What can behaviour really tell us about emotion? Integrating novel physiological and behavioural techniques to advance comparative affective science

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Abstract

Emotion research has gained enormous momentum through the emerging field of comparative affective science, which seeks to uncover important aspects about the emotional life of nonhuman animals. This chapter reviews the limitations of relying solely on behavioural information to derive information on affective states in animals. Instead, it emphasizes the value of combining behavioural coding methods with novel non-invasive physiological methods. We specifically explore advances in automated behavioural tracking, facial action coding, infrared thermography (IRT), infrared videography (IR) and microwave radar technologies. These promising new tools offer insights into internal states without restraining or potentially harming animals, thus providing more ethical empirical assessment. We argue that multi-dimensional approaches that combine behavioural and physiological data enable richer and more accurate interpretations of animal emotions. As future avenue, we propose "behaviour-physiology profiles" to uncover biological and evolutionary foundations of affective processes across species. We believe such an integrated framework holds great promise for advancing animal welfare, communication science and our understanding of the complex emotional life of animals.

Introduction

In recent years, a growing body of research has converged on the consensus that nonhuman animals (hereafter animals) experience emotions, which they communicate to social audiences through multimodal signals related to the body, face, and voice, as well as via behavioural cues (Briefer, 2012; Briefer et al., 2015; Heesen, Austry, et al., 2022; Kret et al., 2020, 2022; Slocombe & Zuberbühler, 2007; Soldati et al., 2022). The increasingly widespread recognition that animals have emotions is reflected in the emergence of comparative affective science as a vibrant new discipline, its growing popularity reflecting broader trends in the psychological sciences towards an era of 'affectivism' (Dukes et al., 2021). In particular, many studies now aim to illuminate the evolutionary origins and mechanisms underlying the emotional lives of animals and humans, using a range of methodological approaches, including behavioural, cognitive and physiological assessments (Briefer et al., 2015; Chotard et al., 2018; Demuru et al., 2015; Dezecache et al., 2017; Ermatinger et al., 2019; Heesen, Austry, et al., 2022; Kret et al., 2020, 2022; Mendl et al., 2009; van Berlo et al., 2023).

One prominent and increasingly influential approach in comparative affective science focuses on how animals *express* emotional states, thereby highlighting the communicative and adaptive role of potential emotional signals (Descovich et al., 2017; Heesen, Austry, et al., 2022; Kret et al., 2020). At the same time, there is increasing research on the *perception* of such expressions, assessed mainly using behavioural indicators of attention, such as through eye movements and head direction, or through match-to-sample tests (Heesen et al., 2024; Kret et al., 2016; Kret & van Berlo, 2021; Parr, 2004; Parr et al., 1998, 2007; van Berlo et al., 2023). Studies on the *expression* and *perception* of (presumable) emotional states span multiple taxonomic orders within the animal kingdom, including carnivores (Maglieri et al., 2024), ungulates (Briefer et al., 2015; Camerlink et al., 2018; Smith et al., 2016) and rodents

(Dolensek et al., 2020), with a particular focus on nonhuman primates (primates hereafter) (Davila Ross et al., 2007; Demuru et al., 2015; Heesen et al., 2024; Kret et al., 2016; Parr et al., 1998; Pritsch et al., 2017). Studies typically focus on bodily, facial, and vocal expressions in order to derive conclusions about autonomic arousal (ranging from low to high activation) and valence (ranging from pleasant to unpleasant) dimensions based on the use of these expressions across varying social or ecological contexts. While valence is often estimated from the expression's contextual use, such as during conflict or play (Demuru et al., 2015; Heesen, Austry, et al., 2022), arousal is typically assessed based on behavioural markers of underlying physiological states, including self-manipulatory behaviours (Kret et al., 2016; Sclafani et al., 2012), or more directly via physiological measures related to the body and skin temperatures (Descovich et al., 2017; Kano et al., 2016; Parr, 2001).

Reflecting the ethological tradition, the use of observational behavioural assessments has historically been, and remains, highly relevant to our understanding of animal cognition, emotion and welfare (Feighelstein, Ehrlich, et al., 2023; Matthews et al., 2016), notably as it avoids restraining animals and using invasive measures. In this way, an observational approach can be applied across numerous settings, including in captivity and the wild, thus offering greater ecological and ethical validity. However, despite important contributions in this area (Darwin, 1993; Goodall, 1986; Tinbergen, 1963), behavioural observations alone can only offer limited insights into underlying mechanisms, and may sometimes even be misleading (Waller et al., 2017). In long-linguistic subjects, including both animals as well as pre-verbal human infants, the identification of emotional states through behaviour is often speculative, unless supplemented by additional measures and tightly controlled experimental paradigms. Because such individuals cannot be directly asked about their subjective experiences, researchers rely on indirect indicators of emotional states, such as bodily and facial expressions. A possible exception are extensively trained or enculturated animals, such as language-competent great apes (e.g., Washoe, Nim, Kanzi, Koko: Krause & Beran, 2020). For instance, in a recent study, the language-competent bonobo Kanzi was able to successfully match playbacks of conspecific alarm calls to the associated lexigram (symbols for scare and snake) indicative of his ability to make affect-based judgements (Lahiff et al., 2025). However, with all such language-competent apes now sadly deceased, and their language-training programmes no longer in operation, the field's empirical focus has already (rightly) shifted focus towards the more ecologically valid intent to understand animal emotions under natural conditions and their evolutionary foundations.

While there is growing agreement that many animals, particularly vertebrates and some invertebrates, are capable of valenced experience, also known as sentience (Browning & Birch, 2022), we still lack definitive methods to identify and characterize the nature of these subjective experiences, including emotions, across species (Feldman Barrett, 2017; Kret et al., 2022). Research must therefore rely on a combination of physiological and visible (i.e., codable) behavioural data, to generate estimations of animal inner experience. The need to understand how physiology drives behaviour is still emerging and calls for the development of new methodologies to carefully and reliably determine under which circumstances certain behaviours may, or may not, serve as valid indicators of emotions. Even in human adults, facial expressions can be produced deliberately (known as "posed expressions, e.g., Elfenbein et al., 2007) and may not accurately reflect a person's internal state, leaving recipients vulnerable to misinterpretation and deception (Zloteanu et al., 2018). Although expressive behaviour is an essential component of emotional experiences, emotions predominantly originate at the physiological and neural level (although there are critical debates on causality Anderson & Adolphs, 2014). This underscores the need to incorporate more than just behavioural markers in comparative studies to avoid potential pitfalls.

