studies ($\approx 1\text{m}$, e.g., Okada et al., 2013; Church et al., 2014). However, due to the thermal imaging camera's narrow field of view ($25^\circ \times 19^\circ$, 31° diagonal), a further distance was necessary to decrease instances of the subject going out of frame and the camera position and angle having to be readjusted.

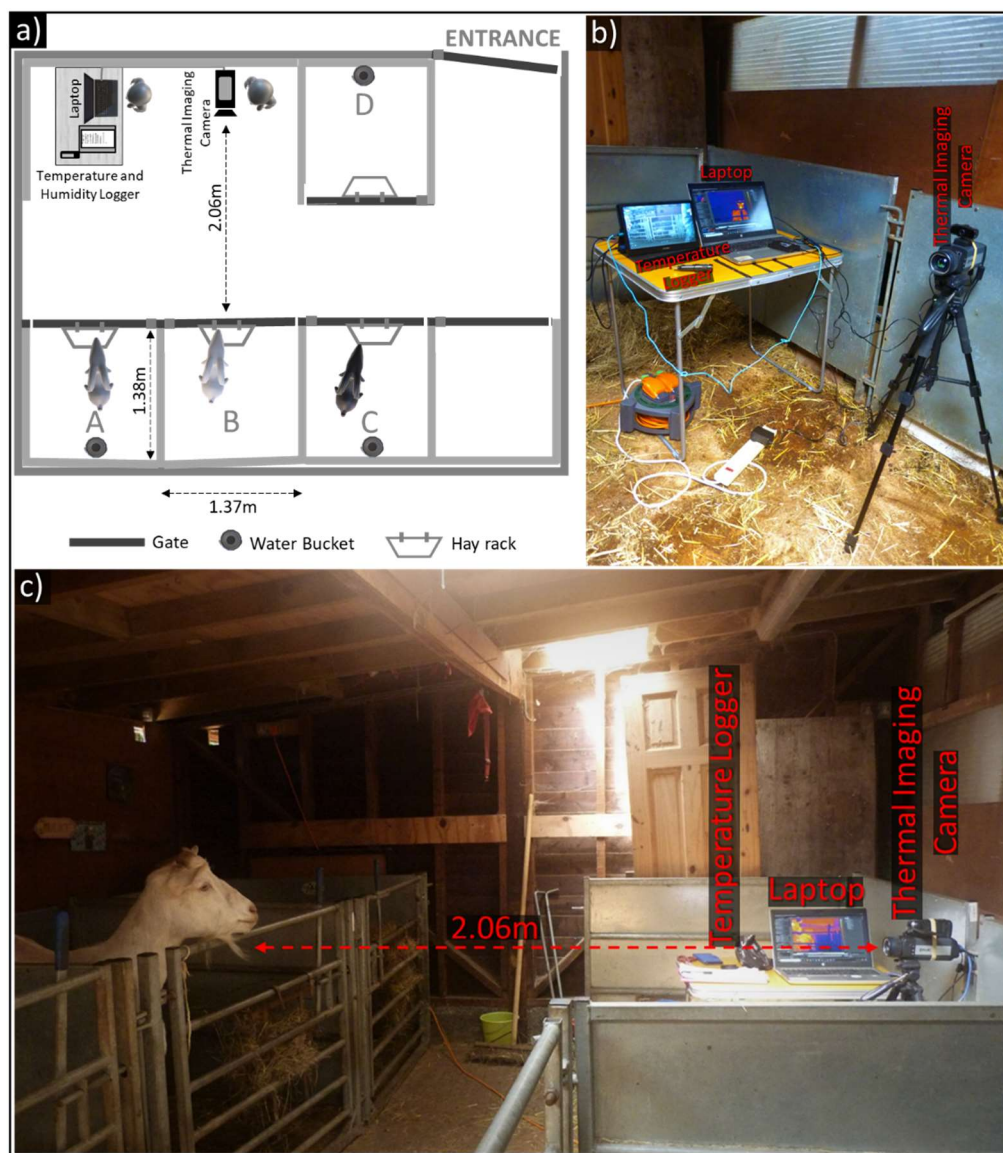


Figure 1. a) Schematic of stable where experiments took place. The thermal imaging camera was positioned 2.06m from the front of Pen B, where subjects were held during testing. b) Photograph demonstrating the set-up of the thermal imaging camera, laptop and temperature logger. c) View of experimental set-up indicating relative locations of the subject and thermal imaging camera, along with other equipment.

2.4. Experimental Preparation & Testing Procedure

We tested goats in seven groups of three individuals each. Each group was tested in one session per day over five consecutive weekdays, with the exception of one group whose final trial was carried out on Monday of the following week. Two to three groups of goats were tested per week over three weeks, with the order in which we tested groups on any given day being randomised, as was the order in which goats were tested within groups.

Before onset of testing, a group of goats were led one-by-one into the stable and we placed each in separate pens, with the goat to be tested in pen B. Once the last group-member had been placed in their designated pen, we waited 10 minutes before testing to minimise effects of physical activity, human disturbance and direct sunlight exposure on temperature readings, as well as giving animals the opportunity to habituate to the test set-up. After 10 minutes had passed, we filmed the subject's face continuously for four minutes. Mistakes made during recording meant that although most trials were recorded at a rate of 6.25 FPS, 12 out of 100 trials had a higher frame rate (maximum 24.97 FPS). Throughout a four minute trial the first experimenter silently maintained the goat's attention (without food or tactile reinforcement), while the second experimenter manually focused the thermal imaging camera. If a subject moved out of frame during their trial, we quickly adjusted the camera's position or height and, if necessary, its angle accordingly. After four minutes had passed, the subject was moved to an adjacent pen, and the next goat to be tested was moved into pen B. To minimise the effect of disturbance and movement artefacts on temperature measures, once the goats had been re-arranged, we waited five minutes before we began the next trial. Once all three subjects had been tested, they were released from the stable.

2.5. Video Processing & Image Analysis

Temperature data was extracted from the thermal imaging videos by a single coder using ResearchIR. Firstly, as suitable frames were not always available (e.g., the goat was not looking at the camera), we broke each four minute video into approximately 12s segments and one still image each was extracted for five consecutive segments. This measurement period generally took place within (approximately) the first 60s of an experimental trial but was shifted until later if we could not find a sufficient number of suitable frames. A frame was considered suitable if all ROIs (left eye, right eye and nose) were fully visible, the image was in focus and the subject's head was oriented at the camera, with images where the snout exceeded a 45° angle from the nasal plane being excluded from analysis.

Furthermore, as the pattern of inhalation and exhalation affect temperatures in the nasal region especially, when it was possible to visualise a goat's breathing cycle, we prioritised extracting frames just prior to onset of inhalation (where nasal temperature began to drop: e.g., Pereira et al., 2018).

Once five frames had been extracted per trial video, each image was calibrated according to the ambient temperature and humidity at the time of its collection. We obtained this environmental data using a EasyLogTM USB-2-LC Humidity and Temperature Data Logger which recorded ambient temperature and humidity in the stable at 10s intervals during testing (to the nearest 0.5°C; mean temperature \pm SD = 25.22°C \pm 3.02, range = 21-31.5°C; mean relative humidity \pm SD = 62.50% \pm 7.17, range = 41.5-75.5%). The emissivity of the image was set to 0.98, a value generally considered to reflect that of biological tissues (Steketee, 1973), while the distance was specified as 2.06m and the reflective temperature, 20°C. Once an image had been appropriately calibrated, we used the elliptical tool to manually position ROIs. To minimise noise in temperature measures, ellipses were drawn tightly around the eye, incorporating only a thin, hairless border around each (see Figure 2). For the nose, only the tip was included, positioned in-between both nostrils. Once the ROIs had been identified, we extracted the mean, maximum, and minimum temperature from each ROI. If part of the ROI was obscured, it was not included in analysis.

To summarise, goats underwent five trials each, with five frames analysed per trial. We aimed to extract nine temperature measurements per frame, the mean, maximum and minimum temperatures from each eye and the nose tip. Of the 21 goats tested, one was excluded for consistently not looking towards the thermal imaging camera during tests. Removing 46 instances where suitable frames could not be found, we included a total of 454 thermal images in analysis.

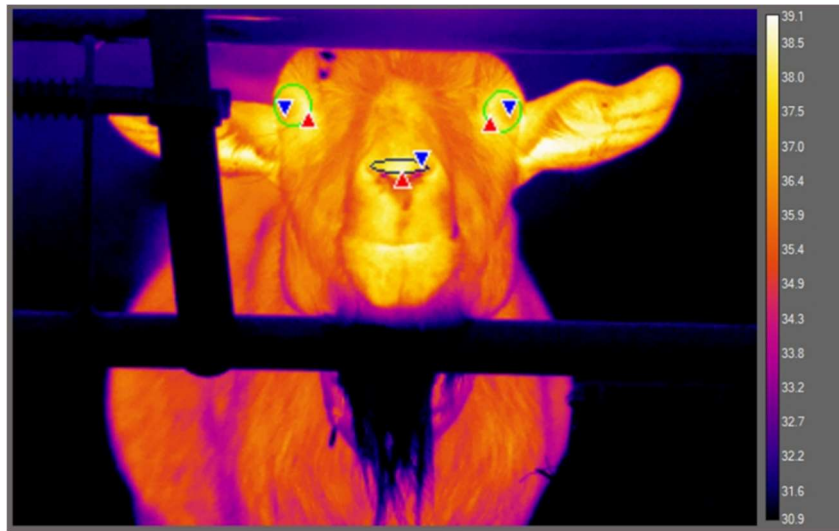


Figure 2. Example thermal image showing regions of interest: left eye, right eye, and nose tip (colour palette: “Fusion”). The red and blue triangles indicate the position of the pixel with the maximum and minimum temperature value respectively for each ROI.

2.6. Statistical Analysis

2.6.1. Repeatability of Goat Surface Temperatures Within a Single Measurement Session

We carried out all analyses using R version 4.2.1 (R Core Team, 2022) and these were based on analyses conducted by Byrne et al. (2017). Using the package rptR (Stoffel et al., 2017) we conducted intraclass correlation analyses (ICC) to investigate repeatability of temperature measurements taken for a particular combination of ROI (left eye, right eye and nose) and measure (mean, minimum or maximum) from a single goat, in a short time frame (approximately one minute) and therefore, under relatively consistent conditions. Temperature data used in these analyses were collected during each goat’s final measurement session on the fifth day of testing. We fitted random effects models, with goat individual identity specified as the random effect (temperature $\sim 1 + (1 | \text{goat ID})$). Models were used to partition variance explained by temperature differences between goats, which was compared against total variance, to calculate repeatability (R):

$$R = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_e^2} (\times 100)$$

where σ_g^2 refers to the between-goat variance and σ_e^2 , the error variance. R was multiplied by 100 to calculate the percentage variance explained by between-goat differences in temperature measures. 95% confidence intervals were computed around R using 10,000 bootstrapping iterations, and we employed likelihood ratio tests to investigate whether the addition of goat identity as a random effect improved model fit relative to null models excluding it.

We used the following formula to calculate the coefficient of variation (CV), for each combination of ROI and temperature measure:

$$CV = \frac{\sigma_g}{\mu} \times 100$$

where σ_g was the standard deviation of between-goat differences in temperature and μ the overall mean of temperature measurements taken from the particular ROI and descriptive measure in question.

