Bonobo Emotions Unveiled — Insights into cognitive, behavioural, and welfare components

Thesis for the degree of Doctor in Science: Biology
To be defended by: Daan Willem Laméris

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Bonobo Emotions Unveiled:

Insights into cognitive, behavioural, and welfare components

Bonobo Emoties Onthuld:

Inzichten in cognitieve, gedrags- en welzijnscomponenten

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Summary

Animal emotions have been a controversial topic for a long time and this discussion continues until today. Although most people associate emotions with subjective feelings, emotions are foremost mechanisms that fine-tune an individual’s behaviour: a process that can aid in better navigating their (social) environment. Emotions are responses to rewarding and aversive stimuli, events, or conditions. They are highly personal, and the elicitation of emotional responses is informed by the individual’s relation to the stimulus. This enables individuals to produce flexible responses in ever-changing environments. Emotions typically start with the evaluation, or appraisal, of the stimulus. The outcome of this appraisal process elicits a cascade of neurophysiological, cognitive, and motivational processes. The synchronisation of these processes prepares the body and mind to produce appropriate behavioural responses towards the rewards and threats.

While the significance of emotional states in the animals’ daily lives has become evident, acknowledging, and investigating their role in animal welfare is a more recent development. Additionally, the individual and species-specific nature of emotional responses makes measuring emotions across different species a significant challenge. This thesis focuses on the assessment of various emotional components in bonobos (*Pan paniscus*), as they offer a unique opportunity due to their emotional expressivity and regulatory behaviours. However, the scarcity of bonobos in captivity has hindered the validation and investigation of bonobo-specific emotional and welfare indicators.

Following the different steps within an emotional episode, in Chapter 2 I focus on appraisal of different salient stimuli by looking at attention biases. Employing a touchscreen-based pictorial emotional Stroop task, the study investigated how cognitive performance of the bonobos was influenced by distractor images. Attention of the bonobos was attracted by non-social images like leopards, food items, and flowers, as well as positive facial expressions. These results align with bonobo socio-ecology where predator detection and food acquisition benefit survival, and where social play holds an important role in regulating social dynamics. The bias for flowers possibly reflects a novelty effect. We furthermore noted that individuals differed in their sensitivity for these attention biases.

In Chapter 3, I elaborated on this individual variation, and explored the possible modulatory role of emotional states on attention biases. I designed an eye-tracking study in which I primed emotions and subsequently studied preferential looking at facial expression in a modified ‘face in the crowd’ paradigm to study affect-congruent attention

biases. Emotions were primed using positively, negatively, and neutrally valenced videos of bonobos and humans. The effectiveness of these primers was assessed using pupillometry. While primer videos generally induced pupil dilation, there was inconclusive difference between the valence loading. In terms of sustained attention, there was no evidence for an effect of the primer videos, perhaps because they did not sufficiently elicit changes in emotions. However, the bonobos generally paid more attention to the negative facial expressions. This contrasts my previous findings of Chapter 2, but may be explained by the nature of different attentional processes.

The subsequent sections delve into the behavioural outputs of emotional episodes. Chapter 4 examined abnormal behaviours, a traditional indicator of negative emotional states and impaired welfare, in a large dataset of observations on zoo-housed bonobos. Results indicate that abnormal behaviours are not universally applicable as emotional indicators. Sex, rearing history, and different personality traits were identified as factors that explain the occurrence of abnormal behaviours. I furthermore address discussion points as to why certain behaviours may be more suitable as indicators of negative emotions than others. This provides a more nuanced perspective of the use of abnormal behaviours in welfare assessments.

In Chapter 5, I assessed another common behavioural indicator of negative emotions, being self-directed behaviours. These behaviours are often observed and assumed to correlate with negative emotions, but this has not clearly been validated for bonobos. The occurrence of three self-directed behaviours was studied when the bonobos were completing touchscreen tasks. Nose wiping was found to be the most common self-directed behaviour, and increased when the bonobos made incorrect responses, suggesting a link with negative emotional arousal. Rough self-scratching similarly increased with incorrect responses, while gentle self-scratching increased with correct responses. The lateralised production of rough self-scratching provided further evidence for a link with negative arousal.

In order to develop a novel welfare assessment tool, Chapter 6 developed a Qualitative Behavioural Assessment to study how humans perceive emotional expressivity in bonobos. Across two studies, I first let bonobo experts and students view bonobo videos and let them use their own terminology, following Free Choice Profiling, to describe bonobo expressivity to determine which terms are most commonly and most reliably used. In the second study, I created a list of fixed terms, informed by the prior study, and let the observers use these terms to score a new set of videos. While in both studies the observers could identify two meaningful dimensions in the bonobo's

expressive qualities, and agreement on these dimensions was moderate to good, the use of the individual terms in the second study was less consistent. Knowledge of the bonobo as a species by the expert observers likely facilitated more coherent recognition of bonobo expressivity and enabled to perceive differences between age classes. Within an applied welfare context, I tested if the developed Qualitative Behavioural Assessment was able to detect differences in the emotions of the bonobos after moving to a new enclosure. This also appeared to require experience with studying the behaviour of bonobos as only bonobo experts perceived changes in the bonobos expressivity. Additional validation and the inclusion of bonobo caretakers is recommended for further development.

The final study of this thesis, presented in Chapter 7, integrated different measures of emotions in bonobos within an animal welfare context. Specifically, the management of the bonobos in Planckendael Zoo initiated fission-fusion activities. Using the response slowing task, I recorded shifts in the cognitive correlates of negative emotions and linked these to behavioural patterns. Fusion events were associated with increases in agonistic interactions and elicited shifts towards negative emotions, shown by response slowing effects. Socio-sexual behaviours similarly increased, suggestive of behavioural strategies to avoid escalated aggression. Changes in emotional states were only of short duration as behavioural and cognitive measures returned to baseline levels on the day afterwards. General correlations between negative emotions and socio-sexual and social play behaviours were furthermore found. Higher levels of daily negative emotions also correlated with more socio-sexual interactions and fewer social play interactions, suggesting emotional consequences of these behaviours.

In summary, the results of the different studies in this thesis addressed multiple components of emotions in bonobos and highlight the importance of species-specific measures. I furthermore discussed different individual factors that influence different processes in an emotional episode. This has important implications in the way we measure animal emotions and assess their welfare.

Samenvatting

Dierlijke emoties zijn lange tijd een controversieel onderwerp geweest, en deze discussie gaat door tot op de dag van vandaag. Hoewel veel mensen emoties associëren met subjectieve gevoelens, zijn emoties in de eerste plaats mechanismen die het gedrag van individuen sturen en zo helpen om te navigeren in hun (sociale) omgeving. Emoties zijn reacties op belonende en bedreigende stimuli, gebeurtenissen of omstandigheden. Daarnaast zijn emoties zeer persoonlijk en worden gevormd op basis van de verhouding van het individu tot de stimulus. Deze persoonlijke invalshoek van emoties maakt het mogelijk dat individuen zich flexibel kunnen gedragen in steeds veranderende omstandigheden. Emoties beginnen met de evaluatie of beoordeling van de stimulus. Het oordeel van zo’n stimulus leidt tot allerlei neurofysiologische, cognitieve en motivationele processen. De synchronisatie van deze processen bereidt het lichaam en de geest voor op een passende gedragsmatige reactie op de beloningen en bedreigingen.

De relevantie van emoties in het dagelijks leven van dieren wordt steeds duidelijker, hoewel de erkenning en het bestuderen van hun rol in dierenwelzijn een relatief recente ontwikkeling is. Bovendien maakt de individuele en soort specifieke aard van emoties het meten bij verschillende soorten een aanzienlijke uitdaging. Dit proefschrift richt zich op het onderzoeken van verschillende emotionele componenten bij bonobo’s (*Pan paniscus*). Bonobo’s zijn een geschikte studiesoort voor emoties omwille van hun emotionele expressiviteit en emotie regulerende gedragingen. Echter, omdat bonobo’s vrij zeldzaam zijn in gevangenschap, is validatie en de studie van bonobo-specifieke emotionele en welzijnsindicatoren beperkt.

De hoofdstukken van deze thesis volgen de verschillende stappen binnen een emotionele episode. Hoofdstuk 1 richt zich op de beoordeling van verschillende relevante stimuli door te kijken naar aandachtsprocessen. Met behulp van een picturale versie van de emotionele Stroop taak werd op touchscreens onderzocht hoe de cognitieve prestaties van de bonobo’s werden beïnvloed door afleidende foto’s. Hierbij werd duidelijk dat niet-sociale foto’s, zoals luipaarden, voedsel en bloemen, maar ook positieve gezichtsuitdrukkingen, de aandacht trokken. Deze resultaten passen binnen de (sociale) ecologie van bonobo’s in het wild, waarbij het snel detecteren van roofdieren en voedselverwerving voordelig is voor de overleving van het individu, en waar sociaal spelgedrag een belangrijke sociaal regulerende functie vult. Het aandachtseffect voor de bloemen weerspiegelt mogelijk een nieuwheidseffect. Individuele verschillen in deze aandachtmechanismen waren overigens verder waarneembaar.

Hoofdstuk 3 bouwt voort op deze individuele variatie in aandachtmechanismen voor sociale stimuli en verkent de mogelijke regulerende rol van de emotionele status van een individu. Ik heb een eye-tracking studie ontworpen waarin ik aanvankelijk emoties induceerde en vervolgens keek naar mogelijke effecten op de voorkeur van aandacht voor gezichtsuitdrukkingen in een aangepaste versie van het ‘face in the crowd’ paradigma. Emoties werden geïnduceerd door middel van videoclips die een positieve, negatieve en neutrale lading, die zowel bonobo- als menselijke modellen liet zien. Of deze video’s succesvol waren in het induceren van emoties werd gemeten met pupillometrie. Hoewel de videoclips over het algemeen leidden tot pupil vergroting, waren er geen duidelijke verschillen tussen de video types. Deze video’s hadden overigens geen effect op de aandachtmechanismen van de bonobo’s, mogelijk doordat ze niet krachtig genoeg waren om sterke verandering in emoties te veroorzaken. Over het algemeen hadden de bonobo’s meer aandacht voor de negatieve gezichtsuitdrukkingen. Dit contrasteert mijn eerdere resultaten, maar kan mogelijk verklaard worden door verschillende aandachtmechanismen.

De verdere onderdelen van deze thesis gaan in op de gedragsmatige gevolgen van emotionele episoden. In Hoofdstuk 4 werd gekeken naar abnormale gedragingen, een traditionele indicator voor negatieve emoties en beperkt welzijn, in een bestaande dataset van gedragsgegevens van bonobo’s in dierentuinen. De resultaten toonden aan dat niet alle abnormale gedragingen betrouwbare indicatoren zijn voor emoties en welzijn. Het geslacht, opvoedingswijze en verschillende persoonlijkheidsfactoren werden geïdentificeerd als factoren die het voorkomen van abnormale gedragingen kunnen verklaren. Ik bespreek verder argumenten waarom bepaalde gedragingen betere indicatoren zijn voor negatieve emoties dan andere. Dit geeft een meer genuanceerd beeld van het gebruik van abnormale gedragingen bij welzijnsevaluaties.

In Hoofdstuk 5 werd gekeken naar een andere gebruikelijke gedragsindicator voor negatieve emoties, namelijk zelfgericht gedrag. Ondanks dat deze gedragingen vaak worden geobserveerd en doorgaans worden geassocieerd met negatieve emoties, zijn ze nog niet specifiek gevalideerd voor bonobo’s. Vier vormen van zelfgericht gedrag werden bestudeerd tijdens touchscreen sessies. ‘Nose wiping’ was veruit het meest voorkomende zelfgerichte gedrag en werd vaker vertoond nadat de bonobo’s fouten maakten in de touchscreen taken, wat suggereert dat het mogelijk verband houdt met negatieve emoties. ‘Rough self-scratching’ nam ook toe na foutieve antwoorden, terwijl ‘gentle self-scratching’ juist toenam na juiste antwoorden. ‘Rough self-scratches’ waren overigens meer gericht naar de linker kant van het lichaam, wat bewijs biedt voor een link met negatieve emoties.

Om een nieuw middel te ontwikkelen om welzijn bij bonobo’s te meten, maakte ik in Hoofdstuk 6 gebruik van de Qualitative Behavioural Assessment (QBA) procedure om te bestuderen hoe mensen de emotionele expressiviteit bij bonobo’s waarnemen. In twee opeenvolgende studies liet ik videoclips van bonobo’s zien aan bonobo experts en studenten. Vervolgens liet ik de deelnemers, met behulp van Free Choice Profiling, de emotionele expressie van de bonobo’s beschrijven op basis van hun eigen terminologie. Op basis hiervan bepaalde ik welke termen het meest gebruikt worden en het meest betrouwbaar zijn. In de tweede studie stelde ik een lijst met vooraf bepaalde termen op, gebaseerd op de vorige studie, en liet de deelnemers een nieuw aantal videoclips beoordelen. Zowel bonobokenners, als niet-kenners identificeerden in beide studies twee betekenisvolle dimensies in de expressie van de bonobo’s, en de herkenning deze dimensies was matig tot goed. Het gebruik van de individuele termen in de tweede studie was echter minder consistent. Over het algemeen bleek kennis van de bonobo als soort nuttig en waren bonobokenners nauwkeuriger en consistenter in het beoordelen van de emotionele expressiviteit van bonobo’s. Bonobokenners merkten ook verschillen in emoties op tussen sub-adulte en volwassen bonobo’s. Binnen de studie heb ik verder getest of de ontwikkelde QBA geschikt was op toe te passen in een welzijnscontext. Tijdens de studieperiode waren de bonobo’s namelijk verhuisd naar een ander verblijf, en alleen bonobokenners waren in staat subtiele verschillen in de expressiviteit van de bonobo’s waar te nemen. Verdere validatie en het betrekken van bonobo-verzorgers wordt aanbevolen om de QBA verder te ontwikkelen.

In de laatste studie van deze thesis, gepresenteerd in Hoofdstuk 7, combineer ik verschillende maten van emoties bij bonobo’s binnen een dierenwelzijnscontext. Tijdens deze studie begon het management in Planckendael Zoo met het huisvesten van twee subgroepen van de bonobo’s volgens een fission-fusion dynamiek. Ik testte de bonobo’s op de ‘response slowing’ taak om zo cognitieve aspecten van negatieve emoties te meten. Deze cognitieve maten werden vervolgens gekoppeld aan gedragsmaten. Fusion-momenten leidden tot negatieve emoties, wat bleek uit het response slowing effect en een toename in agonistische interacties. Ook sociaal-seksueel gedrag nam toe, wat mogelijk wijst op strategieën om geëscaleerde agressie te vermijden. De veranderingen in emoties waren echter kort van duur, aangezien de gedrags- en cognitieve maten de dag erna terugkeerden naar normale niveaus. Er werden ook algemene correlaties tussen negatieve emoties en sociaal-seksueel en sociaal spelgedrag gevonden. Hogere dagelijkse maten van negatieve emoties waren gecorreleerd aan meer sociaal-seksuele interacties en minder sociaal-spel gedrag, wat emotionele gevolgen van deze gedragingen suggereert.

In conclusie behandelden de resultaten van de verschillende studies in dit proefschrift verschillende componenten van emoties bij bonobo’s en benadrukken ze het belang van soort specifieke indicatoren. Verder besprak ik verschillende individuele factoren die de processen in een emotionele episode beïnvloeden. Dit heeft belangrijke implicaties voor de manier waarop we emoties bij bonobo's meten en hun welzijn beoordelen.

1

General introduction

Daan W. Laméris

This thesis seeks to enhance our current understanding of emotions in the bonobo. Emotions are an integral component of the daily lives of animals. Examining animal emotions does not only hold fundamental relevance but is also a significant determinant of their welfare. Hence reliably measuring emotions is important in optimising the welfare of animals. In the first part of this general introduction, I will give a brief overview of historical perspectives on animal emotions and discuss different frameworks that describe emotions. In the second part, I will illustrate how emotions are embedded in current animal welfare science and then describe an emotional episode in more detail: what triggers emotional responses, describing the different processes that shape emotions and its measurable correlates. In the third and final part, I introduce the bonobo as a study species and review current knowledge about how emotions can reliably be measured in them.

Historical perspectives on animal emotions

Emotional states are an intriguing yet elusive area of study. Despite their apparent self-evident and integral role in our human daily lives, objectively describing and measuring emotions, both in humans and non-human animals, poses significant challenges. Where human studies heavily rely on verbal self-reports, animal studies on emotions need to refer to different methods. Throughout history, humans have demonstrated a keen interest in the emotional lives of animals. Philosophers such as Pythagoras (570 – 495 BC), Aristotle (384 – 322 BC) and René Descartes (1596 – 1650) have discussed emotions in animals, but scientific approaches to describe animal emotions emerged later. Herbert Spencer (1855) proposed that emotions, in combination with memory, allowed animals to flexibly react to situations, rather than showing fixed reflexes. However, probably the most influential work in this field came from Charles Darwin's seminal book *The Expression of Emotions in Man and Animals* (Darwin, 1872) in which he laid the foundation for the study of animal emotions. Darwin's work established a theoretical framework that viewed animal behaviour as functional, playing a crucial role in individual adaptation to diverse situations and environments. Emotional states, within this framework, were no longer perceived as dysfunctional but rather as facilitating flexibility and ultimately benefiting survival. Consequently, an ongoing scientific debate emerged concerning whether animals possess and experience emotions. Prominent behaviourists in America, including Skinner, sought to explain behaviour based on operant conditioning, while European ethologists like Konrad Lorenz and Nikolaas Tinbergen advocated for disregarding anything considered sentimental or imprecise, such as emotions (Bekoff, 2000; de Waal, 2011).

The debate regarding animal emotions persists to this day. While it is widely accepted that all vertebrates experience emotions to some extent (Bekoff, 2000; Panksepp, 2011), the acceptance of emotions in invertebrates is much less prevalent (de Waal & Andrews, 2022; Perry & Baciadonna, 2017). Interest in the emotional lives of animals stems from various scientific disciplines, including psychopharmacology, neuroscience, pain research, (evolutionary) zoology, philosophy, and animal welfare science. Consequently, the scientific community has accumulated a wealth of information on animal emotions.

Concepts and definitions of animal emotions

The multidisciplinary nature of animal emotion research has led to a vast array of theories and definitions, driven by the diverse motivations of each discipline. In the following section, I will provide a brief overview of the primary current conceptual frameworks concerning animal emotions and present the definitions used in this thesis.

Defining and conceptualising animal emotions has proven to be a notorious problem. In 1981, Kleinginna & Kleinginna compiled 92 different definitions and classified these into 11 categories, based on the emphasised affective phenomenon or theoretical perspective (Kleinginna & Kleinginna, 1981). This extensive compilation illustrates the inherent difficulties in conceptualising affect. Furthermore, authors often fail to provide systematic and consistent definitions, and when they do, these definitions continue to frequently vary among different authors (de Vere & Kuczaj, 2016). This lack of consensus ultimately slows the progress in the field and hinders the discussion whether animals have and experience emotions at all. Through this thesis, I consider an emotion as a short-lived, stimulus-driven, positive or negative experience that is associated with a particular pattern of physiological activity and behavioural response (Schacter et al., 2011). Short-lived is a relative term, but limited by the fact that emotions are driven by an internal or external stimulus. Emotions persist beyond the stimulus that elicit them, but eventually fade away (Anderson & Adolphs, 2014). Positive or negative experiences can be determined whether the experience is pleasant or unpleasant, or rewarding or unrewarding. The definition of other common terms will be provided as I discuss them further in the next paragraphs and are summarised in Box 1.

Contemporary theories of animal emotions can broadly be separated in three frameworks: discrete emotions, dimensional and appraisal theories. A prominent characteristic shared by these theories is that emotions are recognised as multifaceted phenomena encompassing a subjective experience (the individual's direct perception or feeling of the emotional state), cognitive evaluation, behaviour, neurophysiology, and motivation. The distinctions among these theories lie in their emphasis on different aspects, such as the categorisation of emotions, the underlying mechanisms, or the specific components of emotion (Désiré et al., 2002). The ‘discrete emotions theory’ argues that there are primary, or discrete, emotions that are generalised, automatic and unconscious responses to emotional stimuli (Panksepp, 2011) which are wired in evolutionary old subcortical regions in the brain, such as the amygdala (MacLean, 1970; Panksepp, 1998). There is currently no consensus about how many and which basic emotions exist, but examples include seeking, anger, fear, panic, calm, lust, care, play and happiness (Coria-Avila et al., 2022; Ekman, 1999). In addition to these unconscious primary emotions, discrete emotion theorists argue that the ability to consciously experience emotions is restricted to mammals and involves higher brain centres in the cerebral cortex (Damasio & Carvalho, 2013). These experienced, or ‘felt’, emotions are referred to as ‘secondary emotions’ (de Waal, 2011) and come after the appraisal and reflection of primary emotions (LeDoux & Hofmann, 2018). However, the discrete emotions approach, in a way, limits the study of animal emotions as it would only allow

Box 1: Glossary

Affective state: A general term that covers the short-term ‘emotions’ and longer-lasting ‘moods’, *including* the experience of them.
Appraisal: A transactional process between the individual and the environment, in which the relevance of a stimulus is evaluated.
Arousal: The intensity, or level of activation, of an affective state.
Demeanour: A way of looking and behaving.
Emotion: A stimulus-driven response to a stimulus that guides an individual towards rewards and away from danger. This is accompanied with behavioural, physiological, and cognitive changes.
Emotional state: A general term that covers the short-term ‘emotions’ and longer-lasting ‘moods’, *excluding* the experience of them.
Mood: Longer-lasting emotions, lacking action tendencies and appraisal-induced responses to emotion-eliciting situations.
Valence: The positive/pleasant/rewarding or negative/unpleasant/aversive quality of an affective state.

the identification of emotions that are known to humans, and therefore strongly influenced by social and/or cultural values of emotions (Mesquita & Boiger, 2014). Moreover, discrete emotions are not able to provide a priori predictions about how these emotions are established, and hence how they are measured (Mendl et al., 2010). As such, the discrete emotions approach lacks an overarching structure of emotions that can integrate a continuum of emotions, provide *a priori* predictions, and can be applied across taxonomic groups.

‘Dimensional’ theories are proposed to offer such framework (Russell, 2003) and are based on the deconstruction of emotions in two or three dimensions. While variations of dimensional theories propose slightly different dimensional axes two overarching dimension can be identified: one of valence (positive versus negative) and arousal (high versus low activity) (Russell, 2003; Watson et al., 1999). Valence is challenging to define (Walle & Dukes, 2023), but I consider valence as a bipolar dimension that is characterised as either positive/pleasant/rewarding versus negative/unpleasant/aversive. Some extend this by adding a dimension of persistence (short versus long states) (Anderson & Adolphs, 2014). Dimensional theories have been prominent in the human literature as much evidence for these theories are based on reports of subjective emotional experiences. Because these measures are based on verbal reports, accurately measuring animal emotions on such dimensions is challenging. Nonetheless, these dimensions can still be relevant for conceptual frameworks, especially when integrated with other theories, as discussed later.

Finally, ‘appraisal’ theories are based on the idea that emotions are generated by the cognitive evaluation of internal and external stimuli (Scherer, 2005). These theories focus on the different components of emotions, such as the appraisal component with evaluations of internal and external stimuli; a motivational component with action tendencies; a somatic component with peripheral physiological responses; a motor component with expressive and responsive behaviours; and a subjective component with subjective experiences or feelings (Moors et al., 2013). According to this theory, the different components continuously influence each other over time and induce a subjective experience which is subsequently established as emotional states, moods, or affective traits.

These three main frameworks for emotions are not mutually exclusive, and it is reasonable to consider a combined and integrative approach as the most fruitful for studying animal emotions. By integrating these theories, researchers can develop methods to assess a broader range of emotions in animals than what discrete theories can achieve individually. A framework that integrates components of both discrete and dimensional theories is the 'core affect' framework (Russell & Barrett, 1999). According to core affect theorists, the continuous core affective state (defined in terms of valence and arousal) is integrated with appraisals of present conditions, giving rise to a subjective state that can be expressed using discrete emotion terms (Barrett, 2006). For instance, emotions characterised by negative valence and high arousal can be identified as *fearful* or *anxious*, while those characterised by negative valence and low arousal can be described as *sad* or *depressed*. Conversely, positive valence and high arousal can be associated with *excitement* and *happiness*, whereas positive valence and low arousal can be characterised as *relaxed* or *calm* (Figure 1.1: Mendl et al., 2010). The core affect framework also incorporates the subjective experience of emotions, and labels them henceforth as affective states (Barrett et al., 2007; Russell, 2003).

Apart from the short-lived emotions that are induced by the appraisal (i.e. evaluation) of stimuli or events, animals have moods, which are longer-lasting emotions that lack action tendencies and do not need emotion-eliciting situations to be induced (Mendl et al., 2010). The core affect framework assumes that moods are the cumulative product of short-term emotions, and as such represent an informative background of the core affect framework. In other words, mood states are not induced by the appraisal of emotion-relevant situations but are a reflection of the current status, shaped by previous experiences, providing information for predictive judgement or expectation in situations. Within the core affect framework, an individual’s reaction to emotional stimuli can be conceptualised through combining its longer-lasting background mood state with the appraisal of current stimuli that creates emotions (Barrett, 2006; Panksepp, 2007; Tellegen et al., 1999). Hence, animals experience emotions as a result of appraising emotional stimuli, which is guided by their mood. For example, an individual can be in a ‘happy’ mood but can temporarily feel ‘sad’ emotions when it misses out on a feeding or mating opportunity. After the short-lived emotion, the animal returns to its mood state, in this example ‘happy’.

One of the central points of discussion in the field of animal emotions revolves around the question of whether animals are capable of subjectively experiencing their emotions, in other words, whether they have *feelings*. I have already touched upon the concept of 'felt' emotions when discussing secondary emotions, as proposed by discrete theorists and the core affect framework uses the term ‘affective state’ to refer to the experience of emotions and moods together (Russell, 2003). Based on neural circuits associated with subjectively experiencing emotions in humans, homologous structures can be found in mammals, leading some scientists to assert that the capacity for subjective feelings may be a shared trait among, at least, all mammals (Panksepp, 2011). Others propose that this view is too restrictive and that subjective feelings may also extend to non-mammalian vertebrates (Kittilsen, 2013; Papini et al., 2019) and invertebrates (de Waal & Andrews, 2022; Perry & Baciadonna, 2017). Even if subjective feelings are shared across species, identifying them and quantifying the level of complexity is currently difficult, if not impossible. Even in humans, where verbal self-reports are currently the standardised method to measure experienced emotions, these methods are not flawless and likely do not capture the full complexity of subjective feelings (Diener et al., 2018; Robinson & Clore, 2002). While it remains possible that one day we may develop the means to measure feelings in animals, at present, reliable

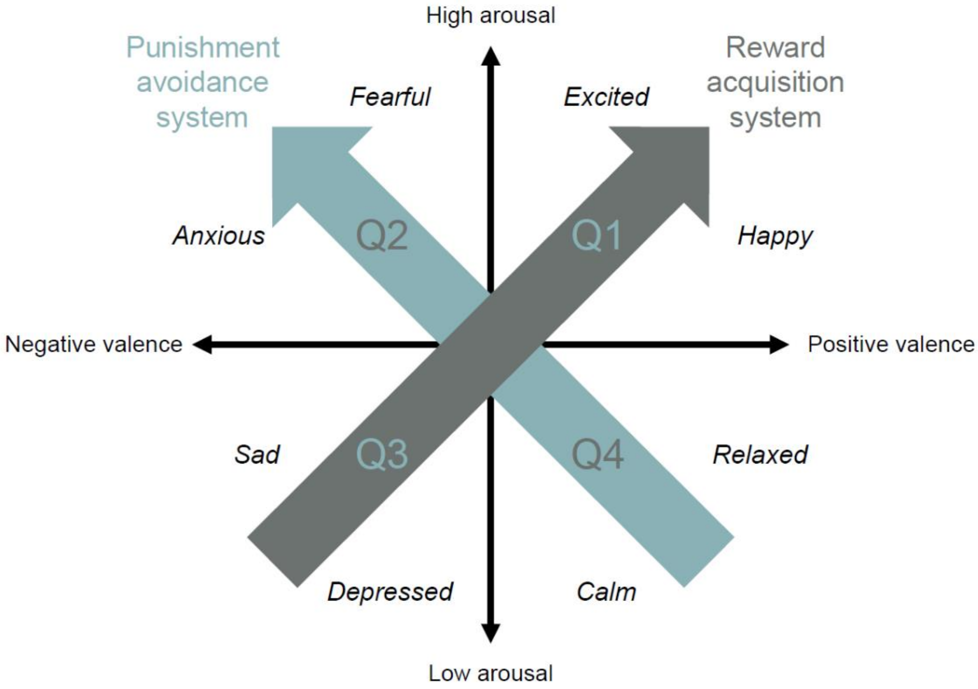

Figure 1.1: Core affect represented in a two-dimensional space (valence and arousal). Possible discrete emotions are written in italics. Positive affective states are in quadrants Q1 and Q2, and negative states in Q3 and Q4. The arrows indicate assumed behavioural systems (Mendl et al. 2010)

methods for doing so are lacking. Hence, emotions and moods are clearly distinguished by a temporal component, and affective states and emotional states can be distinguished based on whether the animal has a subjective experience. However, the terms affect and emotion (or affective and emotional state) are used interchangeably throughout the literature (Paul et al., 2005). As such, I will use them in this way, assuming that subjective experiences are possible in other non-human species. When I make a clear distinction between for example short-lasting emotions and longer-lasting mood states, I will explicitly mention this.

Animal welfare and emotions

Emotions and moods are currently considered at the centre of animal welfare. However, the inclusion of emotions within animal welfare concepts is a recent development. The field of animal welfare science started in the 1960s after the exposure of the treatment of factory farm animals in Ruth Harrison's book *Animal Machines* (Harrison, 1964) which prompted the appointment of a committee to look into the welfare of farm animals. This committee published the Brambell Report which stated that animals should have the freedom "to stand up, lie down, turn around, groom themselves and stretch their limbs" (Brambell, 1965). From this perspective, animal welfare has traditionally been defined in terms of basic health and biological functioning, but only later extended to natural living and emotional states (Fraser, 2009). These viewpoints have long been considered the main cornerstones of animal welfare (Fraser, 2008), and the importance of these viewpoints may vary between stakeholders and depend on human interests, ethical assumptions, and culture. Acknowledging these different perspectives highlight the complex nature of animal welfare, and hence it is important that although the different components of animal welfare are distinct, they are not mutually exclusive.