In animals, there is now ample evidence that communicative signals can be flexibly used even when produced in (presumable) high-arousal contexts ranging from pleasant to unpleasant valence (Dezecache & Berthet, 2018; Heesen, Sievers, et al., 2022). For instance, chimpanzees detecting a snake – a dangerous predator that represents a serious threat to survival – seem to be able to suppress the emission of alarm calls if the audience is already aware of the threat (Crockford et al., 2012, 2017; Schel et al., 2013). Several primate species can modulate facial expressions during social play by adjusting their duration and intensity depending on whether a social partner is visually attentive (bonobos: Demuru et al., 2015; gibbons: Scheider et al., 2016; orangutans: Waller et al., 2015) or depending on the play type, age of the partner, or presence of specific individuals in the audience (Cordoni & Palagi, 2011; Demuru et al., 2015; Flack et al., 2004). While the degree of conscious volitional control is difficult to assess, the findings nevertheless suggest that these expressions function to inform about subsequent or future actions and events, rather than only offering honest readouts of emotions (Waller et al., 2017). Like human expressions, animal expressions thus need not to be strictly tethered to specific emotional states as in "emotion *X* causes expression *Y*" (Berthet et al., 2023; Heesen, Sievers, et al., 2022), though the nature of – specifically clarity in - this relationship may vary across species (Dolensek et al., 2020). Hence, the affective underpinnings of a behaviour in question need to be carefully examined across varying socio-ecological contexts and carefully compared against additional neurobiological or physiological data. Descovich et al. (2017 p. 410) argue that voluntary control of human facial expressions weakens as emotional intensity increases, resulting in so-called 'emotional leakage' (Porter et al., 2012). Similar patterns may also occur in animals, insofar as heightened arousal could lead to stronger or more conserved expression patterns (Heesen, Sievers, et al., 2022). This calls for a new multi-dimensional affective-cognitive approach (Heesen, Sievers, et al., 2022), which avoids drawing generalized conclusions *a priori* based on behavioural contexts and prevents anthropomorphism by prioritizing instead a careful, objective, and case-by-case analysis.

In this chapter, our stance is that the term 'emotional expression', which is readily used across the literature both in animals and humans and dates back to even Darwin himself (Darwin, 1872; Kret et al., 2020; Kret & van Berlo, 2021; Shariff & Tracy, 2011; Walker et al., 2010) may be unclear, incomplete or even misleading unless supported by additional neurobiological or physiological evidence. For example, the bared-teeth facial expression in primates is often assumed to indicate fear or apprehension. This is because it is typically produced by subordinates (though the directionality in production might depend on the hierarchy dynamics of the respective group or species) during tense situations, such as following aggression (Kim et al., 2022; Vlaeyen et al., 2022). Although some researchers even refer to it as "fear grimace" (Gothard et al., 2004), research indicates this expression may be driven by multiple internal states of varying arousal and valence categories depending on the context (Heesen, Sievers, et al., 2022). For example, when a bonobo produces the bared-teeth face in response to an aggressive attack by a dominant conspecific, this might be taken as evidence of distress or fear (Heesen, Austry, et al., 2022). However, bonobos also emit this expression during sexual interactions with varying social partners and across various contexts, including upon food discovery, which could reflect positive and/or negative valence states and varying arousal levels (Vlaeyen et al., 2022). Because behavioural and contextual data alone may be insufficient to accurately identify and differentiate physically similar expressions, researchers should thus adopt a more informative and holistic approach that combines multiple behavioural and physiological measures. Historically, this has been reserved to more invasive laboratory studies, such as with rodent models, where underlying physiology and its relation to behavioural and neural correlates can be investigated in restrained animals. Although it is now possible to gather physiological data in more ethical manners, such as from tethered or freely moving domestic animals who are willing to tolerate wearable physiological devises like heart rate belts (e.g., farm animals: Briefer et al., 2015), collecting equivalent data from nondomesticated unrestrained subjects, especially in the wild, is much more challenging from a practical and ethical standpoint. On a positive note, this challenge has catalysed the emergence of novel, contact-free non-invasive methods which, combined with other measurement approaches, now offer promising new insights into animal emotions.

Our goal, in this chapter, is to review successful efforts in the emerging field of comparative affective science that exemplify a combinatorial approach in the comparative study of affect and emotions, and from there, to provide novel ideas on how the field could move forward. We first review the latest advances on behavioural and analysis tools, including state-of-the-art use of ethogram annotations, systematic facial expression coding and analysis techniques and automated behavioural tracking technologies. We then focus on emerging infra-red-related and microwave radar technologies to detect arousal and consider how these technologies could be combined with others to inform on animal emotional experiences across various settings. While recent studies have delivered important findings investigating physiological arousal in primates (Dezecache et al., 2017; Ermatinger et al., 2019; Kano et al., 2016), physiology on its own likewise represents one component necessary for the study of emotional experiences and communication. With further validation and refinement, the integration of non-invasive physiological methods with state-of-the-art behavioural assays will offer an enhanced and richer comparative perspective on animal emotion. By revealing how physiological states correlate with observable behaviours, a holistic approach – as discussed here - can offer new insights into the biological and evolutionary underpinnings of emotional experiences.

State-of-the-art behavioural analyses: From manual coding to automated tracking

In recent years, machine learning and computer vision techniques have substantially advanced the automatic extraction of behavioural information from images and videos of animals. Traditionally, behavioural video coding remains largely constrained by manual efforts and is often negatively affected by observer fatigue, bias, or mistakes. Beyond the significant time investment, human coders are also limited by the quantity and quality of information that can be perceived by human senses - particularly when studying fast-paced behavioural processes or species whose anatomy or *umwelt* (Uexküll, 2013) differs markedly from our own. While the field of animal behaviour is still gradually introducing automated methods in their data collection pipelines, a lot of innovations have already allowed the collection of finer scale data in a fraction of the conventional annotation times.