Residuals of all random effects models were visually inspected and in combination with the DHARMA package, we evaluated how closely they conformed to assumptions of normality (Hartig, 2021). Error structures for temperature measures taken from both eyes were approximately normally distributed, with the exception of the mean and maximum temperatures for the right eye and the maximum temperature of the left. To address these deviations, we investigated the presence of influential observations or outliers using Cook's Distance (D) in each model (car package: Fox & Weisberg, 2019). To meet assumptions of normality we excluded two observations exceeding eight times the average Cook's D, four observations exceeding five times average Cook's D and the most extreme multivariate observation for the mean and maximum temperature of the right eye and maximum temperature in the left, respectively. More extreme deviations from normality were observed in goat nasal temperature measures, specifically in respect to the assumption of homoscedasticity in model residual distribution. However, as temperature is a continuous variable, transformations were ineffective at improving normality and because alternative error structures such as Poisson distributions are more sensitive to violations of assumptions (e.g., overdispersion), we assumed a Gaussian

distribution for all analyses (Knief & Forstmeier, 2021). It must be noted, although effects of heterogeneous residual variance tend not to bias variance estimates explained by random effects (from which we calculated repeatability), these estimates may become less precise (Schielzeth et al., 2020). Therefore, repeatability measures of nasal temperatures are likely to be less reliable than those of goat eye temperatures. Furthermore, although Gaussian models tend to be more robust to violations against distributional assumptions, they are still sensitive to multivariate outliers with high leverage. After plotting residuals of preliminary models, we identified and removed outliers exceeding four times the average Cook's D (nose mean temperature: 8 observations excluded; maximum temperature: 4 observations excluded; minimum temperature: 7 observations excluded). Although exclusion of these influential outliers helped improve conformation of error residuals to assumptions of normality (although issues remained), they also would have increased repeatability estimates due to the removal of temperature values less in-line with other observations.

2.6.2. Precision in Temperature Estimates

Precision was defined using the following formula:

$$P_n = 1.96 \times \sqrt{\frac{\sigma_e^2}{n_{\in(1,5)}}}$$

where σ_e^2 was the error variance and n was the number of thermal images (1-5). The right side of this formula calculates the standard error, and altogether it estimates the 95% confidence interval range for which the average temperatures measured from 1-5 images was expected to fall in relation to the average of five replicate measurements (Field, 2014; Byrne et al., 2017).

2.6.3. Reproducibility of Temperature Measures Taken Over Multiple Sessions

To investigate how temperature measures in each ROI varied over five days we again used ICC analyses, this time specifying measurement session and the individual goat tested as random effects (temperature $\sim 1 + (1 | \text{measurement session}) + (1 | \text{goat ID})$, $n = 10,000$ bootstraps):

$$R = \frac{\sigma_s^2}{\sigma_g^2 + \sigma_s^2 + \sigma_e^2} (\times 100)$$

where σ_s^2 refers to the variance in temperature readings between sessions, σ_g^2 to that explained by inter-goat differences and σ_e^2 , the error variance. As conditions for each measurement session were not uniform between goats (e.g., session 2 did not take place at the same time or day for each goat), we nested measurement session within individual by giving every measurement session a unique ID (Schielzeth & Nakagawa, 2013). Given this nesting pattern, the effect of measurement session can be interpreted as the temperature variance explained by measurement session alone, combined with that explained by the interaction between goat identity and measurement session, or how readings from individual goats varied over the five days they were imaged (Schielzeth & Nakagawa, 2013). We used likelihood tests to investigate whether adding measurement session as a random effect significantly improved model fit against reduced models excluding this variable.

To ensure temperatures measured in the eye were approximately normally distributed we excluded observations exceeding 10 times Cook's D when analysing mean (6 observations excluded), maximum (2 observations excluded) and minimum temperatures of the left eye (9 observations excluded), as well as the mean of the right eye (7 observations excluded). In addition, we excluded the single most extreme observation for minimum temperatures measured in the right eye. When fitting linear random effects models to predict variance in nasal temperatures, deviations from normality were again more extreme so a more stringent criteria of excluding observations exceeding four times Cook's D was employed (for mean, maximum and minimum nasal temperatures, 15, 16 and 15 outliers were excluded respectively).

3. RESULTS

3.1. Repeatability of Goat Surface Temperatures Within a Single Measurement Session

Adding an individual-level random effect to investigate inter-goat differences significantly improved fit of models predicting surface temperature measured on each goat's fifth day of testing for all combinations of descriptive measure and ROI (all $p < 0.0001$: Table 1). Overall, eye temperatures were restricted to a narrower range of values, than those measured in the nose tip (Table 2), with the latter showing greater variability in temperature around the sample average for each measure (higher CVs: Table 1). This variability in nasal temperatures can largely be attributed to inter-individual differences between goats, with within-goat differences over five repeated measures (error variance) being comparable to those found in eye temperatures. Consequently, repeatability of nasal temperatures was slightly higher than in either eye, but was nonetheless excellent for mean and maximum temperatures across all ROIs (rough rule of thumb: <0.5 poor repeatability, $0.5-0.75$ moderate repeatability, $0.75-0.9$ good repeatability and >0.9 excellent repeatability: Koo & Li, 2016), with between 93.50% (maximum temperature of right eye) and 99.81% (mean nasal temperature) of total variation in temperature being attributed to the individual goat tested (Table 1).

In respect to descriptive measures, variability was highest in minimum temperatures (larger temperature range and higher CV), which included greater variation both between- and moreover within-goats, across repeated measures (Tables 1; 2). Accordingly, minimum temperature values for the left and right eye showed lower repeatability, although it was still moderate to good, with 76.51% and 75.19% of total variation in surface temperatures respectively explainable by the individual goat tested (Table 1). However, in respect to nasal temperatures, although repeatability was slightly lower (and likely negligibly so), it was still excellent, with 99.47% of temperature variance explained by differences in surface temperature between goats. By comparison, differences in repeatability between mean and maximum temperatures were more negligible across all ROIs (confidence intervals feature substantial

Table 1. Between-goat variance, within-goat error variance, coefficient of variation, proportion of variance explained by between-goat differences (repeatability: R), 95% confidence intervals for R and *p*-values associated with the addition of between-goat differences versus null models excluding this effect for temperatures measured in each region of interest and descriptive measure on the fifth day of testing.

Region of Interest	Measure	Individual Variance (°C ²)	Error Variance (°C ²)	CV (%)	R	CI	<i>p</i> -value
Left Eye	Mean	0.440	0.018	1.815	0.960	[0.915, 0.979]	<0.0001
	Maximum	0.353	0.019	1.587	0.949	[0.890, 0.973]	<0.0001
	Minimum	0.968	0.297	2.817	0.765	[0.569, 0.867]	<0.0001
Right Eye	Mean	0.368	0.014	1.659	0.964	[0.921, 0.981]	<0.0001
	Maximum	0.270	0.019	1.387	0.935	[0.858, 0.966]	<0.0001
	Minimum	0.546	0.180	2.117	0.752	[0.546, 0.859]	<0.0001
Nose	Mean	11.612	0.023	9.691	0.998	[0.996, 0.999]	<0.0001
	Maximum	6.812	0.019	7.201	0.997	[0.994, 0.999]	<0.0001
	Minimum	16.498	0.089	12.027	0.995	[0.988, 0.997]	<0.0001

Table 2. Average temperature, standard deviation and temperature range for each region of interest and measure taken within a single session (day 5) and across all five sessions.

Region of Interest	Measure	Measured Within a Single Session		Measured Across All Sessions	
		Average ± SD (°C)	Range (°C)	Average ± SD (°C)	Range (°C)
Left Eye	Mean	36.554 ± 0.680	35.200 - 37.984	36.541 ± 0.791	34.226 - 38.441
	Maximum	37.443 ± 0.610	36.359 - 38.850	37.434 ± 0.687	35.213 - 39.257
	Minimum	34.918 ± 1.111	31.709 - 36.854	34.941 ± 1.221	30.678 - 37.639
Right Eye	Mean	36.537 ± 0.602	35.295 - 37.854	36.440 ± 0.839	33.660 - 38.513
	Maximum	37.457 ± 0.528	36.418 - 38.856	37.320 ± 0.726	34.698 - 39.150
	Minimum	34.903 ± 0.834	32.803 - 36.638	34.775 ± 1.277	30.497 - 37.793
Nose	Mean	35.163 ± 3.466	25.616 - 38.290	34.508 ± 4.011	21.885 - 38.691
	Maximum	36.243 ± 2.428	28.553 - 38.804	35.770 ± 3.194	24.828 - 39.091
	Minimum	33.772 ± 4.041	23.710 - 37.888	32.584 ± 4.985	20.196 - 38.158

overlap); although repeatability was slightly higher and within-goats differences, slightly lower for mean eye temperatures, with this especially being the case for the right eye. The opposite was true for nasal temperatures, with differences across repeated measures being slightly lower for maximum temperatures.

3.2. Precision in Temperature Estimates

The magnitude of standard error was consistently higher (hence precision was lower) for minimum measures, meaning more replicate thermal images would be required to achieve a similar level of precision as when using mean or maximum temperatures, across all ROIs (Table 3). For example, if we were to extract the minimum temperature of a goat's left eye from three images, we would be expected to obtain an average temperature within $\pm 0.62^{\circ}\text{C}$ of the average of five images 95% of the time. However, if we extracted the mean temperature in the same ROI from a single image, we would be expected to be within $\pm 0.26^{\circ}\text{C}$ of the average of five images 95% of the time. Differences in precision between mean and maximum temperatures were less, but slightly higher for goat mean eye temperatures and the maximum temperature measured in the nose tip. The ROI and measure for which we observed the highest levels of precision was in the mean temperature of the right eye ($0.231\text{--}0.103^{\circ}\text{C}$), which also showed the least variability across repeated measures (lowest error variance; Tables 1; 3).

Table 3. Precision, i.e., the standard error (°C) within which the average of one to five replicate thermal images (P_{1-5}) for each region of interest and measure is expected to fall in relation to the average of five image replicates 95% of the time.

Region of Interest	Measure	P_1	P_2	P_3	P_4	P_5
Left Eye	Mean	0.264	0.187	0.153	0.132	0.118
	Maximum	0.270	0.191	0.156	0.135	0.121
	Minimum	1.068	0.755	0.617	0.534	0.478
Right Eye	Mean	0.231	0.163	0.133	0.115	0.103
	Maximum	0.269	0.190	0.155	0.134	0.120
	Minimum	0.832	0.588	0.480	0.416	0.372
Nose	Mean	0.294	0.208	0.170	0.147	0.132
	Maximum	0.272	0.192	0.157	0.136	0.122
	Minimum	0.584	0.413	0.337	0.292	0.261

3.3. Reproducibility of Temperature Measurements Taken Over Multiple Sessions

Adding the random effect ‘measurement session’ increased fit of models predicting variation in goat surface temperatures measured over five days for all combinations of ROI and measure (all $p < 0.0001$; Table 4). The effect of measurement session (1-5) was strongest in the nose tip, but still accounted for a substantial proportion of variation in eye temperatures. For instance, between-session effects explained around 80.83% and 85.85% of variance in mean and maximum nasal temperatures respectively and between 61.71% and 67.01% of variation in mean and maximum eye temperatures (between-session effects similar for both eyes).

When considering across ROIs, goat minimum temperatures were more variable (larger temperature range; Table 2), including between measurement sessions, and moreover within a session, across repeated measures taken from the same goat (Table 4). For example, within-goat variation accounted for 17.10% of total variation in minimum temperature of the right eye, but only 2.51% and

6.08% of that in mean and maximum temperatures in the same eye respectively. Indeed, the proportion of unexplained variation was slightly larger for maximum, compared to mean temperatures across ROIs. However, although slight differences were observed between ROIs, the effect of measurement session explained a similar proportion of the total variation in goat mean and maximum surface temperatures (confidence intervals featured substantial overlap), with measurement session explaining less variation in minimum temperatures.

Table 4. Between-measurement session variance, coefficient of variation and proportion of temperature variance associated with between-session effects (repeatability: R), 95% confidence intervals for session repeatability, *p*-values associated with the addition of between-session effects against models excluding it, proportional variance associated with individual-level effects only and that associated with within-goat error variance for each region of interest and measure.