After the Brambell Report, one early seminal development in describing and conceptualising animal welfare is the 'five freedoms' concept which concentrates on aspects of animal husbandry that potentially compromise welfare; i.e. freedom (1) of thirst, hunger or malnutrition; (2) of discomfort and exposure; (3) of pain, injury, and disease; (4) of fear and distress; and (5) to express normal behaviour (Webster, 1994). The traditional focus was on avoiding negative affective experiences (Broom, 1991). However, these freedoms largely ignore factors that actually promote animal welfare (McCulloch, 2013). To overcome this limitation, the five freedoms concept has been translated into the Five Domains model (Mellor & Reid, 1994). The Five Domains model focusses on similar, yet distinct, domains of potential compromise; i.e. (1) Nutrition; (2) Environment; (3) Health; (4) Behaviour; (5) Mental State. At the time, the major focus of animal welfare science was on optimising the biological functioning of animals and thereby preventing negative outcomes. Later, it was proposed that completely eliminating negative states is not favourable, or sufficient. First, some negative states are biologically adaptive, e.g., hunger leads to feeding behaviours. Second, to achieve good welfare it is not enough to reduce negative states, but additionally requires positive states (Boissy et al., 2007). As it became more accepted that good welfare required positive experiences to compensate negative ones, the Five Domains model was extended to incorporate positive welfare states (Mellor & Beausoleil, 2015). The model is continuously updated as welfare perceptions and priorities shift (Mellor, 2016a, b). For example, recently, domain 2 was renamed to ‘Physical environment’ and domain 4 was renamed to ‘Behavioural interactions’ to include how an animal interacts with the physical environment, but also with other animals and humans (Mellor et al., 2020). Generally speaking, the internal (patho)physiological changes due to nutritional, environmental, or health-related problems are represented in domains 1-3, and the interactions with external physical biotic and social conditions in the animal’s environment are represented in domain 4.

Here, a discrepancy can be noted in which there is opportunity for an animal to experience agency, i.e., the ability to consciously and voluntarily engage in self-generated or goal-directed behaviour. The experience of agency is determined by the degree of control (i.e., the ability to predictably produce desired results) when encountered with challenges (i.e., the opportunity that requires use of certain skills to achieve a goal) (Englund & Cronin, 2023). While more limited in domains 1-3, animals arguably have the most opportunity to perceive agency within domain 4, i.e., how it interacts with the (social) environment. Agency is a significant determinant of how domains 1-4 influence domain 5, and as such considered a key component of welfare (Špinka, 2019). For example, the capacity of an animal to self-select goal-oriented behaviours when interacting with the (social) environment, and subsequently achieving these goals may result in positive affect as it creates a sense of control over their environment. Promoting the perception of agency through the ability to express preferences and to make choices about their own life is becoming important in welfare concepts (Špinka, 2019).

The perception of agency, and welfare in general, is however not static and changes as the mental and physical capacity to adequately react to instant and lasting internal and external stimuli, events, or conditions vary over time. This highlights the dynamic nature of animal welfare (Arndt et al., 2022). It is important to recognise that acute negative stimuli/interactions do not per se reflect compromised welfare (Browning & Veit, 2023). As long as the animal can adequately react to negative states, i.e. cope, there is opportunity for agency and it is likely that their welfare is not acutely impacted (Arndt et al., 2022; Englund & Cronin, 2023). That is not to say that there are no long lasting consequences as positive and negative, or pleasant or unpleasant, experiences from domains 1-4 accumulate over time. From this perspective, a balance between positive and negative states is considered important (Spruijt et al., 2001), albeit challenging to study objectively. For example, it is unclear how and if negative experiences with varying severities can be compensated for by positive experiences (Bateson & Poirier, 2019). Assessing the cumulation of emotional experiences is still in its infancy, but is arguably an important future direction as this reflects the animal's welfare of its life time (Reimert et al., 2023; Webb et al., 2019).

Welfare assessments

The section above applies the Five Domains model as a concept to describe animal welfare. The actual assessment of welfare in animals is a complex matter as there is not one indicator that encompasses the full spectrum of an animal's welfare. Early welfare assessments focused on resource-based indicators, relating to the animals' environment such as space, temperature, food presentation and nutritional value. Later, focus shifted towards more animal-based indicators, such as physical, behavioural and physiological indicators, which can complement resource-based indicators (Whitham & Wielebnowski, 2013). Here, a combination of resource- and animal-based indicators are likely to capture a more holistic assessment of animal welfare, and is reasonably feasible to implement (Wolfensohn et al., 2018).

Different welfare assessment tools are circulating, and depending on what is considered important to ensure good welfare these tools focus on different aspects (Jones et al., 2022; Tallo-Parra et al., 2023). The Five Domains model was initially developed as a conceptual model to describe animal welfare. The outputs of the model can be used to identify negative and positive welfare impacts associated with the different domains. This conceptual way of using the model is can be thought as a tool to promote animal welfare discussions. However, the Five Domains model gradually evolved in a quantitative assessment tool. To apply the Five Domains model it offers captive animal facilities a grading system to determine how the first physical domains positively or negatively affect the fifth mental state domain, which represents an individual animal’s affective experiences. However, recently limitations of the application of the Five Domains model as an assessment tool have been addressed. Some of these limitations include rating subjective experiences using objective scores, biases in the selection of raters, general lack of repeatability testing, the aggregation of scores in different domains to reach an overall welfare outcome, and uncertainty regarding the confidence of scores (Hampton et al., 2023).

Furthermore, the Five Domains model is by default a generic framework, and not species-specific. A species-specific approach to welfare is increasingly being considered important (Browning, 2023) as not all imbalances or opportunities in domains 1-4 may lead to similar affective experiences in domain 5 for all species. This is why knowledge of the species becomes essential to determine the quality of the conditions and interactions in domains 1-4. One good example to illustrate this is that of mules and hinnies. Mules and hinnies are hybrids between donkeys (*Equus asinus*) and horses (*Equus caballus*) and as such contain genetic material of both species. This implies that mules and hinnies are more similar to either a horse or a donkey, however comparison based on cognition, health, nutrition, behaviour (e.g., foraging, social) indicates significant differences between all four species (McLean et al., 2019). Given that mules, hinnies, donkeys and horses are all working equid (Burn et al., 2010), but clearly differ on many aspects, they may respond differently to working environments. Applying similar welfare standards or indicators may therefore lead to over- or underestimation of their welfare status. Unfortunately, for many species insufficient information is available to inform species-specific welfare approaches. This challenges the assessment of the affective component of animal welfare.

Emotional states represent a holistic reflection of an animal's welfare state and are therefore at the core of ensuring their welfare. However, the study of animal emotions is challenging given that emotions cannot be directly identified in animals. The Five Domains models, for example, does not explicitly mention how affective states are elicited and what processes are involved, therefore generally lacking guidelines as to how animals emotions can actually be studied. Scientists have developed approaches that approximate or infer emotions, based on observable measures that correlate with emotions. Figure 1.2 presents the Five Domains model to approach animal welfare, but provides more detail on the affective states domain by illustrating an emotional episode. In the next section, I will focus in more detail on emotional responses: what they are, the processes that result in emotions, how correlates can be measured, and lastly what is currently known in bonobos, the study species of this thesis.

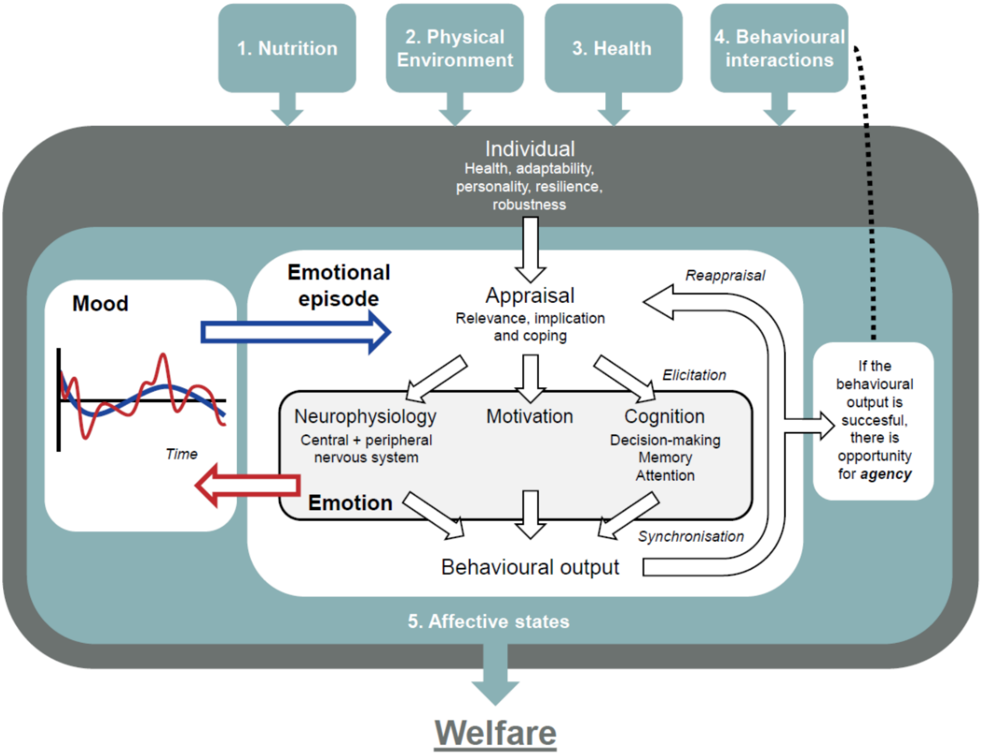

Figure 1.2: An integrated framework illustrating the Five Domains model by Mellor et al. (2020). The Affective states domain is described in more detail by integrating the different processes during an emotional episode, based on the model by Crump et al. (2020).

Processes in an emotional episode

Emotions are complex, multi-dimensional processes that include valence, arousal, and duration. Because of this complex nature, I will follow the core affect framework as its integrative approach allows for a more inclusive perspective on animal emotions, including their individual and flexible nature. In the next section, I will describe how and why this flexibility plays a crucial role in the adaptive value of emotions. Crump et al. (2020) describe the function of emotions within animal contest and illustrate the process of an emotional episode. I will use this model to walk through an emotional episode, examine its triggers, the effects it has on physiological, motivational, and cognitive mechanisms, and ultimately, its impact on behaviour. Instead of explicitly describing specific emotional states, my focus will be on elucidating the general underlying processes of an emotional episode.

Appraisal

Emotions begin with the appraisal, or evaluation, of stimuli. These stimuli can be either internal, external stimuli, or a mixture of both. Appraisal is a multi-faceted and transactional process between on the one hand, the individual and on the other hand the body's state and/or the environment (Faustino et al., 2015). The main purpose of this cognitive process is to determine the relevance, potential implication and possible coping with regards to the stimulus. Appraisal interacts with an individual's motivational and physiological state and therefore presents a relational process (Smith & Kirby, 2009a). This means that appraisal is based on stimulus characteristics, but in relation to the individual's current emotional state and personal set of needs, goals, resources and abilities (Faustino et al., 2015; Smith & Kirby, 2009b). As mentioned before, mood states enable predictive judgement or expectation in situations and as such inform appraisal processes which is also visualised in Figure 1.2. Appraisal is not a single event triggered by internal or environmental changes, but a dynamic process in which reappraisal reflects on the individual's current position and its relationship with the constant influx of information (Faustino et al., 2015). As such, appraisal, and subsequent reappraisal, allow for the flexibility of emotions and enables continuous emotional updating. This highlights the adaptive and flexible nature of the elicitation of emotions (Moors et al., 2013). Depending on how successful the behavioural output is, the degree of coping can be reassessed which can give opportunity for a sense of agency (Englund & Cronin, 2023). After the appraisal of stimuli, a cascade of neurophysiological, motivational, and cognitive processes follows which enable adaptive behavioural responses. I will discuss each of these three processes below.

Neurophysiology

The neurophysiological mechanisms are numerous and complex, and are mediated by neural networks, including interactions between various brain regions. The complexity of these networks varies greatly among species, and a detailed review is beyond the scope of the current introduction. Yet, a number of brain regions appear dominant and evolutionary conserved across species (LeDoux, 2012a). The activity of the autonomic nervous system (ANS) is broadly viewed as the major component of emotional responses (Dantzer et al., 1983; Kreibig, 2010). Generally responsible for the maintenance of the body's organs, the ANS can be divided into two main branches that control emotional responses: the parasympathetic nervous system (PNS), and the sympathetic nervous system (SNS). The PNS is responsible for the physiological processes that are active when an individual is in a low-activity state and is sometimes coined as the 'rest-and-digest' system. Examples of bodily processes controlled by the PNS include but are not limited to the slowing of the heart rate, airway constriction, and increased digestion of food and metabolism (e.g., storage of nutrients). The SNS is concerned with physiological processes that occur when the body is in an active state and is also known as the 'fight-or-flight' system. In contrast to the PNS, the SNS is responsible for increased heart rate, vasodilation, dilating of airways and the release of energy-mobilising hormones such as cortisol, and adrenaline (Ekman et al., 1983; Paul et al., 2005; Reefmann et al., 2009). The two prominent pathways that are activated in this response are the hypothalamic-pituitary-adrenal (HPA) and sympathetic-adrenal-medullary (SAM) pathways (Davis & Whalen, 2001; LeDoux, 1995; Paul et al., 2005). The SNS and PNS do not function mutually exclusive, but in a complementary fashion. Kreibig (2010) published an extensive review on the empirical evidence of ANS reactivity for different discrete emotional states. A major highlight of this review is that activation of the ANS is not valence-specific. For example, the SNS is activated in both positively and negatively valenced arousal, such as in response to sexual activity and fear inducing situations. This makes indicators linked to these systems challenging to interpret.

Two other, closely related, systems that regulate emotions are the dopamine and opioid system. Both systems are typically known for their role in the emotional promotion of behaviours that actively approach rewards by eliciting pleasurable sensations which fosters subsequent repetition of the behaviour. Dopamine is often considered the primary neurotransmitter that promotes reward seeking behaviour (Burgdorf & Panksepp, 2006), whereas opioids are considered to play a role in the rewarding sensation of actually achieving those goals (Panksepp et al., 2002). While closely related, the two systems function independently in producing rewarding experiences (Hnasko et al., 2005). The opioid system, for example, is not only found to promote approach-oriented emotions, but also reduces withdrawal-oriented emotions (Nummenmaa & Tuominen, 2018). Moreover, whether opioids increase or decrease the behavioural output of an emotional response is more so determined by motivational factors (Berridge et al., 2010).

Cognitive processing

Appraisal is a cognitive process which requires the recognition and evaluation of stimuli. Simultaneously, the appraisal of emotional stimuli induces changes in cognition, namely how information is gathered and processed (Bush et al., 2000; Dolan, 2002; Dolcos et al., 2011; Pessoa, 2008). These changes in cognition, also known as cognitive biases, are predominantly studied within the context of attention, memory and judgement under ambiguous situations, but also extend to more complex capacities, such as decision-making, problem solving and planning (Pessoa, 2008). Cognitive biases have been used in human studies as proxy for emotions (Davis & Whalen, 2001; Floresco, 2015; Lang et al., 1998; Mathews & MacLeod, 1994; Murray, 2007; Pessoa, 2008). Studies reveal emotion-congruent cognitive biases in the way people attend to, interpret and recall information about the world (Bar-Haim et al., 2007; Mathews et al., 1989). In the following section, I will briefly discuss how changes in attention, memory and judgement are linked to emotional episodes. In reality, these cognitive biases are much more complex than I can describe in this introduction, yet as these cognitive biases can be measured in animals it is important to provide the general framework that can be used to inform studies. More details regarding specific cognitive biases will be described in the chapters in which they are investigated.

First, since sensory systems are limited by the amount of input they can process, a rapid selection of relevant stimuli is necessary for adaptive behaviours (Anderson, 2005; Pourtois et al., 2013; Schupp et al., 2003). This selective processing of information is known as attention, and human studies indicate that people more readily pay attention to valenced stimuli than neutral stimuli (Strauss & Allen, 2009; Todd et al., 2012;

Vuilleumier, 2005; Yiend, 2010). By rapidly attending to a stimulus, individuals maximise their opportunity to act upon the stimulus, while failing to rapidly attend to a stimulus may result in a missed opportunity to obtain a reward or to avoid a punishment. This phenomenon is referred to as attention bias and describes the fast and sometimes automatic attention allocation towards relevant stimuli (Vuilleumier, 2005). The significance of stimuli is determined by a multitude of factors, including evolutionary pressures (Öhman, 2009), goal congruence (Vogt et al., 2013), but also emotional state (Pool et al., 2016; Yiend, 2010). Based on the relational component of emotions (Faustino et al., 2015), the individual's emotional state determines the significance of a stimulus, and hence what is worth paying attention to as this in return may promote either the reward acquisition or punishment avoiding behavioural mechanisms. Additionally, such attention biases play a crucial role in the reappraisal process, as they modulate attention for stimuli which subsequently feeds back into the appraisal process. For example, individuals in a negative affective state may benefit from enhanced attention for negative stimuli to effectively avoid exposure to this punishment and circumvent even worse affect, while individuals in positive affect may be able to cope with the punishment. Such emotion modulation of attentional processing can be see at different stages, including engagement, maintenance and disengagement (Koster et al., 2005, 2006)

Second, the literature on the relationship between memory bias and emotions indicates that an individual's emotional state may either enhance or impair the formation, reconsolidation and retrieval of memories (Cahill & McGaugh, 1996; Christianson, 1992; Mendl et al., 2001). Memory formation is influenced by increased activity in the HPA and SAM systems in response to emotional stimuli (Packard & White, 1990). Short-term, moderate elevations of adrenaline and cortisol stimulate hippocampal receptors, leading to enhanced memory formation (O'Keefe & Nadel, 1978). Additionally, increased activity in the amygdala in response to emotional stimuli is also associated with improved memory formation (Hamann et al., 1999). However, chronic high concentrations of cortisol and adrenaline can impair learning and memory storage (Cahill & McGaugh, 1996; Roozendaal et al., 2009). From an evolutionary perspective, enhanced memory of emotionally arousing events is an adaptive phenomenon that aids in remembering information which contributes to the survival of an individual (Cahill & McGaugh, 1996; Paul et al., 2005). For example, human studies found that depressed individuals show enhanced retrieval of mood congruent (i.e. sad, upsetting) memories (Clark & Teasdale, 1982; Lewis et al., 2005). This mood-congruent memory retrieval is relevant for these individuals as it prepares them for upcoming emotional stimuli or events. Vice versa, enhanced memory for actions that resulted in a reward (e.g., food resources, mating opportunities) can facilitate future acquisition of such rewards.

The last cognitive bias that will be discussed is judgement bias. Judgements are complex cognitive processes that often involve attention, memory, expectation of reward and other aspects of perception. Judgement biases can be expressed on multiple levels, including interpretations of ambiguous stimuli, expectations about future events, and risk-taking (Mathews et al., 1989). As the cumulation of rewards/punishments determines an individual’s affective state, they represent a source of information about the likelihood of encountering rewards and threats. Affective states are therefore indirectly a representation of the environment which the animal inhabits, but also the degree in which it has been able to cope with that environment (Carver, 2001, 2003). From this perspective, affective states are a valuable source of information that can guide future behaviours, especially in situations when there is a level of ambiguity in their potentially rewarding or punishing outcomes (Mendl et al., 2009).

Motivation

In addition to the changes in neurophysiology, emotions also have an impact on an individual's motivation. Motivation refers to the willingness of an individual to invest effort in order to obtain rewards or avoid punishments. These changes in drive can be triggered by either internal or external stimuli. Internal stimuli, such as deviations from homeostasis, are detected by the individual, leading to the activation of action programs aimed at satisfying basic needs (such as hunger, thirst, libido, exploration, play, care, etc.) with the ultimate goal of restoring homeostasis (Craig, 2003; Denton et al., 2009). Since actions to achieve homeostasis require active engagement, motivational systems ensure that this goal is attained. As such, some consider emotions as fundamentally a disposition to act (Bradley, 2009). This motivational system is closely linked to changes in approach or avoidance behaviours in response and often difficult to empirically measure distinctly.

Behavioural output

Within an emotional episode, the previously discussed changes in neurophysiology, motivation and cognition work together to facilitate the behavioural responses to rewards and punishments (LeDoux, 2012b; Nesse & Ellsworth, 2009). These behavioural responses ultimately contribute to the survival of an individual (Schacter et al., 2011). Short-term emotions have an immediate function, as they result from the appraisal of emotional stimuli, whereas longer-lasting moods provide information about the environment where the individual is living (Carver, 2001; Mendl et al., 2009). This potential adaptive value of an animal's affective state can be further integrated in the core affect framework when the response to an emotional stimulus is deconstructed and linked to reward and punishment (Nesse & Ellsworth, 2009). An appropriate emotional reaction to rewarding or punishing stimuli can increase the acquisition of potential fitness-enhancing rewards and minimise the exposure to fitness-threatening punishers (Burgdorf & Panksepp, 2006). Here, the actual behavioural output is a combined product of changes in valence and arousal, as produced by the neurophysiological, cognitive, and motivational processes.

An individual's position along the dimensions of valence and arousal is believed to be associated with specific behavioural patterns (Figure 1.1). On the one hand, behavioural strategies are observed that aim to minimise the individual's exposure to threat. Negative high arousal states coordinate appropriate responses to threats or danger, often facilitated by the activation of the HPA-axis and sympathetic nervous system (McEwen, 2007). Enhanced attention, and quick memory retrieval enable the body to swiftly make judgements about the stimulus and neurophysiological changes facilitate quick responses (e.g., fighting, fleeing, or freezing). Conversely, positive low arousal states are associated with low levels of threat (Carver, 2001), and enable maintenance and recovery activities (Fredrickson, 2003). On the other hand, behavioural outputs of emotional episodes aim to optimise the individual's acquisition of rewards. Positive high arousal states are closely linked to appetitive motivational states and play an important role in facilitating the process of actively seeking and obtaining rewards (Burgdorf & Panksepp, 2006; Carver, 2001). These states motivate individuals to engage in goal-directed behaviours that lead to reward attainment. In contrast, negative low arousal states may promote strategies to conserve energy in conditions where resources are lacking, or lost (Mendl et al., 2010).

Considering the individual

In Figure 1.2, I included an additional level of the ‘individual’. I have mentioned before that emotions are highly personal, and that the appraisal of stimuli is guided by the significance of a stimulus. However, the extent to which stimuli impact the affective states of individuals is partly determined by internal factors that are specific to an individual. Examples of these internal factors include health, personality (i.e., consistent individual differences over time and context), adaptability (i.e., the capacity to adjust, change or evolve in response to new situations/stimuli), robustness (i.e., the capability to maintain a state in the presence of disturbances), and resilience (i.e., the ability to recover to regular functioning after experiencing disturbances) (Reimert et al., 2023). These factors are not components of an animal’s emotional or welfare state but instead interact with the four physical or functional domains of the Five Domains model that may impact the emotional state. For example, animals with specific personality traits may be more prone to explore environments which makes them more likely to discover rewards/punishers, that subsequently impact their affective state.

To conclude this part, it becomes evident that emotions are non-fixed responses to rewards and punishers, informed by the individual’s relation to the context which allows for flexible behaviours in complex and fluctuating environments. In this regard, emotions are commonly perceived as functional (Kremer et al., 2020; LeDoux, 2012a; Nettle & Bateson, 2012; Öhman & Mineka, 2001). After the appraisal of a stimulus, a cascade of neurophysiological, motivational, and cognitive processes is elicited and synchronise to produce behavioural responses that either aim to increase the acquisition of potential fitness-enhancing rewards and minimise the exposure to fitness-threatening punishers. This approach to emotions provides a framework for scientists to investigate emotions in animals by exploring behavioural, physiological and cognitive correlates (Paul et al., 2020). However, both what stimuli elicit emotions, and how these are manifested can be highly species-specific. Studying emotions in animals and integrating this within their welfare therefore requires a species-tailored approach. In the next section, I will introduce the study species of this thesis: the bonobo.

Bonobo as a study species

In this dissertation, I will investigate different components of emotions in bonobos (*Pan paniscus*). Bonobos share a common ancestor with humans from approximately 5-6 million years ago (Prado-Martinez et al., 2013), and share 98.7% of their DNA with modern humans (Prüfer et al., 2012). They lead rich emotional lives (Clay & de Waal, 2013a; Issa et al., 2019; Kano et al., 2015), providing an opportunity to study various aspects of emotions. Despite their potential, bonobos have received relatively little attention in affective research. This lack of information can be attributed to historical factors, such as their official recognition as a separate species only in 1933 (Stevens, 2020), and limited availability of long-term field sites due to civil unrest in the Democratic Republic of Congo, where bonobos are endemic. In the wild, bonobos are classified as endangered on the IUCN Red List (Fruth et al., 2016), with estimates ranging between 15,000 – 20,000 individuals (IUCN/ICCN, 2012). Additionally, captive populations of bonobos are relatively rare (Stevens & Pereboom, 2020). Therefore, a comprehensive understanding of bonobo emotions is yet to be achieved. I will first provide a brief overview of the socio-biology of bonobos, and then go over the significance of emotions in bonobo society.

Bonobos form multi-male/multi-female communities consisting of 10 to 63 individuals (Furuichi & Thompson, 2008; Kano, 1992; Stevens, 2020). These communities exhibit fission-fusion dynamics, where individuals temporarily disperse into smaller sub-parties (fission) and later reunite to larger groups (fusion) (Hohmann & Fruth, 2002). The aggregation patterns of bonobos are fluid and vary across populations and communities, with highly flexible and complex intra-community relationships (Samuni et al., 2022). Community territories overlap considerably (Idani, 1990), and bonobos are considered nonterritorial (Furuichi, 2020). Inter-community encounters are characterised by a mix of tolerance and competition, influenced by ecological factors such as food availability and resource distribution, with favourable conditions reducing competition over food resources (Lucchesi et al., 2021; Moscovice et al., 2022). These encounters can last for several consecutive days in some instances (Sakamaki et al., 2018) during which members of the opposite communities engage in affiliative behaviours such as grooming and playing (Behncke, 2015; Cheng et al., 2022), and in some instances share high-value food items (Fruth & Hohmann, 2018). When inter-community aggression occurs, male bonobos tend to contribute more and mostly target out-group males, potentially reflecting competition over mates or mate defence

(Tokuyama et al., 2019), although this may vary between populations (Cheng et al., 2021).

Bonobos are often characterised as a relatively tolerant and peaceful species (Fruth & Hohmann, 2018; Hare et al., 2012; Tan et al., 2017). This perception is partly attributed to lower levels of aggression observed during inter-group encounters in comparison to chimpanzees (Samuni et al., 2017). Additionally, bonobos have been described as more ‘empathising’ compared to chimpanzees, who are considered more ‘systemising’ (MacLean, 2016). These labels were assigned based on studies that found bonobos to score higher on specific components of theory of mind, such as gaze following (Hare et al., 2007; Herrmann et al., 2010), display increased attention towards faces and eyes relative to chimpanzees (Kano et al., 2015), engage in food sharing (Hare et al., 2007) and play more as adults (Palagi & Cordoni, 2012). On the other hand, chimpanzees excel in tool use, causal reasoning and spatial memory (Herrmann et al., 2010; Rosati & Hare, 2012). However, it is important to note that aggression does occur among bonobos (Cheng et al., 2021; Hohmann & Fruth, 2003), and more recent experimental studies do not provide substantial evidence for consistent tolerant and prosocial tendencies in adult bonobos (Cronin et al., 2015; Verspeek et al., 2022a, b). In other words, the popular image of bonobos as exclusively tolerant and peaceful needs to be more nuanced. Within this context, exploring the role of emotions, their regulation, and how bonobos intentionally employ emotional expressions to direct social interactions becomes particularly intriguing.

What is known about bonobo emotions?

Currently, animal emotions cannot be measured directly (Kret et al., 2022). However, as described by the processes involved in an emotional episode, there are a number of physiological, cognitive, and behavioural correlates that can be studied empirically which subsequently give insights in the animal’s emotional state. By utilising a combination of these measures, researchers can better approximate and understand the emotional states experienced by animals. However, it is essential to consider the limitations and challenges associated with each measure and to continue refining and developing new methods for assessing animal emotions in a reliable and non-invasive manner. In this final part, I will list what is currently known about emotional measures for bonobos. However, when considered relevant, I will introduce concepts that will lay the foundation for the empirical chapters in this thesis.

Behavioural correlates

Behavioural measures have a long history in animal science, and remain until today the most commonly used indicator to assess animal welfare (Binding et al., 2020; Boissy et al., 2007; Dawkins, 2015). These indicators involve observing an animal's action, reaction, and changes in behaviour that are associated with specific emotional states. They are readily visible, quantifiable, typically non-invasive, and often require minimal training for observers. Data collection, on the other hand, may require lengthy observation periods and are open to subjective interpretation. Behavioural measures traditionally include general changes in activity budgets (Tallo-Parra et al., 2023), stereotypical or abnormal 'negative' behaviours (Hosey & Skyner, 2007; Lutz et al., 2003), and more recently include species-typical positive behaviours such as play (Boissy et al., 2007; Held & Špinka, 2011) or affiliative behaviours (Mellor, 2015). They can also extend to more subtle changes in, for example body posture (Gerdemann et al., 2022; Neal Webb & Schapiro, 2023; Woody et al., 2021). Animals may also express and communicate their emotional states. It has been hypothesised that emotional expressions initially evolved as cues providing bystanders with information about the expressor's emotional state, without intentional communication of information (Shariff & Tracy, 2011). Over the evolutionary course, as bystanders benefited from recognising and responding appropriately to these emotional cues, the expressions became ritualised, becoming more visible exaggerated and importantly, evolved into signals specifically intended for communication. Structural and automatic recognition of vocalisations and facial-expressions additionally revealed high context-dependency, suggesting a promising avenue for future studies (Seyfarth & Cheney, 2003; Waller & Micheletta, 2013).