Within the field of animal welfare and livestock management, computer vision technology has already been widely applied to attain more accurate and automated assessments of livestock behaviours, health and welfare (Tzanidakis et al., 2023), including of the behavioural recognition of pain, aggression and fear, such as in pigs, cows, chickens and other farm animals (Alameer et al., 2020; Chen et al., 2023; Matthews et al., 2016; Yang & Xiao, 2020). Such automated systems are particularly valuable for early detection of health and welfare concerns, such as diseases and injuries, contributing to more ethical and sustainable husbandry practices. Recently, methodological advances have expanded automatic recognition from simpler individual state-level behaviours, like resting or feeding, to more complex social interactions with simultaneous tracking of multiple individuals. For instance, Gan et al. (2021) developed a system for quantifying social nosing and play in pigs using keypoint estimation, while An et al. (2023) introduced a method for predicting the three-dimensional shape of multiple pigs concurrently, allowing quantification of individual and social behaviours, including potential communicative signals. The posture and motion of pig tails, for example, have been proposed as indicators of the animals' physical and emotional states (Camerlink & Ursinus, 2020), leading to the development of automated methods to detect tail movements or health issues related to tail injuries and biting events (D'Eath et al., 2021; Liu et al., 2020). For now, the advances described here are mostly targeted for applied applications to assess pain, fear and aggression; however, they clearly present exciting scope for broader application to understand the relationship between affect, communication and sociality in other animals and settings, particularly species living in open environments, whose behaviour can be reliably tracked.

Another methodology where automated coding is showing promising advances is the Facial Action Coding System (FACS). This methodology, informed by objective anatomical analysis, aims to detect distinct facial muscle movements, known as action units, which underlie facial expressions. Although FACS was originally developed to analyse human facial movements (Ekman & Friesen, 1984), it has since been adapted for use across multiple species and taxa, including macaques (Morozov et al., 2021; Parr et al., 2010), chimpanzees (Vick et al., 2007), cats (Caeiro et al., 2017), horses (Wathan et al., 2015) and dogs (Waller et al., 2013), see Waller et al. (2020) for review. Thanks to computational advances, FACS analysis for human faces can now be done automatically using a number of specialised softwares, including iMotions (iMotions.com) and FaceReader (noldus.com/facereader) as well as open-source software, including OpenFace (https://github.com/TadasBaltrusaitis/OpenFace). Note, however, that there is still room for improvement to increase diversity into the ground truth coding for such algorithms as they were largely trained from expressions of western populations. To our knowledge, there is currently no dedicated systematic automated tool available for analysing FACS in animals. One recent study with captive gorillas applied OpenFace software to analyse play faces (Cordoni et al., 2025), but the accuracy in applying this method to quantify primate facial expressions still requires further careful validation. Also in monkeys, automated classification of facial action units and expressions has been explored (Tlaie, Hay, et al., 2025), though again this remains largely limited to more controlled, captive settings (but see Carugati et al., 2025 for research on wild lemurs). Given the extensive effort and time investment needed for manual FACS coding, further validation and development of suitable software to analyse animal faces represent important methodological directions for comparative affective science. Despite its early stages, the automatization of FACS in animals thus represents a promising and important future research line.

Another emerging computational approach involves the use of machine learning classifiers to automatically detect facial or bodily landmarks of animals, which can then be used to infer possible emotional states based on the relative position of each landmark. This machine-learning based method has already been effective in detecting potentially pain-related behaviour of domestic cats (Feighelstein, Henze, et al., 2023; Martvel, Lazebnik, et al., 2024; Martvel, Shimshoni, et al., 2024), dogs (Ferres et al., 2022), and horses (Hummel et al., 2020). A potentially simpler and more powerful emerging method is the use of deep learning models on inputted images and videos to directly analyse behaviours identified as potentially representing internal states. This approach eliminates the need to extract higher level data, like action units or landmarks, and instead directly allows models to learn subtle patterns from all the available information contained in one or multiple images (Boneh-Shitrit et al., 2022; Corujo et al., 2021; Feighelstein, Ehrlich, et al., 2023; Feighelstein et al., 2022). This bottom-up approach has already demonstrated impressive results and even outperformed human coders in some cases (Feighelstein et al., 2025). Nevertheless, deep learning models should still be treated with caution, as they may struggle to generalize across different systems and species and often require large amounts of training data, typically coded by humans, thus introducing potential bias (see above). In this respect, while machine learning offers more systematic and efficient analysis, its performance hinges on the quality of human input (or “ground truth”), rendering it prone to flaws if the original training data is inaccurate or inconsistent. Therefore, while machine learning represents a promising new direction in behavioural analysis, careful consideration and rigorous validation are essential steps to ensure reliability and accuracy.

Compared to other animals including birds or quadrupedal mammals, identifying and tracking behaviour in wild primates can be especially challenging due to the flexible use of their limbs, mixed use of substrates (arboreal and terrestrial) and the noisy or low-light nature of their forest environments. Especially in the latter setting, algorithms may struggle to reliably separate subjects from each other or from the background (Wiltshire et al., 2023). Despite these challenges and variability in model performances, several methods and datasets have now been developed to automatically monitor and quantify behaviours in primates, including locomotion, resting, grooming, and foraging, using video footage from camera traps in the wild (Brookes, Mirmehdi, Stephens, et al., 2024), drones (Duporge et al., 2024) and in zoos (Ma et al., 2023). This reflects a broad array of advancements in automated tracking of primate behaviour over the past decade (Vogg et al., 2025), from posture estimation (Bala et al., 2020; Kaneko et al., 2024; Wiltshire et al., 2023; Xing et al., 2024), to behavioral classification (Brookes, Mirmehdi, Kuhl, et al., 2024; Fuchs et al., 2024; Ma et al., 2024), and facial recognition (Loos & Ernst, 2013; Schofield et al., 2019; Schofield et al., 2023). Thanks to rapid pace of improvements in AI-assisted research, we predict that behaviours in primates and beyond may soon be monitored and measured with unprecedented detail with the advent of a new era in automated behavioural monitoring.

Despite exciting advances, we would argue that researchers interested in animal emotions still need to retain some caution in their interpretations of automatically coded behavioural data, given that external behaviours may not always be reliable indices of underlying affect. In the next section we discuss how combining such techniques with non-invasive psychophysiological technologies such as infra-red thermography could support a deeper understanding of the nature and expression of animal emotion. We describe two different applications of thermography that can be applied to address the underlying affective and physiological processes driving human and animal behaviour. First, we introduce infrared thermography (IRT) to assess thermal correlates of autonomic arousal, and second, infrared videography (IR) to study sleep, well-being, and behaviour in low-light conditions. Last, we briefly discuss another emerging method – microwave radars - which may be used to get insights into physiological processes like heart rates of primates without having to establish contact with the animals' skin or body.