Region of Interest	Measure	Measurement Session					Other Effects	
		Variance (°C ²)	CV (%)	R	CI	<i>p</i> -value	Goat ID R	Proportional Error Variance
Left Eye	Mean	0.397	1.724	0.617	[0.429, 0.842]	<0.0001	0.359	0.024
	Maximum	0.318	1.506	0.667	[0.477, 0.872]	<0.0001	0.291	0.043
	Minimum	0.772	2.515	0.514	[0.354, 0.704]	<0.0001	0.340	0.147
Right Eye	Mean	0.483	1.907	0.670	[0.475, 0.889]	<0.0001	0.305	0.025
	Maximum	0.361	1.611	0.661	[0.476, 0.863]	<0.0001	0.278	0.061
	Minimum	0.799	2.570	0.496	[0.341, 0.680]	<0.0001	0.333	0.171
Nose	Mean	14.123	10.891	0.808	[0.612, 0.997]	<0.0001	0.189	0.002
	Maximum	8.640	8.216	0.858	[0.665, 0.997]	<0.0001	0.138	0.003
	Minimum	19.140	13.426	0.746	[0.546, 0.958]	<0.0001	0.249	0.005

3.4. Summary

To summarize, although inter-individual differences and short-term repeatability was higher for temperatures measured in the nose tip, between-goat effects explained a large proportion of total variation in mean and maximum eye, as well as nasal temperatures. When measuring goat surface temperature across five days, measurement session also had a stronger effect on goat nasal temperatures, but still accounted for a substantial proportion of variation in eye temperatures. Differences between mean and maximum measures and between the left and right eye were more negligible, although mean temperature of the right eye were slightly more precise and showed lower variability across repeated measurements overall. In respect to descriptive measures, minimum temperatures were not only less precise, but were more variable across sessions, between individuals, and moreover within a single session over repeated measures than mean and maximum temperatures.

4. DISCUSSION

The use of thermal imaging in the fields of animal health and welfare research has increased hugely over the last decade, but there remains a lack of consensus of how this technology should be best applied, including which regions and measures should be favoured when quantifying animal surface temperatures (reviews: Mota-Rojas et al., 2021; Travain & Valsecchi, 2021; McManus et al., 2022). To address this, we investigated repeatability and precision of goat mean, maximum and minimum eye and nasal temperatures taken from five thermal images collected in quick succession from videos (at 12 second intervals for approximately one minute), as well as the reproducibility of temperature estimates across five measurement sessions taking place over consecutive days. From these measurements we assessed which combinations of ROI and temperature measure are the most reliable for quantifying differences in goat surface temperatures. Our results indicate that although replicate measurements taken from individual goats in the short-term showed substantial repeatability and high precision (though measures differed in suitability), surface temperatures from individual goats were not readily reproducible across days.

4.1. Repeatability of Goat Surface Temperatures Within a Single Measurement Session

When evaluating reliability of a specific measure and/or ROI for quantifying goat surface temperature, it is necessary to determine how much variation in temperature can be attributed to the individual animal imaged, versus other factors specific to the time of imaging (Byrne et al., 2017). This is achieved through comparing the temperature variation that can be explained by differences among individuals, against total variation in animal surface temperatures (e.g., Byrne et al., 2017; Scoley et al., 2019). Repeatability of five thermal images taken in quick succession was excellent for mean and maximum temperature across all ROIs, with between 93.50% (maximum temperature of right eye) and 99.81% (mean nasal temperature) of variation being attributed to the individual goat. By contrast,

minimum temperatures were less repeatable and more variable both between-goats and moreover, within-goats across repeated measures. Indeed, as minimum temperature is derived from the value of a single pixel within a specified ROI, it is thought to be particularly vulnerable to measurement errors, the positioning of the ROI, and presence of debris or moisture on the animal's surface (Metzner et al., 2014; Byrne et al., 2017; Uddin et al., 2020). Ultimately, given the greater variability and lower repeatability of minimum temperatures, and in line with recommendations made by similar investigations (e.g., Metzner et al., 2014; Byrne et al., 2017; Uddin et al., 2020) we advocate against use of minimum temperature measures when carrying out thermal imaging in goats.

In respect to mean and maximum temperatures, given the high proportion of variation explainable by between-, compared to within-goat differences across repeated measures, on the face of it, both appear appropriate for quantifying nasal and eye temperatures in goats over a short period. However, temperature variation across repeated measures was slightly lower, and precision higher for mean over maximum eye temperatures (and in the right eye especially). This could suggest using the mean is more reliable for measuring eye temperatures, and as for nasal temperatures, given the slightly lower within-goats differences and higher precision observed in maximum temperatures, the latter may be more suitable. As mean temperatures are estimated from all pixels within a ROI, one key consideration affecting repeatability is the consistency with which ROI boundaries are defined across thermal images (e.g., the ROI's size, shape and position; Cuthbertson et al., 2019). By contrast, measuring maximum eye temperatures can often be achieved by extracting the maximum temperature of thermal images as a whole (e.g., Jerem et al., 2015), substantially reducing processing time. This is especially important for video analysis where a large number of measurement frames can be gathered in a short time (Hoffmann et al., 2013; Cuthbertson et al., 2019). However, maximum, like minimum temperatures are calculated from the value of a single pixel, so are more sensitive to measurement inaccuracies than the mean. Indeed, according to manufacturer specifications, temperatures measured by the camera used for the current investigation are expected to be within 2°C of an object's genuine

surface temperature. These issues can to an extent be overcome by ensuring thermal images are of highest quality, that the camera is calibrated to ambient conditions (Kim & Cho, 2021), and/ or through using data processing techniques to smooth raw temperature data and reduce influence of outliers (e.g., Cuthbertson et al., 2019 using video footage). Ultimately, although the current research can make recommendations regarding the suitability of mean and maximum temperatures, we found negligible differences in repeatability between these measures. Researchers must carefully weigh the advantages and disadvantages of each when deciding which measure best suits their needs.

When comparing between ROIs, we found that between-goat differences against total variation was greater for nasal temperatures than for either eye. However, whether observed differences in repeatability are genuine is difficult to verify given differences in suitability of methods used to process and analyse nasal and eye temperature data. Specifically, the repeatability estimates for temperatures of the nose tip may be less precise than those measured in the eyes (Schielzeth et al., 2020; Knief & Forstmeier, 2021), and the more stringent removal of outliers in the former likely boosted repeatability. What can be concluded however, is that nasal temperatures were far more variable between goats, with eye temperatures being restricted to a narrower range of values.

4.2. Precision in Temperature Estimates

Goats have been reported to show an increase in eye temperature of 1.1°C following exposure to a stressor (Bartolomé et al., 2019) and 1-2.2°C differences in rectal temperature between febrile and non-febrile animals (Van Miert et al., 1984; Zwart et al., 1991). Although changes in core temperature may not be perfectly mirrored in peripheral regions, in order to better detect fever, emotional experiences, and other physiological processes, we must reduce uncertainty in surface temperature estimates. Through averaging temperature across multiple thermal images collected in quick succession (assuming temperature is approximately stable over time), standard error will decrease proportionally

with an increasing number of measurement frames, thereby increasing precision (Byrne et al., 2017). Obtaining a large number of measurement frames in a short time window is feasible when collecting thermal imaging videos (Hoffmann et al., 2013; Cuthbertson et al., 2019), but device memory and RAM capacity, as well as time needed to process video frames can still limit the number of replicate measures it is practical to take.

We found that minimum temperatures measured from one image can differ by as much as 1.07°C from our gold standard, i.e., the average of five images, limiting its efficacy for making even broad distinctions, such as between stressed versus unstressed, or sick versus healthy goats. To achieve a similar precision in minimum temperatures as was found for mean and maximum temperatures, more images would be required. By contrast, a single image may be sufficient (although not recommended) to measure large temperature changes when using mean and maximum measures. We were able to attain a maximum precision of $\pm 0.10^{\circ}\text{C}$ from five images using the mean temperature of the right eye. Given this region and measure also showed lower variability across repeated measures, this may highlight the suitability of this combination in particular when measuring goat surface temperatures over a single session. More broadly, mean temperatures were slightly more precise when measuring goat eye temperatures, with maximum values performing slightly better for nasal temperatures. The observed precision gained through measuring mean and maximum temperatures repeatedly over multiple thermal images may enable future researchers to effectively measure subtle surface temperature changes associated with less arousing emotional experiences (Proctor & Carder, 2015; Tamioso et al., 2017) and earlier stages of diseases in goats.

4.3. Reproducibility of Temperature Measurements Taken Over Multiple Sessions

As well as short-term consistency in repeated measures taken within a single session, we investigated reproducibility of goat surface temperatures when measured over five sessions taking place

on consecutive days. Variability was always greatest (hence, reproducibility lowest) in minimum temperatures across all regions measured, including variation from unknown sources not explained by between-goat differences or session effects (e.g., measurement errors and variation in ROI placement across thermal images). Altogether, our results bring into question the suitability of minimum temperatures when using thermal imaging, both in the short- and longer-term.

Unlike eye temperatures, which were restricted to a narrower range, goat surface temperatures measured in the nose tip were highly variable. When measurements were taken across five days a good proportion of variation in nasal temperatures could be attributed to between-session effects (74.61-85.85%), i.e., the effect of measurement session alone and how temperatures from individual goats changed across days. If not due to the more stringent removal of outliers in nasal temperature data, given the significance of measurement session, it appears surface temperatures in this region might be highly sensitive to ambient conditions specific to the time of imaging (e.g., temperature, humidity, emotional arousal and goat position: Church et al., 2014; Proctor & Carder, 2015; 2016; Ijichi et al., 2020). By contrast, given the proximity of the orbital region to the brain and its ample blood supply, eye temperatures often have a stronger association with core body temperatures compared to other peripheral regions (George et al., 2014; de Ruediger et al., 2018; Bleul et al., 2021; Kim & Cho, 2021), including in goats (preliminary study, eye-rectal temperature: $r = 0.956$: Marques et al., 2021). Nonetheless, although lower than for nasal temperatures, we found a substantial proportion of variation in eye temperatures could be attributed to differences in surface temperatures between sessions (between 49.59-67.01%). Some of this variation could be associated with shifts in core temperature (in relation to e.g., circadian rhythm: Giannetto et al., 2020; emotional arousal: Beausoleil et al., 2004; Lees et al., 2020), but it is likely that eye temperatures were, like nasal temperatures, strongly influenced by imaging conditions.

The high variability in surface temperatures between goats and apparent sensitivity to imaging conditions observed in the nose tip especially, likely limits effectiveness of this ROI for detecting meaningful differences between goats (i.e., larger temperature differences, or sample sizes will be required to observe differences between treatment groups: Ledolter & Kardon, 2020). However, pre-existing variation in peripheral temperatures inherent to a sample of goats can, to an extent, be controlled for by focusing measures at the individual-level. Indeed, for such a purpose, sensitivity of a particular region to various external and internal parameters can be an asset. For example, temperatures in a chickens' comb and wattle (which play key roles in thermoregulation), unlike eye temperatures, changed with stressor intensity, enabling finer grained measurements of emotional responses (Herborn et al., 2015). Similarly, in ewes, more pronounced changes in temperature were observed in the muzzle, relative to the eyes, so the former was considered a more practical region for detecting ovulation (de Freitas et al., 2018). As well as across repeated measures taken from a single subject, temperatures measured in the eye especially, have been used to compare among groups of animals, in relation to for example, exogenous factors, like breed and sex (Jansson et al., 2021), and screening febrile from non-febrile animals (e.g., Schaefer et al., 2007; de Diego et al., 2013; Bleul et al., 2021). However, given the importance of imaging conditions on eye, as well as nasal temperatures it suggests such comparisons should be made with caution.