Behavioural correlates are most often used as indicators of emotional states in bonobos. Starting with more traditional behaviours of emotions and welfare indicators, abnormal behaviours have been investigated in a number of studies. Most studies that report on abnormal behaviours in bonobos focused on hair plucking (Brand et al., 2016; Brand & Marchant, 2015, 2018), and regurgitation and reingestion (Miller & Tobey, 2012; Stevens & Wind, 2011). Besides self hair plucking, self-injurious behaviours are not widely reported, except for one case in which a bonobo developed self-mutilating behaviours (Prosen & Bell, 2001; Wallace et al., 1998). Behavioural and medical interventions successfully alleviated these behaviours.

Displacement behaviours are another group of behaviours that are generally considered to result from frustration and/or internal conflict (Pavani et al., 1991;

Tinbergen, 1952). These include behaviours such as yawning and self-directed behaviours (e.g., self-scratching, self-grooming). Changes in displacement behaviours are reported in welfare studies (Caselli et al., 2023), or in fundamental studies (e.g., Clay & De Waal, 2015; Palagi & Norscia, 2013; Verspeek & Stevens, 2023). Because displacement behaviours are typically linked to negative emotions, separate behaviours are often combined together, despite the fact that subtle changes between individual behaviours exists (Leeds & Lukas, 2018). A detailed study into the different types of displacement behaviours, and their potential link to emotional states, in bonobos is currently lacking.

Play behaviour received considerable scientific attention in bonobos as evidence suggests that play remains relatively frequent in adult bonobos (Behncke, 2015). Adult-adult play is more frequent in female-female dyads compared to female-male and male-male dyads (Palagi, 2006; Palagi & Paoli, 2007), suggesting a link with their strong social bonds. Play among adult bonobos is suggested to have an affiliative function to promote social bonds (Enomoto, 1990; Palagi & Paoli, 2007), reduce tension during food competition (Asensio et al., 2022; Norscia & Palagi, 2011; Palagi et al., 2006; Yamanashi et al., 2018), social insecurity (Antonacci et al., 2010) or social crowding (Crast et al., 2015; Tacconi & Palagi, 2009), and therefore facilitate social tolerance (Palagi, 2023) and overall regulate emotions on a group-level. Such play interactions are accompanied by the production of play signals, such as play faces or vocalisations which may signal positive affective experiences. These expressions are more common during adult-adult play (Palagi, 2008), and are produced more when the play partner is able to see the expression, suggesting a degree of intentionality (Demuru et al., 2015). However, at least in chimpanzees, adult social play does not necessarily indicate positive emotions or welfare (Yamanashi et al., 2018).

Another behaviour that is commonly linked to emotions and emotion regulation, and widely studied in bonobos, is socio-sexual behaviour. These behaviours are frequently observed during heightened social tension such as feeding competition (Hohmann & Fruth, 2000; Paoli et al., 2007; Parish, 1994), employed to reconciliate and console after conflict (Clay & De Waal, 2015; Hohmann & Fruth, 2000), and promote social bonding (Moscovice et al., 2019; Parish, 1994; Wrangham, 1993). Bonobos may furthermore display emotional expressions to communicate their internal states, and which may inform researchers about their experience. For example, bonobos frequently exhibit bared-teeth displays during sexual interactions, or after aggression potentially signalling appeasement or reassurance (de Waal, 1988; Vlaeyen et al., 2022), irrespective of dominance (Vervaecke et al., 2000).

Physiological correlates

Physiological indicators focus on the physiological changes that occur during emotional states. These measures encompass various aspects including the activity of the HPA-axis, such as glucocorticoids and adrenocorticotropic hormone levels (Ralph & Tilbrook, 2016), as well as changes in sympathetic and autonomic function (e.g. cardiovascular measures, respiratory rate, catecholamine levels, skin conductance and temperature, pupil size and neuroendocrine activity (Ekman et al., 1983; Kinner et al., 2017; Paul et al., 2005; Reefmann et al., 2009) and immunological measures (D'Acquisto, 2017). Despite the vast number of physiological measures that have been linked to emotional states, not all of these measures can be collected non-invasively and often require specialised equipment. Perhaps more importantly, physiological measures have limitations in terms of interpretation as many of these measures solely identify the arousal of emotions but cannot distinguish between positive or negative emotions. As a result, only few studies have measured physiological correlates of emotions in bonobos.

Cortisol is likely the most widely studied physiological indicator. Cortisol can be measured in different media, e.g. saliva, urine or faeces (Behringer & Deschner, 2017), which may tap into different temporal dimensions of emotional states. In relation to possible emotional states, cortisol is typically positively linked with negative states, during, for example, competition (Cheng et al., 2021; Surbeck et al., 2012), after a psychological stressor (Verspeek et al., 2021), abnormal behaviours (Brand et al., 2016), or transition into siblinghood (Behringer et al., 2022a). Associations with cortisol are, however, also found in more ambiguous situation such as the birth of a new group member (Behringer et al., 2009), or with positive events such as enrichment (Behringer et al., 2022b).

Salivary alpha-amylase (sAA) is another measure that is associated with negative affective states. sAA is positively correlated with salivary cortisol outside of stressful events (Behringer et al., 2012). This correlation is no longer present when bonobos experience stress (i.e., introduction of a new female, birth and a transfer), but sAA levels increased (Behringer et al., 2012).

The last endocrinological measure that I will discuss are oxytocin levels. Oxytocin is a neuropeptide that is often associated with social bonding (Ross & Young, 2009), which may have emotional consequences and promote positive welfare (Boissy et al., 2007). Oxytocin is measured in bonobos in a number of studies, and find that oxytocin administration enhances social attention (Brooks et al., 2021), and promotes social grooming (Brooks et al., 2022). Socio-sexual behaviours are furthermore associated with increased levels of urinary oxytocin (Moscovice et al., 2019), and infant handling also showed positive correlates with oxytocin (Boose et al., 2018) However, measuring circulating levels of oxytocin is challenging (Valstad et al., 2017) and a review paper expresses that caution should be taken with oxytocin as an emotional correlate and welfare indicator, as links to both positive and negative states are found (Rault et al., 2017).

Although not yet commonly applied to measure emotions or welfare, novel developments in non-invasive electrocardiograms allow to measure heart rate and rhythm in bonobos (Olds et al., 2023).

Cognitive correlates

Cognitive indicators involve assessing an animal's cognitive processes and information processing biases that are influenced by emotions. Cognitive measures of emotions have only been developed for animals since the early 2000s (Harding et al., 2004). Numerous animal studies have since shown that different forms of cognitive biases are linked to expected positive or negative emotional states (reviewed in: Crump et al., 2018; Roelofs et al., 2016) and are therefore considered a promising tool in animal welfare as they can objectively measure and distinguish positive and negative emotions (Marchant-Forde, 2015). To this date, no study investigated affect-related cognitive biases in bonobos. Some studies examined attention biases for other's emotions in bonobos (Kret et al., 2016; van Berlo et al., 2023), but did not explicitly test whether this was driven by underlying emotional states. Hence, for the cognitive measures, I will divert to other primate species and describe current methods that could be applied in bonobos to study cognitive correlates of emotions.

The vast majority of animal welfare studies has focused on judgement biases, or differences in decision-making under ambiguous contexts (Roelofs et al., 2016). Judgement bias tasks typically involve the training of animals to exhibit distinct responses towards two unidimensional stimuli, resulting in positive and negative outcomes. In experimental trials, intermediate "probe" stimuli with ambiguous characteristics are introduced. The animals' response to these probes, resembling that towards the positive stimulus, is interpreted as an optimistic judgment bias associated with positive-valence states. Conversely, a response resembling that towards the negative stimulus is considered as a pessimistic judgment bias indicative of negative-valence states. Judgement bias tasks have been conducted with a few primate species, including marmosets (*Callithrix jacchus*; Gordon & Rogers, 2015)), rhesus macaques (*Macaca mulatta*; Bethell et al., 2012)), capuchins (*Cebus apella*; Pomerantz, Terkel, et al., 2012; Schino et al., 2016)), chimpanzees (*Pan troglodytes*; Bateson & Nettle, 2015)), and gorillas (*Gorilla gorilla*; McGuire et al., 2017)). One disadvantage of judgement bias tasks, however, is that they require extensive training periods which can be impractical in applied settings and may lead to attrition of subjects. This can unconsciously create a selection bias in participating animals (Mendl et al., 2009). Additionally, with repeated testing, subjects can gain insensitivity to the ambiguous cues with makes their responses unreliable of their emotional state (Doyle et al., 2010).

Another cognitive correlate that recently received more interest is attention bias. Attention bias tasks may overcome some limitations of judgement bias tasks, such as the lengthy training periods as attention bias tasks require little or no training, and do not depend on interpreting optimistic or pessimistic responses (Crump et al., 2018). The most commonly applied paradigm in primate studies is the response slowing task (Bethell et al., 2016). This paradigm measures how attention is distracted from an original task (i.e., to touch a neutral target). During test sessions, a social control stimulus (i.e., an averted gaze of an unknown conspecific) is embedded in the target, as well as a mildly threatening social stimulus (i.e., a direct gaze of an unknown conspecific). In this study, the attention of rhesus macaques with neutral or positive emotions, was not biased towards the mildly threatening stimulus, however, macaques with negative emotions showed attention biases for low threat stimuli, such as the direct gaze (Bethell et al., 2016). Although such direct gazes do not signal clear emotional information, individuals with negative affect show altered attentional processing for these stimuli and interpret them as potentially threatening. This paradigm has been applied in a number of studies, indicating that macaques in negative states show enhanced attention for the direct gaze of conspecifics after, for example, veterinary inspections (Bethell et al., 2016), or exposure to anthropogenic noise (Cronin et al., 2018). Using a different task, the dot-probe task, Cassidy et al. (2021) tested how affective states mediate attention biases towards neutral or aggressive expressions in long-tailed macaques (*Macaca fascicularis*). On touchscreens, the macaques were presented with a stimulus pair: a neutral and aggressive facial expression for a either 100 or 1,000 ms. Afterwards, a ‘dot-probe’ appears in the location of one of the two stimuli, and the latency to touch this probe is measured. Faster latencies to touch the target indicate that attention was likely already allocated towards the stimulus it replaced. Slower latencies suggest attention shifted from another location. Results showed that anaesthesia procedures altered attentional processing of threatening facial expressions in the long-tailed macaques and shifted from vigilance during normal days, to avoidance of threatening facial expressions (Cassidy et al., 2021). Chimpanzees showed similar effects when completing a pictorial emotional Stroop task (Allritz et al., 2016). In this task, participants are presented with two identical images, except that they are embedded in different coloured frames. Participants are trained to touch the stimulus with their personal target colour frame while ignoring the other stimulus. When the chimpanzees were presented with images of the veterinarian, the chimpanzees showed altered performance on this task, and this effect was stronger in individuals with more recent medical interventions (Allritz et al., 2016).

In conclusion, there are critical gaps in our understanding of bonobo emotions. Despite the significance of emotional states in animal welfare, the specific indicators of emotions in bonobos have been understudied. Behavioural measures are most common but are often based on studies of closely related species, while bonobo-specific validation is lacking. Cognitive measures are currently not being applied to study emotions in bonobos. This thesis seeks to provide a more holistic understanding of bonobo emotions. By expanding our knowledge in these areas, we can develop a more accurate and comprehensive picture of bonobo emotional experiences, which contributes to improve their welfare under human care.

Dissertation outline

This dissertation comprises six empirical chapters, consisting of published articles or those currently being prepared for publication in international peer-reviewed journals. The primary objective of this dissertation is to expand our current understanding of emotions in bonobos by looking at different components of emotions, and examining how these can be applied to measure their welfare. The empirical chapters are structured following the steps within an emotional episode.

As such, I will first present **Chapter 2** that examines attention biases, as an inherent process involved in the appraisal of stimuli. Specifically, it investigates the emotional responses of bonobos to valenced stimuli. By employing a modified Emotional Stroop task on a touchscreen setup, the study investigates how positive, negative, and neutral social and non-social stimuli influence task performance.

Chapter 3 builds on these results and specifically studies the influence of emotions on social information processing using an eye-tracking paradigm. I attempt to induce emotional states by priming the bonobos using valenced videos. Changes in the neurophysiological processes involved in emotional arousal are measured using pupillometry, and subsequent attention biases towards socio-emotional information are examined by looking at gaze patterns as measured by the eye-tracker.

Chapter 4 focuses on the behavioural output of an emotional episode. Specifically, in this chapter I will focus on a more traditional measure of emotions by looking at abnormal behaviours, which are commonly used to identify potential welfare issues. There is currently no overview of what abnormal behaviours are present among zoo-housed bonobos, and little is known what might explain why certain individuals show abnormal behaviours. As such, in Chapter 4 I examine the prevalence of abnormal behaviours in European zoo-housed bonobos and investigate potential links between intrinsic factors and their occurrence.

In **Chapter 5**, I evaluate self-directed behaviours as indicators of emotional arousal. While self-directed behaviours are generally considered stress-related, their species-specific validation is often lacking. To address this gap, I opportunistically utilised the bonobos' interactions with touchscreens, during which they occasionally made mistakes. This allowed me to experimentally assess the emotional consequences of these mistakes and validate reliable self-directed behaviours as indicators of emotional arousal in bonobos.

Chapter 6 takes a different approach by exploring whether humans can reliably perceive and characterise emotional expressivity in bonobos through a Qualitative Behavioural Assessment. This chapter also relates to how animal welfare can be measured through understanding bonobo emotional expressions.

Chapter 7 will integrate cognitive and behavioural measures of emotions in bonobos. In this Chapter I will study how emotions influence social information processing by implementing a response slowing task. Within an applied welfare context, I examine how putative emotionally arousing social events influence social information processing, record the bonobos' behavioural strategies, and correlate these measures to study the emotional consequences of the behaviours.

Finally, in **Chapter 8**, I discuss the overall findings and implications of these studies and discuss the limitations and future perspectives of this work.

2

Social and non-social stimuli alter the performance of bonobos during a pictorial emotional Stroop task

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Abstract

The emotional Stroop task is a paradigm commonly applied in human studies to investigate how emotionally laden stimuli interfere with cognitive processes. Recent modifications of this task have enabled researchers to study similar Stroop effects in zoo-housed primates. Across three experiments using a pictorial emotional Stroop task, we investigated if the attention of bonobos was influenced by social (facial expressions during play, conflict, and neutral events) and non-social stimuli (a preferred food item, predator, and flower). Four bonobos successfully learned to complete the task on a touchscreen. First, we tested the bonobos on a standard colour-interference Stroop task and found that they made more errors in colour-congruent trials. Second, we included facial expressions of unknown conspecifics and found that it took the bonobos longer to select targets with play facial expressions compared to neutral expressions. Lastly, we included objects and found that the negative, positive, and neutral objects altered performance. Our findings show that the cognitive processes of bonobos are influenced by both relevant social and non-social stimuli. Specifically, play faces interfered with the bonobos' attention suggesting that these facial expressions form a salient stimulus within bonobo society. Non-social stimuli also altered accuracy and reaction times during the task which may be explained by their evolutionary relevance. Our results help us to better understand the (socio-)emotional competencies of bonobos and how they respond to external stimuli. Future studies can further examine how a wider range of biologically relevant stimuli interfere with attentional processes in bonobos.

Introduction

Attention is a limited cognitive resource and selective processing facilitates enhanced attention for relevant visual stimuli while ignoring irrelevant distractors. Evolutionary pressures have shaped attentional processes enabling adaptive responses which will ultimately enhance the survival of the individual. For example, Japanese macaques (*Macaca fuscata*) rapidly detect snake images (Shibasaki & Kawai, 2009), but not spiders (Kawai & Koda, 2016) and show preferential engagement of attention to snakes (Masataka et al., 2018). Interestingly, these macaques were born in captivity and therefore had likely no prior experience with snakes, suggesting an innate rapid detection mechanism. However, another study did not find that snake images distracted Japanese macaques during an emotional Stroop task, although the attention of chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla gorilla*) was influenced (Hopper et al., 2021a).

There is a body of evidence that attention is also enhanced towards socio-emotional information. Especially for social species, rapid detection, and accurate recognition of emotional expressions in conspecifics is beneficial and triggers corresponding action tendencies which facilitate group-living. Primates express a range of facial expressions that may share similar features in a variety of species, although their use and function differ among species (Kret et al., 2020; Preuschoft & Van Hooff, 1995), driven by the socio-ecology of the species (Dobson, 2012). Facial expressions present a combination of cues (Öhman, 2002) and inform bystanders about the expressor’s internal state and future behaviour (Waller et al., 2017). For example, in crested macaques (*Macaca nigra*) lipsmacking increases the probability of affiliative behaviours (Micheletta et al., 2013). Play faces are also thought to coordinate and maintain play in gorillas (Waller & Cherry, 2012) and bonobos (*Pan paniscus*) (Palagi, 2008). Facial expressions are therefore salient communication signals that help predict social outcomes (Waller et al., 2016) and enhanced attention to conspecifics’ facial expressions may benefit reproduction and survival.

Attention biases towards emotions in primates have been investigated in a number of studies employing different paradigms. Rhesus macaques (*Macaca mulatta*) showed attention biases towards threatening faces of conspecifics during the dot-probe task (King et al., 2012; Lacreuse et al., 2013; Parr et al., 2013). In contrast, chimpanzees did not show a bias for threatening facial expressions in a dot-probe task (Kret et al., 2018; Wilson & Tomonaga, 2018) but did so during a visuo-spatial cueing experiment (Tomonaga & Imura, 2009). Not only facial expressions, but also whole-body stimuli can bias attention in primates, and this can also include positive social scenes, as suggested in a study on bonobos which found a bias towards affiliative but not aggressive whole-body stimuli, which may reflect differences in the socio-ecology of the species as compared to the closely-related chimpanzee (Kret et al., 2016).

The emotional Stroop task is another paradigm commonly used in human psychology to assess attentional biases, specifically by measuring how accuracy and reaction time during a simple task is influenced by emotionally valent distractor stimuli. In this task, human participants are instructed to name the colours in which emotionally-loaded words are written and typically find that, due to automatic attention processes, humans take longer to name the colours of negative stimuli (Bar-Haim et al., 2007; McKenna & Sharma, 2004). Only few studies have so far employed an emotional Stroop task in primates. Allritz et al. (2016) designed a pictorial version of the emotional Stroop task and tested chimpanzees' responses to pictures of humans (veterinarian, caretaker, and stranger). In this modified version, the chimpanzees were trained to choose between two identical stimuli, based on the colour of their border. Similar to the human Stroop task, this version measures attentional interference of stimuli on the performance of a simple task, in this case a colour discrimination task. The chimpanzees showed longer reaction times to pictures of the veterinarian, and this effect was more pronounced in those individuals who had a more recent anaesthetization experience. Hopper, Allritz, et al. (2021) used a similar approach and tested the responses of chimpanzees, gorillas, and Japanese macaques when presented with positively valenced (preferred food items) and negatively valenced (snakes) images. Both apes and monkeys showed lower accuracy scores when presented with positive images compared to neutral images, however, only apes made more mistakes during negative trials.

This study aimed to employ a pictorial emotional Stroop task (Allritz et al., 2016) and to investigate in a series of three experiments if biologically relevant social and non-social stimuli cause attention biases in zoo-housed bonobos. Overall, we expected that the bonobos have more difficulty in swiftly and correctly indicating the target stimulus when the stimulus is a potential threat, preferred food item or of social value, as such stimuli capture attention. First, we replicated the colour-interference Stroop task to test if the performance of the bonobos during a simple discrimination task is influenced by task-irrelevant images of neutrally valenced geometric shapes. We expected to find a typical Stroop effect in which colour incongruency causes interference during the task (as measured by lower accuracy scores and/or longer reaction times) (Allritz et al., 2016). Second, we included facial expressions of unfamiliar bonobos that differed in emotional valence (negative, positive, and neutral). While bonobos do console individuals in distress (Clay & de Waal, 2013b; Palagi & Norscia, 2013), the only study to date on attention bias to emotional stimuli in bonobos did not find a bias towards social scenes depicting bonobos in distress (Kret et al., 2016). The same study did report a bias towards affiliative emotional scenes and together with the knowledge of the communicative role of play faces in bonobos (Demuru et al., 2015; Palagi, 2006, 2008), we predicted that bonobos show an attention bias towards play faces (i.e. lower accuracy scores and/or longer reaction times) but not towards individuals in distress. Lastly, we investigated how performance was influenced by emotionally valenced non-social stimuli. We selected biologically relevant stimuli that were negatively valenced (i.e., leopards), positively valenced (i.e., a preferred food item), and neutrally valenced (i.e., flowers). Leopards are one of the largest predators and pose an evolutionary-relevant threat to bonobos (Corredor-Ospina et al., 2021; D'Amour et al., 2006). We, therefore, predicted that bonobos would show Stroop effects when presented with leopard images (i.e., lower accuracy scores and/or longer reaction times). We also expected that the bonobos have an attention bias for preferred food items (i.e. lower accuracy scores and/or longer reaction times), similar to chimpanzees, gorillas, and Japanese macaques (Hopper et al., 2021a).

Methods

Subjects and housing conditions

Four adult bonobos (one female and three males; mean age = 14.7 years; range = 7-22 years old), that were new to cognitive studies using touchscreen technology, housed at Planckendael Zoo (Belgium) in a social group of 18 individuals, participated in the current study (Table 2.1). The bonobos were housed in an indoor enclosure (total surface 422 m^2) consisting of four main enclosures that were visible for zoo visitors, as well as six additional off-exhibit enclosures. From March – November they had access to an outdoor enclosure (3000 m^2). Fresh vegetables, fruits, browse, and primate chow was provided four times per day and the bonobos had access to water *ad libitum*.

Touchscreen sessions took place four to five times per week between 12:00 and 15:00 in the off-exhibit enclosures to avoid disturbance by zoo visitors (Huskisson et al., 2021). Participation in the touchscreen sessions was voluntary and they were conducted in social settings, i.e. the animals were not separated from group members (Cronin et al., 2017). Sessions were conducted using positive reinforcement training and conform to the guidelines of the Ex-situ Program (EEP), formulated by the European Association of Zoos and Aquaria (EAZA). This study furthermore passed the Ethics Committee of the Royal Zoological Society of Antwerp (EC-2/SGZ(10-12-19)) and conformed to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

Table 2.1: Group composition and the training phases which the individuals passed. Individuals in bold indicate the subjects who participated in this study

Subject	Sex	Age	Habituation	Shaping	Colour discrimination	Transfer task
Busira	**Female**	**16**	**Passed**	**Passed**	**Passed**	**Passed**
Habari	**Male**	**14**	**Passed**	**Passed**	**Passed**	**Passed**
Mokonzi	**Male**	**7**	**Passed**	**Passed**	**Passed**	**Passed**
Zamba	**Male**	**22**	**Passed**	**Passed**	**Passed**	**Passed**
Hortense	Female	42	Passed	Passed	Failed	
Moko	Male	4	Passed	Passed	Failed	
Nayoki	Female	8	Passed	Passed	Passed[a]	
Vifijo	Male	26	Passed	Passed	Failed	
Djanoa	Female	25	Passed	Failed		
Banya	Female	29	Failed			
Kianga	Female	15	Failed			
Kikongo	Male	6	Failed			
Sanza	Female	3	Failed			
Unabii	Female	1				
Binti [b]	*Female*	25				
Bina [b]	*Female*	4				
Balina [b]	*Female*	1				
Nayembi [b]	*Female*	14				
Nila [b]	*Female*	4				

[a] This individual was transferred to another zoo before she could complete the training

[b] These individuals arrived in Planckendael ZOO during a later training phase and were therefore not included in this study

Apparatus and general procedure

All sessions were conducted on a 22’’ Viewsonic TD2220 touch-sensitive monitor (1920 x 1080 resolution) connected to the researcher’s (DWL) computer (Figure 2.1). A second monitor allowed the researcher to review the subject’s responses in real-time. The touchscreen setup was mounted on an adjustable cart, placed outside an off-exhibit enclosure. The touchscreen was placed parallel to the enclosure mesh, allowing the bonobos to work on the touchscreen through the mesh (Figure S2.1). Training and testing tasks were designed using *OpenSesame* (Mathôt et al., 2012). Stimuli preparation was done in Adobe Photoshop version 21.2.2.

The apes were rewarded on correct responses with automatic delivery of a DK Zoological Trainings Biscuit (small) triggered by a custom-made pellet dispenser. A secondary reinforcing tone was played via two speakers behind the touchscreen. Primary and secondary reinforcers were delivered with every correct response (i.e., a 100% fixed reinforcement ratio). Additionally, we manually provided a raisin through a PVC tube on every fifth correct response to maintain the bonobo's interest. If an individual finished all trials within a session, (s)he received three peanuts. Each response was followed by a 1500 ms inter-trial interval (ITI). In case the bonobo made an incorrect response, no reinforcement was provided, and the trial was followed by an extended ITI of 3500 ms in total.

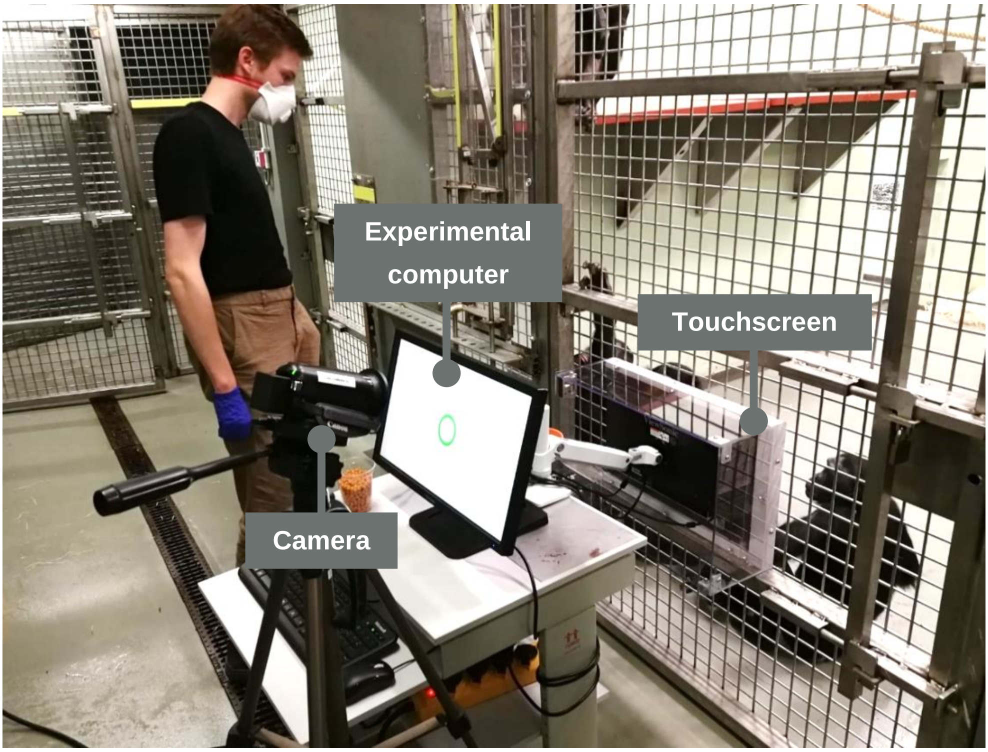

Figure 2.1: Schematic overview of the touchscreen setup placed parallel to the enclosure of the bonobos

Experiment 1: Colour-interference Stroop task

In July 2019 we started introducing the bonobos to the touchscreen setup. We habituated eight bonobos to the touchscreen setup and shaped their touching behaviour to reliably touch small targets (Table 2.1). Of these eight bonobos, five completed a colour discrimination training in which they were presented with two identical stimuli (random human objects), but that had a different colour of border. The bonobos were trained to select stimuli with a red border (RGB 254, 0, 0) over stimuli with a blue border (RGB 0, 0, 254), regardless of the content of the stimuli. The screen was divided into four quadrants, and the stimuli appeared randomly in two of the four possible locations. One bonobo was transferred to another zoo before she could finish the training, and the remaining four bonobos completed this training phase in September 2020 (accuracy >80% in 1-2 sessions (i.e., 24-48 trials) per day, over two consecutive days). A more detailed description of the different training phases is provided in the ESM.

In Experiment 1, following Allritz et al. (2016) and Hopper et al. (2021), we presented the four bonobos in each trial with two stimuli, just like in the training phases. Yet, instead of the training stimuli, we designed test stimuli to assess colour interference during the task to measure a Stroop effect (i.e., interference of the test stimuli as measured as altered accuracy scores and reaction times). The purpose of this task is to examine whether the subjects' performance, in this case selecting stimuli with a red border, would be influenced by the task-irrelevant content (i.e., the colour of the geometric shapes) within these borders. We created four, full-coloured, geometric shapes (a square, a triangle, a circle, and a diamond) in the same red and blue colour as the border colours. Each stimulus was created with a red and a blue border, resulting in 16 unique stimuli. The combination of the shape and border colour created two different conditions: congruent and incongruent trials (Figure 2.2a). For congruent trials, the shape and border colours matched for the target (red shape in red border), but not for the distractor (red shape in blue border). In incongruent trials, the shape and the border colours matched for the distractor (blue shape in blue border), but not for the target (blue shape in red border). We additionally created six control stimuli which were five randomly selected stimuli that were presented in the training transfer task and a blank with only the border. All test and control trials were presented in random order.

In September 2020, all four bonobos completed 12 test sessions, each consisting of 28 trials, over 5 days with a maximum of 3 sessions per day. If a session was not finished, it was repeated on another day. Complete blocks of unfinished sessions were included in the analyses.