Going beyond behavior: Using novel technologies to investigate physiological parameters non-invasively in animals

Infrared thermography as a measure of physiological arousal

Animals, like humans, behave in response to changes in their surrounding environment – notably the social one (Byrne, 1996; Smith, 1965; Whiten, 2000) – and these behaviors are often driven by underlying psychological and affective states, which some argue to be comparable to human emotions (Anderson & Adolphs, 2014; de Waal, 2011). Traditionally, observations of visible or audible behaviours have served as the primary source of data for linking behaviours to specific contexts and interpreting their function. However, the absence of observable behavior does not imply the absence of internal states. Animals continuously acquire and process diverse information about others, updating their knowledge of the world and others - especially of social relationships - to adjust their behavior accordingly (Byrne & Bates, 2007; Seyfarth et al., 2005). Yet, when cognitive and emotional processes cannot be directly accessed through behavioural correlates, new methods are needed.

One recent technology increasingly adopted in comparative research is infrared thermography (IRT), which enables researchers to measure changes in skin surface temperature in both humans and animals, providing insights into emotional responses (Fernández-Cuevas et al., 2015; Mccafferty, 2007). Like other key scientific technologies (e.g., fMRI), IRT was originally developed for industrial applications, such as detecting heat leaks in buildings, before being adapted by cognitive researchers (Cilulko et al., 2013). Prevalently used in controlled environments like laboratory settings and zoos at first (Proctor et al., 2013), IRT is increasingly being adopted in the wild to study a variety of species, including insects, birds, mammals, and primates (Stewart et al., 2005; Tattersall, 2016; Tattersall & Cadena, 2010). As reviewed by Brügger and Burkart (Chapter in this Book), IRT represents a new contactless and portable method to estimate underlying arousal states through measures of skin temperature, with a focus on Regions of Interest (ROIs) in the face (Ioannou et al., 2014; Kano et al., 2016; Nakayama et al., 2005). Through activation of the sympathetic nervous system, vasoconstriction reduces blood flow into the peripheral vessels, yielding detectable temperature changes in certain ROIs, including the nose tip and peri-orbital regions (Ioannou et al., 2014). Some studies have found that stress or fearful experiences like hearing conspecifics' screams (Dezecache et al., 2017; Kano et al., 2016) elicit changes in facial temperatures in primates, presumably correlated with changes in internal states. Negatively valenced stimuli or contexts such as hearing screams or observing an injury typically result in drops in nasal temperature, although the direction of temperature change can differ across studies. For instance, other studies with humans have found temperature increases linked to negative emotional arousal (Aureli et al., 2015; Ioannou et al., 2016; Vreden et al., 2025), as well as temperature decreases for positive emotions (Nakanishi & Imai-Matsumura, 2008). In primates, drops in nasal temperature have also been detected in relation to playful experiences (Chotard et al., 2018). At present, the reasons underlying this apparent variability in temperature change directionality is not well understood. It appears that, while IRT can be used as indicator of arousal, its applicability to identify valence currently remains questionable and requires further validation and testing. Additional to the nasal area, other facial areas such as the periorbital, upper lip, or nose bridge areas have been investigated (Chotard et al., 2018), as well as fingertip temperatures: Moritz and Dominy (2012) revealed profound temperature changes in the characteristic middle digit of the nocturnal aye-aye (*Daubentonia madagascariensis*) – a specialized touch sensory structure used during percussive and foraging – whenever it was actively used during touching behaviours.

Despite the advances offered by IRT, there are limitations which need to be carefully addressed and mitigated, especially when applying this technology with wild animals. Early IRT studies were conducted under highly controlled – but sometimes ethically problematic – laboratory conditions, where animals were physically restrained while being exposed to negative or stressful stimuli (Nakayama et al., 2005). As growing evidence shows that the socio-ecological environment (i.e., captivity, sanctuary, wild) influence primate behaviours (Leavens et al., 2010), including their communication (Fröhlich et al., 2021), it is essential to acknowledge the challenges of studying animal emotions across diverse settings (de Vere & Kuczaj II, 2016). Since environmental factors, such as ambient temperature and humidity can significantly impact infrared measurements (but see Berthier et al., 2025), researchers conducting studies in controlled environments like zoos and laboratories can better control and regulate these variables (e.g., via air conditioning) and hence carefully validate the respective method (Fig 1 A and B). In contrast, field researchers must frequently monitor and control for these variables, either by manually inputting temperature, distance, and humidity into the cameras' to automatically correct atmospheric transmission (available in specific FLIR camera models for example), or by using the camera built-in sensors to automatically recording and correcting these variables, or by statistically adjusting for variation after data collection (de Vevey et al., 2022). Nonetheless, even with these corrections, data may still be noisy, which can be further compromised by additional external variation caused by unpredictable weather changes and sun exposure. Although careful monitoring of conditions and minimizing variations are crucial in both captive and wild settings, inconsistencies in published studies are being reported (Church et al., 2014), leading some researchers to question the validity and reliability of IRT findings (Ioannou et al., 2014; McCafferty, 2013). Given potentially greater variability in environmental conditions in naturalistic settings when compared to the more controlled environments, data in the wild should be interpreted with more caution.