Our results suggested a high repeatability in surface temperatures measured from a single subject in the short-term (within one session) where conditions were consistent, so intuitively to compare among goats it may be better to test multiple animals under similar conditions (e.g., through testing subjects in quick succession) and preferably over multiple sessions (Uddin et al., 2020). Tighter control over environmental conditions should not only be recommended for between-subjects designs, with one investigation finding that an animal's baseline temperature influenced the magnitude of subsequent skin temperature changes following exposure to a stressor (Herborn et al., 2015). For practical reasons, we imaged goats at a distance of just over two metres and at 90° to the nasal plane

(frontal view). However, as distance between the camera and target object increases, intervening gases absorb a greater proportion of the radiant heat emitted by that object, so less is detected (Okada et al., 2013). Because goats were imaged at a distance exceeding that widely recommended for thermal imaging research ($\approx 1\text{m}$), and at a probably less than optimal angle (recommended angle: 90° to the sagittal plane) measured surface temperatures would likely have been lower than actual temperatures, and less accurate (Okada et al., 2013; Church et al., 2014; Jorquera-Chavez et al., 2019; Ijichi et al., 2020). Moreover, as subjects were free to move, the exact distance, and angle between camera and subject will have varied between goats and across repeated measures, introducing a less systematic source of variation into temperature estimates. Additional considerations include how best to define eye temperature in particular. In the eye, the posterior border of the eyelid and lacrimal caruncle especially are known to be richly supplied by a dense array of capillary beds (Kim & Cho, 2021; Mota-Rojas et al., 2021). Indeed, investigations subsetting the eye into multiple orbital regions have found ROIs associated with specific areas (e.g., medial canthus and lacrimal sac) correlate better with rectal temperature than whole-eye measurements (Kim & Cho, 2021; Shu et al., 2022). Ultimately through exerting greater control over the environmental component of animal surface temperatures, future investigations may be able to achieve greater reproducibility in temperature estimates (Church et al., 2014).

4.4. Conclusion

We found that goat mean, and maximum surface temperatures measured in the eyes and nose tip to be highly repeatable, at least in the short-term. In addition, these temperature measures showed high levels of precision, with a single image potentially being enough to make broad distinctions, such as sick from healthy, or stressed from unstressed animals; although using more than one image is recommended to enhance precision. However, given the strong influence of measurement session, goat

surface temperatures were not readily comparable across days, highlighting the importance of ambient imaging conditions on temperature estimates. Researchers using thermal imaging in small ruminants should consider focusing measurements at the individual-level, and/ or further refining the methodology used here (e.g., using a more optimal measurement distance and angle), as well as exerting tighter control over ambient conditions and perhaps using a more precise ROI (e.g., localised to a specific orbital region). Given the non-invasive nature of thermal imaging and importance of animal body surface temperatures as an indicator of animal health and welfare, investigations like ours are becoming increasingly important to identify approaches in which to effectively exploit this technology to its fullest potential.

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CHAPTER 5: General Discussion

1. OVERVIEW OF FINDINGS

This thesis started with a comprehensive literature review detailing our current understanding of emotions, cognition and personality in goats and their implications for welfare (**Chapter 1**). Throughout that chapter I focussed on the rich emotional lives of goats, how they apply their impressive repertoire of cognitive abilities to cope and even thrive in their challenging day-to-day environments, as well as the inter-individual differences in strategy that emerge as they do so (e.g., Miranda-de la Lama et al., 2011; Briefer et al., 2014; 2015a; 2015b; Pitcher et al., 2017; Baciadonna et al., 2020; Raoult et al., 2021). Goats are naturally curious and motivated to engage with cognitive challenges (Langbein et al., 2009; Rosenberger et al., 2020) emphasizing the significance of complex and cognitively-stimulating environments on their welfare. Indeed, the importance of learning and problem-solving opportunities is well recognized, which is especially clear given the extensive use of physical enrichment to stimulate the minds of captive animals (Oesterwind et al., 2016; Clark, 2017). However, for goats, as a gregarious species, we must also consider the challenges posed by their social environment and how these might affect welfare. For example, social conditions in a domestic setting are often distinct from those that would occur naturally, with larger group sizes and frequent mixing of individuals between groups potentially impairing their ability to form stable dominance hierarchies and social relationships between group members (Miranda-de La Lama & Mattiello, 2010; Patt et al., 2012; Stanley & Dunbar, 2013). Indeed, goats are known to express social preferences, and bonding is thought to be important in reducing stress, creating opportunities to experience positive emotions and to promote prosocial behaviour (Schino, 1998; Stanley & Dunbar, 2013; Briefer et al., 2015a). However, conspecifics cues are not the only socially relevant stimuli in the domestic environment.

How human cues are perceived during day-to-day handling and management could have key implications for the welfare of goats and other domesticated species (Mota-Rojas et al., 2020; Rault et

al., 2020). Whether intentionally or not, vocalisations are a key channel for communication between humans and livestock, but how goats perceive the human voice had not yet been investigated (Tallet et al., 2018; Celozzi et al., 2022). As well as neglecting perception of the human voice, research to date has focused on the capacity of goats to perceive cues common to all humans, such as facial expressions, attentional states and our gestural cues (Kaminski et al. 2005; Nawroth et al., 2015; 2016a; 2016b; 2020; Nawroth & McElligott, 2017). Accordingly, over the course of this PhD research I investigated goat perception of the human voice, and their discrimination of more individual-specific cues, including how these might affect goat behaviour. Firstly, I studied whether goats could combine vocal and visual cues to discriminate between familiar people (**Chapter 2**), and secondly, whether class-level recognition (familiar versus unfamiliar) affected their ability to discriminate between human voices conveying different emotional valence (**Chapter 3**).

The welfare implications arising from goat perception of human cues result from how they affect goat emotional experiences, which can be assessed through indicators operating at multiple levels of an integrated emotional response (cognitive, behavioural or physiological). In **Chapter 1**, I focused on two relatively rapid and non-invasive physiological indicators, namely cardiac responses (heart rate and heart rate variability: HRV) and skin temperature changes assessed through thermal imaging. Accordingly, I measured cardiac responses in conjunction with behaviour in **Chapters 2 and 3** to investigate changes in physiological arousal in relation to human cues (Briefer et al., 2015b). Finally, in **Chapter 4** I examined reliability of various combinations of measure (mean, maximum and minimum temperatures) and region of interest (ROI: eyes and nose) in quantifying goat surface temperatures using thermal imaging in the short- and long-term. A more detailed summary of each thesis chapter is provided below:

1.1. Chapter 2: Goats May Recognise Humans Cross-Modally

Goats can discriminate among conspecific social partners using a variety of cues (Ruiz-Miranda, 1993; Poindron et al., 2007; Briefer & McElligott, 2011a; Briefer et al., 2012; Keil et al., 2012), enabling them to attribute past interactions to certain group members and tailor their behaviour accordingly (Schino, 1998; Kaminski et al., 2006; Tibbetts & Dale, 2007; Wiley, 2013; Yorzinski, 2017). In contrast, although goats are also sensitive to human behaviour, from our attentional (Nawroth et al. 2015; 2016a; 2016b; Nawroth & McElligott, 2017), gestural (Kaminski et al., 2005; Nawroth et al., 2015; 2020) and emotional cues (Nawroth et al., 2018; **Chapter 3**), how they represent us as individuals and discriminate between us had not previously been investigated. To address this gap, given goats can recognize conspecific social partners using visual and vocal cues (Pitcher et al., 2017), in **Chapter 2** I used a congruency paradigm to evaluate whether goats can likewise apply cross-modal recognition for discriminating between familiar people. Subjects were presented with a facial photograph and two repeated voice recordings that either came from the same (was congruent) or different familiar people (were incongruent; based on experiments in dogs and cats: Adachi et al., 2007; Takagi et al., 2019). When facial and vocal cues were incongruent, goats were predicted to look faster and for longer after playbacks reflecting a violation of expectations. In addition, I expected behaviour to change in tandem with physiology, with increases in arousal, i.e., raised heart rate and a drop in HRV when human identity cues were incongruent (Briefer et al., 2015b; Baciadonna et al., 2020). In contrast to predictions, goats were slower to look following the second, compared to the first voice playback, but importantly, this increase in time taken to respond was greater when goats were experiencing incongruent facial and vocal cues. Although differences in behaviour between conditions did not conform to predicted patterns and were only observed in one response measured, the fact that goat behaviour did change with congruency could suggest that they were capable of perceiving differences in human identity information presented.

1.2. Chapter 3: Goat Discrimination of Emotional Valence in the Human Voice

Goats can discriminate human and conspecific emotions visually using facial expressions (Bellegarde et al., 2017; Nawroth et al., 2018); however, goat facial musculature is less developed compared to humans, meaning expressions are more subtle and further, how they are expressed appear poorly conserved across taxa (Waller & Micheletta, 2013). In contrast, as emotional experiences often affect vocalisations in similar ways in different species, vocal communication may be a particularly important channel for cross-species transfer of emotional information (Faragó et al., 2014; Filippi et al., 2017; Bryant, 2021). Goat vocalisations convey a range of information about the caller (Briefer & McElligott, 2011a; 2011b; Briefer & McElligott, 2012), including their emotional state (valence and arousal: Briefer et al., 2015b). Given goats can discriminate positively from negatively valenced conspecific calls (Baciadonna et al., 2019), in this chapter I investigated whether they could perceive analogous differences conveyed in human speech. As familiarity with the individual expressing emotional cues has been shown to facilitate discrimination in other species (e.g., Merola et al., 2014; Briefer et al., 2017), I examined whether voice familiarity affected goat behavioural and physiological responses (heart rate and HRV). Goats were presented with a habituation-dishabituation-rehabilitation playback paradigm, where they listened to several playbacks of a familiar or unfamiliar voice conveying the same emotional valence (e.g., happy; habituation phase), before the valence changed (e.g., to angry; dishabituation phase) and then reversed back to that of the habituation phase (e.g., back to happy; rehabilitation phase; based on Baciadonna et al., 2019). Having shown robust evidence of habituation over the habituation phase (decreased likelihood, time spent looking and time taken to look), goats were less likely to respond following a change in voice valence (dishabituation phase), but importantly, those which did looked for longer, suggesting these goats had perceived the shift in valence. Familiarity with the voice presented also affected goat behaviour, although it did so in complex ways, which are difficult to interpret. I found no changes in cardiac responses in relation to voice valence or familiarity. Discrimination of human emotions has more extensively been investigated in companion species, but

research in goats and other livestock suggests these cues are salient for animals living closely with us, irrespective of whether they were domesticated as household companions, for work or for their products (Nawroth et al., 2018; Jardat & Lansade, 2021).

1.3. Chapter 4: Thermal Imaging in Goats: Reliability & Precision of Temperature Measurements Taken from Facial Regions

Thermal imaging is a technology increasing in prominence in animal health and welfare research, being used to non-invasively track changes in animal peripheral temperatures over time (e.g., in response to an emotional event) or between individuals (e.g., sick versus healthy animals). However, there is a distinct lack of consistency in which body regions are sampled (region of interest: ROI) and measures used (mean, maximum or minimum temperature) between thermal imaging studies (Stewart et al., 2008a; 2008b; Proctor & Carder, 2015; 2016; Dai et al., 2015; Herborn et al., 2015; Kano et al., 2016; Brügger et al., 2021). Accordingly, in **Chapter 4** I investigated short-term repeatability (measurements taken within a single session), precision, as well as reproducibility (measurements taken over five consecutive days) of mean, maximum and minimum goat surface temperatures measured in the eyes and nasal ROIs from thermal imaging videos. I found that goat minimum temperatures were not only the least precise, but were more variable across sessions and individuals, and over repeated measurements from the same individual in a single session. By contrast, for mean and maximum measures short-term repeatability and precision was high across five repeated measures (taken within approximately one minute) with between 93.50% and 99.81% of total variation in surface temperature attributable to differences between goats across ROIs. However, when sessions were repeated across five days, temperature measurements taken from individual goats were not readily reproducible with the effect of measurement session explaining between 61.71% to 85.85% of variation in mean and maximum surface temperatures. Although some of this variation could be associated with changes in

body temperature (in relation to e.g., circadian rhythm: Giannetto et al., 2020; emotional responses: Beausoleil et al., 2004; Lees et al., 2020) it is highly likely that temperatures measured in the eyes and nose tip are highly sensitive to ambient imaging conditions. Based on my findings, I recommended that future research using thermal imaging in small ruminants should consider concentrating measurements at the individual-level (i.e., before, during and after stimulus exposure: e.g., Bartolomé et al. 2019; Proctor & Carder, 2015; 2016), using for example, a more optimal measurement distance or angle (Okada et al., 2013; Church et al., 2014; Jorquera-Chavez et al., 2019; Ijichi et al., 2020), exercising tighter control over environmental conditions and perhaps using a more specific ROI (e.g., localised to a particular orbital region: Kim & Cho, 2021; Shu et al., 2022).