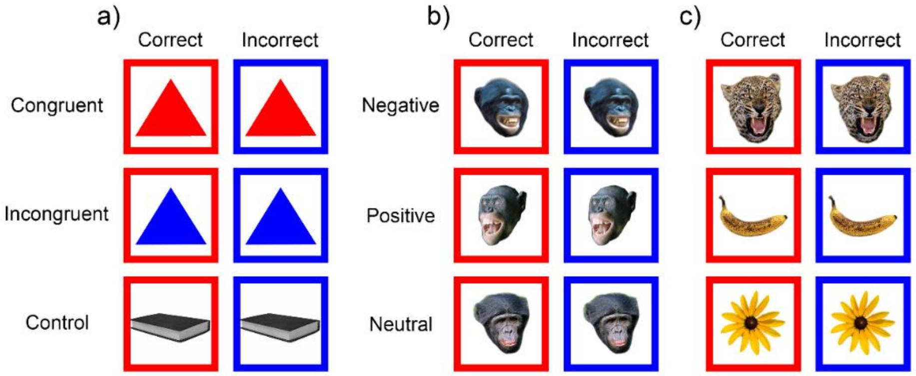

Figure 2.2: Examples of stimuli pairs used in the three experiments. (a) In Experiment 1, trials were either congruent (i.e. the correct stimulus had a red shape and red border) or incongruent (i.e. the correct stimulus had a blue shape and red border). (b) Experiment 2 included facial stimuli of unknown bonobos that were either from negative, positive, or neutral contexts. (c) In Experiment 3, stimuli consisted of valenced objects

Experiment 2: Social pictorial emotional Stroop task

For Experiment 2, we applied a pictorial emotional Stroop task (Allritz et al., 2016). Experiment 2 implemented the same methodology as Experiment 1, but instead of determining colour interference, this experiment aimed to explore the interference of socio-emotional stimuli. We, therefore, selected full-colour images of unfamiliar bonobos from a personal database (provided by JMGS). These images were categorized as either negative, positive, or neutral based on the context in which the photo was taken. Negative emotional scenes included images of individuals in distress, e.g., during conflict. Positive emotional scenes included play events. Neutral scenes included images of bonobos resting. For each category, we selected 15 images in which the bonobo showed a facial expression according to its context (examples in Figure 2.2b). We made sure that none of the images included bonobos showing a direct gaze towards the camera, as this could induce attentional biases compared to an averted gaze (Bethell et al., 2016). Within a category, each image came from a different individual. Across the categories, one individual was presented twice due to limitations in our image dataset. Images were cropped so that only facial expressions of single bonobos were visible. We then asked 9 bonobo experts (3 caregivers and 6 researchers) to score these images based on their valence (7-point Likert scale ranging from ‘extremely negative’ to ‘extremely positive’) and intensity (5-point Likert scale ranging from ‘not intense at all’ to ‘very intense’) (Kret et al., 2016). The raters showed a high intraclass correlation ($ICC(3,k)_{valence} = 0.92$, $ICC(3,k)_{intensity} = 0.95$). Based on these ratings, we selected the eight most suitable images for each category for a total of 24 images. These selected images were then trimmed so that only the bonobo's face was visible, superimposed on a white background, and checked for luminosity and colour hue values (Table S2.1).

Following Allritz et al. (2016), each testing session consisted of small test blocks as this results in the most pronounced Stroop effects in human studies (McKenna & Sharma, 2004). Each block consisted of five trials, with each trial showing two matched stimuli. Within a block, four trials were from the same category (negative, positive, or neutral), followed by one control trial (blank with coloured borders) to avoid carry-over effects. Control blocks consisted of five control trials. Each test session began with a control block, followed by three randomly selected test blocks (negative, positive, or neutral) until each test block was shown twice. Thus, each test session consisted of a total of seven blocks, or 35 trials: 8 negative, 8 positive, 8 neutral, and 11 control trials. Within each session, each stimulus was used once to avoid habituation to the images. The target and distractor could appear again in two of the four locations which were randomly determined for each trial.

We tested the four bonobos on Experiment 2 at the start of October 2020. Again, unfinished sessions were later repeated and complete blocks within these sessions were included in the final analyses. All bonobos ultimately completed 12 sessions that consisted of 35-trials.

Experiment 3: Non-social pictorial emotional Stroop task

Experiment 3 had a similar design as Experiment 2, but instead of showing facial expressions, presented non-social stimuli (Figure 2.2c). The stimuli used in Experiment 2 were similar in colour hue and luminance, and we wanted to select non-social stimuli that likewise shared such features between each other. As negative stimuli, we used images of leopards as they pose a threat in wild-living bonobos (Corredor-Ospina et al., 2021; D'Amour et al., 2006) and zoo-living bonobos also show strong responses to a leopard model (Staes et al., 2016). As positive stimuli, we decided to select images of a banana, which is a highly preferred food item among zoo-living bonobos with little between-individual variation (Verspeek & Stevens, 2020). For the neutral stimuli, we selected images of *Rudbeckia hirta* flowers. For each category, we selected eight unique stimuli, resulting in 24 test stimuli in total. Like in Experiment 2, the stimuli were trimmed so that only the object was visible, superimposed on a white background, and checked for luminosity and colour hue values (Table S2.1).

The same four bonobos completed Experiment 3 in mid-October 2020. Unfinished sessions were repeated and complete blocks within these sessions were included in the final analyses. All bonobos completed 12, 35-trial sessions.

Data preparation and statistical analyses

All testing sessions were video recorded and coded afterward to exclude outlier trials. In Experiment 2, 51 trials were not recorded due to a technical error and therefore also excluded from analyses. Next, we filtered our data on extreme values (RT < 250 ms) and detected individual RT outliers based on the median plus or minus 2.5 times the median absolute deviation (Leys et al., 2013). For the RT analyses, we only considered correct responses. The total number of trials excluded, and the number of trials entered for analyses in the three experiments are presented in Table S2.2.

We analysed two aspects in each of the three experiments: the accuracy and the reaction time. To analyse the accuracy across conditions, the software recorded for each trial whether the participant made a correct (coded as 1) or incorrect (coded as 0) response. We built generalized linear mixed models (GLMMs) using a binomial distribution with a logit link function and included subject ID, stimulus ID, and session as random intercepts. For Experiment 1 (the colour-interference test), we included colour congruency (levels: congruent, incongruent, and control) as a fixed factor. For Experiment 2 (social test) and Experiment 3 (non-social test), we included image category (levels: negative, positive, neutral, and control) as a fixed factor. We built similar models to analyse the reaction time of the bonobos but used a Gamma distribution with a log-link function instead. We then ran subject-level analyses using similar models as described above, except that the random intercept for subject ID was not included.

All models were created using the *glmmTMB* package (Brooks et al., 2017) in R version 2.15.2 (R Core Team, 2016). Post hoc analyses were performed using the *multcomp* package (Hothorn et al., 2008) using the Tukey correction for multiple comparisons. Diagnostic plots (residuals vs fitted and QQ plots) were used to examine assumptions of normality and homogeneity of variances and we additionally tested uniformity and dispersion of the residuals using the *DHARMa* package (Hartig, 2020).

Results

Experiment 1: Colour-interference Stroop task

In Experiment 1, we aimed to test for the classic Stroop effect in which task-irrelevant stimuli (i.e., geometric shapes either congruent or incongruent in colour with the target border) interfere with the original task (i.e., selecting the stimulus with the target border colour). Our model showed a significant effect of colour congruency on the accuracy (Figure 2.3a; $\chi^2 = 41.901$, df = 2, $P < 0.001$), but not on the reaction time (Figure 2.3b; $\chi^2 = 2.655$, df = 2, $P = 0.265$). The bonobos made more errors in congruent trials compared to incongruent trials ($t_{1085} = -4.065$, $P < 0.001$) and compared to control trials ($t_{1085} = -6.382$, $P < 0.001$). There was no difference in accuracy between control and incongruent trials ($t_{1085} = 1.963$, $P = 0.122$).

Subject-level analyses showed that only Busira and Habari had lower accuracy scores for congruent trials compared to control trials (both $P < 0.001$) and compared to incongruent trials ($P = 0.012$ and $P = 0.007$, respectively). Furthermore, Habari had lower accuracy scores for incongruent trials compared to control trials ($P = 0.046$). Accuracy scores for Mokonzi and Zamba were similar across conditions ($P > 0.05$). None of the bonobos showed differences in their reaction time between the conditions ($P > 0.05$). Full subject-level model outputs are presented in Table S2.3-4.

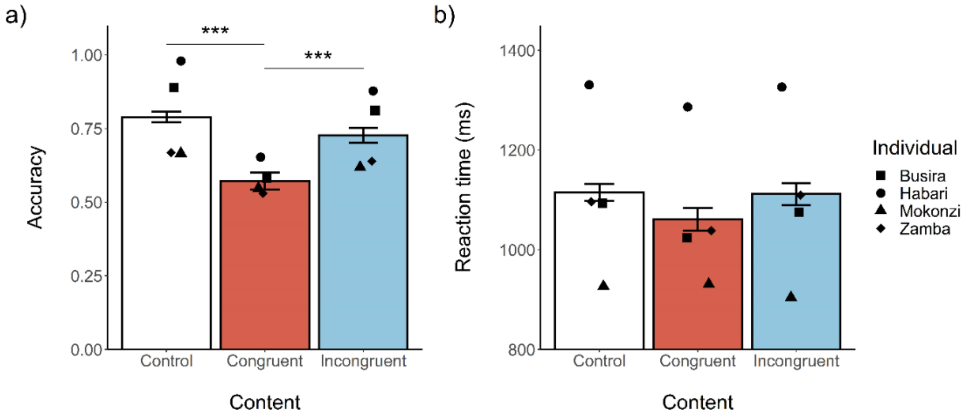

Figure 2.3: Subject average (a) accuracy scores and (b) reaction time during the colour-interference Stroop task (Experiment 1). *** P < 0.001

Experiment 2: Social pictorial emotional Stroop task

In Experiment 2, we assessed how socio-emotional stimuli, i.e., facial expressions, interfere with the performance on the pictorial emotional Stroop task. We found no effect of social stimuli on the accuracy of the bonobos during the test (Figure 2.4a; $\chi^2 = 4.887$, df = 3, $P = 0.180$), but reaction times were influenced by the social stimuli (Figure 2.4b; $\chi^2 = 12.741$, df = 3, $P = 0.005$). Specifically, bonobos were slower in touching the target when a positive social stimulus was present compared to neutral social stimuli ($t_{1013} = -3.525$, $P = 0.003$) and tended to respond faster to neutral social stimuli compared to the blank control trial ($t_{1013} = 2.331$, $P = 0.092$).

For the subject-level analyses, we found that Habari, Mokonzi, and Zamba had longer reaction times for positive trials compared to neutral trials ($P = 0.043$, $P = 0.057$, and $P = 0.047$ respectively). Habari had longer reaction times for positive trials compared to blank control trials ($P < 0.001$). Zamba was slower in touching the target in neutral trials compared to blank trials ($P = 0.001$). Busira did not show a difference in her reaction time during Experiment 2 ($P > 0.05$). Furthermore, the accuracy scores for none of the bonobos were affected by the different social stimuli ($P > 0.05$). Full subject-level model outputs are presented in Table S2.5-6.

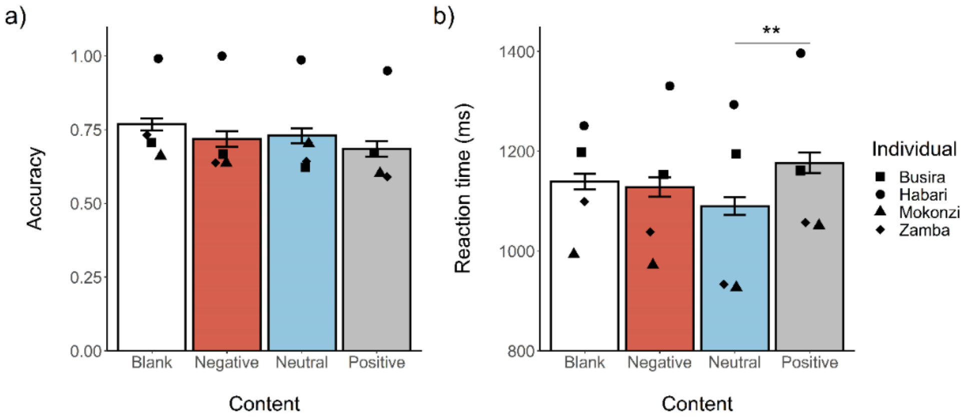

Figure 2.4: Subject average (a) accuracy scores and (b) reaction time during the social pictorial emotional Stroop task (Experiment 2). $^{**}P < 0.01$

Experiment 3: Non-social pictorial emotional Stroop task

Experiment 3 looked at how non-social stimuli interfered with the performance of the bonobos. Non-social stimuli had an effect on both the accuracy (Figure 2.5a; $\chi^2 = 33.531$, df = 3, $P < 0.001$) and the reaction time (Figure 2.5b; $\chi^2 = 27.589$, df = 3, $P < 0.001$). The

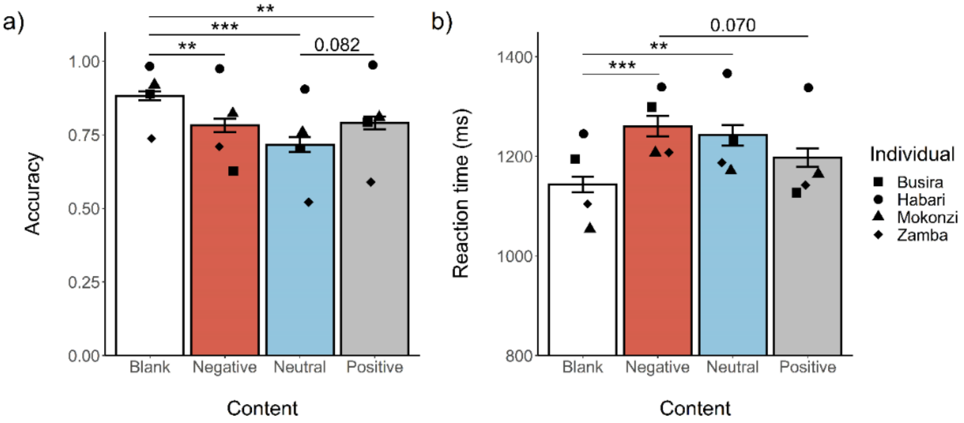

Figure 2.5: Subject average (a) accuracy scores and (b) reaction time during the object pictorial emotional Stroop task (Experiment 3). ** $P < 0.01$ and *** $P < 0.001$

bonobos made more errors with negative stimuli ($t_{1428} = 3.712$, $P = 0.001$), positive stimuli ($t_{1428} = 3.402$, $P = 0.004$), and neutral stimuli ($t_{1428} = 5.757$, $P < 0.001$) when compared to the control stimuli. The bonobos also tended to make fewer errors during positive trials compared to neutral trials ($t_{1428} = 2.376$, $P = 0.082$). The bonobos furthermore responded slower on trials with negative stimuli ($t_{1037} = -4.901$ $P < 0.001$) and neutral stimuli ($t_{1037} = -3.624$, $P = 0.003$) compared to control trials. Reaction times also tended to be slower with negative stimuli compared to positive stimuli ($t_{1037} = 2.441$, $P = 0.070$).

For subject-level accuracy scores, we found that only Busira had lower scores during negative non-social trials compared to blank trials ($P = 0.001$). Busira, Mokonzi and Zamba had lower accuracy scores during neutral trials compared to blank trials ($P = 0.019$, $P < 0.001$, $P = 0.012$ respectively). Mokonzi also had lower accuracy scores during positive non-social trials compared to blank trials ($P = 0.05$) and Zamba showed a tendency for lower neutral non-social trials compared to negative trials ($P = 0.063$). For the reaction time analyses on a subject-level, we found that both Habari and Mokonzi had slower reaction times during negative ($P = 0.033$ and $P = 0.001$) and neutral ($P = 0.009$ and $P = 0.027$) compared to blank trials. Reaction times during positive trials were also marginally slower for Habari ($P = 0.077$) and significantly slower for Mokonzi ($P = 0.037$) when compared to blank trials. Busira showed a near-significant longer reaction time for negative non-social stimuli compared to positive stimuli ($P = 0.058$). Zamba did not show any differences in his reaction time in response to any non-social stimuli ($P > 0.05$). Full subject-level model outputs are presented in Table S2.7-8.

Discussion

In the current study, we found that, when completing a colour-interference Stroop task, the bonobos made more mistakes in colour-congruent trials. We also found that the performance of bonobos during a pictorial emotional Stroop task was influenced by positive socio-emotional conspecific stimuli as well as multiple valenced non-social stimuli. Our findings reveal patterns in bonobo attention allocation that may be linked to their behavioural ecology.

We employed a Stroop paradigm that was previously used by two studies with chimpanzees, gorillas, and Japanese macaques (Allritz et al., 2016; Hopper et al., 2021a). Similar to these studies, we examined colour-interference during the Stroop task (Allritz et al., 2016; Lauwereyns et al., 2000; Washburn, 1994). Contrary to our predictions based on these studies, we found that bonobos had lower accuracy scores when presented with colour-congruent trials. Our results are, however, similar to those reported by a more recent study by Hopper et al. (2021), which also found that apes and monkeys made more errors in colour-congruent trials. Like the study of Hopper et al. (2021), our trial design differed from Allritz et al. (2016), which could potentially explain these differences. Namely, within a trial, the colours of the shapes in the two stimuli were matched while in the original study of Allritz et al. (2016) the colours of the shapes were different within a trial. This could mean that during congruent trials, the colour contrast of incorrect stimuli (i.e., red shape with a blue border) may have facilitated attention, resulting in the bonobos to select the distractor. Alternatively, during incongruent trials, the contrast of the target stimulus is higher (blue shape in red border) than the distractor stimulus, which may also have influenced the accuracy scores. We furthermore found no evidence for colour interference on the reaction time of the bonobos. This is again similar to the results reported by Hopper et al. (2021) who suggest that in their study, the familiarity of the subjects to touchscreen tasks may have caused ceiling effects in their reaction times. In our study, the bonobos were naïve to touchscreens at the start of this study, which may indicate that previous experience does not play a major role in the subjects’ reaction times. Other potential explanations addressed by Hopper et al. (2021) include too few trials to detect differences, or potential other distractors within the zoo environment. The presence of zoo visitors, for example, can alter the performance of primates on touchscreen tasks (Huskisson et al., 2021), but this is unlikely in our study as we tested the bonobos out of sight of the visitors. We furthermore filtered the reaction time data when the bonobos seemed distracted (i.e., they were not attending to the screen), which gives reason to believe that distractors do not explain the lack of reaction time effects. While Stroop effects on reaction times may be more difficult to measure in general (Beran et al., 2007), it is possible that the different trial design in the study of Hopper et al. (2021) and our current study versus the original study of Allritz et al. (2016) may explain why we did not find differences in reaction time. This suggests that when researchers are looking to find colour-interference effects on reaction times, trial design must be carefully considered.

In Experiment 2, we used valenced facial expressions of unknown bonobos as stimuli and found that positive facial expressions, i.e., play faces, led to longer reaction times. Hence, during this Stroop task, positive social information elicited stronger interference with attentional processes in bonobos than neutral stimuli. In other words, bonobos process play faces faster and/or pay more attention to them than other facial expressions. Previous cognitive studies have reported biases towards negative facial expressions in primates (King et al., 2012; Lacreuse et al., 2013; Parr et al., 2013; Tomonaga & Imura, 2009). Our observed positive bias in bonobos is therefore remarkable. However, in a study using a different paradigm, bonobos have previously shown attention biases towards affiliative whole-body scenes, such as scenes showing bonobos mating and grooming, but not towards scenes of playing bonobos (Kret et al., 2016). Our study thus gives additional support to the view of a positive attention bias in bonobos. This further suggests that play face expressions on their own, hence without other body cues, are sufficient to attract attention. Bonobos are highly social with complex social dynamics (Gruber & Clay, 2016), and emotional expressions play a pivotal role within their society. Eye-tracking studies have shown that bonobos generally pay more attention to faces and gazes than chimpanzees (Kano et al., 2015; Kano & Call, 2014), and play faces are more common during social play in bonobos (Demuru et al., 2015; Palagi, 2006, 2008), suggesting a significant communicative role of play faces in bonobo socio-ecology. Our results extend our current knowledge by adding that positive facial expressions, namely play faces, alone are sufficient to attract the bonobos' attention. Although bonobos console distressed group members (Clay & de Waal, 2013b; Palagi & Norscia, 2013), we did not find evidence that facial expressions of unknown conspecifics in distress elicited attention biases. Our results are like those reported by Kret et al. (2016), suggesting that bonobos do not show immediate attention bias towards conspecifics in distress. It is important to be aware that in our study, we limited the stimulus categories to play, distress, and neutral facial expressions. But, the repertoire of bonobo facial expressions is wider than that, and we encourage future studies to include other expressions such as aversion or disgust in response to food (Kret et al., 2020).

In Experiment 3, we found that the attention of the bonobos was altered in response to valent non-social stimuli. Regardless of the stimulus type, bonobos showed lower accuracy scores when presented with objects compared to blank trials and made marginally fewer mistakes when presented with a preferred food item, compared to presumed neutral flowers. Reaction times were also slower in trials with negative, i.e., leopards, and neutral, i.e., flowers, stimuli compared to blank trials. Positive objects, i.e., preferred food, did not influence reaction times. Human studies reporting Stroop effects typically compare valent stimuli to neutral stimuli. It is possible that the altered accuracy scores and reaction times towards valent stimuli, compared to blank trials, may not reflect a Stroop effect but rather indicate enhanced attention to these stimuli in general. Future studies could overcome this by including a category with known neutral stimuli (Hopper et al., 2021a). In our case these could have been the human objects on which the bonobos were trained. Additionally, the bonobos tended to respond slower to the leopard than to the food item. Leopards are natural predators of bonobos in the wild (Corredor-Ospina et al., 2021; D'Amour et al., 2006), and although the participating bonobos were zoo-born and have therefore never encountered a real-life leopard before, the images appeared sufficiently relevant to elicit an attentional bias. Animal studies investigating fear responses to ecologically relevant predators often use snake images (Hopper et al., 2021a; Kawai & Koda, 2016; Masataka et al., 2018; Shibasaki & Kawai, 2009). For this study, we used leopard images as zoo-housed bonobos showed strong behavioural responses to a taxidermied leopard, but not to a snake model (Staes et al., 2017). The observed effects of the leopard images on task performance indeed suggest that leopards may be ecologically relevant threats for bonobos. Lastly, the bonobos showed decreased accuracy when presented with a putative neutral object stimulus, i.e., flowers, although marginally significant. Flowers are commonly used as non-valenced stimuli in primate cognition studies (Kawai & Koda, 2016; Shibasaki & Kawai, 2009), and while the bonobos probably never encountered this specific species of flower used in this study, they are familiar with several flower species that grow in their outdoor enclosure. Recent behavioural observations on this group furthermore indicate that the bonobos do not actively consume flowers in the outdoor enclosure. At present, it remains unclear as to why flower images elicited a Stroop effect in the bonobos.

Some differences in the performance of the bonobos during the Stroop task in response to social and non-social stimuli were observed. To start, the accuracy of the bonobos was not affected when presented with social stimuli but did so with non-social stimuli. We furthermore report more significant differences between the non-social categories, although mostly compared with the blank control trials. The basis of these findings is currently unclear. One possible explanation is that the stimuli in the two experiments differed in their salience levels. For example, we limited the social stimuli to only facial cues, while in natural situations individuals typically use a combination of cues (e.g., vocal, body and facial). Nonetheless, a number of previous studies processed facial stimuli in a similar manner (Bethell et al., 2016; Parr & Heintz, 2009), suggesting that such stimuli are valid and relevant for the participating animals. We also limited social stimuli to images of individuals with an averted gaze, by means to standardize our stimulus set, which are potentially less salient. However, emerging studies indicate that differences in the degree of cognitive interference between direct and averted gaze stimuli depends on the individual's affective state, i.e. primates in negative affective state experience higher interference with a direct gaze (Bethell et al., 2016; Cronin et al., 2018). Alternatively, it is possible that low-level features, such as colours, contrasts or line orientations, can explain these difference (Tomonaga & Imura, 2015), although we controlled for such factors within the two experiments, but not between them.

One limitation of our study is our sample size. Although our sample size falls within the average range of participating subjects in great ape studies using touchscreen technology (Egelkamp & Ross, 2018), we should be cautious to draw broad ecological conclusions, also taking the limited stimulus categories into account. The fact that all the individuals in this bonobo group were naïve to, not only this paradigm, but to touchscreens in general arguably played a role in the low training succession ratio. Despite that, we believe that this type of cognitive research, including ours, in zoological institutions yields informative and scientifically valid data which is often not feasible to collect in other settings. Studies like this on endangered species, or those that are rarely found in captive settings, such as the bonobo, are therefore highly relevant to the scientific community (Hopper, 2017) and, on top of that, can be enriching for the participating individuals which contributes to their welfare (Cronin et al., 2017).

One important aspect that is often not addressed in similar studies, but that we report, are subject-level effects. Especially in studies with smaller sample sizes, individual subjects may influence group-level effects. Hence, these kind of studies showcase the added value of considering individual differences and subsequent potential subject-level effects (see also Vonk (2021), this issue). Indeed, we found individual variation in the accuracy scores and reaction times in response to the test stimuli across the three experiments. Given the current sample size, we cannot link these variations to individual variables, such as sex or personality traits, although this would be interesting for future studies. On top of that, while innate attention biases may be species-wide, they can also be affect-driven in animals (Crump et al., 2018), and the pictorial emotional Stroop task may be able measure changes in internal affective states. The original study by Allritz et al. (2016), for example, found that the performance of the chimpanzees was most influenced in individuals that were most recently anesthetized. While we cannot make such conclusions from the current study, it is noteworthy that three out of four bonobos had longer reaction times to positive facial stimuli. Future studies in bonobos and other species could use state-induction procedures to examine how attention biases are modulated by internal affective states. While humans show a significant, albeit moderate, bias towards positive emotional stimuli (Pool et al., 2016), positive biases to facial stimuli were associated with positive affectivity and heightened optimism (Mauer & Borkenau, 2007), positive emotions (Sanchez & Vazquez, 2014; Strauss & Allen, 2009), higher trait emotional intelligence (Lea et al., 2018) and higher tendencies for prosocial behaviour (Troller-Renfree et al., 2015). These are interesting directions for future research as bonobos are often considered more empathizing than chimpanzees (MacLean, 2016).

Conclusions

In conclusion, the bonobos in our study showed altered attentional processing towards positive social stimuli and different non-social stimuli. The presented stimuli were selected for their biological relevance to bonobos specifically, and the reported attention biases indeed confirm their significance. The observed positive bias towards social stimuli supports previous studies that highlight the importance of affiliative behaviours and expressions among bonobos. Our results further extend our knowledge by reporting that, compared to facial expression of distress, play faces may especially occupy a significant role in bonobo society. Apparent attention biases towards non-social stimuli were also observed and may give some insight into innate attention allocation related to the behavioural ecology of bonobos. Ultimately, this enhances our understanding of bonobo emotion recognition and attentional processing.

3

Affect-congruent attention biases in bonobos: Investigating the impact of emotional priming

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Laura S. Lewis, Jonas Verspeek, Jeroen M. G. Stevens

Abstract

Within group-living species, efficient social orienting plays a major role in directing social dynamics between individuals. Attention biases toward socio-emotional stimuli facilitate this process as they trigger corresponding action tendencies. However, little is known about how emotional states modulate the attention of great apes to facial expressions of conspecifics. In this study, we sought to investigate the impact of viewing valenced video scenes on emotional arousal in bonobos and if this influences subsequent social information processing. To address this question, we used a combination of pupillometry and a novel modified version of the 'face in the crowd paradigm'. We primed emotional states in 12 bonobos by showing them valenced videos of a) bonobos engaging in positive, negative, or neutral interactions, and b) humans with whom they have positive, negative, or neutral associations. These videos were then followed by a series of configurations of competing static facial expressions of unfamiliar bonobos displaying positive, negative, or neutral emotions. We first analysed changes in pupil size in relation to the stimuli. Using the percentual change in pupil size and time course analysis, we found that bonobo primer videos generally resulted in pupil dilation, whereas human primer videos led to pupil constriction. Time course analysis revealed minor differences in the trajectory of pupil sizes between the primer videos, but ultimately showed no significant differences. Next, we studied whether these valenced video scenes influenced the bonobos' attention biases for static facial expressions. We found that the bonobos showed a general emotion bias, and preferentially attended to images of conspecifics expressing distress signals. This negativity bias was not influenced by the priming condition. These findings contribute to our understanding of attentional processing in bonobos, but overall did not find support for affect-congruent attention biases.

Introduction

Sensory systems are limited by the amount of input they can process, and rapid selection of relevant stimuli is necessary for adaptive behaviours (Anderson, 2005; Pourtois et al., 2013; Schupp et al., 2003). Such attention biases are widespread across species and are typically shaped by evolutionary pressures. For example, attention biases aid in navigating the environment by rapidly locating potential threats (Öhman, 2009). Social dynamics are characterised by a complex interplay of cognitive processes and behavioural responses to socio-emotional stimuli (Kret et al., 2020). Judging emotional expressions can inform group members about the expresser's internal state and future behaviours (Shariff & Tracy, 2011; Waller et al., 2017). The ability to efficiently discriminate relevant social cues of conspecifics is critical for maintaining group cohesion and ensuring adaptive decision-making (Laméris et al., 2020; Öhman, 2002; Vuilleumier, 2005; Whitehouse et al., 2017; Yiend, 2010).

Biased attention for emotional expressions in others is shared across primate species (Lacreuse et al., 2013; Laméris et al., 2022b; Pritsch et al., 2017). Facial expressions among primate societies evolved depending on their socio-biology (Dobson, 2012), and while many homologies exist, their use and function may differ between species (Kret et al., 2020). Social styles can influence patterns of attention biases for emotional expressions across species. For example, rhesus macaques (*Macaca mulatta*) and long-tailed macaques (*Macaca fascicularis*), who are relatively despotic (Matsumura, 1999; Thierry, 1985), have been experimentally shown to exhibit biased attention for threatening faces (King et al., 2012; Lacreuse et al., 2013; Parr et al., 2013). In contrast, bonobos have been shown to exhibit attention biases towards affiliative scenes (Kret et al., 2016), play faces (Laméris et al., 2022b), and sustained attention for facial expressions signalling distress (van Berlo, 2022), which may be linked to their social style which is often described as egalitarian (de Waal, 1997), and tolerant (Fruth & Hohmann, 2018; Hare et al., 2012; Tan et al., 2017). However, the latter is disputed and bonobos are also considered as semi-despotic (Stevens et al., 2007) and intolerant (Jaeggi et al., 2010).