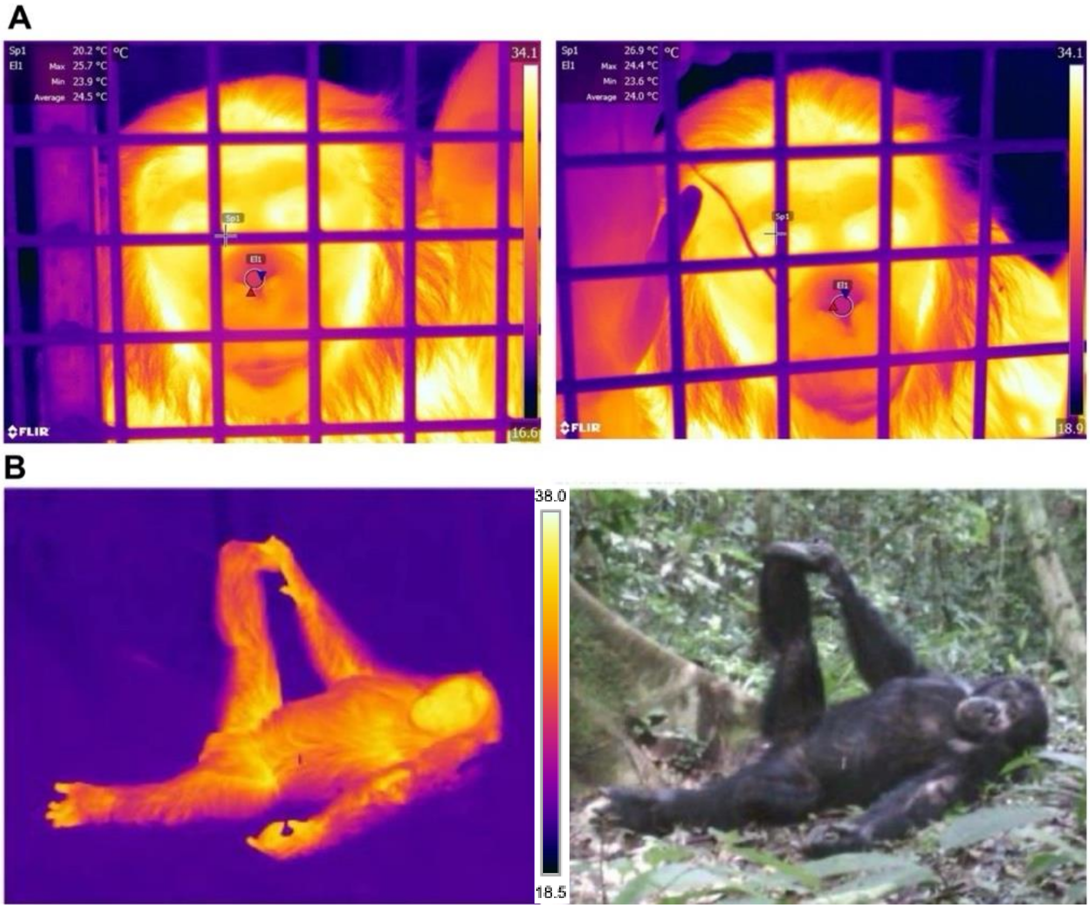

Figure 1. Example images from infrared thermography cameras used to measure facial and bodily temperatures of bonobos and chimpanzees. A: Nasal tip temperatures of a bonobo with a circled Region of Interest (ROI). Footage taken at La Vallée des Singes, France, captured with a FLIR T865 camera; left and right images show a bonobo face before and after a cooperation task, respectively. B: An adult male chimpanzee resting on the ground in the

Budongo Forest, Uganda, captured using the infrared sensor of a FLIR T530 camera (left); simultaneous capture of the same scene using the visible light sensor of the same FLIR T530 camera (right). The temperature scale in C° is shown to the right of the infrared images. *Image credits*: *Raphaela Heesen (A) and Adrian Soldati (B).*

Another current IRT limitation is lack of precision as to the physiological mechanisms underlying skin temperature changes. As noted above, directional changes in temperature across specific facial areas when comparing baseline and post stimulus presentations are not consistently replicated across studies, calling for further validation (Chotard et al., 2018; Ioannou et al., 2014; Kano et al., 2016). Although research on human emotions, physiology, and neurology provides useful reference points, these findings do not always translate directly to animals. The addition of complementary physiological measures alongside IRT, including endocrinology, pupil dilation, skin conductance, and heart rate monitoring can offer valuable insights (Guevara et al., 2022; Harrap et al., 2018; Kano et al., 2016). Emerging technologies for real-time monitoring of cognitive processes may also help clarify how physiological responses relate to emotion and cognition. For instance, Testard et al. (2024) combined behavioural observations with wireless neural recordings in free-ranging rhesus macaques (*Macaca mulatta*) during social interactions and found that responses to aggression, both behaviourally and neurally, were modulated by the presence of social partners, patterns aligning with results in chimpanzees (Barrault et al., 2022). However, many of these new methods currently involve varying degrees of invasiveness, undermining one of IRT's ethical advantages. In sum, while IRT offers valuable physiological data, its full potential may only be realized when integrated within ethically valid frameworks integrating neurological, behavioural, and other physiological measures. Such a multi-dimensional approach would leverage knowledge of emotional and cognitive processes in animals.

Night-vision IR videography to quantify animal welfare and behaviour in low-light conditions

A related application of IRT, infra-red videography (IR) – commonly known as "night vision"- has also been instrumental in advancing the study of animal behaviour under low-light conditions. Even though both IR and IRT operate within the infrared spectrum, IR specifically relies on near-IR wavelengths, which require some active illumination, while IRT relies on far-IR radiation emitted as heat by objects. Near-IR light is undetectable to most mammals (Ma et al., 2019), making it a suitable tool to study behaviour without researcher interference, especially in nocturnal animals. Since the late 20th century (Conner & Masters, 1978), researchers have employed IR technology to observe nocturnal activities without disturbing natural behaviors. In recent years, the growing accessibility and affordability of IR equipment have significantly expanded its use in behavioral research (Goolsby et al., 2024; Stafstrom & Hoy, 2024). Today, IR videography is pervasive, spanning studies in industry (Fukasawa et al., 2018), zoo settings (Seyrling et al., 2022), and field research (Funkhouser et al., 2025).

IR videography has been pivotal in advancing video-based actigraphy to assess sleep quality non-invasively. While sleep is not *per se* an affective state, its direct impact on cognition, behaviour, and emotions has been widely acknowledged (Goldstein & Walker, 2014; Hickman et al., 2024). Most notably, disturbed sleep in humans is considered a robust risk factor for psychopathologies, and its disruption is associated with anxiety, bipolar disorder, depression, psychosis, obsessive-compulsive disorder, dissociation, alcoholism, and eating disorders (Tkachenko et al., 2014; Watson, 2001). In this way, assessing sleep quality and processes can provide crucial insights into the wellbeing, behavior and cognition of the studied animals. Importantly, the mechanism underlying the association between sleep disruption and psychopathologies is emotional regulation (Goldstein & Walker, 2014). Thus, disrupted sleep could impact the regulatory capacities of an animal to control emotions and to perform during cognitive or behavioral tasks, which may drastically impact results in comparative cognitive studies. Sleep can therefore be an objective target behavior to assess emotional well-being in nonverbal agents such as primates, which are notably hard to assess with traditional tools based on verbal assessment (Úbeda et al., 2021).