2. INFLUENCES OF LEARNING & DOMESTICATION ON SOCIAL COGNITION IN GOATS

Following research in dogs, cats and horses (Adachi et al., 2007; Proops & McComb, 2012; Takagi et al., 2019), my investigation, presented in **Chapter 2** may further emphasize the adaptability of complex cross-modal recognition systems to categorise members of a morphologically very different species (Ratcliffe et al., 2016). Indeed, recognition systems are thought to evolve in tandem with signalling systems, promoting communication between, for example, mates, kin, group members and competitors (e.g., Miller et al., 2020; Tibbetts et al., 2020). In humans and primates, recognition mechanisms become attuned to processing conspecific stimuli over development (e.g., Lewkowicz & Ghazanfar, 2009; Simpson et al., 2011; 2017). However, this perceptual narrowing can be slowed or offset through exposure to heterospecifics during this sensitive period (e.g., Pascalis et al., 2005; Sugita, 2008; Adachi et al., 2009; Scott & Monesson, 2009). For livestock like goats, humans, as well as conspecifics can be perceived as important features in an animal's early social environment. Through early exposure to humans, perhaps combined with learning in later life, we may expect goats to develop recognition systems to accurately discriminate among human, as well as conspecific social partners. For sheep, a fellow small ruminant, although cue use is more complex in the conspecific context, (Peirce et al., 2000; 2001), even less tame breeds show evidence of robust and holistic face-processing abilities, recognizing people from photographs irrespective of angle and hairstyle (Knolle et al., 2017). As well as a role for learning, goat dependence on humans for food, shelter and protection from predators over thousands of generations, may have predisposed them to develop more advanced perception of human cues to facilitate interspecific communication, including in the context of recognition (Avarguès-Weber et al., 2013).

Previous research investigating cross-modal recognition of humans has been limited to related species (Sliwa et al., 2011) and companion animals (Adachi et al., 2007; Proops & McComb, 2012; Takagi et al., 2019). Unlike companion animals, which have been domesticated as working animals or as

household pets, goats have largely been bred for their meat, milk and hair products (MacHugh & Bradley, 2001). We may, therefore, expect goats to be under weaker selection to discriminate among us and interpret our cues. However, although more robust evidence has been observed in cats, dogs and horses (Adachi et al., 2007; Proops & McComb, 2012; Takagi et al., 2019), this does not mean these species are better able to apply cross-modal recognition to discriminate among familiar people. Indeed, these differences could be due to my experimental approach. For example, I used a photographic representation over a live person which provided less information for goats to make distinctions (e.g., Lampe & Andre, 2012; Proops & McComb, 2012). Furthermore, using a physical photograph, instead of an electronic display, which would have allowed human visual and vocal stimuli to be presented in two short stages may have increased goat likelihood of habituating to the stimuli array compared to the latter approach (e.g., Adachi et al., 2007; Takagi et al., 2019). If goats can use complex cross-modal mechanisms to recognize human, as well as conspecific social partners, it will add to the growing body of evidence emphasising social cognition of human cues between livestock and companion species are less distinct than might be assumed (for review, see Jardat & Lansade, 2021). There is further empirical research supporting this idea, suggesting that selective breeding exclusively for reduced emotional reactivity towards humans is sufficient to develop heightened social cognition of our cues (Hare et al., 2005). Domestic heritage may also in part underlie the apparent ability to discriminate emotional valence observed in goats in **Chapter 3**, and indeed, domestic pigs, but not wild boar likewise respond differently to human voices based on their emotional valence (Maigrot et al., 2022). However, only some goats seemed to respond to a change in valence of human voice playbacks, which may point towards individual-level explanations for such abilities, rather than ones that apply to domestic goats as a whole.

If not due to for example, differences in how strongly valence was conveyed across playbacks, or in cognitive ability or level of attention among goats, variation in their responses to the playback paradigm could stress the importance of learning on an individual's ability to interpret human emotional

cues. Experiences of human voices of differing valence and how these have been linked with previous positive and negative events will have varied among the goats tested, potentially affecting their ability to discriminate such cues. Indeed, horses and pigs can learn to associate human voices with previous positive and negative experiences (Tallet et al., 2016; d'Ingeo et al., 2019) and dogs discriminate more relevant human emotions (e.g., happiness over fear) with greater ease, as well as those expressed by an owner over those of a stranger (Merola et al., 2014).

Ultimately, the research presented in **Chapters 2 & 3** add to what we know about the impressive repertoire of social cognitive abilities goats have developed to navigate the anthropogenic environment (e.g., Nawroth et al., 2015; 2016a; 2016b; 2016c; 2018; 2020; Nawroth & McElligott, 2017). Thus far, research into the abilities enabling domesticated species to perceive our cues and interact with us heavily favour companion animals (and horses and dogs especially). However, this gap is started to be bridged in goats and other livestock, with preliminary evidence suggesting social cognitive abilities governing perception of human cues are comparable between these two groups (for review, see Jardat & Lansade, 2021). Ultimate explanations for goat ability to perceive human cues likely comprise a blend of their domestic background and learning over an individual's lifetime (among other factors) to varying degrees dependent on the social cognitive ability in question. Further research is needed to disentangle their relative influences. Understanding the extent to which livestock perceive human cues is important from a welfare perspective, as these social cognitive abilities underpin the human-animal relationship.

3. WELFARE IMPLICATIONS AND THE HUMAN-ANIMAL RELATIONSHIP

Humans are hugely important in the lives of many farm animals, and as such how these animals perceive and interact with us has strong implications for their welfare (Nawroth, 2017; Nawroth et al., 2019). Although isolated human-animal interactions often only have transient effects on animal emotional experiences and welfare, through multiple repeated interactions relationships may develop, affecting how animals perceive human cues in the long-term (Hinde, 1976; Sankey et al., 2010; Somavilla et al., 2016; Mota-Rojas et al., 2020; Rault et al., 2020). Negative human-animal relationships (HARs), resulting from a negative perception of humans have not only been linked to poor welfare, but can be detrimental to animal health and productivity, with fear of humans being the primary driving factor (reviewed by: Mota-Rojas et al., 2020). In contrast, in a positive HAR, interactions with certain people may develop rewarding properties, providing opportunities for animals to experience positive emotions, a buffer against stressful situations (e.g., husbandry procedures) and potentially increasing an animal's long term stress resilience (reviewed by: Rault et al., 2020). As behaviour differs among people (based on e.g., attitudes, gender, skills and experience: Hemsworth et al., 2000; Hemsworth & Coleman, 2010; Ceballos et al., 2018; Celozzi et al., 2022) and positive and negative interactions do not necessarily have equal value when determining the valence of the HAR (positive or negative: Hemsworth et al., 1987), the specificity with which goats discriminate among humans has key implications for the form of the HAR, and as a result animal welfare.

In **Chapter 2** I provided evidence that goats may combine visual and vocal cues to recognize familiar people. Possession of such complex recognition mechanisms would not only imply that goats can accurately discriminate among humans but also suggests they develop internal representations of familiar people, a pre-requisite for individual recognition (Proops et al., 2009). With increasing specificity of recognition, goats will be better able to attribute positive and negative interactions to certain people and tailor their own behaviour accordingly (Tibbetts & Dale, 2007; Wiley, 2013; Yorzinski, 2017). This is

as opposed to producing generalised responses to people sharing similar characteristics (class-level recognition: familiar versus unfamiliar, vets versus non-vets) or all people (although generalisations may still be made to less familiar individuals: Destrez et al., 2013; Brajon et al., 2015). Ultimately, the HAR is shaped by what an animal anticipates as the outcome of interacting with humans, and as such is affected by the predictability of these interactions (de Passillé et al., 1996; Destrez et al., 2013; Brajon et al., 2015; Rault et al., 2020). As well as a history of interactions with a certain individual, or humans in general, goats can gauge a person's future behaviour in a more proximate sense through interpreting their emotional expressions (Schmidt & Cohn, 2001).

My findings in **Chapter 3** indicate goats can discriminate emotional valence in the human voice, although only some goats showed the predicted change in behaviour with valence. In a social species like goats, recognizing and responding to emotional cues of group members and humans may play key roles in mediating intra- and interspecific social relationships (Schmidt & Cohn, 2001). For example, horses and dogs have been shown to process valence information from human vocal stimuli in a functionally relevant way (e.g., through producing lateralised responses: Smith et al., 2018; Siniscalchi et al., 2018), and horses, dogs and cats adjust their behaviour towards a person based on the valence of emotional cues they had expressed (Galvan & Vonk, 2016; Proops et al., 2018; Albuquerque et al., 2022). Similarly, goats have been shown to selectively approach and interact with human facial photographs expressing a positive (happy) over a negative (angry) emotional valence (Nawroth et al., 2018). Indeed, if animals can discriminate between and are sensitive to human emotional states, it may affect their own emotional experiences and welfare. This could be because animals perceive human voices of differing valence as possessing inherently rewarding or aversive properties, as predictors of positive or negative events (e.g., Schmidt & Cohn, 2001; Merola et al., 2014; d'Ingeo et al., 2019), or even through transmission of emotional state from humans, as seen in dogs (emotional contagion: e.g., Katayama et al., 2019). Negatively-valenced human voices (e.g., shouting, growling and use of a stern voice) can provoke fear and vigilance in domestic animals (Waynert et al., 1999; Merkies et al., 2013;

Smith et al., 2018). By contrast, voices conveying a positive valence (e.g., soothing voices) may have a calming effect (Lange et al., 2020), as well as potentially eliciting approach (Nawroth et al., 2018) and social bonding between humans and animals. Ultimately, the ability to discriminate between and remember social partners, be they conspecific or human, paired with an understanding of their emotional state and motivations will have significant implications for the quality and richness of a goat's social life (Nawroth et al., 2019). Such abilities may also serve as a foundation for more sophisticated social cognitive phenomena, such as prosocial behaviour, cooperation and even empathy (Nawroth, 2017; Nawroth et al., 2019). However, in order to properly understand the welfare implications of having such social cognitive abilities, we must move beyond demonstrating the capacity to discriminate human cues and towards an understanding of how goats perceive us (Nawroth, 2017). To access these experiences, we require behavioural and physiological indicators with which to measure animal emotional responses (reviewed in **Chapter 1**).

Emotions are complex multifaceted phenomena comprising neural, cognitive, behavioural, physiological and (in some species, and humans at least) subjective components (Špinka, 2012). Behavioural responses are generally directly observable, but accessing physiological changes often requires excessive handling to equip animals with wearable sensors (to monitor e.g., brain and cardiac activity: Gyax et al., 2013; **Chapters 2 & 3**), or use of more invasive methods (e.g., blood sampling: Carbonaro et al., 1992a; 1992b). The process of fitting measurement devices to animals can itself elicit emotional responses, especially in individuals less accustomed to human handling; this therefore requires careful regimes to habituate animals to the device (which may not be successful in all individuals), with more invasive methods often being painful and difficult to habituate to. Thermal imaging offers a remote alternative, enabling data collection with less need for human handling or proximity (e.g., Hoffmann et al., 2013).