Interestingly, a number of experimental studies did not find evidence for attention biases for emotional information in chimpanzees (Kret et al., 2018; Wilson & Tomonaga, 2018), and orangutans (Laméris et al., 2022a). While these studies discuss methodological explanations, an increasing number of animal studies indicate that different factors may modulate attention biases which may obfuscate effects within populations. For example, attention is stronger for emotional expressions in unfamiliar individuals in bonobos (van Berlo et al., 2023), or is attracted to the dominant sex in chimpanzees, bonobos (Lewis et al., 2021), and rhesus macaques (Watson et al., 2012). Age of the individual may also modulate attention as indicated by infant rhesus macaques who preferentially orient attention towards female macaques (Paukner et al., 2009).

The variation between studies can also potentially be explained by the affective state of the individual perceiving the stimulus. While it is known that in humans an individual's affective state can modulate many (subtle) cognitive processes, including attention (Yiend, 2010), this factor is rarely taken into account in animal studies. Human studies report evidence for affect-congruent attention biases in which people with affective disorders detect affect-congruent faces faster (Becker & Leinenger, 2011; Unruh et al., 2018) and show maintained attention to, and impaired capacity to disengagement with negative information (Koster et al., 2005). Negative affect also decreases attention for positive social information (Sears et al., 2010) and can have extended effects on positive information processing (Li et al., 2016). Moreover, some evidence exists that positive affective states may enhance attention for positively valenced social stimuli (Mauer & Borkenau, 2007; Sanchez & Vazquez, 2014; Strauss & Allen, 2009), although these positive affect-congruent effects are generally not as strong as those found in people with negative affect (Pool et al., 2016).

In studies of primates, a limited number of studies find support for similar affect-driven attention biases (Crump et al., 2018). Macaques in negative affective states show enhanced attention for the direct gaze of conspecifics (Bethell et al., 2016; Cassidy et al., 2021; Cronin et al., 2018). Although such direct gazes do not signal clear emotional information, individuals with negative affect may interpret them as potentially threatening, leading to enhanced attention. Chimpanzees show altered performance on a pictorial Stroop task when presented with images of the veterinarian, and this effect is stronger in individuals with more recent medical interventions (Allritz et al., 2016). In our previous study, using the same Stroop task, bonobos showed a general attention bias for play faces, although individual-level analyses revealed that not all bonobos exhibited this effect (Laméris et al., 2022b). This raises the question if other factors, such as an individual's affective state, modulate the attentional processing of facial expressions, just like the affect-congruent attention biases observed in human studies (Bar-Haim et al., 2007; Pool et al., 2016).

In the current study, we sought to examine if attention biases for emotional facial expressions in bonobos can be influenced by their affective states. Repeatedly and reliably priming changes in affective states is challenging in animal studies. Environmental enrichment is often used to induce shift towards positive affect (Bethell et al., 2012a), while veterinary visits may be perceived as negative and can induce changes in cognitive (Allritz et al., 2016; Bethell et al., 2016) and physiological (Verspeek et al., 2021) correlates of negative affect. However, these primer methods tap into different affective mechanisms, complicating the direct comparisons of the effects within a similar paradigm. Within the human literature, the most effective method to induce emotions makes use of valenced video clips (Fernández-Aguilar et al., 2019; Schaefer et al., 2010; Siedlecka & Denson, 2019). Different types of video clips can be used, depending on the direction of the desired affective shift. Several studies have investigated how primates view video clips (Kano & Tomonaga, 2010; Parr, 2001). Physiological markers suggest that primates show affective responses when viewing emotional scenes, including changes in skin temperature (Kano et al., 2016; Parr & Hopkins, 2000) and heart rate (Wang et al., 2023). Pupillometry is another physiological correlate of emotional arousal, guided by the autonomic nervous system, but has not yet been widely applied to measure emotional arousal in response to viewing video scenes in primates.

The aim of this study was to examine whether viewing emotionally charged videos elicits emotional arousal in bonobos and, in turn, how this influences socio-emotional information processing. As such, we first investigate whether valenced scenes induce emotional arousal in bonobos. Second, we examine whether watching valenced videos subsequently leads to affect-congruent attention biases. We hypothesised that both positively and negatively valenced video sequences would lead to pupil dilation in bonobos, as in other species pupils tend to dilate in response to emotional arousal, regardless of emotional valence (Bradley et al., 2008). Furthermore, based on existing human literature, we hypothesised that the bonobos would allocate more attention to positive facial expressions after viewing positive videos (Pool et al., 2016). and would allocate more attention to negative facial expressions after viewing negative videos (Bar-Haim et al., 2007; Yiend, 2010).

Methods

Ethical statement

Eye-tracking sessions were conducted using positive reinforcement and conform to the guidelines of the Ex-situ Program (EEP), formulated by the European Association of Zoos and Aquaria (EAZA), and complied with the ASAB guidelines (ASAB, 2020). Participation in these sessions was voluntary, and the bonobos were never separated from group members for the purpose of this study. This study was furthermore approved by the Ethics Committee of the Royal Zoological Society of Antwerp (EC-2/SGZ(10-12-19)) and conformed to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

Subject and housing

Twelve bonobos (7 females and 5 males; mean age = 10.9 years, range = 2-30 years), at Zoo Planckendael (Belgium) participated in the current study (Table 3.1). The bonobos were housed in an indoor enclosure (total surface 422 m^2) consisting of ten enclosures of which four main enclosures were visible for zoo visitors. When temperatures allowed, the bonobos had access to an outdoor enclosure (3000 m^2). Fresh vegetables, fruits, browse, and primate chow was provided four times per day and the bonobos had access to water *ad libitum*.

Table 3.1: Subject information

Subject	Sex	Birth year	Age
Banya	Female	1990	30
Bina	Female	2015	5
Moko II	Male	2016	4
Nila	Female	2015	5
Sanza	Female	2017	3
Unabii	Female	2019	2
Habari	Male	2006	14
Kianga	Female	2005	15
Kikongo	Male	2014	6
Mokonzi	Male	2013	7
Nayembi	Female	2006	14
Vifijo	Male	1994	26

Figure 3.1: Overview of the eye-tracking setup

Eye tracking setup

Following previous studies in other species (Hopper et al., 2021b), we tested the bonobos using established restrain-free eye-tracking procedures, by presenting visual stimuli on a 23” monitor, approximately 60 cm outside of their enclosure (Figure 3.1). The bonobos viewed the stimuli on the monitor through a transparent polycarbonate panel. A nozzle delivering diluted fruit juice to the bonobos was placed on the panel to keep the bonobos in position directly in front of a Tobii X60 eye-tracker (Tobii Technology AB, Stockholm, Sweden). This eye-tracker was positioned below the monitor and tracked the eye movements and pupil diameter of the bonobos, through Tobii Studio on a connected laptop. We used an external webcam to record the behaviour of the bonobos while they were tested.

Each bonobo completed a two-point calibration in the outer corners of the monitor. Calibrations were manually checked for accuracy prior to each testing session using nine fixed points on the screen.

Stimuli

We presented the bonobos with two types of stimuli: videos and still-images. Video stimuli included 10 s long scenes of bonobo or human models. The bonobo scenes consisted of unfamiliar conspecifics showing positive, negative, or neutral emotional expressions. Positive scenes included playful interactions; negative scenes included scenes of individuals showing signs of distress; and neutral scenes showed individuals resting or locomoting. We matched the bonobo videos for the number of individuals present and background settings. To see if the bonobos showed differential emotional reactions depending on the model in the video, and because we wanted to control for the possible matching-effect of bonobo video scenes and subsequent image stimuli, we decided to also include videos with familiar human models, with whom we predicted the bonobos to have positive (i.e., caretaker), negative (i.e., veterinarian) or neutral (i.e., zoo-guide) associations. All human videos were recorded from the upper body, and the human models were asked to wear similar clothing to control for low-level features such as contrast and luminance. Because the caretakers and veterinarian usually wear a facemask, we asked all human models to wear a facemask. Although apes likely categorise humans with facemasks (Leinwand et al., 2022), we wanted to ensure that the bonobos made the correct association and asked the human models to interact with an object that is typical for them. For the caretaker, this was a bowl with rewards used during daily training, for the veterinarian a sedation dart, and for the zoo-guide this was a booklet. Both bonobo and human scenes were checked for video-average luminance by calculating frame-by-frame luminance values and if considerable deviations were present, we manually corrected the luminance.

Still-image stimuli consisted of cropped facial expressions of bonobos, unfamiliar to the test subjects. We selected facial expressions based on our previous findings (Laméris et al., 2022b), which included play faces, bared-teeth faces and neutral expressions. We applied a modified version of the ‘face in the crowd’ paradigm, using conflicting emotional stimuli (Halamová et al., 2022). We created a 2-by-2 matrix of one positive, one negative and two neutral stimuli. All stimuli were matched based on facial direction, luminance (Table S3.1), and were selected from a larger database of pictures based on their valence and arousal ratings (Table S3.2). Location of the stimuli within the matrix was randomised.

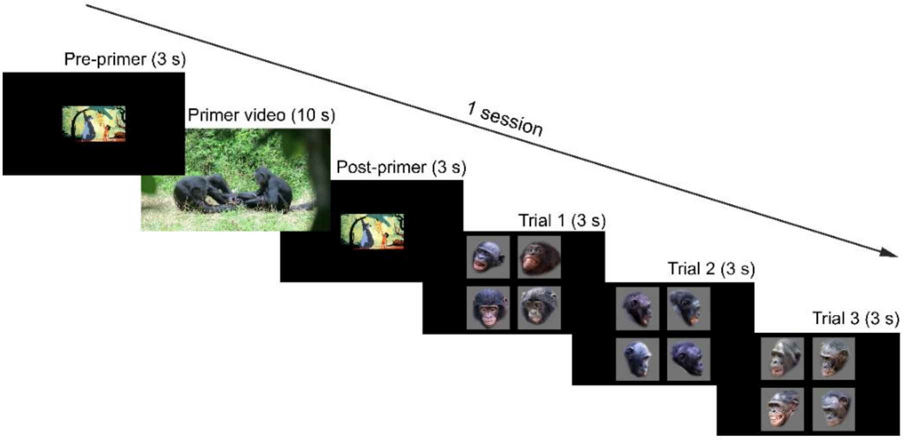

Figure 3.2: Session outline. The calibration screen at the beginning of the session, and the fixation points before each of the trials are not shown here

Procedure

Most bonobos in this study had participated in previous eye-tracking studies (Lewis et al., 2021). We habituated newly participating individuals over a couple of days by presenting them with videos non-related to this study.

We created a total of 18 different sessions. Each session consisted of the following sequence (Figure 3.2): 1) a 9-point calibration screen to manually check the accuracy of the participant's calibration, 2) a 3 s pre-primer video fragment of a cartoon that was included as a baseline measure for pupillometry data, 3) a 10 s primer video of either the bonobo or human model, 4) a 3 s post-primer video cartoon fragment, 5) a series of 3, 3 s trials of the 2-by-2 matrix. Apart from the 9-point calibration sequence, which was manually controlled, all other sequences continued automatically. Each 2-by-2 trial was preceded by a 0.5 s fixation point in the middle of the screen. The primer videos consisted of either bonobo or human videos with a positive, negative, or neutral valence. For each category (model x valence), we created three versions, totalling 18 videos.

We planned for each participant to complete all 18 sessions. However, because participation was entirely voluntary, not all bonobos completed all sessions. We also manually checked whether fixations occurred in the different segments and based on this we decided to repeat sessions if deemed necessary, so some bonobos did more than 18 sessions.

Data processing and statistical analyses

Fixations were calculated using Tobii Studio’s I-VT Filter. Data processing and analyses were done in RStudio (R Core Team, 2020). We pre-processed the pupillometry data following recommendations (Kret & Sjak-Shie, 2019; Mathôt et al., 2018) and removed blinks, including 100-ms before and after. We furthermore applied a quantile cut-off filter (removing the upper 10% of sample to sample differences) and a linear interpolation to sample gaps up to 500 ms (Hepach et al., 2017, 2021). Finally, data for both left and right eyes were averaged, filtered, and interpolated again.

Within each session, we analysed three components. First, we analysed changes in pupil size in two different analyses. We used data from 396 sessions (mean per individual = 37.0, SD = 11.2) to measure changes in pupil size before and after viewing the primer videos. Second, we also ran additional exploratory time course analysis to test for changes in pupil size while watching the 10 s primer videos, using data from 502 sessions (mean per individual = 47.8, SD = 14.2). Third, to test for changes in social information processing, we analysed gaze patterns for the facial expressions in the trials with the static images. Data from 338 sessions (mean per individual = 28.2, SD = 7.9) were entered in the analyses.

To analyse the percentual change in pupil size after viewing the primer videos, we calculated the mean pupil size for each pre- and post-primer fragment. We used Generalised Linear Mixed Models (GLMMs) with a Gamma distribution and log link, and set mean post-primer pupil size as dependent variable, and included pre-primer pupil size as a control variable to correct for differences in baseline pupil size (Gelman & Hill, 2006). We included the following independent variables: primer valence (levels: negative, neutral, positive); primer model (levels: human, bonobo); the number of times the session was repeated. The primer ID, as well was the session nested within subject were included as random intercepts. Because participants differed in the extent to which they attended to the eye-tracking sessions, we calculated weights for each session by dividing the data quality (i.e., proportion of datapoints registered over the possible amount of datapoints) by the average data quality per participant.

We ran additional exploratory analysis on the change in pupil size during the primer video itself. For this, we conducted a subtractive baseline correction, based on the pupil size during the pre-primer fragment (Mathôt et al., 2018). We fitted a Generalised Additive Mixed Model (GAMM) with a Gaussian error structure (van Rij et al., 2019), with baseline corrected pupil size as the dependent variable. We created a six-level categorical predictor named Condition which implements the interaction between valence and model (levels: Bonobo Neutral, Human Neutral, Bonobo Positive, Human Positive, Bonobo Negative, Human Negative). Condition was included in the model as a linear term, as well as a non-linear term over time (with the upper limit for the number of knots set to 20). To account for differences in pupil size caused by gaze position, we included a non-linear interaction between the X and Y gaze positions (Mathôt et al., 2018; van Rij et al., 2019). To correct for autocorrelation in the data, we included an additional random smooth factor for each individual Session time series (Sóskuthy, 2017), and an AR1 error model for the residuals ($\rho = 0.92$). To further account for not normally distributed residuals, we modelled the data following a scaled *t* distribution (Wood et al., 2016). We assessed the model fit by inspecting the correlations between the residuals and the lagged residuals, a QQ-plot of residuals as well as the residuals against the fitted values using the functions 'gam.check' of package 'mgcv' and 'acf' of package 'stats'. We again applied weights in a similar fashion as described above.

To analyse gaze patterns, we defined areas of interest (AOIs) for the four images in each trial, including a 50-pixel buffer on each side of the image. We only performed gaze analyses on trials in sessions where the participant viewed the primer video. We determined the total fixation duration for each AOI in each trial and calculated the proportion looking duration (PLD) for each of the three stimulus categories (neutral: PLD_{Neu}; negative: PLD_{Neg}; and positive: PLD_{Pos}). To measure the level of attention for the different facial expressions, we used Bayesian mixed modelling. We ran three models, one for each of the stimulus categories. The first model, with the neutral facial expressions as the dependent variable (PLD_{Neu}) examined if the bonobos showed a general attention bias for emotional facial expressions over neutral ones. Given that two neutral images were included in each trial, PLD values below, and credible intervals not encompassing, 0.5 indicates a bias away from neutral images, and hence towards either of the two emotional images. For PLD_{Neg} and PLD_{Pos}, a threshold of 0.25 was maintained. We included the following independent variables in the models: primer valence (levels: negative, neutral, positive), primer model (levels: human, bonobo) and their two-way interaction. Primer valence and primer model were sum-coded. Trial order (first, second, third) was added as a continuous control variable. Trial ID, nested in Session ID, nested in subject ID was included as random intercept, as well as a random intercept for primer ID. Bayesian models included a zero-one-inflated beta distribution to account for proportional data. We used weakly informative priors, including a prior with a normal distribution (M = 0, SD = 1) for the intercept and *b* estimates. Another prior with a half cauchy distribution (M = 0, SD = 1) was included for the standard deviation. We ran 4 chains and 4000 iterations, including 1000 warm-up iterations. Each model included a weight control based on the total fixation duration while looking at the images. To ensure that the bonobos viewed the primer video, we only analysed trials in sessions where >30% of the possible data in the primer were recorded.

To test the model fit, we followed the guidelines set out in the WAMBS checklist (Depaoli & van de Schoot, 2017). We found an accurate reflection of the original response values by the posterior distributions, acceptable R-hat statistics <1.05, sufficient effective samples >1000, and no divergent transitions in MCMC chains. Bayesian models were performed using the brms package (Bürkner, 2017). We report Bayesian results according to the Bayesian Analysis Reporting Guidelines (Kruschke, 2021), and describe the effects based on the median estimate, median absolute deviation (MAD) and 89% credible intervals (CrIs), following recommendation by McElreath (2018). We also report the probability of direction (pd), which reflects the certainty with which an effect goes in a specific direction, using the bayestestR package (Makowski et al., 2019).

Results

Change in pupil size

In the model assessing whether the pupil size differed in the post-primer fragment compared to the pre-primer fragment, we found no significant interaction effect of primer valence by model (Figure 1A: $\chi^2 = 4.652$, df = 2, $P = 0.098$). A reduced model without the interaction revealed a significant main effect of primer model ($\chi^2 = 7.668$, df = 1, $P = 0.006$) where the pupil size was larger after watching bonobo videos compared to human videos ($z = 2.616$, $P = 0.009$). Repetition of the primer video furthermore had no impact on change in pupil size ($\chi^2 = 1.977$, df = 1, $P = 0.160$)

Time course analysis

The model summary showed a significant change of baseline corrected pupil size over time for each of the Conditions (Figure 3.3B-C, Table 3.2). Difference curves indicated some differences in the pupil size between the conditions (Figure S3.1). Specifically, when watching bonobo videos, between 3,625 - 3,936 ms, pupils were larger for negative videos compared to neutral videos, whereas between 5,492 - 6,736 ms pupils were smaller when viewing positive videos compared to neutral videos. When comparing pupil sizes between positive and negative videos, pupils were smaller for positive videos between 3,936 - 4,247 ms, and between 5,284 - 6,425 ms. For the human videos, bonobos had smaller pupils during negative than neutral videos between 1,655 - 8,706 ms, and likewise smaller during positive than neutral videos between 1,862 - 4,144, between 5,907 - 6,425, and between 9,255 - 10,000 ms. When comparing positive and negative videos, pupil sizes were larger between 6,529 – 6,944 ms during positive videos.

Table 3.2: Results of the GAMM model

Parametric coefficients	*Estimate*	*SE*	*t-value*	*P-value*
(Intercept)	-0.214	0.026	-8.342	<0.001
Condition: Bonobo Neutral	-0.029	0.038	-0.789	0.430
Condition: Bonobo Positive	-0.072	0.039	-1.868	0.062
Condition: Human Negative	-0.225	0.038	-5.930	<0.001
Condition: Human Neutral	-0.016	0.038	-0.434	0.664
Condition: Human Positive	-0.188	0.378	-4.973	<0.001
Smooth terms	*edf*	*Ref.df*	*F*	*P-value*
s(Time)Condition: Bonobo Negative	18.25	18.72	57.98	<0.001
s(Time)Condition: Bonobo Neutral	18.55	18.86	62.38	<0.001
s(Time)Condition: Bonobo Positive	18.53	18.87	87.04	<0.001
s(Time)Condition: Human Negative	18.60	18.88	156.60	<0.001
s(Time)Condition: Human Neutral	18.35	18.80	117.55	<0.001
s(Time)Condition: Human Positive	18.62	18.90	160.67	<0.001
s(Ygaze, Xgaze)	26.80	28.61	39.03	<0.001
s(Time, SessionID)	3439.84	4079.00	68.25	<0.001

Notes: Reference category of condition: Bonobo Negative

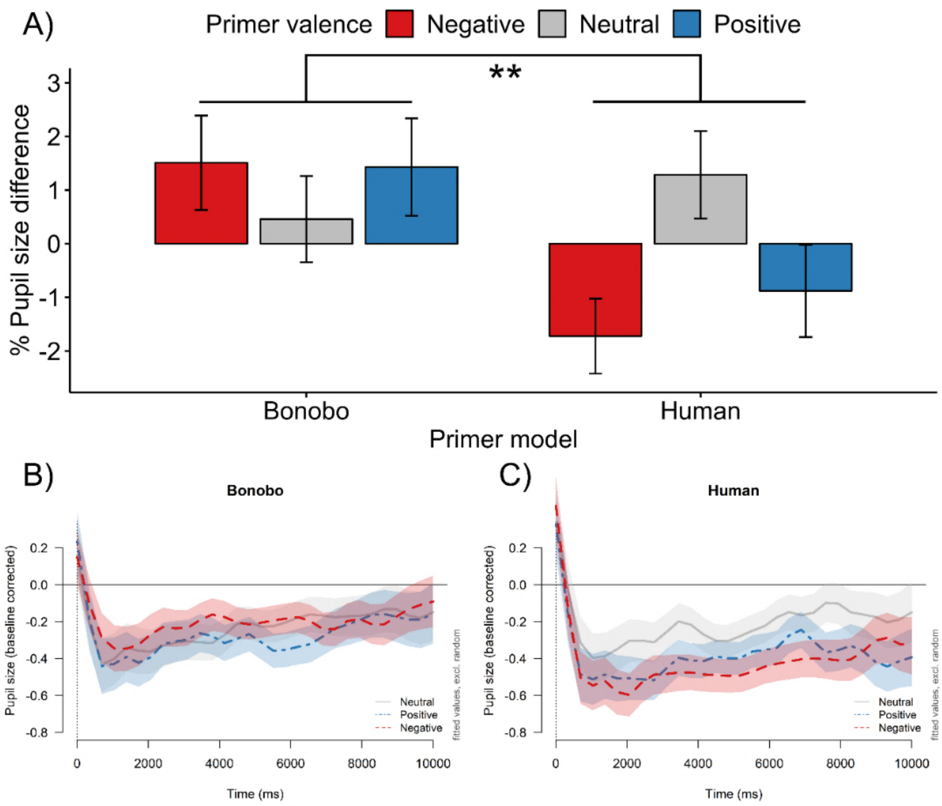

Figure 3.3: Pupil size across the different primer video depending on valence and model, expressed in percentual change (± SE) based on the pre- and post-primer measures (A), and time series plots for baseline corrected pupil size (± SE) during the primers for bonobos (B) and human models (C). ** *P* < 0.01

Gaze patterns

When looking at the gaze patterns of the bonobos after viewing the different valenced primer videos, we found an overall emotion bias, which was foremost driven by negative facial expressions (Table S3.3, Figure 3.4). There was no evidence for an interaction effect between primer model and valence on either of the attention biases (Table S3.4), and attention bias was generally unaffected by the type of primer video (Table S3.5). We did however see that, as stimulus presentation progressed within a session, attention shifted as bonobos paid more attention to the negative facial expressions (β = 0.14 ± 0.05, 89% CrI [0.06, 0.22], pd = 99.60%), and less to neutral facial expressions (β = -0.16 ± 0.05, 89% CrI [-0.24, -0.08], pd = 99.87%).

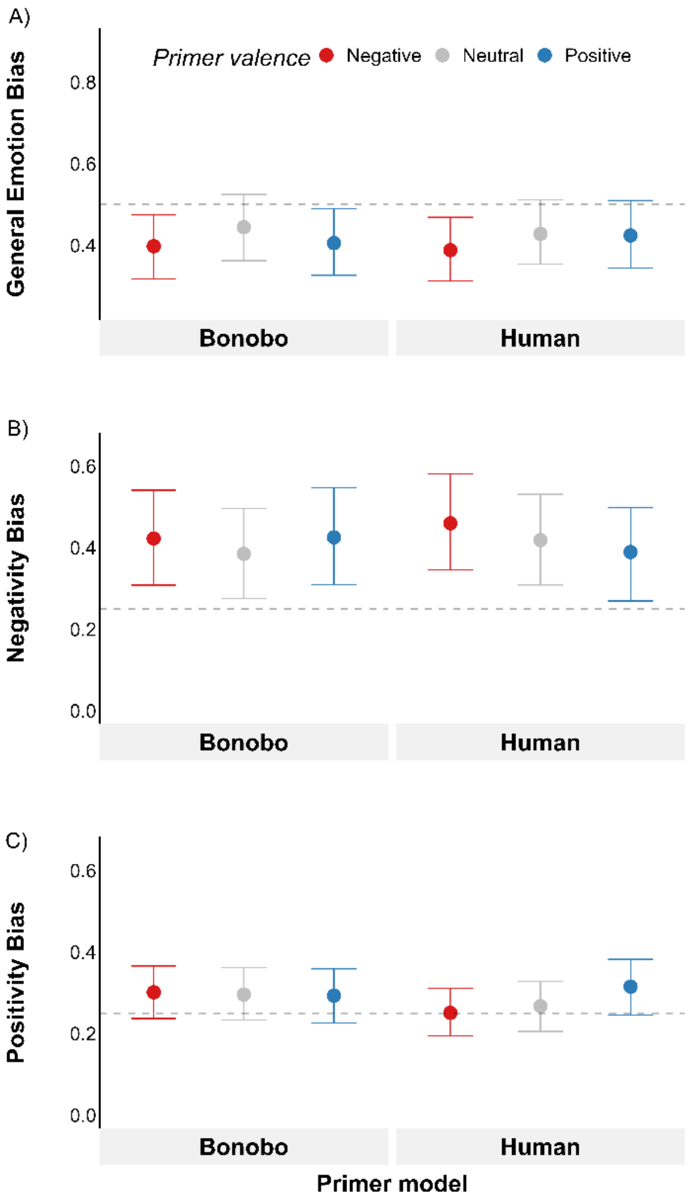

Figure 3.4: Proportion Looking Duration (± CrI) for emotional stimuli in general (A), negative facial expressions (B), and positive facial expression (C), depending on the primer valence and model. Threshold for an emotion bias is if median < 0.5 and 89% CrI does not involve 0.5. Threshold for a negativity and positivity bias is if median > 0.25 and 89% CrI does not involve 0.25

Discussion

This study sought to investigate whether viewing valenced videos induces emotional arousal in bonobos and, subsequently, if this affected their socio-emotional information processing. While we found an increase in pupil size following the viewing of bonobo primer videos, there was no discrimination between positive, negative, and neutral valenced scenes. Time course analyses revealed certain changes in the trajectory of pupil sizes during the primer video between the conditions, but this ultimately did not lead to overall significant differences. We found that bonobos preferentially attended to negative facial expressions of unfamiliar conspecifics, as opposed to positive or neutral expressions. This effect was not modulated by the specific type of primer video shown prior, suggesting we found no clear evidence for affect-congruent attention biases.

Apes have been shown to respond emotionally to valenced videos in a number of studies (Kano et al., 2016; Kano & Tomonaga, 2010; Parr, 2001; Parr & Hopkins, 2000; Wang et al., 2023), and our results add to this body of literature to some extent. However, the results for the changes in pupil size were rather ambiguous. Our analyses of relative changes in pre- and post-primer fragments, suggest that the bonobos' pupils dilated when viewing videos of conspecifics, whereas they constricted when viewing human videos, with no clear modulatory effect of primer valence. However, when we used time course analysis to look at the trajectory of change in pupil size while watching the primer videos, it appeared that pupils slightly dilated for all videos, regardless of primer model or valence. This furthermore revealed that pupils initially showed a rapid constriction within the first second, and then gradually increased. Interestingly, this initial drop, known as the initial light reflex (0 ~ 2,000 ms, Goldwater 1972), appeared weaker for the Neutral Human videos compared to all the other videos. Although pairwise comparison did not indicate any significant differences (Figure S3.1), it is still worth addressing possible explanations for this discrepancy. The initial light reflex is highly influenced by low-levels features, such as luminance (Hess et al., 1975). We carefully calculated frame-by-frame luminance values for each of the primer videos, and if needed adjusted overall luminance values. The average luminance value of the Neutral Human videos did not divert much from the other videos, which makes this an unlikely explanation for the observed effect (Table S3.1). It could be that other compositional differences can explain this discrepancy. We visually matched the videos based on contrast and overall colour hue, but it is possible that other, more fine-grained features influenced the light reflex, such as local contrast or brightness values (Bradley et al., 2017).

The light reflex may also be modulated by emotional content (Snowden et al., 2016), but typically the initial light reflex is attenuated (Bradley et al., 2017; Henderson et al., 2014), rather than exaggerated as we observed in the analyses of pupil size in the human videos. Hence this does not seem to explain this difference. Alternatively, previous studies have shown that novelty can impact the initial light reflex (Bitsios et al., 1996; Henderson et al., 2014). We selected human models for the primer videos based on their presumable familiarity for the bonobos, and their predicted associations. It is possible that the zoo guide was not appropriate for this purpose. He works in the zoo for several decades and has often been in the public area of the bonobo house but has never directly interacted with the bonobos. This could explain why the change in pupil size shows a different, albeit not significant, pattern compared to the Positive and Negative Human videos, as great apes show different attentional processing of humans based on their familiarity (Leinwand et al., 2022). When focusing on the late pupil response (> 2,000 ms, Kinner et al., 2017), some differences in pupil dilation occurred, yet mostly between the Human primers. That is, pupils dilated more for the Neutral Human video compared to the Positive and Negative ones, although this is likely the result of the attenuated light response for the Neutral videos. No meaningful differences were observed between the Bonobo videos. Altogether, while it seems reasonable to conclude that the bonobos affectively responded to conspecific videos, we should be careful in the interpretation of the change in pupil size between the bonobo and human videos.

In terms of attention biases, we found that bonobos look more at emotional facial expressions compared to neutral ones. This is not surprising, as evolutionary theories predict a general bias for emotional expressions over neutral expressions (Öhman, 2002; Pourtois et al., 2013; Vuilleumier, 2005). However, our study is the first to apply this novel paradigm in great apes with multiple competing emotional stimuli (Halamová et al., 2022). Instead of contrasting one emotional stimulus with a neutral one, our study design arguably presented a more socio-ecologically relevant situation, which could have resulted in altered attentional processing. The fact that the general emotion bias holds in more complex stimulus configurations suggests that this is a deeply rooted cognitive process. This offers perspectives for future testing of attention biases in great apes. Additionally, we found that the bonobos' attention was captured by negative facial expressions, specifically those of individuals in distress. This contrasts previous studies that found implicit attention biases towards affiliative scenes in bonobos (Kret et al., 2016), including our own results reported in Chapter 2 where we found an attention bias for play faces (Laméris et al., 2022b). In the current study we used similar stimuli as in

Chapter 2, yet we found no evidence for an attention bias for play faces. This may initially seem surprising, however it is possible that we captured different attentional processes. That is, the emotional Stroop task presented in Chapter 2 captures implicit attention processes or degrees of distraction, whereas the current eye-tracking study measured explicit or sustained attention. In this regard, our results converge with a previous eye-tracking study with bonobos that similarly found enhanced sustained attention for bared-teeth face expressions (van Berlo, 2022). Comparable evidence is also found in orang-utans (Pritsch et al., 2017), suggesting that sustained attention for individuals in distress may be shared among great apes.