Thus far, the state-of-the-art for IR video-based actigraphy mainly applies to humans (Heinrich et al., 2013; Long et al., 2019; Scatena et al., 2012), especially neonates and preterm infants (D. Zhang et al., 2023). Traditional methods like polysomnography, while highly accurate, require sleeping in an unfamiliar lab setting, which can be intrusive and stressful for subjects (Long et al., 2019). Although polysomnography is the gold standard in measurements of sleep, it requires cumbersome equipment, including electrodes attached to participants. Additionally, because preterm infants' skin is fragile, adding such sensors to the skin can be hazardous (Long et al., 2021). By contrast, IR video-based actigraphy allows for the unobtrusive recording of sleep behaviors in more diverse (non-lab) settings, including in field settings with wild animals. In humans at least, it can also be coded automatically, which offers substantial advantages, as previous described, over manual coding methods (e.g., Anders et al., 1992). Such methods rely either on interpreting overall body movement as a proxy for activity (Heinrich et al., 2013), or the extraction of key visual features that are indicative of behaviors that aid in sleep classification, like breathing (Sun et al., 2019; D. Zhang et al., 2023). To date, most studies with animals are still reliant on manual IR scoring (Funkhouser et al., 2025; Seyrling et al., 2022), though some studies have also attempted automated coding. For example, Lund et al. (2024) showed that DeepLabCut and Create ML – two different Machine Learning algorithms - automatically classify nocturnal behavior in captive elephants with high similarity to expert manual coding. The study included several behavioral categories such as foraging, drinking, laying down, standing, and playing with environmental enrichment. In addition, automated methods have also been used to classify sleeping behavior in canids (Schork et al., 2024), suggesting it may be suitable for primate studies as well. There is hence clearly exciting scope for the development and expansion of automated IR methods in the field of comparative science, including for the study of animal affect.

As noted, the biggest strength of video IR technologies is observing nocturnal behaviour without disrupting it, thus making it ideal for the study of nocturnal primates. Although still in its infancy, IR also stands great potential to enhance our understanding of animal communicative behaviour. A good example is the enhancement of visual signals emitted in low-light conditions such as facial expressions (Tlaie, Abd El Hay, et al., 2025; Zhao et al., 2011). Illumination from visible-spectrum light sources can alter or obscure the visual cues necessary for interpreting facial expressions, for example by changing colour tones or creating shadows that obsvtruct visual access to facial features. Shadows, especially, can make it difficult to perceive facial expressions. These disruptions are eliminated or greatly diminished when analysing IR footage, preserving the integrity of the visual signal during recording, which is especially relevant in view of the need for high quality and resolution data to study facial expressions (Vick et al., 2007). In IR videography, colours are reduced to grayscale and contrast is maximized. Thus, the effects of changes in lighting and shadows (e.g., a shadow partially or completely covering a facial expression) are much less obtrusive in IR compared to conventional videography. Therefore, IR videography is particularly beneficial when studying communicative signals low or inconsistent illumination environments (e.g., under the canopy, during dusk or dawn). When used in combination with other techniques, IR videography has the potential to illuminate rich insights into animal behaviour and psychophysiological processes, including assessment of emotional states (IRT: Kano et al., 2016; microwave radar sensors: Yuan et al., 2024).

Microwave radars as non-contact measure to examine physiology

Microwave radars have recently emerged as another promising technology to noninvasively measure aspects of physiology in primates without contact. Radars work by emitting electromagnetic waves and measuring minute changes in the reflected signal caused by subtle movements of the chest or body movements that are caused by breathing and heartbeat. Technologies like Impulse Radio Ultra-Wideband (IR-UWB) or Frequency-Modulated Continuous Wave (FMCW) have already been leveraged to estimate breathing and heart rates non-invasively in macaques (Minami et al., 2024; J. Zhang et al., 2024), chimpanzees (Matsumoto et al., 2024), and bonobos (Yuan et al., 2024). While they are still being validated and established for generic use, radars are becoming increasingly reliable and promising. Like with IRT, the main advantage of radars is the contactless acquisition of physiological data, thus minimizing unwanted influence on animal physiology through stressful procedures. Unlike IRT, radars output a continuous stream of data for heart and breathing rate instead of relying on manual annotation of video frames. These data can be quickly processed with Fourier or wavelet-based algorithms, or machine learning, resulting in real-time readings. Another interesting aspect of radars is that they seem to perform adequately through barriers (e.g., plexiglass: Yuan et al., 2024), which can be especially useful in captive settings that tend to include such substrates. In short, while further validation is needed, radars represent an exciting emerging method that can be applied for physiological measurements, particularly due to their suitability to measure through physical barriers and in real-time, setting them apart from other existing technologies.

Drawing a bigger picture of affect: combinations of behavioral and physiological data

So far, we have considered how emerging methods in automated behavioural analysis and infra-red promote exciting advancements in the field of comparative affective science. In what follows, we describe examples of how the combination of IRT with behavioural analyses can be used to inform on internal states. We focus here on responses to acoustic signals, given this has been a topic of increased research attention especially in primates. We argue that IRT offers a non-invasive method to assess how primates process acoustic information, notably when combined with behavioural measures.