The use of thermal imaging to assess goat emotional responses to human cues has been limited to date. Eye temperatures have been shown to change in response to an experimenter herding goats noisily with large arm movements to an adjacent pen (Bartolomé et al. 2019), and a preliminary study demonstrated a drop in eye temperature in relation to a painful husbandry procedure (ear tagging: Zebaria et al., 2021). However, central to many modern welfare concepts is the idea that welfare reflects a balance of positive and negative experiences, and in particular to foster 'positive welfare' the former must outweigh the latter (Green & Mellor, 2011; Mellor & Beausoleil, 2015). Within the scope of the HAR, to best exploit this technology and promote 'positive welfare' we must identify positive, as well as negative components of human-animal interactions using changes in peripheral temperature. The use of thermal imaging to measure positive human-animal interactions is limited, but changes in body surface temperatures in cows and sheep have been shown in response to human stroking and brushing, respectively (Proctor & Carder, 2015; Tamioso et al., 2017). This technology has also been applied in other species to investigate responses to more complex social phenomena, such as emotional contagion in chickens (Edgar et al., 2011; Edgar & Nicol, 2018), as well as influences of the wider social environment on emotional responses to social interactions (presence of females and dominant males: de Vevey et al., 2022) and third-party social evaluation in primates (Brügger et al., 2021). Furthermore, the combination of playbacks and thermal imaging in experiments to measure emotional responses towards social stimuli (Kano et al., 2016; Ermatinger et al., 2019; Brügger et al., 2021) highlight the potential of this approach to further investigate the implications of the human voice on welfare in goats and other domesticated species.

Temperature estimates obtained through thermal imaging are affected by a range of endogenous (e.g., individual, sex and level of physical activity: Rizzo et al., 2017; Jansson et al., 2021), environmental (e.g., temperature, humidity and wind speed: Church et al., 2014; Jansson et al., 2021) and extraneous factors (e.g., distance, measurement angle, ROI and measure: Church et al., 2014; Ijichi et al., 2020; Byrne et al., 2017; Scoley et al., 2019). Therefore, to effectively measure changes in surface

temperatures in response to human cues, we clearly need reliable methods to track the time course of goat emotional responses. Indeed, **Chapter 4** demonstrates that goat mean and maximum surface temperatures are highly repeatable in the short-term (under consistent conditions), and thus may be suitable for measuring individual-level responses to human stimuli. However, magnitude of associated temperature changes may be linked to an animal's baseline peripheral temperatures (measured before exposure to the experimental stimulus: Herborn et al., 2015), with these temperatures seeming to be heavily influenced by ambient imaging conditions (goat peripheral temperatures were not readily reproducible across days: **Chapter 4**). Through knowledge of my results, along with further refinement of methodology and tighter control over ambient conditions, future researchers will be in a better position to examine goat emotional responses to positive and negative human-animal interactions among other cues.

4. A NOTE ON THE STUDY SITE

All experiments took place at Buttercups Sanctuary for Goats (<https://www.buttercups.org.uk/>) where animals are kept in a large herd (of 100+ individuals throughout the study period), given ready access to a large outdoor paddock and where their health care and dietary needs are carefully met. Although Buttercups houses rescue goats, some of which have experienced past mistreatment and neglect, previous research conducted at the same study site suggest females suffering poor welfare in the past expressed an optimistic bias when presented with ambiguous cues, relative to control females (Briefer & McElligott, 2013). Further, males showed similar levels of optimism regardless of their past experiences. Together this suggests that the environment of the sanctuary has positive effects on goat rehabilitation, including on stress resilience and the ability to cope with challenges posed by their environment. Part of this will be because of the strong positive relationship between humans and goats that exists at Buttercups. The goats used for testing had varied and frequent contact from staff, volunteers as well as members of the public and so were well-habituated to human handling, often actively sought contact with people (personal observations and e.g., Briefer et al., 2015a; Baciadonna et al., 2016), and with their preferred person in particular. Indeed, many goats possessed strong bonds with certain people (this being a selection criterion for **Chapter 2**), including staff members and guardians (members of the public with special privileges). These HARs often featured preferential contact between humans and goats including provision of preferred food, as well as human grooming and stroking. Ultimately, the strength of the HAR and the level of exposure to human cues may have made human behaviour especially salient to the goats at Buttercups, which may partly underlie the sensitivity to our cues evident in my own PhD research (**Chapters 2 & 3**), as well as in other investigations (e.g., Nawroth et al., 2016b; 2016c; 2018; 2020; Nawroth & McElligott, 2017). Although further research is needed to investigate the impact of prior human experience on perception of our cues, close positive HARs of the kind seen at Buttercups are not unique to that site. This is especially the case given the number of goats kept as pets (Cornall & Wall, 2015; Weaver, 2021), as working animals

(e.g., pack goats: in ancient history: Sutliff, 2019; contemporarily: Weaver, 2021) or in zoos, and moreover because of the increasing recognition of a positive HAR on animal welfare, health and productivity (Rault et al., 2020).

5. FUTURE DIRECTIONS

Given the significance of the HAR (Mota-Rojas et al., 2020; Rault et al., 2020), from an animal welfare perspective, identifying mechanisms through which animals discriminate between and mentally represent humans should be a key area for future research. My results from **Chapter 2** provide an indication, but further evidence is needed to more conclusively establish whether goats can use cross-modal recognition to discriminate among familiar people. For **Chapter 2**, I used a photographic representation rather than its live human counterpart. Photographs exclude olfactory, body (facial photographs were used), depth, perspective and motion cues and alter colour, all of which limits the amount of information goats would have had available to distinguish between individuals (Hill et al., 1997; Poindron et al., 2007; Fagot & Parron, 2010; Keil et al., 2012; Lansade et al., 2020). Aside from it being more difficult for non-human animals to recognize objects from photographs, in order to have registered incongruencies between the visual and vocal identity information presented, goats would have also had to treat the photographs as representations of the people they depict (Fagot & Parron, 2010). One obvious means to reduce task difficulty and potentially provide a stronger indication of whether or not goats are capable of cross-modal recognition of humans would be to substitute photographs with the live people they represent. Along with steps taken to minimise the influence of unintentional human cuing, for example providing noise cancelling headphones to prevent people acting as stimuli from being aware of the experimental condition (congruent or incongruent: Proops & McComb, 2012), I would recommend using multiple pairs of familiar people. Through demonstrating goats can match congruent cues and preferentially respond to incongruent ones using multiple pairs of people as stimuli, we would be in a better position to establish whether recognition is at the individual-level or whether goats are likely to be using broader class-level cues (e.g., size, gender, age and degree of familiarity: Proops et al., 2009; Taylor et al., 2011; Ratcliffe et al., 2014; Pitcher et al., 2017; Jardat et al., 2022; Korzeniowska et al., 2022).

In **Chapter 3**, I provided evidence that goats can discriminate between human voices based on their emotional content, however predicted patterns of behaviour were only seen in some goats and an ultimate explanation for these social cognitive abilities remains lacking. Teasing apart potential mechanisms underlying the observed pattern of behaviour will necessitate comparison of the ability of different goat populations to discriminate human emotional cues based on their historical or contemporary associations with people. Specifically, we may choose to measure these social cognitive abilities in domestic goats and compare them to that of their wild progenitor species, the bezoar goat, to investigate the effect of domestication on goat ability to perceive human cues (e.g., in zoo populations, like: Maigrot et al., 2022). To investigate the effect of individual experiences with people on social cognition of human cues, it may be advised to compare discriminatory abilities between individual animals differing in their level of exposure to human handling. For example, through investigating responses of feral goats to human emotional cues and comparing against those of individuals from intensively managed flocks, or responses of hand-reared goats, to less intensely human-socialised individuals. As well as exploring the underlying mechanisms, it is of note that if goats can discriminate among humans and conspecifics at the individual-level and interpret their mental state (emotions, and by extension motivations) it may suggest they are predisposed towards more complex social cognitive abilities.

Group living animals like goats may benefit from avoiding antisocial herd members, or humans which hinder goal directed behaviour or act selfishly in cooperative situations, and instead associate with more cooperative, or prosocial individuals (Abdai & Miklósi, 2016). Identifying cooperative tendencies in social partners can be achieved either through interacting with an individual directly (direct social evaluation) or indirectly, through observing their behaviour towards a third party (third party social evaluation). Indeed, goats show sensitivity both to their immediate social environment, adjusting behaviour based on previous interactions with certain individuals (Kaminski et al., 2006), and to their wider one, intervening in aggressive encounters between other group members (Keil &

Samraus, 1998). Furthermore, when unable to solve a task independently, goats have been shown to adjust the frequency of human-directed behaviours based on a person's level of attention (gaze alternations: Nawroth et al., 2016b), which can be interpreted as goats showing sensitivity to a person's perceived willingness or ability to cooperate. Social evaluation is assumed to be taxonomically widespread, but has thus far mainly been investigated in dogs, primates and humans (e.g., Anderson et al., 2017), and never in ungulate livestock. However, in addition to expanding our knowledge of the upper limits of goat social cognitive capacities and identifying mechanisms underpinning their ability to discriminate human cues, from a welfare perspective it is also important to develop objective means to measure how these cues affect goat emotional experiences. Thermal imaging as a remote technology may be a suitable indicator for measuring emotional responses in different populations of goats, varying in level of acceptance of human handling (e.g., feral populations and wild progenitors).

Given the prevalence of the dimensional framework in modelling animal emotion (Russell, 1980; Mendl et al., 2010), to assess the potential of thermal imaging to investigate goat perception of human cues among other emotional experiences, we must understand how peripheral temperature changes in relation to both arousal and valence. This can be achieved by measuring goat surface temperatures in relation to situations differing in both of these dimensions (i.e., positive and negative contexts of low and high arousal: Briefer et al., 2015b; Baciadonna et al., 2020). Through using thermal imaging videos, it is possible to collect more detailed information regarding the time course of an emotional response (e.g., how quickly a temperature change occurs), with this and the magnitude of temperature responses likely being important in contextualising changes in relation to arousal, and perhaps valence (discussed in **Chapter 1**; Stewart et al., 2007; 2008b; Herborn et al., 2015; Proctor & Carder, 2016). To assess the sensitivity of thermal imaging for measuring goat emotional responses, we would need to compare skin temperature data gathered against a suite of competing emotional indicators (Briefer et al., 2015b; Baciadonna et al., 2020), as well as examining the suitability of different ROIs (eyes and nose) and measures (mean and maximum; **Chapter 4**). It could be that like many physiological indicators (e.g.,

cardiac responses: Briefer et al., 2015b), surface temperatures are more sensitive to changes in emotional arousal, rather than valence and other (e.g., behavioural) measures will be needed to provide valence information. From here, we would be able to measure more salient components of human-animal interactions, and perhaps whether they are perceived as positive or negative, using thermal imaging alone, or preferably in combination with other emotional indicators.