This differential processing of facial expressions in different attentional stages may be explained by the context in which these expressions are displayed. Play faces are typically produced during playful interactions, in which they are intentional and directed to the play partner (Demuru et al., 2015). Across primates, rapid facial mimicry of such play faces are observed which facilitates successful play sessions (Davila Ross et al., 2008; Mancini et al., 2013; Palagi et al., 2019). Swift detection and recognition of these expressions is therefore essential. In contrast, bared-teeth displays are often produced by bonobos when in distress, e.g. during sexual interactions or after aggression to signal appeasement or reassurance (de Waal, 1988; Vervaecke et al., 2000; Vlaeyen et al., 2022). As such, facial expressions likely convey information regarding potential (social) threats, and enhanced sustained attention may be beneficial (Öhman et al., 2001; Pourtois et al., 2004) which may improve processing at the location of the potential threat (Carlson & Reinke, 2014). Additionally, bonobos respond to distress in others by consolation behaviours (Clay & de Waal, 2013b). The overall bias for negative facial expressions may therefore be adaptive within bonobos. Alternatively, this result may also provide support for a number of studies that dispute the common characterisation of bonobos as peaceful, tolerant and prosocial, suggesting that this view is more nuanced (Cronin et al., 2015; Jaeggi et al., 2010; Stevens et al., 2007; Verspeek et al., 2022a, b).

Interestingly, as the stimulus configurations progressed within a session, the bonobos exhibited an increased attentional preference for distress facial expressions. One plausible explanation for this pattern could involve carryover effects (Gladwin et al., 2020). However, it is worth noting that some studies suggest that the processing of fear-related stimuli is not influenced by carryover effects (Maxwell et al., 2022) and the randomised location of the stimuli should have, to some extent, avoided spatially driven carryover effects (Gladwin & Figner, 2019). Alternatively, the heightened focus on negative facial expressions could potentially be attributed to a shift in affective state triggered by the initial preferential looking at these expressions, subsequently modulating following attentional patterns (Bradley et al., 2017; Carroll & Young, 2005; Murphy & Zajonc, 1993; Snowden et al., 2016). While further investigations are necessary to establish whether this cumulative attention bias towards distressed faces indeed represents a carryover effect, it also offers valuable insights into possible ecologically relevant attention processing in bonobos. That is, attention for emotions is not only a reaction to the saliency of the stimulus, but may also be goal-driven (Anderson, 2013) and as such be a proactive process in shaping perceptual experiences (Todd et al., 2012). In light of our current findings, this could imply that whereas the preferential processing of one distressed individual conveys information about potential threats (Pourtois et al., 2004), the observation of multiple distressed individuals increases this saliency and potentially alters the perceived urgency or severity of the threat, for which enhanced attention may be beneficial. While it is unclear at this point whether the accumulative negativity effect is due to the study design, it may also present behaviourally relevant attentional processes and future studies are encouraged to further explore this.

Our current findings do not support the presence of a modulating effect resulting from the viewing of valenced videos prior to observing competing facial expressions. Several potential explanations can be addressed to account for this observation. Firstly, it is possible that the primers were not salient enough to evoke changes in affective states. Although the pupil dilation suggests that the bonobos were aroused by the primer videos, it remains plausible that this response was not robust enough to subsequently influence the processing of emotions. Notably, human studies often employ primer videos of longer duration, ranging from 30 seconds to several minutes. However, this length was considered unfeasible given the voluntary participation of the bonobos, the social setting in which testing occurred, and their overall short attention span. Nevertheless, previous human studies did reported changes in pupil size in response to viewing still-images with varying durations (100 ms – 6000 ms) (Bradley et al., 2017; Snowden et al., 2016). This suggests our selected primer videos were of adequate length to induce emotional responses in bonobos.

Secondly, analogous to humans, primates exhibit distinct processing of social information contingent on their emotional state (Bethell et al., 2016; Cronin et al., 2018). In Chapter 7 of this thesis we provide similar evidence for bonobos. Nonetheless, it is essential to recognise that attention is a complex cognitive process encompassing a multitude of components. Remarkably, no prior study has directly investigated affect-congruent attention biases in primates Thus, even though the bonobos in this study did not exhibit a preferential shift in attention towards affective congruent information aligned with the primer video, we cannot exclude the possibility that other attentional processes were altered. In our current study, we exclusively focused on assessing looking duration towards facial expressions. However, past research has demonstrated that emotions can impact diverse attention-related variables, including fixation duration and counts (Gere et al., 2017), as well as different stages of attention such as engagement, maintenance or disengagement (Koster et al., 2005; Okon-Singer, 2018). Emotions can also influence whether information is processed globally or locally (Gasper & Clore, 2002; Schmid et al., 2011; Wadlinger & Isaacowitz, 2006). Unfortunately, our current dataset is not detailed enough to comprehensively analyse these different attentional processes. Nevertheless, this opens up intriguing directions for future research, and offers promising suggestions for more in-depth analyses that can reveal valuable insights in the interplay between emotions and attention in primates.

Conclusions

In conclusion, this study aimed to investigate the impact of viewing valenced videos on emotional arousal in bonobos and how it might influence subsequent social information processing. The findings indicate that while pupil size increased after watching bonobo and human primer videos, this effect was independent of the valence of the primer. Notably, bonobos exhibited sustained attention toward negative facial expressions, regardless of primer type, suggesting an evolved bias for emotional stimuli over neutral ones, and particularly for distress-related facial cues. This finding is consistent with the idea that sustained attention to distress signals might aid in threat detection and social cohesion within the bonobo society. The enhanced attention for distressed stimuli within a session raises questions about the proactive nature of attention processes in shaping perceptual experiences. The absence of a clear modulating effect of primer videos on subsequent attention biases suggests that the emotional response induced by the primers may not have fully carried over to influence subsequent emotional processing. However, it is worth considering that the complexity of attentional processes extends beyond mere gaze duration and future investigations should explore additional aspects of attention. This study, which pioneered the use of valenced videos to study attention biases in bonobos, contributes valuable insights into their emotional responses and attentional preferences, prompting further inquiries into the nuanced interplay between emotion and attention in non-human primates.

4

The influence of sex, rearing history, and personality on abnormal behaviour in zoo-housed bonobos (*Pan paniscus*)

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Abstract

Abnormal behaviours are often used as a welfare indicator in zoo-housed great apes. While previous studies report on the occurrence of abnormal behaviours in zoo-housed chimpanzees (*Pan troglodytes*), there is currently a lack of knowledge about such behaviours in the closely related bonobo (*Pan paniscus*). Here we report on the prevalence, diversity, and frequency of abnormal behaviours, based on 1531 hours of observations in 51 adult bonobos, living in six zoos. We also investigate the potential influence of age, sex, rearing history and four previously established personality traits (Activity, Boldness, Openness and Sociability) on the diversity and frequency of abnormal behaviours. Our results document the presence of a total of 13 abnormal behaviours in the population, with the five most frequent ones being *Coprophagy*, *Poke anus*, *Social hair pluck*, *Regurgitation* and *Head shake*. We find that wild-born bonobos show a higher diversity of abnormal behaviours compared to mother-reared individuals, likely due to their abnormal early-life experiences. Mother-reared individuals and males show lower frequencies of *Poke anus*. The frequency of abnormal behaviours is also linked to personality. Bonobos scoring lower on Activity, associated with more self-scratching and lower activity, engage more in *Coprophagy* and *Head shaking*. More sociable individuals, on the other hand, had higher frequencies of *Social hair pluck*, which follows a previous finding that this behaviour is embedded in grooming. Finally, more sociable individuals also had lower frequencies of *Coprophagy*, an indicator that higher sociability might cause higher resilience to stressors. Our study provides a first overview of the abnormal behaviours in zoo-housed bonobos. We discuss that not all abnormal behaviours may be suitable indicators of poor welfare. These results form an important base in our understanding of the repertoire of abnormal behaviours in zoo-housed bonobos, which is a crucial step for optimising their welfare.

Introduction

Abnormal behaviours in captive animals are defined as those that deviate qualitatively (i.e. by kind) or quantitatively (i.e. by degree) from behaviours observed in wild-living individuals (Birkett & Newton-Fisher, 2011; Bloomsmith et al., 2019; Wallace et al., 2019). Factors that may trigger the development of abnormal behaviours include the inability to perform species-specific behaviours (Browning, 2019; Clubb & Mason, 2007), lack of environmental control (Hosey, 2005) and atypical social experiences, like the absence of maternal care during early-life periods or limited contact to conspecifics (Bellanca & Crockett, 2002; Freeman & Ross, 2014). In contrast, attempts to improve the welfare of animals can reduce abnormal behaviours, for example through positive reinforcement training (Pomerantz & Terkel, 2009), more complex and naturalistic enclosure designs (Ross et al., 2011) and enrichment programs (Mason et al., 2007; Swaisgood & Shepherdson, 2005).

Behaviour, in general, is currently the most used parameter to assess zoo animal welfare (Binding et al., 2020) and because abnormal behaviours often arise as a result of past or present suboptimal (social) conditions, they are often used as an indicator for negative welfare (Mason, 1991). Despite their importance in identifying potential welfare issues (Dawkins, 2015; Rose et al., 2017), the study of abnormal behaviours remains challenging (Mason & Latham, 2004). One major difficulty is identifying their underlying aetiologies and assessing their actual effect on the psychological wellbeing of the animal. Behaviours that are relatively well-understood in terms of their impact on animal welfare include self-injurious behaviours which are linked to early life stressors such as maternal separation (Novak et al., 2013; Polanco, 2016) and abnormal repetitive behaviours which are associated to a failure to cope with stressful events or environments (Bacon, 2018; Rose et al., 2017). Yet, for many other behaviours considered abnormal, the evidence is lacking to associate them with the animal’s welfare. On top of that, some abnormal behaviours are socially learnt (Hook et al., 2002; Hopper et al., 2016) and as such their presence no longer represents a response to stressors.

Interestingly, the occurrence of abnormal behaviour varies between individuals within a specific environment. Studying what factors are associated with patterns of abnormal behaviours can help to better understand their aetiologies and can help to inform welfare practices. Factors including sex, age and the species itself are linked to abnormal behaviours (Bloomsmith et al., 2019; Kummrow & Brüne, 2018; Lutz, 2018). For example, studies on nonhuman primates report that males perform more abnormal behaviours in general (Mallapur & Choudhury, 2003; Trollope, 1977). However, a recent study on a large sample of two macaques species (*Macaca fascicularis* and *Macaca mulatta*) and baboons (*Papio hamadryas*) report that male macaques exhibited more abnormal appetitive behaviours while in baboons, the females exhibited more of these behaviours (Lutz, 2018). Age also influences abnormal behaviour, especially on active abnormal behaviours (e.g., motor stereotypies) since these can be linked to the animal's physical abilities. More physically active stereotypical behaviours sometimes decrease with age, as shown in macaques (Gottlieb et al., 2013, 2015; Lutz, 2018) but not in baboons (Lutz, 2018), while other behaviours such as self-directed behaviours and self-injurious behaviours increase with age (Lutz et al., 2003).

Additionally, the individual's personality can play a role. Defined as contextually and temporally consistent differences in the behaviour across individual members of the same species, personalities are known to have a physiological basis (Koolhaas et al., 1999) and as such are associated with the sensitivity to environmental challenges (Carere et al., 2010; Nettle, 2006). Personality is described in a wide range of taxa, including amphibians (Kelleher et al., 2018), insects (Amat et al., 2018), fish (Toms et al., 2010), birds (Groothuis & Carere, 2005), felids (Gartner & Weiss, 2013) and non-human primates (Freeman & Gosling, 2010). Yet, few studies to date have investigated the link between abnormal behaviour and personality. Motor stereotypic behaviours are linked to personality traits characterised by heightened activity in rhesus macaques (*Macaca mulatta*) (Gottlieb et al., 2013) and are more frequent in bold individuals (Gottlieb et al., 2015). Anxious and/or inhibited rhesus macaques also experience more hair loss, likely through a higher expression of self hair plucking (Coleman et al., 2017). In orange winged Amazon parrots (*Amazona amazonica*), neuroticism-like traits are linked to feather damaging behaviour, while more extraverted birds were more resilient to environmental stress as they developed less diverse and less frequent stereotypical behaviours (Cussen & Mench, 2014).

Abnormal behaviours are species-specific as are the risk factors that are associated with their occurrence. According to a survey including 68 primate species across 108 zoos, apes more frequently show abnormal behaviours (Bollen & Novak, 2000). Most studies on great ape abnormal behaviour have focused on chimpanzees (*Pan troglodytes*) (Kummrow & Brüne, 2018), of which a majority of the individuals show at least one abnormal behaviour (Birkett & Newton-Fisher, 2011; Bloomsmith et al., 2019; Jacobson et al., 2016). A large-scale cross-zoological study on abnormal behaviour in the closely related bonobo (*Pan paniscus*) is currently lacking, despite some studies reporting on the presence of abnormal behaviours (e.g. Brand et al., 2016; Brand & Marchant, 2018; Miller & Tobey, 2012).

As such, the first aim of this study is to investigate the prevalence, diversity, and frequency of abnormal behaviours in a large multi-group sample of bonobos across European zoological institutions. The second aim of our study is to examine potential links between intrinsic factors, such as age, sex, rearing and personality with the occurrence of abnormal behaviour. Specifically, while most previous studies linked such factors to the prevalence of abnormal behaviours, we were interested in assessing their link to the frequency as this might provide additional information regarding the impact on the animal's welfare (Bloomsmith et al., 2019; Brilot et al., 2010; Pomerantz et al., 2012b). Together, the goal of this study was to create a first overview of abnormal behaviour in bonobos across zoos and to make an initial attempt to understand which factors may contribute to their occurrence, so that this can be used in future management decisions.

Methods

Subjects and housing

Behavioural data were collected between October 2011 and April 2014 on 51 adolescent and adult captive bonobos (32 females and 19 males, Table 4.1), housed in six European zoological parks. The care and housing of all bonobos was adherent to the guidelines of the EAZA Ex-situ Program (EEP). All individuals were socially housed in a multi-male/multi-female structure (median group size = 10; range 6 - 16) with juveniles and/or infants. Information about the bonobos, including their sex, age and rearing history were collected from the International Studbook (Stevens & Pereboom, 2020). The age of the adult individuals ranged from 7-63 years old, with a median of 21 years. The behaviour of infants and juveniles (age <7) was not scored in this project.

Table 4.1: Bonobos in study sample within each sex and rearing category

	Number of individuals	Percentage of the population
Sex		
Female	32	62.7%
Male	19	37.3%
Rearing		
Mother	34	66.7%
Hand	7	13.7%
Wild	10	19.6%

Data collection

We used the Observer (Noldus version XT 10) to score general behavioural patterns of the 51 individuals using 10 min focals, totalling on average for 29.5 h of observation time per animal (ranging between 12.9-58.2 h per individual) (Altmann, 1974) for a total of 1531.8 h. We selected 28 abnormal behaviours (Table 4.2), based on an earlier and similar study on chimpanzees in zoos (Birkett & Newton-Fisher, 2011). Our aim was to give an overview of all possible abnormal behaviour in bonobos and as such opted for an inclusive approach and record all behaviours that traditionally have been considered as abnormal. Data were collected by eight observers over 1-3 observation periods per location. Inter-observer reliabilities were calculated based on two 10-minute focal videos that were scored by all observers and reached a Spearman rank correlation mean of $r = 0.87$ across all observers, and so the observations across observers were highly reliable (Martin & Bateson, 1993).

Table 4.2: Abnormal behaviours used in this study. Behaviours in bold were observed during the observation period and are ordered based on prevalence

Abnormal behaviour	Definition	Number of zoos in which the behaviour was observed
Coprophagy	**Ingest own or other's faeces**	**6/6**
Poke anus	**Insert finger into own anus**	**6/6**
Social hair pluck	**Pulls out hair of other**	**4/6**
Regurgitate	**Vomit voluntarily, then usually re-ingest vomitus**	**5/6**
Head shake	**Repeatedly shaking head**	**6/6**
Self hair pluck	**Pulls out own hair**	**6/6**
Twirl	**Rotate torso on axis for 360 degrees while upright and bipedal**	**6/6**
Drink urine	**Drink own urine**	**2/6**
Posturing	**Deviating posturing without apparent reason**	**3/6**
Flip lip	**Repeatedly flip lower lip outside**	**3/6**
Head toss	**Circular movement of head**	**3/6**
Rock	**Sway repetitively and rhythmically. Usually side-to-side movement, not exclusively. Usually whole body, sometimes just the head.**	**2/6**
Clap hands	**Slap palm of hand or sole of foot, making noise**	**1/6**
Auto-aggression	Act aggressively towards own	0/6
Cling	Clutch own body or object	0/6
Ear cover	Cover one or two ears with hands	0/6
Eye poke	Poke one or more fingers into own eye	0/6
Genital pat	Touch own genitals	0/6
Head bang	Hit own head against solid surface	0/6
Pace	Locomote, usually quadrupedally, on substrate, covering and then re-covering route in stylised fashion, with no clear objective	0/6
Raspberry vocalisation	Push lips together and produce sound similar to flatulence	0/6
Repetitive body movement	Repeatedly moving body part without apparent function	0/6
Self-mutilation	Self-mutilates repeatedly	0/6
Self-slap	Hit self repeatedly	0/6
Spit	Expel saliva through pursed lips	0/6
Stick out tongue	Repeatedly stick out tongue	0/6
Suck self	Suck own body parts, e.g., finger or toes	0/6
Throw	Throw food object to other	0/6

Statistical analysis

Descriptive measures of abnormal behaviour

To describe the abnormal behaviour in zoo-living bonobos we analysed four aspects: 1) the prevalence (i.e. the proportion of individuals that perform a certain abnormal behaviour in contrast to the total number of individuals); 2) the diversity (i.e. the total number of different abnormal behaviours one individual shows); 3) the frequency of all abnormal behaviours combined (i.e. the total number of occurrences of all abnormal behaviours per hour per individual) and 4) the frequency of single abnormal behaviours (i.e. the number of occurrences of single abnormal behaviours per hour per individual). Because some behaviours were coded as events, we did not analyse the duration or proportion for all abnormal behaviours and therefore focus on their frequency.

Personality measures

For 41 bonobos that we collected data on abnormal behaviour on, we used personality profiles that were available from a previous study and constructed based on data that was collected at the same time as the abnormal behaviour data (Staes et al., 2016). The personality profiles were constructed using concurrent naturalistic observations and observations from experimental settings. These included 17 behavioural variables (10 from the naturalistic context and 7 from the experimental contexts) but did not include any of the abnormal behaviours studied here. Data were collected in two consecutive years, allowing to test for temporal consistency using intraclass correlations to determine temporal stability. Only stable variables were used to determine personality structure. Dimension reduction analysis on these variables revealed four factors: Activity, Boldness, Openness and Sociability. Details of the item's loading onto each dimension are shown in Table S4.1. Items that showed cross-loadings >|0.4| on multiple components, were considered part of the dimension on which they had the highest loading (Table 4.3).

Table 4.3: Behavioural contents of the personality traits

Factor	Adjectives loading on to factors
Sociability	+ Grooming frequencies + Grooming density + Neighbours + Grooming diversity − Latency to approach puzzles/durian − Autogroom
Openness	+ Approaches to puzzles/others + Play + Proximity to puzzles + Taste pasta
Boldness	+ Approaches to leopard + Displays to leopard + Proximity to leopard + Aggression received
Activity	+ Activity − Self-scratching

Factors influencing abnormal behaviour

We used Generalised Linear Mixed Models (GLMMs) with backwards selection to identify factors that explain variation in 1) the individual diversity of abnormal behaviour, 2) the frequency of abnormal behaviours combined and 3) the frequency of the most prevalent single abnormal behaviours. To ensure statistical reliability, we only ran GLMMs for single abnormal behaviours that were performed by at least 20 individuals. This criterion was reached for the behaviours *Coprophagy, Poke anus, Social hair pluck, Regurgitation* and *Head shake*. Explanatory factors included in our models were age, sex (female, male), rearing history (mother-reared, hand-reared, and wild-born) and four personality traits (Activity, Boldness, Openness and Sociability). Our dataset for the GLMM analyses was restricted to the individuals for whom we had information for all the independent variables, which we had for 41 individuals. We removed any outliers from our dataset (more than 4 SD above the mean). The models assessing the frequency of abnormal behaviours used a negative binomial distribution and a log link function and included the number of observation hours as offset to correct for sampling effort. For the model assessing the diversity of abnormal behaviours, we used a beta distribution with a logit link function. For descriptive measures and figures of the diversity of abnormal behaviour, we report the actual count data. All models included the identity of the subject as random factor to correct for repeated measures. Multicollinearity between independent variables was tested with a variance inflation factor (VIF) threshold of >5 (O'Brien, 2007), but the variables did not show multicollinearity. All analyses were performed using R 2.15.2 (R Core Team, 2016), with the GLMM calculated using the *glmmTMB* package (Brooks et al., 2017). Diagnostic plots (residuals vs. fitted and QQ plots) were used to examine assumptions of normality and homogeneity of variances and we additionally tested uniformity and dispersion of the residuals using the *DHARMa* package (Hartig, 2020).

Results

Prevalence of abnormal behaviours

Of the 28 abnormal behaviours included in the ethogram from the literature on chimpanzees, only 13 were observed in bonobos. The behaviours *Auto-aggression, Cling, Ear cover, Eye poke, Genital pat, Head bang, Pace, Raspberry vocalisation, Repetitive body movement, Self-mutilation, Self-slap, Spit, Stick out tongue, Suck self* and *Throw* were not recorded. Each of the 51 observed bonobos in our study engaged in abnormal behaviours since all of them performed *Coprophagy*, which was therefore the most prevalent behaviour. The other most prevalent abnormal behaviour we recorded were *Poke anus* (66.7%), *Social hair pluck* (51.0%), *Regurgitate* (49.0%) and *Head shake* (39.2%) (Figure 4.1).

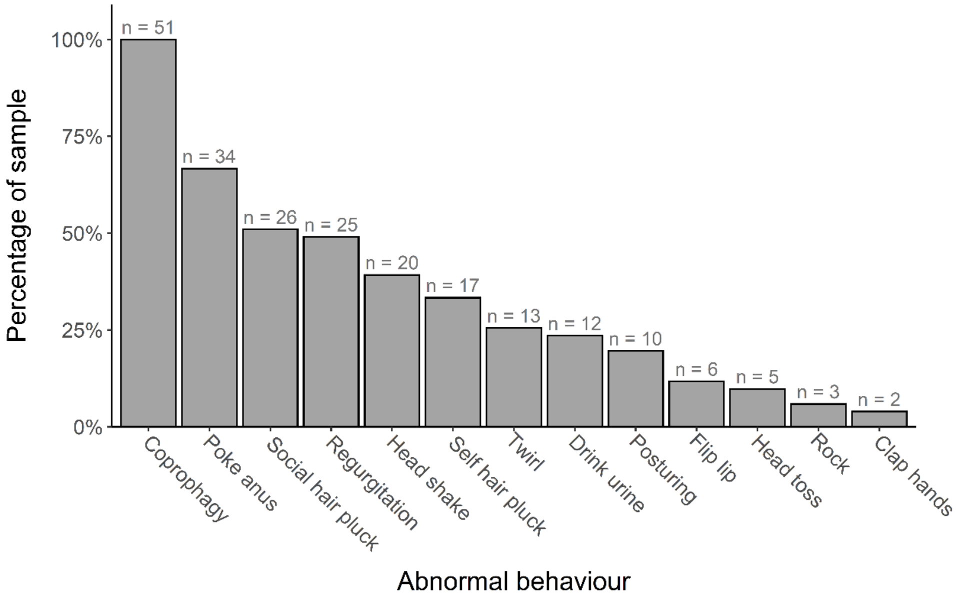


Figure 4.1: Percentage of the bonobos in the sample observed to perform each individual abnormal behaviour at least once during the period of observation

Diversity of abnormal behaviour

The individual diversity ranged from 1-8 abnormal behaviours with a median of 4 abnormal behaviours per individual and was significantly influenced by rearing history ($\chi^2 = 6.478$, df = 2, $P = 0.039$). Specifically, wild-born individuals showed a significantly higher diversity (M = 3.739, SE = 0.303) compared to mother-reared individuals (M = 2.889, SE = 0.172; $t_{74} = -2.039$, $P = 0.045$), see Figure 4.2a. Hand-reared individuals had a similar pattern, with a higher abnormal behavioural diversity (M = 3.727, SE = 0.574) than mother-reared individuals (M = 2.889, SE = 0.172), but the difference was not significant ($t_{74} = -1.937$, $P = 0.057$).

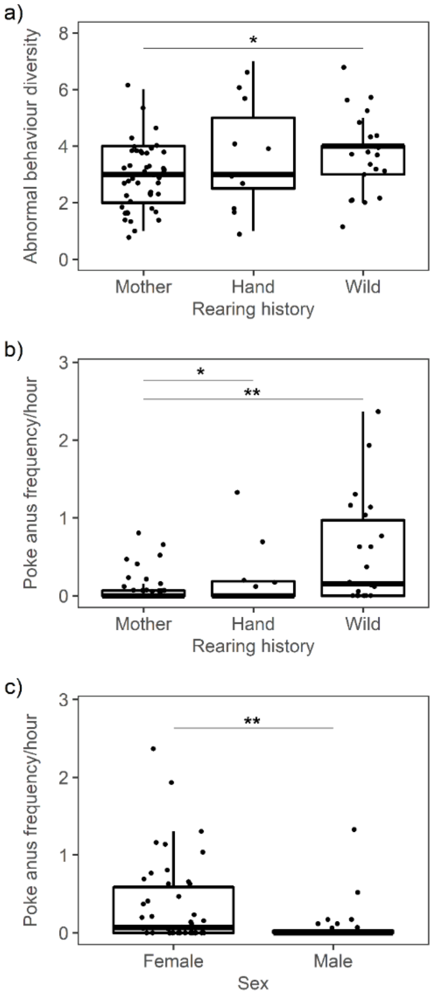


Figure 4.2: Median diversity of abnormal behaviour based on the (a) rearing history and median frequency of *Finger in anus* based on the (b) rearing history and (c) sex. *$P < 0.05$ and ** $P < 0.01$

Frequency of abnormal behaviours

Looking at the frequencies of abnormal behaviours, there was a large inter-individual variation ranging from 0.302 to 15.322 events/hour, with a median of 1.781 events/hour. Variation in the overall frequency of abnormal behaviours could not be explained by any of the predictors (age, sex, rearing history or the personality traits Activity, Boldness, Openness and Sociability).

Rearing history did predict the frequency of *Poke Anus* (χ^2 = 9.780, df = 2, P = 0.008) with wild-born individuals (M = 0.537, SE = 0.147; t_{71} = -2.737, P = 0.008) and hand-reared individuals (M = 0.228, SE = 0.126; t_{71} = -2.113, P = 0.038) showing this behaviour more frequently than mother-reared individuals (M = 0.093, SE = 0.028; Figure 4.2b). *Poke Anus* was also significantly different between sexes, (χ^2 = 7.411, df = 1, P = 0.006) with females (M = 0.344, SE = 0.079) showing higher frequencies than males (M = 0.082, SE = 0.045), see Figure 4.2c.

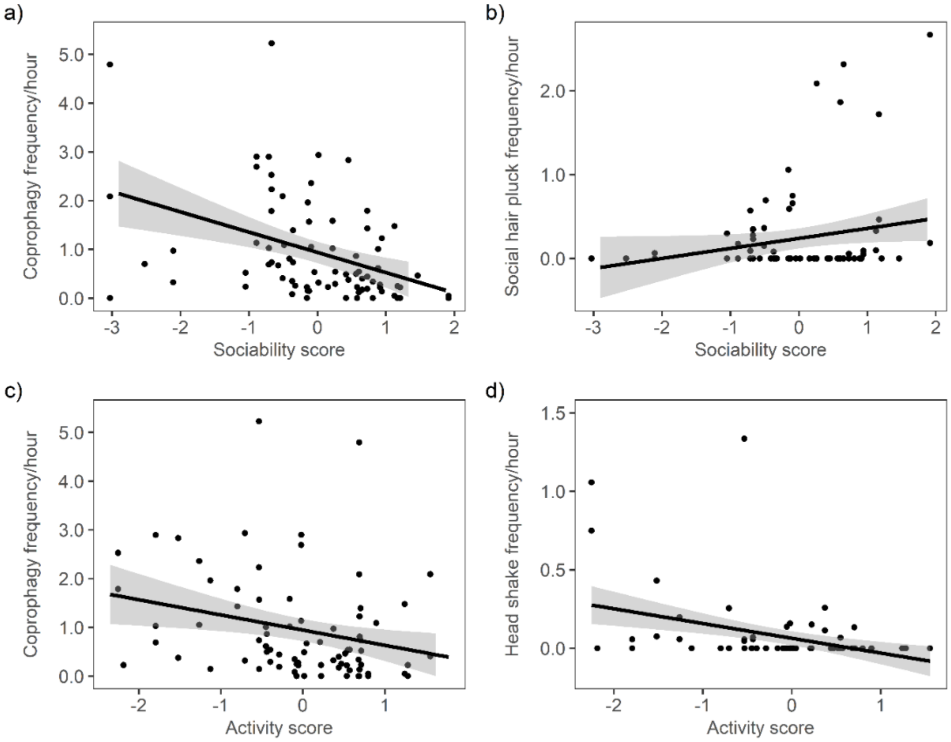


Figure 4.3: The association between the personality score Sociability and the frequency of (a) Coprophagy and (b) Social hair pluck and the personality score Activity and the frequency of (c) Coprophagy and (d) Head shake with the corresponding confidence intervals

Sociability predicted the frequency of *Coprophagy* ($\chi^2 = 15.073$, df = 1, $P < 0.001$) and *Social hair pluck* ($\chi^2 = 4.884$, df = 1, $P = 0.027$). Individuals scoring high on Sociability showed lower frequencies of *Coprophagy* ($\beta = -0.496$, SE = 0.128, Figure 4.3a), but higher frequencies of *Social hair pluck* ($\beta = 0.807$, SE = 0.365, Figure 4.3b).