Marmoset monkeys (*Callithrix jacchus*) are known for their rich and complex vocal interactions (Burkart et al., 2014; Snowdon, 2009; Takahashi et al., 2013) and use specific calls to address particular individuals within their social groups (Oren et al., 2024). Exposure to conspecific vocal interactions has been associated with changes in marmoset nasal skin temperature, suggesting an internal physiological response to social auditory stimuli (Brügger et al., 2021). Interestingly, such thermal responses may occur in the absence of overt beavioural cues, thus offering insights into underlying, implicit affective processes not necessarily visible at the surface. Similarly, chimpanzees (*Pan troglodytes*) engage in vocal exchanges during fission-fusion events (Mitani & Nishida, 1993) using long calls with individual signatures (Marler & Hobbett, 1975). Research has shown that exposure to conspecific vocalizations can lead to physiological responses in wild chimpanzees, such as changes in skin temperature, indicating heightened arousal or alertness (Dezecache et al., 2017). Temperature changes are also visible across different interaction contexts varying from cooperative to competitive (de Vevey et al., 2022). These responses may reflect the chimpanzees' ability to perceive and adjust their understanding of social dynamics and environmental events combining auditory and contextual cues, processing acoustic information in ways more sophisticated than their visible reactions alone would suggest. Relatedly, a recent developmental study with IRT revealed that 10-month-old infants showed significant changes in nasal temperature upon hearing distress cries of aged-matched peers, when compared to thermal responses to control sounds, including acoustically matched aversive noises (Vreden et al., 2025). Interestingly, although infants also showed strong aversive behavioural responses to crying over other stimuli, these behavioural responses were not directly correlated with the thermal responses. The authors suggest at least two possible explanations for this. First, methodologically, assessments of behaviour and physiology could occur on different temporal and mathematical scales. Thermal responses are temporally slower to occur (Kuraoka & Nakamura, 2011), while behavioural responses occur almost immediately. Second, the authors used maximum relative changes (to baseline) as their thermal measurement compared to absolute ratings of behavioural affect. Although these reflect established approaches for each method, such effects raise issues for the compatibility of thermal and behavioural data – an important issue requiring further inspection and clarification. Different measures of emotions thus rarely show strong convergence. This supports the stance that emotions are multiply determined and multi-dimensional, with no one measure being able to capture every aspect, calling for different measures that can – in combination – draw more complete pictures of these complex phenomena.

From the production perspective, integrating IRT with acoustic analyses can nonetheless provide deeper insights into the interplay between arousal and vocal production. It is evident that variations in internal states can increase the informational value of a communicative signal. For example, in human language, the acoustic structure of a sentence is impacted by emotional states, even when the literal meaning of that sentence remains unchanged. The sentence "The train has arrived" can be stated in a sad, happy or neutral way, without impacting its core meaning: there is a train approaching (Oller et al., 2013; Taylor et al., 2022). Here, the emotional tone of the expression can be used to derive pragmatic inferences as it can help listeners better understand subtle details about the situation and adopt an appropriate reaction (e.g., console the speaker who is sad that their friend is leaving).

Similarly, animal signals convey meaning that goes beyond a simple reflection of the emotional state of the individual (see for review Berthet et al., 2023). The meaning can be determined by investigating the features of the circumstances (FoCs) present when a specific signal is emitted (Berthet et al., 2023, 2025) and is reflected in the largest set of FoCs that appear across all occurrences of the signal. Although a call can provide information about the caller's internal state (e.g., "I am scared"), it can also denote a behaviour at the time of emission (e.g., "I start travelling") or after the emission of the call ("I will approach you"), as well as the expected reaction of the receiver (e.g., "Run away") and the presence of external events (e.g., "There is a snake") (Berthet et al., 2023).

Thus, while the acoustic structure of any vocalization can be impacted by a caller's emotional state (Briefer, 2012), this does not mean that all signals are emotional or exclusively convey emotions. Rather than dichotomously naming certain expressions as "emotional", as in the case of a bared-teeth facial expression in primates, a more useful termpinology would be to refer to it as a communicative signal with an *emotional message* or *affective information* along with its referential meaning. Viewed in this light, affective cues accompanying a signal can help receivers draw pragmatic inferences and better navigate their social world as a result (Arnold & Bar-On, 2020; Berthet et al., 2023; Oller & Griebel, 2014). A striking example comes from wild chimpanzees. During social feeding events, chimpanzees show increased social monitoring, especially during competition over contested resources, where they gather information to prepare for potential aggression (Barrault et al., 2022). Under these circumstances, the presence of dominant individuals has been shown to lower nasal temperature in recipients; except when allies are present, which was associated with higher nasal temperature. This is likely because allies act as a buffer and may provide support in case of escalation (Barrault et al., 2022). Although still awaiting further testing, one might speculate that the production of the same call type in the presence of a dominant male may be associated with subtle acoustic variations matching skin temperature changes (e.g., lower nasal temperature) and inform others that the signaller is stressed, while when produced in the presence of friends it may be linked to a different internal state (e.g., higher nasal temperature) and inform others that the signaller is relaxed and “wants to bond”. In summary, combining IRT data with a rigorous investigation of the context of emission of a signal (or multimodal combination thereof) can enhance our understanding of the complex interplay between physiological processes, signal meaning, and pragmatics, with implications for our understanding of primate communicative complexity and underlying cognitive processes.

One further fruitful research direction for which IRT, combined with behavioural data, now offers exciting opportunities is the study of deceptive signalling in animals. A common assumption is that most behaviors are honest rather than strategic attempts to manipulate others, yet primates have been documented to engage in tactical deception (Byrne, 1996). For example, capuchin monkeys (*Cebus apella nigritus*) produce alarm calls when accessing food to deceive dominant individuals into leaving, thereby reducing feeding competition (Wheeler, 2009). While some signals may be more difficult to suppress (e.g., a scream during aggression) or to decouple across modalities, such as in the case of screaming without a concurrent open-mouth facial expression (but see Slocombe & Zuberbühler, 2007), other complex signals can be flexibly produced and structured even during competitive and high-arousal contexts, such as pant hoot sequences accompanying dominance displays in chimpanzees (Soldati et al., 2022). Physiological responses to external events are even harder, if not impossible, to voluntary control. For example, some temperature increases may be externally visible, e.g., cheek blushing or lip reddening in humans (Ioannou et al., 2014), whereas changes in nasal temperature as a result of internal states are typically not. This suggests that such thermal signatures, largely inaccessible to observers, are likely under little selective pressure to be used for deception. This raises the intriguing possibility that the “true” internal state of a signaller may be revealed more accurately with the help of IRT, particularly in deceptive contexts. For instance, a capuchin monkey producing a false alarm call while feeding may display a thermal response that differs from the arousal state triggered by a genuine predator encounter. IRT, therefore, represents a promising tool for exploring the affective and cognitive underpinnings of primate communication through a range of exciting research questions.