6. FINAL REMARKS & CONCLUSION

To refine handling practices and improve welfare, it is imperative that we understand how goats perceive and interact with humans in their day-to-day lives (Nawroth, 2017; Nawroth et al., 2019). The outcome of human-animal interactions may have short-lived effects on animal emotional experiences and welfare, but when repeated over time, they can have cumulative and long-lasting implications for how animals perceive humans through affecting the valence of the HAR (positive or negative: Rault et al., 2020). A positive HAR, for example, is built through a history of (mostly) positive interactions and assumes animals possess the ability to discriminate between humans and associate outcomes of positive and negative interactions with certain people (Hinde, 1976; Sankey et al., 2010; Somavilla et al., 2016; Mota-Rojas et al., 2020; Rault et al., 2020). The specificity of recognition will affect how goats perceive and behave towards individual people (individual recognition), groups of people (class-level recognition: e.g., vets versus stockpeople) or people in general (Tibbetts & Dale, 2007; Wiley, 2013; Yorzinski, 2017). The research I presented in **Chapter 2** provided an indication that goats use sophisticated cross-modal recognition mechanisms to discriminate among familiar people, which suggests they form internal templates for known individuals, a building block of individual recognition (Proops et al., 2009; although further research is needed to confirm my results). Ultimately, within a HAR, goats use previous behaviour of a person to anticipate their future actions, but in a more immediate sense, goats can predict human behavioural motivations through interpreting our emotional cues (Schmidt & Cohn, 2001). Vocalisations are a potent medium for emotional communication in both humans and goats (Briefer et al., 2015b; Baciadonna et al., 2019), but how goats perceive the human voice remains poorly understood (Celozzi et al., 2022). Although not all goats showed predicted patterns of behaviour, my results from **Chapter 3** suggest goats can discriminate emotional valence conveyed in the human voice. Being able to discriminate between conspecifics and humans and perceive their internal state, including emotions and motivations, may affect the quality and richness of a goat's social interactions and perhaps act as a foundation for more complex social behaviour, from prosociality and

cooperation to even empathy (Nawroth, 2017; Nawroth et al., 2019). Human cues expressed during handling, including emotional ones, may have positive or negative effects on behaviour, but how goats perceive such cues and how these affect their emotional experiences requires an objective means of measuring emotions. We found that although goat mean and maximum surface temperatures measured in the eyes and nose were not readily reproducible across days, they were highly repeatable in the short-term. This suggests thermal imaging may be suitable for measuring changes in skin temperature at individual-levels, for example in relation to goat emotional responses before, during and after human handling; although tighter control over ambient conditions and refinement of experimental procedures may be necessary.

Ultimately, positive HARs can evoke positive emotions in goats and other livestock and mitigate against the effects of negative experiences, promoting positive, and long-lasting welfare outcomes (reviewed by: Rault et al., 2020). To achieve this gold standard, we need to develop an understanding of the social cognitive abilities underpinning HARs; from how different domesticated species discriminate between humans and the specificity with which they do so, to what aspects of human behaviour they are sensitive to (including emotional cues) and how this affects formation of these relationships. Finally, given emotional responses are complex, multicomponent phenomena, to gain a complete picture of how animals perceive human cues (in terms of emotional valence and arousal), and the value of the HAR, we need to expand and further refine our repertoire of emotional indicators. Accordingly, my PhD research has offered clues as to how goats discriminate between and internally represent familiar people. Further, I have provided the first evidence that they are sensitive to cues present in our voice, namely emotional valence, as well as identity cues. And lastly, I have presented recommendations to reduce error in surface temperature estimates obtained through thermal imaging in the hope that future goat researchers will exploit this physiological welfare indicator to its fullest potential.

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APPENDIX 1A

PARTICIPANT CONSENT FORM

Title of research project: Goats' Perception of Humans

Title of Study: Face-voice cross-modal individual recognition of humans

Brief description of research project and what participation involves:

Many recognition studies focus on investigating an animal's ability to differentiate a known from an unknown individual (Kriengwatana et al., 2015). However, such experiments can at most support class-level (familiar versus unfamiliar) recognition. To demonstrate *individual* recognition, subjects must be able to distinguish among familiar individuals. Through individual recognition, animals can more effectively track behavioural interactions with other individuals, enabling more complex social relationships to develop (Kappeler 2019).

For livestock, if it is beneficial to adjust behavioural responses on an individual basis, extending individual recognition to humans may be advantageous. More specifically, recognition of individual humans may enable animals to attribute positive or negative experiences to certain individuals and use these past interactions to predict that human's future behaviour (Nawroth et al., 2019). With decreasing recognition, animals may become increasingly likely to generalise experiences with specific individuals to all humans. The ability of livestock to recognise individual humans can therefore have substantial implications for their welfare.

Individual-specific cues are not limited to one modality, creating opportunities for animals to form complex cognitive representations of individual humans in multiple modalities. Only in horses has the ability of livestock to discriminate humans using multimodal cues been empirically demonstrated (Proops & McComb 2012). Pitcher et al., (2017) demonstrated goats were able to match auditory to visual cues of close social partners, suggesting they could form cross-modal representations of these individuals. The proposed research aims to investigate if these recognition mechanisms extend to familiar humans.

For participation in this experiment we will need to take a photograph of your head and shoulders which will be blown up to life-size. In the same session we will also ask to record your voice reading a few provided phrases. The photograph and voice recording provided will be used as stimuli in a set of behavioural experiments with goats at Buttercups Sanctuary for Goats. Participation should take no longer than 45 minutes. Participation consent forms will be kept for six years following completion of the research project, before being destroyed or

retained in an anonymised form. Data provided will be kept for 10 years (or longer if requested by funder or a regulatory body) following project completion, before being archived.

Investigator contact details:

Name: Marianne Mason

Department: Life Sciences

University Address: Whitelands College, University of Roehampton, Holybourne Ave, London SW15 4JD

Email: masonm@roehampton.ac.uk

Consent statement:

I agree to take part in this research, and am aware that I am free to withdraw at any point without giving a reason by contacting Marianne. I understand that if I do withdraw, my data may not be erased but will only be used in an anonymised form as part of an aggregated dataset. I understand that the personal data collected from me during the course of the project will be used for the purposes outlined above in the public interest.

By signing this form, you are confirming that you have read, understood and agree with the University's Data Privacy Notice for Research Participants.

The information you have provided will be treated in confidence by the researcher and your identity will be protected in the publication of any findings. The purpose of the research may change over time, and your data may be re-used for research projects by the University in the future. If this is the case, you will normally be provided with additional information about the new project.

Name

Signature

Date

Please note: if you have a concern about any aspect of your participation or any other queries please raise this with the investigator (or if the researcher is a student you can also contact the Director of Studies.) However, if you would like to contact an independent party please contact the Head of Department.

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APPENDIX 1B

Subject name, year in which they were tested, sex, breed, age, number of years at study site, order of trials included in analysis (C = Congruent, I = Incongruent) and whether cardiac, as well as behavioural data had been successfully taken during experimental trials (Y = Yes; N = No).

Goat ID	Tested	Sex	Breed	Age (years)	Duration at Sanctuary (years)	Trial Sequence	Contributed Cardiac Data?
Bernard	2020	M	Anglo Nubian	9	9	C, C, I, I	Y
Davey	2020	M	Saanen	15	7	C, I, C, I	Y
Dixie	2020	F	Pygmy	11	9	C, I, C	N
Dylan	2020	M	Pygmy	7	5	C, I, I, C	N
Ewok	2020	M	Anglo Nubian	4	3	I, I, C, C	Y
Juliet	2020	F	Toggenburg	8	3	C, C, I, I	N
Luke	2020	M	Anglo Nubian	4	3	C, I, C, I	Y
Natalie	2020	F	Swiss-Alpine Cross	10	9	I, C, I	Y
Nigel	2020	M	Pygmy	9	8 months	I, I, C	N
Princess	2020	F	Anglo Nubian	4	3	I, C, C, I	Y
Spice	2020	F	Anglo Nubian	7-8	3	C, I	N
Tarnie	2020	F	Golden Guernsey	16	4	I, C, I, C	Y
Bill	2021	M	Toggenburg	≈16	4	I, C, I	Y
Bramble	2021	M	Pygmy	Unknown	≈3	I, I, C, C	Y
Cole	2021	M	Mixed Breed	≈8	2	C, I, C	N
Dunstan	2021	M	Pygmy	9	7	I, C, C, I	N
Franky	2021	M	Saanen Cross	5	3	I, C, I, C	Y
Glenda	2021	F	Saanen Cross	≈10	≈1	I, C, C	N
Goesover	2021	M	Saanen	Unknown	1	C, I, C	Y
Heidi	2021	F	Toggenburg	11	9	I, C, C	Y
Jet	2021	M	Pygmy	9	4	I, C	Y
Joseph	2021	M	Pygmy	7+	6	C, I, C	N

Khan	2021	M	Pygmy	9+	4	C, C, I, I	N
Kirk	2021	M	Pygmy	9+	4	C, I, C, I	Y
Mary	2021	F	British Alpine	16+	4	C, I, C	Y
Milly	2021	F	Old English Feral	Unknown	≈4	C, I, C	N
Pooky	2021	F	Pygmy	9	5	C, C, I	N
Sundance	2021	M	Pygmy	13	7	I, C, C	Y

APPENDIX 1C

Goat latency to look at the photograph following voice playbacks in relation to the effect of congruency between human visual and vocal cues, in combination with playback number (results of post-hoc tests for congruency x playback number interaction).

Explanatory Variable	β	S.E.	z-ratio	p-value
• C1 - C2	-0.311	0.006	-53.68	<0.0001****
• I1 - I2	-2.073	0.007	-277.31	<0.0001****
• C1 - I1	0.719	1.227	0.59	0.936
• C1 - I2	-1.353	1.227	-1.10	0.688
• I1 - C2	-1.031	1.227	-0.84	0.836
• C2 - I2	-1.042	1.227	-0.85	0.831

Key: C1= Congruent condition, Playback 1; C2= Congruent Condition, Playback 2; I1= Incongruent Condition, Playback 1; I2= Incongruent Condition, Playback 2. **** $p < 0.0001$

APPENDIX 2: Supplementary Information from Chapter 3

APPENDIX 2A

Subject name, sex (F= Female; M= Male), breed, age, number of years at the study site and playback sequence experienced during experimental trials (AHA = Angry-Happy-Angry; HAH = Happy-Angry-Happy).

Goat ID	Sex	Breed	Age (years)	Duration at Sanctuary (years)	Playback Sequence
Anoushka	F	Pygmy	14+	2	AHA
Arlo	M	Mixed Breed	7	3	HAH
Bear	M	Pygmy	6	2	AHA
Bernard	M	Anglo Nubian	8	8	AHA
Bramble	M	Pygmy	Unknown	1	HAH
Bonnie	F	Pygmy	16	6	AHA
Buttercup	F	Pygmy	≈14	1	HAH
Davey	M	Saanen	14	6	AHA
Del Boy	M	Pygmy	10	6	AHA
Dixie	F	Pygmy	10	8	HAH
Ewok	M	Anglo Nubian	3	2	HAH
Harry	M	Saanen	10	8	HAH
Heidi	F	Toggenburg	9	7	HAH
Luke	M	Anglo Nubian	3	2	HAH
Natalie	M	Mixed Breed	9	8	HAH
Pickle	F	Pygmy	Unknown	2	AHA
Princess	F	Anglo Nubian	3	2	HAH
Rambo	M	Unknown	7	2	HAH
Rosie	F	Saanen	7	1	HAH
Sapphire	F	Toggenburg	8	3	AHA
Shakespeare	M	Saanen – Golden Guernsey Cross	12	9	HAH

Goat ID	Sex	Breed	Age (years)	Duration at Sanctuary (years)	Playback Sequence
Sticky	M	Saanen – Golden Guernsey Cross	6	6	AHA
Sugar	F	Anglo Nubian	7	2	AHA
Tarnie	F	Golden Guernsey	15	3	AHA
Valentine	F	Toggenburg	Unknown	2	AHA
Vern	M	Toggenburg	8	8	AHA
Wendy	F	Toggenburg	Unknown	1	HAH

PARTICIPANT CONSENT FORM

Title of research project: Goats' Perception of Humans

Title of Study: Discrimination by goats of emotional valence in familiar and non-familiar human voices

Brief description of research project and what participation involves:

Recognizing emotions of others enables assessment of behavioural motivations, which is important in guiding future behavioural interactions with those individuals (Schmidt & Cohn 2001). When living closely with humans, such as in the domestic environment, it may be adaptive for animals to discriminate human (as well as conspecific) emotional cues. Although the ability is affected by side biases, goats can discriminate between human facial expressions of different valence (Nawroth et al., 2018). However, relative to humans, goats have less developed facial muscles and although they do appear to discriminate conspecific emotions visually (Bellegarde et al., 2017), vocalisations likely provide a richer medium to assess emotions of others. Both human and goat vocalisations vary with emotional valence and arousal which can potentially be interpreted across communication systems (Scheumann et al., 2014; Briefer et al., 2015).