Lastly, Activity scores predicted the frequency of *Coprophagy* ($\chi^2 = 8.253$, df = 1, $P = 0.004$) and *Head shake* ($\chi^2 = 9.322$, df = 1, $P = 0.002$). Individuals scoring high on Activity had lower frequencies of *Coprophagy* ($\beta = -0.332$, SE = 0.116, Figure 4.3c) and lower frequencies of *Head shake* ($\beta = -1.300$, SE = 0.426, Figure 4.3d). Fixed effects tables for all the GLMMs described in the main text are provided in Table S4.2-3.

Discussion

We studied the abnormal behaviour in zoo-housed bonobos and investigated which factors were related to their occurrence. Variation in the diversity and frequency of individual behaviours could be explained by the individual’s rearing-history, sex and/or personality traits.

Of the 28 abnormal behaviours included in the ethogram, we observed 13 behaviours in the 51 bonobos included in the study. This is lower than the 37 abnormal behaviours previously reported in a study with 40 zoo-housed chimpanzees with similar data collection methods (Birkett & Newton-Fisher, 2011). Similar to other chimpanzee studies (Birkett and Newton-Fisher, 2011; Jacobson et al., 2016; Martin, 2002; Nash et al., 1999, but see Bloomsmith et al., 2019), we found *Coprophagy* to be the most prevalent abnormal behaviour, as all bonobos exhibited this behaviour. On average, bonobos showed 4 abnormal behaviours, performing them 1.78 times per hour. While this number seems high and corresponds to a similar study on chimpanzees (Birkett & Newton-Fisher, 2011), there is the possibility that our data represent an overestimation (Ross & Bloomsmith, 2011). Namely, it is important to acknowledge that for many of the abnormal behaviours, there is currently no clear link to their origin or their effect on animal welfare. To avoid such generalisation, it can be helpful to consider four ways abnormal behaviours can relate to welfare (Cooper & Mason, 1998): as an indicator of poor welfare; an adaptation to captivity; the physical harm of the behaviour; or the behaviour does not have a large direct impact on the quality of life. For example, *Coprophagy* is increasingly questioned as an indicator of negative welfare (Hopper et al., 2016) as accumulating studies suggest that it may be socially learnt (Freeman & Ross, 2014; Jacobson et al., 2016; Nash et al., 1999). *Coprophagy* is also observed in multiple wild bonobo populations (Beaune et al., 2017; Goldstone et al., 2016; Sakamaki, 2010) where it may be an adaptive feeding strategy when food is scarce (Sakamaki, 2010) and a cultural behaviour in some populations to cope with high tannin levels of *Canarium* fruits (Beaune et al., 2017).

Social learning may also play a role in the acquisition of other abnormal behaviours. *Social hair pluck* may be socially learnt as this behaviour is embedded in grooming activities (Brand & Marchant, 2019). Our data provide extra support for social learning of *Social hair pluck*, as it was present in four of the six surveyed locations. Instances of social transmission are also reported for *Regurgitation* in chimpanzees (Kalcher-Sommersguter et al., 2013) and bonobos (Stevens & Wind, 2011) and for *Poke anus* in bonobos (Stevens and Staes, unpublished data). Nonetheless, even if social learning, rather than past or present stressors, explains why individuals acquire certain abnormal behaviours, this does not exclude health implications (Cooper & Mason, 1998) and a potential impact on animal welfare. For example, *Regurgitation* (often followed by reingestion) has health consequences for the throat and teeth (Hill, 2009), *Coprophagy* may contribute to parasitic and bacterial disease transmission (Graczyk & Cranfield, 2003), and hair loss due to hair plucking (either self-directed or social) could interfere with homeothermy (McFarland et al., 2016). Even when such abnormal behaviours are not directly linked to suboptimal (social) environments and thus are not indicators of impaired psychological wellbeing, they can affect the health of an animal, and therefore negatively impact their welfare (Cooper & Mason, 1998).

When looking at the factors influencing abnormal behaviours in bonobos, we found that the absence of maternal care was linked to a higher diversity of abnormal behaviours, as well as to higher frequencies of *Poke anus*. This corroborates other studies reporting a higher diversity of abnormal behaviours in socially deprived chimpanzees (Martin, 2002), as well as a higher occurrence of abnormal behaviour in non-mother reared chimpanzees (but not for *Coprophagy* (Jacobson et al., 2016)). The exact history of the wild-born apes is often unknown, and their experience may vary from being ex-pets to passing through animal dealers. Yet, anecdotal reports suggest that many of these individuals were separated from their mother at an early age and were often deprived of social contact with their peers, resulting in the development of more abnormal behaviours (Martin, 2002) which may persist throughout life (Bloomsmith et al., 2019; Kalcher-Sommersguter et al., 2013). The bonobo breeding program has encouraged mother rearing since the 1990s and the import of wild-caught individuals has been stopped in the 1980s, with only few confiscated individuals from private persons entering the zoo population. Therefore, wild-caught, and hand-reared individuals largely represent past practice, and the latter only happens in life-threatening situations.

Sex effects are repeatedly observed for abnormal behaviours but often vary between behaviours and species (Bloomsmith et al., 2019; Lutz, 2018). We only found a sex effect for the frequency of *Poke anus*, such that females performed this behaviour more frequently than males. While the occurrence of *Poke anus* may be explained by social learning (Stevens and Staes, unpublished data), our observation that females performed this behaviour more often suggests that other mechanisms contribute to the expression of this behaviour, possibly self-stimulation (Vasey & Duckworth, 2006), but this remains to be studied.

We provide additional evidence that personality is linked to abnormal behaviours (Cussen & Mench, 2015; Gottlieb et al., 2013; Schork et al., 2018). Bonobos with lower Activity scores engaged more frequently in *Coprophagy* and *Head shake*. Lower Activity scores are characterised by lower levels of activity and higher levels of self-scratching (Staes et al., 2016). Increased rates of abnormal behaviour, mainly coprophagy in chimpanzees (Bloomsmith & Lambeth, 1995), have been observed in primates before predictable feeding times and were associated with heightened levels of inactivity (Bloomsmith & Lambeth, 1995; Waitt & Buchanan-Smith, 2001), while other studies in contrast report increased food-anticipating activity before feeding moments (Krebs et al., 2017). Taking this into consideration with the findings of our study, it is possible that *Coprophagy* is linked to feeding moments and that less active bonobos perform this behaviour more within these contexts. To better understand *Coprophagy* in bonobos, future research could focus on when exactly this behaviour is performed, and whether it is linked to feeding moments. We also found that less active bonobos showed higher frequencies of *Head shake*. Head shaking behaviour was initially considered an abnormal behaviour (Walsh et al., 1982), but recent studies suggest that this behaviour functions as a communicative gesture for initiating or resuming interactions such as play (Pika et al., 2005) or to prevent group members from engaging in a particular behaviour (Schneider et al., 2010). At this stage, it is unclear why less active individuals showed higher rates of *Head shake* and future research could focus on possible associations between the use of communicative gestures and personality profiles.

Interestingly, more sociable bonobos engaged less frequently in *Coprophagy*. This result seems contradictory to previous studies suggesting that higher sociability (e.g. mother-rearing conditions) facilitate the acquisition of *Coprophagy* through social learning (Freeman & Ross, 2014; Jacobson et al., 2016; Nash et al., 1999). However, it is important to note that we addressed the frequency of *Coprophagy* and not its prevalence. Higher Sociability scores are characterised by more frequent grooming bouts, more neighbours and higher grooming diversities, suggesting that these bonobos have richer social lives while less sociable individuals have fewer positive social interactions (Staes et al., 2016). Less sociable individuals may experience some form of boredom as sociability is considered a pillar contributing to primate welfare (Robinson et al., 2017). Boredom is previously used to explain *Coprophagy* in captive apes (Hoff et al., 1994; Martin, 2002) which could also explain why less sociable individuals engaged more in *Coprophagy*.

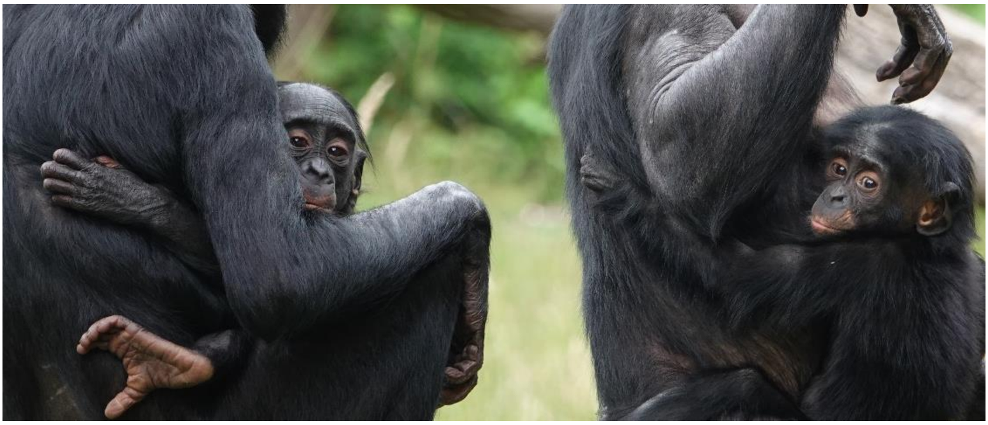
More sociable bonobos also performed more *Social hair pluck*. *Social hair pluck* is embedded in grooming activities of bonobos (Brand & Marchant, 2019), which may explain the positive association between Sociability scores and the frequency of *Social hair pluck*. Bonobos have several social grooming cultures (van Leeuwen et al., 2020) and social hair plucking may be a part of their cultural behaviour in captivity. Although *Social hair pluck* is not related to urinary cortisol levels (Brand et al., 2016), it is currently unclear if it is an appropriate indicator of poor welfare as individuals showing abnormal behaviour within a given environment likely have better welfare than those that do not perform these behaviours (Mason & Latham, 2004). More research is needed to understand how *Social hair pluck* influences bonobo welfare.

Conclusions

All bonobos performed at least one behaviour that is traditionally considered as abnormal. Yet, prevalent behaviours, such as *Coprophagy*, *Poke anus*, *Regurgitation* and *Social hair pluck*, may be acquired through social learning and hence cannot unconditionally be used as welfare indicators, although potential health implications must also be assessed. Variation in the frequency of single abnormal behaviours was observed and can partly be explained by rearing history, sex and/or personality traits. We were able to sample a relatively large number of bonobos, although future studies should aim to increase the sample size even further to look at possible interactions effects between risk factors which can reveal patterns that will further increase our understanding of abnormal behaviours in this species.

Altogether, the results of this study have several implications for the welfare of zoo-living bonobos. First, mother rearing is the most optimal condition in which bonobos can be raised and we encourage the bonobo breeding program to keep this as the standard. Second, social learning of abnormal behaviours complicates the elimination of behaviours such as *Coprophagy*, *Poke anus*, *Regurgitation*, and *Social hair pluck* from the zoo population, especially as they appear to be rather widespread. Still, zoos can attempt to mitigate abnormal appetitive behaviours including *Coprophagy* and *Regurgitation* through dietary manipulations and behavioural enrichment programs, which can be tailored to the personality profiles of the bonobos. Mitigating *Social hair pluck* may be more challenging as it is embedded in grooming activities, which are considered a positive behaviour. Two bonobo groups in our sample did not perform *Social hair pluck* at all and, in theory, one could prevent social transmission of this behaviour by not introducing individuals that engage in *Social hair pluck*. However, from a practical point of view, transfers between zoos are crucial to retain a viable breeding population and isolating the non-performing groups would therefore not be recommended.

Lastly, we suggest that future studies focus on how specific abnormal behaviour impact the psychological welfare of an individual. For example, cognitive bias testing revealed that head twirls, but not pacing, was an accurate indicator of negative emotional states in tufted capuchins (*Sapajus apella*) (Pomerantz et al., 2012b). In the future, cognitive bias testing can also help to identify risk factors for the psychological welfare of individuals, including personality (Asher et al., 2016; Cussen & Mench, 2014). In conclusion, this study gives a starting point for a better understanding of why some individuals show more abnormal behaviours than others. These findings can contribute to a better understanding of abnormal behaviours in zoo-housed bonobos from which the captive care and management for the species can be further optimised.



5

Evaluating self-directed behaviours and their association with emotional arousal across two cognitive tasks in bonobos (*Pan paniscus*)

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Abstract

Self-directed behaviours (SDBs) are widely used as markers of emotional arousal in primates, and are commonly linked to negative arousal, or are used as indicators of stress or poor welfare. However, recent studies suggest that not all SDBs have the same function. Moreover, lateralisation in the production of these behaviours has been suggested to be associated with emotional processing. Hence, a better understanding of the production and the asymmetry of these displacement behaviours is needed in a wider range of species in order to confirm their reliability as indicators of emotional arousal. In the current study, we experimentally evaluated the production and asymmetry of SDBs in zoo-housed bonobos during two cognitive touchscreen tasks. Overall, nose wipes were most commonly observed, followed by gentle self-scratches, and rough self-scratches. The rates of nose wipes and rough self-scratches increased with incorrect responses, suggesting that these behaviours indicate arousal and possibly frustration. Rough self-scratching was additionally more directed towards the left hemispace after incorrect responses. In contrast, gentle self-scratching increased after correct responses in one study, possibly linking it with positive arousal. We also tested if left-handed bonobos showed greater behavioural reactivity towards incorrect responses but found no evidence to confirm this hypothesis. Our results shed light on potential different mechanisms behind separate SDBs. We therefore provide nuance to the use of SDBs as indicator of emotional arousal in bonobos.

Introduction

Self-directed behaviours (SDBs), behaviours that are directed at an animal's own body, are considered to be displacement behaviours that result from frustration and/or internal conflict within an animal (Pavani et al., 1991; Tinbergen, 1952). In non-human primates, SDBs, such as self-scratching or self-touching, have been introduced as behavioural indicators of psychosocial stress (Maestripieri et al., 1992), because (1) pharmacological evidence with anxiogenic and anxiolytic drugs provided support for the link between SDBs and social anxiety, arousal or stress (Schino et al., 1991, 1996); (2) observational studies indicated increased rates of SDBs with social or environmental stressors (Baker & Aureli, 1997; Castles & Whiten, 1998; Diezinger & Anderson, 1986; Maestripieri et al., 1992; Troisi, 2002); and (3) SDBs have been shown to decrease after positive affiliative interactions (Aureli & Yates, 2010; Norscia & Palagi, 2011) or after reconciliation following agonistic interactions (Aureli et al., 1989; Fraser et al., 2008). Other studies found that SDB rates increased with the complexity of cognitive tasks (chimpanzees (*Pan troglodytes*): Leavens et al., 2001); when delay between trials increased (orangutan (*Pongo pygmaeus*): Elder & Menzel, 2001); and when subjects made incorrect responses (chimpanzees: Itakura, 1993; Yamanashi & Matsuzawa, 2010; mandrills (*Mandrillus sphinx*): Leeds & Lukas, 2018), suggesting that SDBs also reveal emotional arousal in non-social contexts when the subjects are not achieving their goals (Tinbergen, 1952).

Due to the rare occurrence of SDBs, and because the differences between them are subtle, many studies combine different SDB types, for example, gentle and rough self-scratching, or combine SBDs with other behaviours, such as self-grooming or self-plucking, into one measure (Fraser et al., 2008; Pomerantz & Terkel, 2009), which obscures their interpretation. On the other hand, several studies have indicated subtle nuances between different SDBs (Leeds & Lukas, 2018), or between individual differences in the rates of SDBs (Yamanashi & Matsuzawa, 2010). For example, some studies suggest that in chimpanzees, rough self-scratches, but not gentle self-scratches or self-grooming, indicate negative arousal (Aureli & De Waal, 1997; Baker & Aureli, 1997; Leavens et al., 2004). Others have suggested that gentle self-scratching may reflect lower levels of negative arousal (Yamanashi & Matsuzawa, 2010). One particular SDB in great apes, that is often overlooked despite being commonly observed, is 'nose wiping' (Jordan, 1977; Marchant & McGrew, 1996). This behaviour is rather inconspicuous, and different studies have referred to this behaviour with different terms, e.g., 'nose gesture' (Yamanashi & Matsuzawa, 2010) or 'rubbing' (Hopkins et al., 2006).

In chimpanzees, there is some evidence that nose wipes appear to increase with errors in cognitive tasks (Yamanashi & Matsuzawa, 2010), but not with cognitive challenge (Clark & Smith, 2013).

To better understand the potential link between SDBs and (negative) affect, researchers have also focused on the asymmetrical production of these behaviours (Leavens et al., 2001, 2004; Wagner et al., 2016). Lateralised behaviours are associated with specialisation of the left or right brain hemispheres, which results in the differential processing of information, perception and production of emotions across vertebrates (Rogers & Andrew, 2002). Although different views exist (Güntürkün et al., 2020), findings largely suggest a similar pattern of a right hemisphere bias for expressing intense emotions (Rogers, 2002), specifically negative emotions, such as stress (Rogers, 2010). Since SDBs are typically executed using one hand, they represent a lateralised behaviour, and looking at such biased production presents a potential key variable in identifying the link between these behaviours and their emotional valence, i.e., whether the SDB reflects positive or negative emotions. Observational studies yield inconsistent evidence for the asymmetrical production of SDBs in great apes. A left-hand bias for face touching has been observed across orangutans, gorillas (*Gorilla gorilla*) and chimpanzees (Dimond & Harries, 1984), whereas a right-hand bias was found for self-scratching in chimpanzees (Hopkins et al., 2006). Other studies found no overall hand preference for SDBs in these species (Hopkins et al., 2006; Hopkins & de Waal, 1995; Marchant & McGrew, 1996). Within the context of measuring arousal in cognitive challenges, studies have reported more right-hand SDBs when the chimpanzees made errors on the task (Leavens et al., 2001, 2004), although a more recent study found that chimpanzees and gorillas had a left-hand bias for SDBs during incorrect trials (Wagner et al., 2016).

In addition to hand preference for SDBs, changes in the target location on the body (i.e., left, or right hemispace) have been associated with asymmetrical processing of emotions in the brain. Chimpanzees and gorillas direct self-scratches more to the left side of their body, supporting the view of right hemispheric processing (Hopkins et al., 2006; Wagner et al., 2016), whereas another study found that in chimpanzees, rubs were more directed to the right hemispace after incorrect responses, while self-scratches (both gentle and rough) were more directed to the left hemispace (Leavens et al., 2004).

Altogether, current evidence suggests that SDBs in primates may reflect arousal, and possibly negative arousal, but that their reliability as an indicator for concepts, such as stress, frustration, or anxiety, may depend on factors such as species, context, SDB type, hand use, and target location. The purpose of this study is to increase our understanding regarding the production of SDBs in great apes, and more specifically, in bonobos (*Pan paniscus*). Bonobos represent an interesting study species for an examination of frequency and asymmetry of SDBs during cognitive tasks for several reasons. Firstly, chimpanzees and bonobos appear to differ in handedness. Several studies indicate that, whereas chimpanzee populations show right-handed bias in gestural communication, unimanual reaching, and bimanual complex coordination, bonobos have individual preferences for left- or right- handedness, but, besides one study (Neufuss et al., 2017), no clear right-hand bias across populations in various contexts (Brand et al., 2017; Chapelain et al., 2011; Hopkins et al., 2011, 2015; Meguerditchian et al., 2015). Nonetheless, greater leftward asymmetries in brain regions associated with the motor skills used for manual actions have been observed (Hopkins et al., 2009). Second, chimpanzees and bonobos may differ in their emotional decision making (Rosati & Hare, 2013), and studies of brain regions have indeed identified differences in neural systems that regulate emotional processing, such as the amygdala (Issa et al., 2019; Staes et al., 2019b; Stimpson et al., 2016). Therefore, investigating bonobos' asymmetry in SDB production can further shed light on the different mechanisms behind these behaviours across species. In addition, a better understanding of the contexts of SDB production and how they relate to (negative) emotional arousal has implications for the use of these behaviours in assessment of affective states and welfare.

In this study, we examine the production of four SDBs (nose wiping, gentle self-scratching, rough self-scratching, and self-touching) in bonobos during two cognitive touchscreen tasks and evaluate the asymmetry of their production in relation to trial accuracy. We expect to find that (1) some, but not all, SDBs will increase with errors made during the tasks; (2) if SDBs are a reflection of internal arousal, they are produced more with the left hand; (3) SDBs that are linked with arousal are targeted more to the left hemispace of the body after incorrect responses, compared to those associated with correct responses; (4) that left-handed individuals show enhanced behavioural reactivity, and thus more SDBs in response to incorrect answers.

Methods

Subjects and housing

The study subjects were eight mother-reared adolescent and adult bonobos (three females and five males; mean age = 15.8 years, range = 7–27 years; Table 5.1) who were part of a social group of 20 individuals, housed at Zoo Planckendael (Belgium). The bonobos were housed in an indoor enclosure (total surface 422 m^2) consisting of ten interconnected rooms, of which four main rooms were visible for zoo visitors, and six rooms off exhibit. When the temperature allowed, the bonobos had access to an outdoor enclosure (3000 m^2). Fresh vegetables, fruits, browse, and primate chow was provided four times per day and the bonobos had access to water ad libitum.

Table 5.1: Subject information of the eight bonobos included in this study

Subject	Sex	Age	Study 1	Study 2
Busira	Female	16	Yes	Yes
Habari	Male	14	Yes	Yes
Kianga	Female	17	Yes	No
Kikongo	Male	7	Yes	No
Mokonzi	Male	7	Yes	Yes
Nayembi	Female	15	Yes	No
Vifijo	Male	27	Yes	No
Zamba	Male	22	Yes	Yes

Testing procedure

Touchscreen sessions took place four to five times per week, between 12:00 and 15:00, in the off-exhibit enclosures. Subjects could choose to participate voluntarily in touchscreen sessions and were not separated from group members for testing.

All sessions were conducted on a 22’ Viewsonic TD2220 touch-sensitive monitor (1920 × 1080 resolution), which was connected to the researcher’s (DWL) computer. A second monitor allowed the researcher to view the subject’s responses. The touchscreen setup was mounted on an adjustable cart, placed outside an off-exhibit enclosure. The touchscreen was placed parallel to the enclosure mesh, allowing the bonobos to work on the touchscreen through the mesh. Training and testing tasks were designed using OpenSesame (Mathôt et al., 2012). Stimulus preparation was conducted in Adobe Photoshop version 21.2.2.

The apes were rewarded for correct responses with an automatic delivery of a DK Zoological Trainings Biscuit (small), triggered by a custom-made pellet dispenser. A secondary reinforcing tone was played via two speakers behind the touchscreen. Primary and secondary reinforcers were delivered on a 100% fixed reinforcement ratio. Additionally, we manually provided a raisin, through a PVC tube, on every fifth correct response to maintain the bonobo's interest. If an individual finished all of the trials within a session, they received three peanuts. Each response was followed by a 1500 ms inter-trial interval (ITI). When a bonobo made an incorrect response, no reinforcement was provided, and the ITI was increased to 3500 ms.

Touchscreen tasks

This study reports observations regarding the production of SDBs across two studies. Eight individuals participated in Study 1, and a subset of four individuals participated in Study 2.

Study 1 was a response slowing task (Bethell et al., 2016), conducted between January and July 2021. In this task, the bonobos were trained to touch grey square target stimuli. During the period of this study, the bonobos were housed in two sub-groups, the composition of which was regularly changed, to mimic natural fission-fusion dynamics. Test sessions for this study were conducted during a pre-fusion, on days with fission-fusion events, and during post-fusion days, one day after the fission-fusion events. The stimuli in the test sessions included images of a frontal bonobo face picture with a neutral expression (i.e., a direct gaze), or a profile view bonobo face picture with a neutral expression (i.e., an averted gaze), see Figure 5.1A. The maximum number of trials per subject, per day, was set to 60.

Study 2 was a pictorial emotional Stroop task (Allritz et al., 2016), conducted between September and October 2020 (Laméris et al., 2022b). Prior to the testing sessions, the subjects successfully completed colour-discrimination training, which was required for participation. The detailed protocol is described in (Laméris et al., 2022b). In short, the bonobos were trained to always touch the stimuli that were framed in a target colour, while an identical stimulus was simultaneously presented and framed in a different distractor colour. Hence, while stimuli were similar, the bonobos could make a correct response (i.e., touching the stimulus with the target colour) or an incorrect response (i.e., touching the stimulus with the distractor colour). The study itself consisted of three parts: (1) a colour-interference Stroop task, in which bonobos were shown

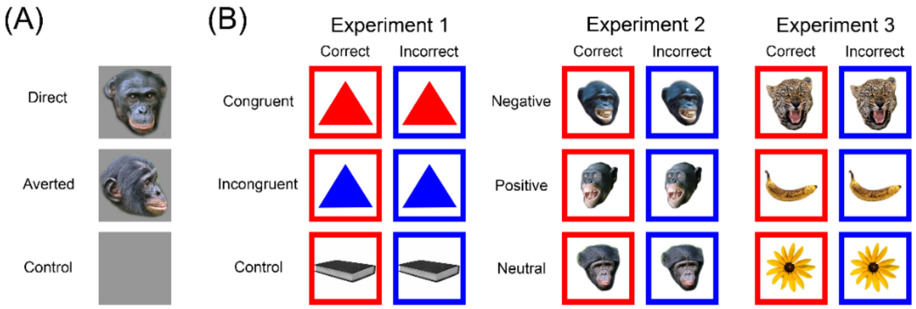

Figure 5.1: Examples of stimuli used in (**A**) Study 1, the response slowing task and (**B**) Study 2, the pictorial emotional Stroop task

geometric shapes that were either the same colour as the frame or a different colour; (2) a social, pictorial emotional Stroop task, in which bonobos were shown images of unfamiliar bonobos that had different facial expressions that are typically expressed in negative, neutral or positive contexts; (3) a non-social, pictorial emotional Stroop task, in which bonobos were shown biologically relevant objects that were predicted to have a negative (i.e., a leopard), neutral (i.e., a flower), or positive (i.e., a highly preferred food item) association, see Figure 5.1B. The maximum number of trials per subject per day was set to 105.

Video coding

All test sessions were video recorded using a Canon Legria HF R88. We followed the same coding protocol for both studies and coded the following factors: (a) hand used to complete the touchscreen trial (left or right); (b) any and all SDBs; (c) hand used to perform the SDB (left or right); (d) hemispace to which the SDB was directed (left, mid, or right). The software automatically recorded the accuracy (i.e., correct, or incorrect response), and the start and end time for each trial.

Based on previous studies on chimpanzees and bonobos (Jordan, 1977; Leavens et al., 2001; Leeds & Lukas, 2018; Wagner et al., 2016; Yamanashi & Matsuzawa, 2010), we identified 4 SDBs: nose wipes, gentle self-scratches, rough self-scratches, and self-touches. Nose wipes include when the subject raises the arm with a relaxed hanging hand and moves the wrist or back of the hand downwards across the nose (Jordan, 1977). Gentle self-scratches were defined as a subject raking their own hair or skin with bent fingers (Baker & Aureli, 1997). Rough self-scratches refer to the raking of one's own hair or skin with fingernails, including large movements of the arm (Baker & Aureli, 1997). A new gentle or rough scratch event was recorded after a period of five seconds without the corresponding scratching behaviour, or if the location of the scratch changed. A self-touch was defined as a single moment of contact between the fingers and another body part, without raking motions. We included self-touch as a separate category, as we considered this different to self-scratches. Example videos of the SDBs are presented in online supplements[1].

To test the reliability of the coding, 16% of the trials were coded by two observers, who were blind to the study aims. The reliability of: hand used to complete the touchscreen, hand used to perform SDBs, and to which hemispace the SDB was directed, were assessed using Cohen's Kappa, and intraclass correlation for the occurrence of the four SDBs using a two-way mixed models with a consistency definition. Inter-observer reliability for hand use on the touchscreen was perfect (=1.00), and almost perfect for hand use to perform SDBs (=0.94) and hemispace (=0.90). Intraclass correlation was moderate for self-touches (=0.70), good for rough self-scratching (=0.80), and excellent for gentle self-scratching (=0.96) and nose wiping (=0.94).

Tube task

One of our aims was to examine if left-handed individuals show greater behavioural reactivity towards incorrect responses. One obvious way to determine handedness is to look at which hand is used to complete the touchscreen task. However, different levels of manual lateralisation are expected based on the complexity of the task; low-level tasks may reveal a hand preference that is not indicative of the specialisation of the contralateral hemisphere (Fagot & Vauclair, 1991). The touchscreen task may represent such a low-level unimanual task. To obtain a more reliable level of hemispheric specialisation, we therefore completed the 'tube task' (Hopkins, 1995). We provided the bonobos with PVC tubes probed with small amounts of honey, which encourages the bonobos to hold the tube with the subordinate hand while removing the honey with their dominant hand, therefore presenting a more high-level coordinated bimanual task.

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[1] https://www.mdpi.com/article/10.3390/ani12213002/s1

Statistical analysis

We analysed Study 1 and Study 2 separately, as they differed in the individuals that participated as well as in task contingency. Before analyses, we excluded outlier trials, i.e., trials where the subject moved out of view, where other bonobos approached and interrupted the subject, or where a behaviour could not be reliably coded (2026 (15.9%) of the trials). Furthermore, we excluded SDBs directed to the mid-line of the face or body from analyses, as no obvious hemispace effect could be assigned (82 (0.6%) of the trials). Self-touches were not analysed due to the low rate of occurrence.