As radars have only recently been applied to measuring physiology, studies combining it with other techniques are scarce. The most common combination at present seems to be with IRT, in the context of healthcare monitoring in humans. For example, Kundu et al. (2023) used IRT in combination with a FMCW radar to enhance signal detection via redundancy – both were employed to measure heart and breathing rates, but were used interchangeably depending on whether one signal was of higher quality than the other. More specifically, while FMCW radars are sensitive to body movement, IRT can underperform in cases of abrupt temperature changes. Owing to this combinatorial approach, Kundu et al.'s method was able to retrieve reliable measures by relying on the signal that was least affected by adverse conditions. A recent study (Del Regno, 2024) employed a combination of radar and IRT to detect apnea, by directing the radar at the chest to measure breathing effort, while IRT measured actual breathing. While combinations of radar and other techniques are still under development, there are some applications in specific scenarios that may find a functional analogue in comparative affective science. For instance, microwave radars could be simultaneously measured with IRT in animal research to examine which changes are pertinent to the emotional state of interest. In addition, given the novel applications of these technologies, the combination of the two methods could help validate the use of either in new settings, or to measure new body areas, akin to how early IRT studies were paired with heart-rate measures (Kano et al., 2016). Given that accessing and measuring emotional states has proven particularly challenging thus far, converging patterns from multiple methods may provide the only reliable way forward.

Conclusion and outlook

The field of comparative affective science is at the verge to venture into an exciting new direction to study animal emotions. As discussed in our chapter, novel technologies like AI-based automated tracking, IRT, IR and microwave radars could enable large-scale and systematic combinatorial analyses (Fig 2 A and B) to uncover physiological processes underlying (communicative) behavior. Although some efforts have been made into this direction, combining IRT with behavioral coding (Barrault et al., 2022; de Vevey et al., 2022), the field needs more detailed validation studies especially during communication events (e.g., (Dezecache et al., 2017). Combinatorial outputs using IRT and regular video analyses may offer insights into how communication in animals might be linked to emotional states, how animals navigate their social worlds, and the extent to which certain species' signalling efforts are driven by a combination of voluntary control and affect. Here, pooling data from the wild and controlled captive settings would be highly beneficial to deliver informed outputs. With sufficient data included, such efforts could enable researchers to derive "behavior-physiology profiles" for certain signals, such as for the bared-teeth facial expression in primates (Fig 2 C), to determine the underlying affective and cognitive mechanisms driving communication.

Although for now only hypothetical, such behaviour-physiology profiles for communicative signals (Fig. 2 C) could be produced across species and socio-ecological contexts once sufficient empirical data has been generated through systematic comparisons. As a result, researchers will be able to derive more informed interpretations based on comprehensive and multi-dimensional data, instead of *a priori* assumptions on whether certain signals are (or are not) "emotional". We hope that, over time and through the use of more controlled combinatorial approaches as outlined in our chapter, researchers will uncover deeper insights into which communicative signals truly qualify as expressions of emotion, or which, contrary to the expected, reveal the remarkable flexibility with which animals coordinate social interactions through the intertwined expression of intent and affect.

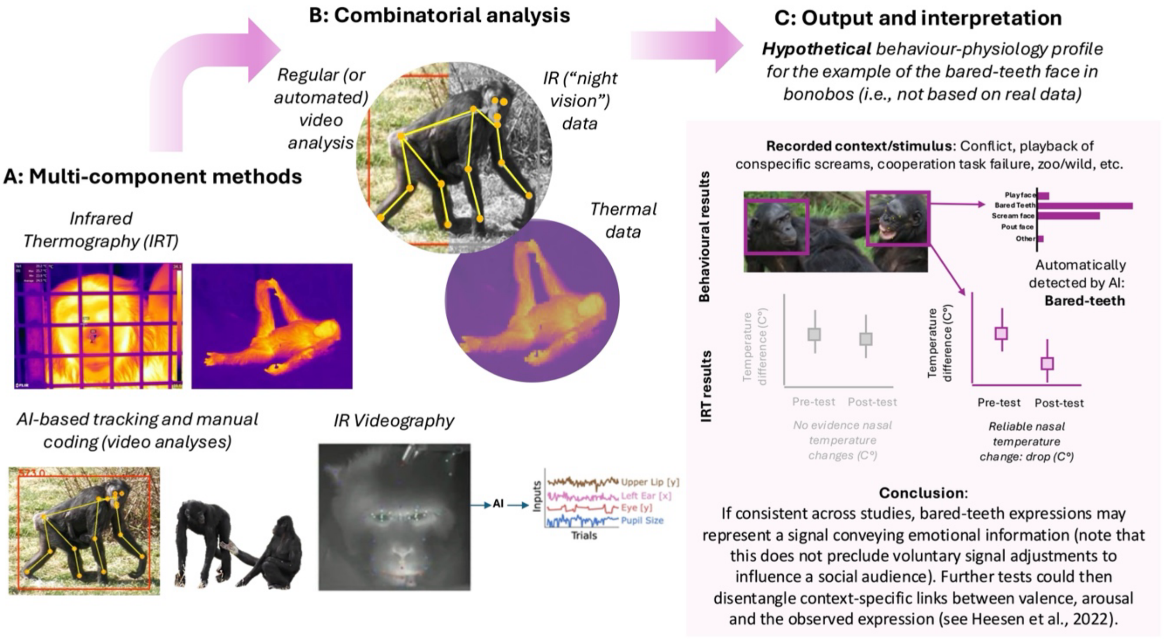

Figure 2. Multi-component methods for comparative research on animal emotions and communication. Illustration of the three steps aimed at combining current methods and technologies to create new behaviour-physiology profiles of communicative signals. A: data is simultaneously collected using available methods including IRT, AI-based posture estimation, behavioural coding, and IR; B: behavioural and physiological data are combined to be analysed together; C: behavior-physiology profiles are created by interpreting behavioural and physiological results together. In the light purple box on the right, we used the bared-teeth face in bonobos to exemplify *hypothetical* results and interpretations that researchers may obtain adopting a combinatorial approach (these results are not based on empirical findings and only server the purpose of showcasing the approach). Macaque face in IR videography and resulting graph adapted from Tlaie et al. (2025) under CC4.0 license (https://creativecommons.org/licenses/by/4.0/). Radar data can also be taken into consideration, though was not included in the figure here given its comparably limited

application in the literature thus far.

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