Baciadonna et al. (*in prep*) demonstrated goats discriminate emotional content of conspecific vocalisations, but whether similar discriminations are possible for the human voice is yet to be investigated. Familiarity has been demonstrated to improve emotional discrimination in other species (e.g., in dogs: Merola et al., 2014), so I will examine whether goats can discriminate human voices of different valence, and if voice familiarity affects this ability.

For participation in this experiment we will record your voice while you read multiple phrases using an 'angry' and a 'happy' voice. The voice samples you provide will be compiled with recordings taken from other people and used as stimuli in a set of behavioural experiment in goats at Buttercups Sanctuary for Goats. Participation should take no longer than 20 minutes. Participation consent forms will be kept for six years following completion of the research project, before being destroyed or retained in an anonymised form. Data provided will be kept for 10 years (or longer if requested by funder or a regulatory body) following project completion, before being archived.

Investigator contact details:**Name:** Marianne Mason**Department:** Life Sciences**University Address:** Whitelands College, University of Roehampton, Holybourne Ave, London SW15 4JD**Email:** masonm@roehampton.ac.uk**Consent statement:**

I agree to take part in this research, and am aware that I am free to withdraw at any point without giving a reason by contacting Marianne. I understand that if I do withdraw, my data may not be erased but will only be used in an anonymised form as part of an aggregated dataset. I understand that the personal data collected from me during the course of the project will be used for the purposes outlined above in the public interest.

By signing this form, you are confirming that you have read, understood and agree with the University's Data Privacy Notice for Research Participants.

The information you have provided will be treated in confidence by the researcher and your identity will be protected in the publication of any findings. The purpose of the research may change over time, and your data may be re-used for research projects by the University in the future. If this is the case, you will normally be provided with additional information about the new project.

Name

Signature

Date

Please note: if you have a concern about any aspect of your participation or any other queries please raise this with the investigator (or if the researcher is a student you can also contact the Director of Studies.) However, if you would like to contact an independent party please contact the Head of Department.

Director of Studies contact details: Name:

Dr Alan McElligott

Department: Life Sciences**University Address:** Whitelands College, University of Roehampton, Holybourne Ave, London SW15 4JD**Email:** alan.mcelligott@roehampton.ac.uk**Telephone:** 020 8392 3000 ext 4480**Head of Department contact details:****Name:** Dr Caroline Ross**Department:** Life Sciences**University Address:** Whitelands College, University of Roehampton, Holybourne Ave, London SW15 4JD**Email:** c.ross@roehampton.ac.uk**Telephone:** 020 8392 3529

RESEARCH PARTICIPANT INFORMATION SHEET FOR INDIRECTLY COLLECTED OR RE-USED PERSONAL DATA

You have previously provided personal data to the University of Roehampton to be included in a research project entitled 'Goat Perception of Human Cues'

We are writing to you because the University intends to use the data you originally provided for a new experiment. Information about the new research project and contact details for the research team are included below.

Title of Research Project: Goat Perception of Human Cues

Title of Study: Discrimination by goats of emotional valence in familiar and non-familiar human voices

The voice samples you provided were used in an experiment to assess whether the domestic goat can discriminate emotional valence (happy versus angry) expressed in the human voice. In order to validate the use these voice samples, we wish to use your samples again to verify whether human participants can correctly categorise recordings according to valence. Samples provided will be combined at random with those of seven other speakers and sent in an anonymised, password-protected form to study participants. Although speaker identity will be anonymised, there is some risk that some volunteers may be recognized through their voice

Following project completion, recordings provided will be kept for 10 years in accordance with the University Records Retention Schedule before being archived in an anonymised form.

Investigator Contact Details:

Name: Marianne Mason

Department: Life Sciences

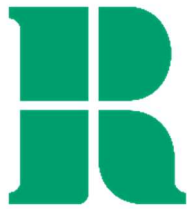
University Address: Whitelands College,
University of Roehampton,
Holybourne Ave, London, SW15 4JD

Email: masonm@roehampton.ac.uk

Privacy Notice:

You have the right to opt-out of your personal data being processed as part of this research project, which you can do by contacting Marianne Mason. If you do withdraw, your data may not be erased but will only be used in an anonymised form as part of an aggregated dataset.

More information about how your personal data will be used can be found in the University's [Data Privacy Notice for Research Participants](#) and its [Data Protection Policy](#).



PARTICIPANT CONSENT FORM

Title of research project: Goat Perception of Human Cues

Title of Study: Validation of Experimental Stimuli Used in a Goat Behavioural Experiment

Brief description of research project:

Background

Recognizing emotions of others enables assessment of behavioural motivations, which is important in guiding future behavioural interactions with those individuals (Schmidt & Cohn 2001). When living closely with humans, such as in the domestic environment, it may be beneficial for animals to discriminate human (as well as conspecific) emotional cues. Goats have been shown to discriminate between human facial expressions of different emotional valence (angry versus happy) (Nawroth et al., 2018). However, relative to humans, goats have less developed facial muscles and although do appear to discriminate conspecific emotions visually (Bellegarde et al., 2017), vocalisations likely provide a richer medium to assess emotions of others.

Baciadonna et al. (2019) demonstrated goats discriminate emotional content of conspecific vocalisations, but whether similar discriminations are possible for the human voice is yet to be established. Over the summer of 2019, goats were exposed to recordings of human voices expressing different emotional valence (angry versus happy) to see whether they could discriminate between these emotional cues. In order to assess the validity of playbacks presented, it is necessary to present experimental stimuli to human participants to see whether they can successfully discriminate the valence expressed in the voice samples used.

Participation

Participation involves listening to a series of 48 voice recordings taken from various speakers (average recording length = 1.43 seconds \pm 0.373) and divided into three blocks of 16 recordings. Each block will be sent to you as a separate audio file via email. You will be requested to complete at least a single block per session (lasting one minute 45s, one minute 51s and one minute 54s) but are otherwise free to complete this task remotely in your own time. Following each recording we ask that you score on a blank piece of paper whether you consider the speaker to be expressing happiness (positive valence; scored as: +) or anger (negative valence; scored as: -). There will be five seconds of silence following each recording to allow you to do this. Participation will take approximately five minutes 30 seconds in total and there is a possibility you may be able to recognize some of the speakers.

Data from your participation will be anonymised and included as part of an aggregated data set. Data will be retained for 10 years in accordance with the University Records Retention Schedule.

Investigator contact details:

Name: Marianne Mason
Department: Life Sciences
University Address: Whitelands College,
University of Roehampton, Holybourne
Ave, London SW15 4JD
Email: masonm@roehampton.ac.uk

Consent statement:

I agree to take part in this research, and am aware that I am free to withdraw at any point without giving a reason by contacting Marianne Mason. I understand that if I do withdraw, my data may not be erased but will only be used in an anonymised form as part of an aggregated dataset. I understand that the personal data collected from me during the course of the project will be used for the purposes outlined above in the public interest.

By signing this form you are confirming that you have been informed about and understand the University's [Data Privacy Notice for Research Participants](#).

The information you have provided will be treated in confidence by the researcher and your identity will be protected in the publication of any findings. The purpose of the research may change over time, and your data may be re-used for research projects by the University in the future. If this is the case, you will normally be provided with additional information about the new project.

Name

Signature

Date

Please note: if you have a concern about any aspect of your participation or any other queries please raise this with the investigator (or if the researcher is a student you can also contact the Director of Studies.) However, if you would like to contact an independent party please contact the Head of Department/ Director of School.

Director of Studies contact details:

Name: Dr Alan McElligott
Department: Life Sciences
University Address: Whitelands
College, University of Roehampton,
Holybourne Ave, London SW15 4JD
Email:
alan.mcelligott@roehampton.ac.uk

Head of Department contact details:

Name: Dr Caroline Ross
Department: Life Sciences
University Address: Whitelands College,
University of Roehampton,
Holybourne Ave, London, SW15 4JD
Email: c.ross@roehampton.ac.uk

Should the Head of Department change over the lifecycle of the research project the new Head of Department will become the independent contact. Contact details for the new Head of Department can be obtained from the investigator



Basic Participant Demographic Information

All data provided through participation will be anonymised and included as part of an aggregated data set

Name: _____

Gender:

- ☐ Male
- ☐ Female
- ☐ Other
- ☐ Prefer not to say

Age Range:

- ☐ 18-24
- ☐ 25-34
- ☐ 35-44
- ☐ 45-54
- ☐ 55-64
- ☐ 65+
- ☐ Prefer not to say

Country of Origin: _____

APPENDIX 2D

Results of post-hoc comparisons for the interaction between playback number and familiarity on goat latency to look at the sound source following a change in emotional valence of human voice samples between the habituation and dishabituation phase (H9-D10) and the dishabituation and rehabilitation phases (D12-R13).

Explanatory Variable	β	S.E.	z-ratio	p-value
H9-D10				
F: H9 – F: D10	-0.467	0.006	-82.58	<0.0001****
U: H9 – U: D10	-2.435	0.008	-291.68	<0.0001****
F: H9 – U: H9	4.269	1.499	2.85	0.023*
F: D10 – U: D10	2.301	1.499	1.54	0.417
F: H9 – U: D10	1.834	1.499	1.22	0.612
U: H9 – F: D10	-4.736	1.499	-3.16	0.009**
D12-R13				
F: D12 – F: R13	-2.405	0.009	-283.10	<0.0001****
U: D12 – U: R13	0.916	0.007	126.82	<0.0001****
F: D12 – U: D12	0.456	2.101	0.22	0.996
F: R13 – U: R13	3.778	2.101	1.80	0.274
F: D12 – U: R13	1.373	2.101	0.65	0.914
U: D12 – F: R13	-2.862	2.101	-1.36	0.523

Significant results are shown in bold. Key: F= Familiar, U= Unfamiliar, H9 = Habituation phase playback 9 (last playback of habituation phase), D10 = Dishabituation phase playback 10 (first playback of dishabituation phase), D12 = Dishabituation phase playback 12 (last playback of dishabituation phase), R13= Rehabilitation phase playback 13 (last playback overall). * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; **** $p < 0.0001$

APPENDIX 3: Supplementary Information from Chapter 4

Subject name, sex (M = Male; F = Female), breed, age, number of years at the study site, group membership and week tested (1, 2 or 3).

Goat ID	Sex	Breed	Age (years)	Duration at Sanctuary (years)	Group ID	Week Tested
Ewok	M	Anglo Nubian	5	4	1	1
Luke	M	Anglo Nubian	5	4	1	1
Princess	F	Anglo Nubian	5	4	1	1
Davey	M	Saanen	16	8	2	1
Mary	F	British Alpine	16+	4	2	1
Goesover	M	Saanen	10	3	3	2
Jeffers	M	Boer Cross	10	3	3	2
Juliet	F	Toggenburg	9	4	3	2
Donald	M	Mixed Breed	8	2	4	2
Hattie	F	Toggenburg	10	10	4	2
Heidi	F	Toggenburg	12	10	4	2
Blossom	F	Nubian Cross	12	8	5	2
Glenda	F	Saanen Cross	12	8	5	2
Natalie	F	Swiss-Alpine Cross	11	9	5	2
Arlo	M	Mixed Breed	9	5	6	3
Dylan	M	Pygmy	8	6	6	3
Franky	M	Saanen Cross	6	5	6	3
Sapphire	F	Toggenburg	11	6	7	3
Topaz	F	Toggenburg	11	6	7	3
Vincent	M	Mixed Breed	11	11	7	3