Handedness and side index

We used counts of left- and right-handed responses to complete the trials during the touchscreen task (HI-screen) and tube task (HI-tube) to quantify individual hand preferences. The Handedness Index score was computed for each subject as follows:

Here, R and L correspond to the count of right and left responses.

$$\mathrm{HI} = {}^{(\mathrm{R}-\mathrm{L})}\big/_{(\mathrm{R}+\mathrm{L})} \qquad (1)$$

HI-values range from −1.0 to +1.0, with positive values reflecting greater right-hand use, while negative values indicate more left-hand use. Side Indices (SI) for gentle and rough self-scratching, and HI for performing combined and separate SDBs, were calculated in a similar way.

Our sample included individuals with varying HI-screen. Therefore, we considered it likely that in-task hand use influences which hand is subsequently used to perform an SDB; we ran a binomial mixed model with subject ID as random intercept to verify this. Indeed, hand use for working on the touchscreen was not independent from the hand use for performing SDBs ($\chi^2 = 262.18$, df = 1, $P < 0.001$). However, hand use while working on the touchscreens did not predict to which hemispace the SDB would be directed ($\chi^2 = 0.054$, df = 1, $P = 0.817$).

Linear mixed models

We assessed the accuracy of the four individuals that participated in both studies to develop a sense of the perceived difficulty of the two tasks. We applied a generalised linear mixed model (GLMM), with a binomial distribution, with trial accuracy as a dependent variable and study (categorical; Study 1 or Study 2) as a fixed factor. The subject ID was included as a random intercept.

To examine the link of the production of SDBs during the touchscreen sessions and emotional arousal, we created LMMs with SDB rates (per trial per second) as dependent variable for each separate SDB type (nose wipe, gentle self-scratch, and rough self-scratch), and trial accuracy (categorical; correct or incorrect) and the hemispace (categorical; left or right side) to which the SDB was directed as independent variables. We included a two-way interaction between trial accuracy and hemispace. As nose wipes are, by definition, directed towards the centre of the face, we only included trial accuracy as a predictor in this model. Subject ID was included as random intercept in all models. We did not include hand use for SDB as an independent variable because this variable was not independent of in-task hand use. We used planned post-hoc testing for significant global effects using simple contrasts, focusing on the effect of trial accuracy. Tukey corrections were applied for multiple comparisons.

To rule out the possibility that condition in Study 1, or stimulus type in Study 1 and Study 2, influenced the production of SDBs, we ran separate LMMs for each SDB, including condition (categorical; pre-fusion, fusion, post-fusion) and stimulus (categorical; direct, averted, control) as the fixed factor for Study 1. For Study 2, we ran separate models for the three experiments, and included stimulus (categorical; Experiment 1—congruent, incongruent, control; Experiment 2—negative, positive, neutral; Experiment 3—negative, positive, neutral) as the fixed factor. Subject ID was again included as a random intercept in all models. Model outputs are presented in Tables S5.1–4, and mostly returned insignificant results. Only the rates of gentle self-scratching were lower during trials when averted stimuli were presented, compared to the control trials. Furthermore, the rates of nose wiping were lower during trials with positive social stimuli, compared to the control trials.

Behavioural reactivity

To examine the difference in behavioural reactivity to incorrect responses, depending on the handedness of the individual, we calculated standardised ratios for each SDB, following previous work (Yamanashi & Matsuzawa, 2010). As such, we calculated the average rate of SDBs after incorrect responses and divided this by the average rate after correct responses. This proportion was then standardised. We ran Pearson’s correlations between these standardised ratios and the HI-screen, and against HI-tube.

Results

Production of SDB types per study

We analysed 10,600 trials (Study 1 = 5876 trials, range = 436–896 per individual; Study 2 = 4724 trials, range = 1134–1220 per individual) and recorded a total of 1537 SDBs. Table 5.2 presents the distribution of observed SDBs per study. Overall, nose wipes occurred most frequently in both studies, followed by gentle scratching, rough scratching, and self-touching. Individual rates of SDBs were typically low, and are presented in Table S5.5.

Table 5.2: Occurrence of the different SDB types per Study

	Nose Wipe	Gentle Scratch	Rough Scratch	Self-Touch
Study 1	69.2%	19.8%	9.1%	1.9%
Study 2	80.6%	11.9%	5.6%	1.9%
Total (% of total)	75.5%	18.4%	7.2%	1.9%

Accuracy in the two studies

To examine the difference in the complexity of the two studies, we only included those individuals that participated in both studies (N = 4). The binomial GLMM showed a significant effect of ‘study’ on accuracy scores ($\chi^2 = 481.08$, df = 1, $P < 0.001$); with accuracy being higher in Study 1 (M = 0.978, SE = 0.006), compared to Study 2 (M = 0.758, SE = 0.003; $t_{8065} = -21.934$, $P < 0.001$). From these results, we concluded that Study 1 was less difficult than Study 2.

Linear mixed models

We present HI- and SI-indices in Table 5.3, from which it can be seen that, based on the HI-screen, our sample of bonobos consisted of two left-, five right-handed individuals, and one ambiguous-handed individual. As the hand used to execute SDBs was not independent of the hand used in the preceding touchscreen task, we decided to focus on laterality effects in the hemispace (Hopkins et al., 2006; Leavens et al., 2004). In order to present a complete perspective, we also present HI-indices for the different SDB types, although it is important to note that these values are dependent on the hand used to complete the touchscreen tasks.

Table 5.3: Individual Handedness- and Side-indices across tasks and SDB types. Please note that the HI indices for the different SDBs are influenced by HI-screen

Subject	HI-Tube	HI-Screen	HI-Gentle Scratch	HI-Rough Scratch	HI-Nose Wipe	SI-Gentle Scratch	SI-Rough Scratch
Busira	−0.01	0.92	0.79	0.77	0.98	0.28	−0.15
Habari	0.61	−0.47	−0.33	−0.69	−0.35	0.25	0.43
Kianga	−0.76	0.00	−0.21	−0.47	0.16	−0.32	0.20
Kikongo	0.15	0.96	−0.27	NA	−0.54	0.45	NA
Mokonzi	0.25	0.52	0.03	−0.50	−0.03	0.10	0.5
Nayembi	1.00	0.72	0.33	0.40	1.00	0.33	−0.20
Vifijo	0.72	0.97	1.00	0.33	0.78	0.00	−0.33
Zamba	0.68	−0.67	0.00	0.41	−0.17	−0.50	−0.76

Study 1

Eight bonobos participated in Study 1. For nose wiping, we only examined the effect of trial accuracy as this behaviour is directed towards the nose, and therefore hemispace effects are irrelevant. Here, trial accuracy had an effect on nose wiping ($\chi^2 = 5.989$, df = 1, $P = 0.014$), with rates increasing after incorrect responses compared to correct responses (Figure 5.2A; $t_{5846} = 2.447$, $P = 0.014$). We did not find a two-way interaction between trial accuracy and hemispace for gentle self-scratching ($\chi^2 = 0.102$, df = 1, $P = 0.750$), or for rough self-scratching ($\chi^2 = 0.146$, df = 1, $P = 0.702$). After removing the insignificant interaction effects, we only found a significant main effect of hemispace for rough self-scratching ($\chi^2 = 3.866$, df = 1, $P = 0.049$) and post-hoc testing showed that rough self-scratches were more directed to the left hemispace (Figure 5.2B; $t_{220} = 1.966$, $P = 0.051$). Full model results are presented in Table 4, and post-hoc results of the final models are presented in Table S5.6.

The participants in Study 2 consisted of a subset of the participants in Study 1, therefore, we ran additional analyses for Study 1, for those four bonobos that participated in both studies. Results were comparable in that we found a significant effect of trial accuracy on nose wiping ($\chi^2 = 16.073$, df = 1, $P < 0.001$), with higher rates after incorrect responses ($t_{3342} = 4.009$, $P < 0.001$), and no interaction effects between hemispace and trial accuracy for both rough self-scratching ($\chi^2 = 1.187$, df = 1, $P = 0.276$) and gentle self-scratching ($\chi^2 = 1.247$, df = 1, $P = 0.264$). In contrast to the analyses on the full dataset, the main effect of hemispace on rough self-scratching was not significant ($\chi^2 = 2.614$, df = 1, $P = 0.106$). Full post-hoc results of the final models are presented in Table S5.7.

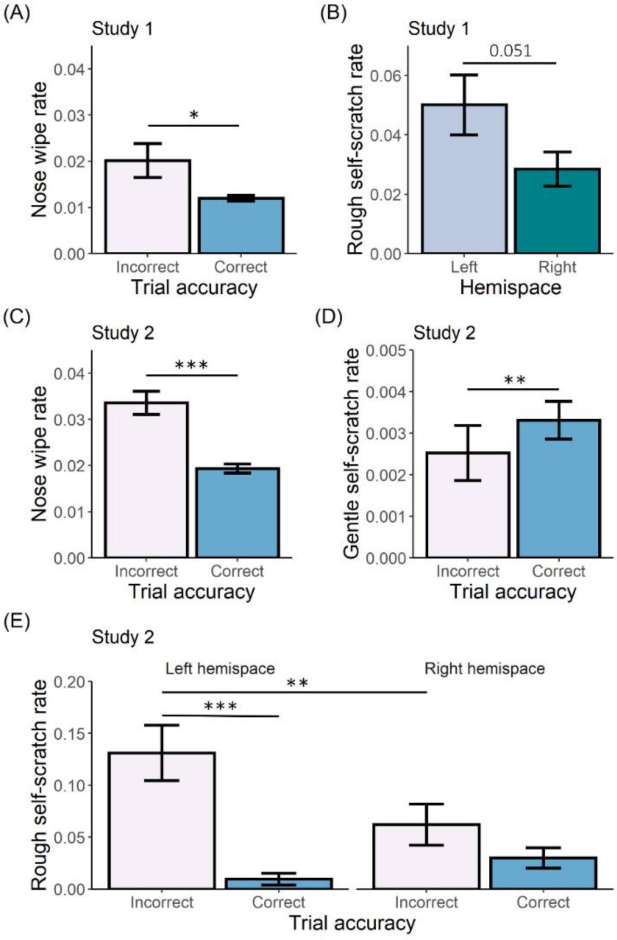


Figure 5.2: Mean rates per trial per second of (**A**) nose wiping in Study 1 in function of trial accuracy; (**B**) rough self-scratching in Study 1 in function of hemispace; (**C**) nose wiping in Study 2 in function if trial accuracy; (**D**) gentle self-scratching in Study 2 in function of trial accuracy; and (**E**) rough self-scratching in Study 2 in function of trial accuracy and hemispace *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$

Study 2

Four bonobos completed Study 2. Trial accuracy showed a significant effect on nose wiping ($\chi^2 = 21.216$, df = 1, $P < 0.001$), with higher rates after incorrect responses (Figure 5.2C; $t_{4696} = 4.606$, $P < 0.001$). Gentle self-scratching was not influenced by the interaction between trial accuracy and hemispace ($\chi^2 = 0.031$, df = 1, $P = 0.860$), but was influenced by the main effect of trial accuracy ($\chi^2 = 8.328$, df = 1, $P = 0.004$). Namely, gentle self-scratching increased after correct responses compared to incorrect responses (Figure 5.2D; $t_{119} = 2.886$, $P = 0.005$). For rough self-scratching, we found a significant two-way interaction between trial accuracy and hemispace ($\chi^2 = 6.469$, df = 1, $P = 0.011$). The bonobos scratched more to their left hemispace after an incorrect response compared to a correct response (Figure 5.2E; $t_{123} = 4.556$, $P < 0.001$). This accuracy effect was not observed in the right hemispace ($t_{145} = 1.311$, $P = 0.192$). Using hemispace as a simple contrast, we found that rough self-scratching was more directed to the left compared to the right hemispace during incorrect trials ($t_{135} = 2.250$, $P = 0.026$), but not during correct trials ($t_{141} = -1.210$, $P = 0.228$). Full model results are presented in Table 5.4, and post-hoc results of the final models are presented in Table S5.6.

Table 5.4: Results of the LMM examining the interaction between trial accuracy and hemispace on the rate of SDBs

Study 1				**Study 2**			
Nose wipe	Chisq	df	*P*	*Nose wipe*	Chisq	df	*P*
Accuracy	5.989	1	**0.014**	Accuracy	21.216	1	**<0.001**
Gentle Scratch	Chisq	df	*P*	*Gentle Scratch*	Chisq	df	*P*
Accuracy[a]	0.277	1	0.599	Accuracy[a]	8.328	1	**0.004**
Hemispace[a]	0.558	1	0.455	Hemispace[a]	0.001	1	0.969
Accuracy * Hemispace	0.102	1	0.750	Accuracy * Hemispace	0.031	1	0.860
Rough scratch	Chisq	df	*P*	*Rough scratch*	Chisq	df	*P*
Accuracy[a]	0.816	1	0.366	Accuracy	15.604	1	**<0.001**
Hemispace[a]	3.866	1	**0.049**	Hemispace	0.086	1	0.769
Accuracy * Hemispace	0.146	1	0.702	Accuracy * Hemispace	6.469	1	**0.011**

[a] Results are from models in which the non-significant interaction effect was removed. Bold values highlight significant results.

Handedness and behavioural reactivity

No correlation was found between the HI-screen and the behavioural reactivity of nose wiping (Pearson's $r_6 = -0.469$, $P = 0.241$), gentle self-scratching (Pearson's $r_6 = 0.146$, $P = 0.731$), or rough self-scratching (Pearson's $r_6 = -0.190$, $P = 0.652$), or between HI-tube and nose wiping (Pearson's $r_6 = -0.311$, $P = 0.453$), gentle self-scratching (Pearson's $r_6 = 0.482$, $P = 0.0.226$), or rough self-scratching (Pearson's $r_6 = -0.130$, $P = 0.758$).

Discussion

We studied the production of SDBs in bonobos during two cognitive touchscreen tasks. As expected, and in line with previous studies, we found that bonobos also respond to arousing events with increased rates of some SDBs, namely nose wiping and rough self-scratching. Interestingly, gentle self-scratching increased with correct responses in one study.

Nose wiping was by far the most recorded SDB, constituting 75.5% of all recorded SDBs, followed by gentle self-scratching (18.4%) and rough self-scratching (7.2%). Despite being the most common SDB in our study, not much is known about nose wiping and its potential link to arousal. Some suggest a link to nervousness or edginess (Marchant & McGrew, 1996). However, with the exception of this report, nose wiping remains overlooked as a possible SDB, and empirical evidence is lacking. We found that rates of nose wiping increased during incorrect trials, and these changes were consistent across the two studies. Similar to other studies, when the bonobos made an incorrect response, they were not given a small food reward and received a short time out, which arguably resulted in increased arousal. A previous study on chimpanzees examined nose wiping and reported changes in rates based on trial accuracy in some subjects, although rates were typically lower than rates of self-scratching (Yamanashi & Matsuzawa, 2010). This could hint at species-specific differences in the expressive patterns of SDBs. It is possible that a mutation in the serotonin receptor, linked to increased rates of self-scratching in chimpanzees, is absent in bonobos (Staes et al., 2019a) and could relate to this difference. The fact that nose wiping was so common in the current sample, combined with the observation that rates also increased with incorrect responses in Study 1, which were relatively rare, could suggest that nose wiping is a behavioural response to low levels of arousal in bonobos. Overall, this could support the idea that, compared to chimpanzees, bonobos differ in their behavioural reactivity towards emotional arousal (Rosati & Hare, 2013). One other study found that one particular bonobo began nose wiping more after viewing emotional images (Kret et al., 2016), yet additional exploratory analyses on our data revealed lower rates of nose wiping after viewing play faces. This is interesting as we previously found that these positive social stimuli specifically grab the attention of bonobos (Laméris et al., 2022b). Our results contribute to the limited knowledge regarding nose wiping and suggest that it can be considered an indicator of arousal in bonobos, and potentially of low levels of arousal, although this, and a possible response to emotional stimuli, warrants further validation.

We further aimed to assess handedness for executing SDBs during the cognitive tasks. Based on previous studies in chimpanzees, we expected to find asymmetry in hand use for executing SDBs in bonobos, especially when arousal was increased, e.g., when making incorrect responses (Hopkins et al., 2006; Leavens et al., 2001; Wagner et al., 2016). However, we found that the hand used to perform SDBs was strongly associated with the hand used to complete the trial preceding these SDBs. Whilst changes in hand use can of course still offer information about these asymmetries (Wagner et al., 2016), because our sample consisted of individuals with varying handedness levels, in both touchscreen performance and in the conventional tube task, we reasoned that this would complicate the interpretation of these results. We therefore refrained from testing the effect of hand use for SDBs, but focused on asymmetries in the hemispace (i.e., to which side of the body the SDBs were directed). Since only gentle and rough self-scratches are clearly directed towards one of the two hemispaces, and nose wipes are by definition directed towards the middle of the face, we limited our hemispace analyses to these two behaviours. Results from these analyses only revealed an arousal-related hemispace effect for rough scratching. Namely, when the bonobos made an incorrect response, rough self-scratches were directed to the left hemispace. This suggests that there is a left hemispace bias with increased arousal, which is consistent with previous work on chimpanzees (Hopkins et al., 2006; Leavens et al., 2004), and follows the idea of right hemisphere asymmetries for emotional responding (Rogers, 2002, 2010), which then has consequences for asymmetries in cutaneous sensations (Leavens et al., 2001). However, it is important to note that we only observed this arousal-related hemispace effect in Study 2, while a general left hemispace bias was found in Study 1. This can have multiple explanations. Study 2 was perceived by the bonobos to be more challenging, as indicated by the lower accuracy scores in this task. Baker & Aureli (1997), despite assessing rough self-scratching in different contexts, reported that rough self-scratching may reflect higher levels of anxiety (Baker & Aureli, 1997), and Troisi et al. (1991) raised the idea that self-scratching and arousal are associated in an inverse-U fashion (Troisi et al., 1991). Although we were unable to test this, the difference in the effect of trial accuracy on rough self-scratching between the two studies could suggest that the frequency of incorrect responses is a modulating factor in the expression of rough self-scratching. However, one drawback of our study is that Study 1 and Study 2 differed in the number of participants, making it difficult to truly distinguish between the effect of task complexity and the subject sample. Therefore, we re-ran the analysis of Study 1, with only the bonobos that also participated in Study 2 and found that the general hemispace effect on the entire sample disappeared, suggesting that this effect was sample-specific. This is in agreement with an earlier study that focused on individual differences in which subjects are sensitive to incorrect responses (Yamanashi & Matsuzawa, 2010). However, due to the relatively low sample size, interpretation of the results should be met with caution.

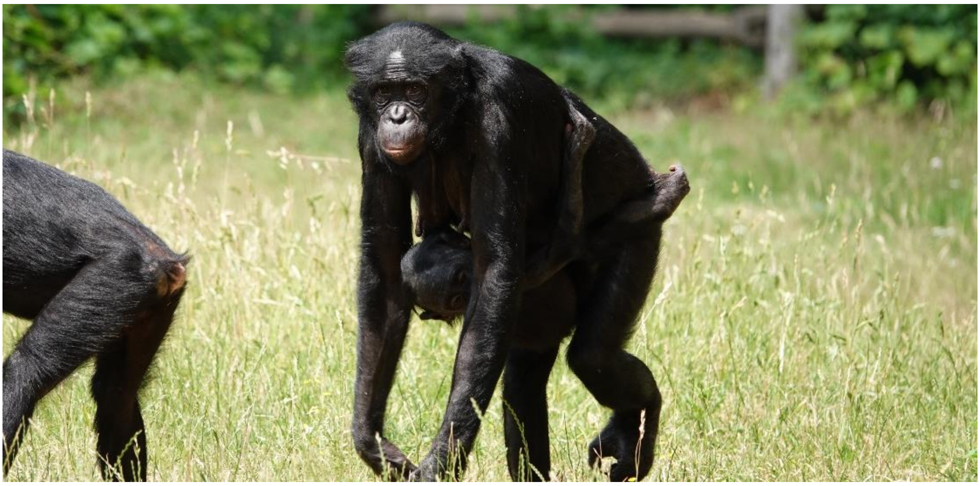
One individual factor that could explain differences in behavioural reactivity when experiencing arousal is hemispheric specialisation. Several lines of evidence suggest an association with hemispheric specialisation and the stress response (Braccini & Caine, 2009; Gordon & Rogers, 2015). We predicted that individuals showing right handedness would show stronger behavioural responses after incorrect trials. We measured handedness during the touchscreen task as a proxy for hemispheric specialisation and tested its effect on behavioural reactivity to incorrect responses. Contrary to our prediction, we found no evidence for an association between handedness and behavioural reactivity. However, hand preference may vary between tasks (Lilak & Phillips, 2008), and it could be that the hand preference measured in the unimanual touchscreen task is not correlated with hemispheric specialisation (Fagot & Vauclair, 1991). For this reason, we additionally correlated behavioural reactivity with incorrect responses to handedness during the tube task, a standardised task to approach hemispheric specialisation in primates (Hopkins, 1995). Based on this, we saw that handedness while working on touchscreens was not correlated with handedness measures based on the tube task. This may confirm that the unimanual nature of working on touchscreens taps into different mechanisms than more complex bimanual tasks, such as the tube task, and therefore does not reflect hemispheric specialisation. Nonetheless, handedness based on the tube task also did not show an association with behavioural reactivity during incorrect trials. Evidence on the putative link between handedness and stress response is inconsistent (e.g., higher levels of plasma cortisol were observed in right-handed rhesus macaques (Westergaard et al., 2001) and common marmosets (Vaughan et al., 2019)), and may not be straightforward.

Furthermore, although the increased rates of some SDBs after incorrect responses suggest heightened levels of arousal, it remains unclear which emotions the bonobos were experiencing, and if whether is in fact linked to increased activation of one of the two brain hemispheres.

Interestingly, the bonobos had higher rates of gentle scratching during correct trials in Study 2, compared to incorrect trials. Although this result should be interpreted with caution due to the lower sample size, this finding is consistent with a study on common marmosets (*Callithrix jacchus*), which reported increased rates of self-scratching in positive conditions (Neal & Caine, 2016). Specifically, the authors of the latter study found increased rates during social play, but decreasing rates during food foraging, and no change during food anticipation. The differential patterns of self-scratching in this study highlight the complex nature of self-scratching. We could reason that the increase of gentle self-scratching in our own study may be linked to the anticipation for the food reward. Prior to taking part in these studies, the bonobos were conditioned on an auditory reinforcer, which was accompanied with a small food reward. However, these rewards were automatically triggered and delivered immediately after a bonobo gave a correct response, and we consider it most likely that any scratching occurred after the delivery of these rewards. The timing of food rewards (i.e., immediate, delayed or no reward) in a similar context previously did not affect gentle self-scratching in chimpanzees (Leavens et al., 2004), and we are therefore unsure if the increased rates of gentle self-scratching reflect positive anticipation. Alternatively, because the bonobos participated in the touchscreen sessions in a social setting, it could be possible that they experienced arousal due to competition with other group members when receiving a food reward. However, we trained the bonobos to complete their tasks individually, and paused sessions when they were interrupted by other individuals, in an attempt to avoid competition over the food rewards. The fact that we only observed this effect in Study 2, and not in Study 1 (which was perceived as easier), could suggest that the more frequent incorrect responses enhanced the relative rewarding experience during correct trials, although this is purely speculative. This raises more questions regarding the mechanisms behind this behaviour, and several hypotheses remain to be tested regarding the increase in gentle self-scratching with correct responses, as it could be some form of anticipation, positive arousal of receiving food rewards, or a possible contrast effect due to the ratio of correct and incorrect responses.

Conclusions

In conclusion, despite having a reputation for being less emotionally responsive than chimpanzees, bonobos also show higher rates of SDBs in response to emotional arousal. Whereas self-scratching appears the most common SDB in chimpanzees, the bonobos in this study most commonly performed nose wipes. The fact that nose wipes were so common among the bonobos, and are potentially indicative of low levels of arousal, could hint to a species-specific difference in emotional reactivity. Although more research is necessary to better comprehend these expressive patterns of SDBs and their reliability as indicators of emotional arousal in bonobos, we were able to provide evidence that some, but not all SDBs, increase with putative negative arousal, namely nose wiping and rough self-scratching. Arousal-related hemispace effects for rough self-scratching provide further reason to believe that this behaviour may indicate negative arousal. In contrast, we found that gentle self-scratching increased with possible positive arousal. Overall, we encourage future studies to investigate SDBs while taking into account the nuances laid out in this study.



6

Human perception of bonobo emotional expressivity using a Qualitative Behavioural Assessment

Daan W. Laméris, Marina Salas, Marcel Eens, Lisa Gillespie, Nicky Staes, Jonas Torfs, Jonas Verspeek, Hilde Vervaecke, Samantha Ward, Jeroen M. G. Stevens

Abstract

Human perception of animal emotional expressivity can inform animal welfare. While Qualitative Behavioural Assessment (QBA) has been applied to domesticated and some non-domesticated animals, its use in great apes is limited, despite their emotional expressivity. Here we develop a QBA for bonobos via two consecutive studies. In Study 1, a group of students and bonobo experts viewed 20 video clips of zoo-living bonobos of both sexes and different age classes, before and after moving to a new enclosure. Free Choice Profiling was used to investigate the bonobos' expressive qualities. Multiple Factor Analysis revealed two meaningful dimensions. Students described dimension 1 as ranging from 'quiet/calm' to 'angry/active', and dimension 2 as 'sad/anxious' to 'happy/loving'. Experts described dimension 1 from 'quiet/relaxed' to 'nervous/alert', and dimension 2 from 'nervous/bored' to 'playful/happy'. To establish a fixed list of descriptors, 21 reliable and commonly used terms were retained, and three terms from QBA literature were added. Study 2, similarly involved students and experts who used this final list to rate 40 video clips, resulting, again, in two dimensions. Students described dimension 1 from 'quiet/calm to 'agitated/frustrated', and dimension 2 from 'sad/stressed' to 'happy/positively engaged'. Experts described dimension 1 from 'quiet/calm to 'active/excited', and dimension 2 from 'sad/bored to 'happy/positively engaged'. Students and experts scored adult and subadult bonobos on different terms, and experts in Study 2 rated bonobos higher on 'active/excited' in their new enclosure. Reliability was moderate to good for the dimensions, but low to moderate for individual descriptors. Additionally, observers' animal-directed empathy influenced scores on dimension 1. Our results indicate the potential of a great ape QBA but further validation against cognitive and physiological measures is needed before regular application to measure welfare.

Introduction

Measuring animal emotional states has been of interest for many scientific fields, including animal welfare science (Mellor, 2012) and comparative psychology (Kret et al., 2022). Because of this widespread interest, numerous measures have been developed to estimate emotions in animals. Emotional states correlate with behavioural and/or physiological responses, of which a number can be identified and can be measured relatively easily. Consequently, behaviour remains one of the most commonly utilised welfare measures (Binding et al., 2020; Dawkins, 2004). Anthropomorphism is often considered a methodological concern for behavioural observations that should be avoided (de Waal, 1999; Williams et al., 2020). However, judgements that are quantified and validated can provide practical and scientific advantages (Meagher, 2009). A prominent approach herein is the Qualitative Behavioural Assessment (QBA) method, developed to evaluate animal welfare in the early 2000s, which focuses on the ‘whole-body’ expressive qualities of an animal (Wemelsfelder et al., 2000). Instead of focusing on separate facets of information and measuring only the animal’s behaviour, QBA is a holistic and integrative approach to examine how animals respond to the environment and how they deal with it (Wemelsfelder et al., 2001). Two QBA methods currently exist: the Free Choice Profiling (FCP) method, originating from food sciences, allows raters to use their own descriptive terminology to score animal emotional expressions, whereas the Fixed-list method provides a list with predetermined descriptors used by all raters. QBA finds similarities with rater-based animal personality scores as similar terms are used, but allows for the temporal variation of emotional states when repeatedly measured (Wemelsfelder et al., 2000).

QBA was initially developed as a welfare indicator for farm animals to supplement other quantitative measures (Wemelsfelder et al., 2000). A major benefit of QBA is that assessments can be done rapidly, on-site (through live observations) or off-site (using video footage), on individual or group-level. High inter- and intra-observer reliability, and validation against other behavioural and physiological indicators of welfare states have proven the value of QBA as additional welfare measure (Carreras et al., 2016b; Skovlund et al., 2023; Stockman et al., 2011; Wickham et al., 2015).

QBA is based on the human ability to interpret the expressive qualities, or demeanour (i.e. a way of looking and behaving), of an animal and this may be modulated by several characteristics of the observer. This can include the level of experience with the species (Duijvesteijn et al., 2014), which for non-domesticated species may present a challenge as the shared co-evolution and enhanced familiarity with domesticated species facilitates our interpretation and responses to these animals (Prguda & Neumann, 2014; Westbury & Neumann, 2008). Another factor that may influence how humans perceive animals is their empathy for animals, which can be a concern for the generalisability of observer judgements (Meagher, 2009). Perceiving and assessing emotional states of other individuals involves a certain degree of ability to put oneself in the place of the other (Preston & de Waal, 2002), which varies among individuals and as such may influence their judgements. Nonetheless, QBA has been shown to be a valuable additional tool to assess the welfare of non-domesticated species, for example in zoo-settings or wildlife rescue centres (Rose & Riley, 2019). Recently, QBAs have been gaining momentum for such species, and a number of studies developed and tested QBAs for non-domesticated species, including giraffes (Patel et al., 2019), elephants (Pollastri et al., 2021; Webb et al., 2020; Yon et al., 2019), bears (Skovlund et al., 2023; Stagni et al., 2022) and dolphins (Warner et al., 2022). Non-human primates (from now on “primates”) have so far received limited attention, with only one study applying a QBA following the Fixed-list method (Gartland et al., 2022), while no previous study used FCP to study primate emotional expressivity.

Primates may be particularly interesting to use as species for QBA as emotional expressions play a pivotal role in maintaining and regulating social relationships in many primate societies (Kret et al., 2020). Some of these expressions exhibit continuity among species, including humans, and homologous traits can be identified, whilst for other expressions this is not the case (Kavanagh et al., 2022). Socio-ecological factors, for example, may shape the function and use of expressions of emotions, resulting in species-specific expressions (Dobson, 2012). Subjective welfare assessments have previously been applied to different primate species to address emotional states and generally found good reliability between expert observers (e.g., people with behavioural observation experience or caretakers) (King & Landau, 2003; Robinson et al., 2016; Stevenson-Hinde et al., 1980; Weiss et al., 2002), but the use of QBA is limited (Gartland et al., 2022). On one hand, their phylogenetic proximity and physical similarity to humans may facilitate human recognition and perception of primate body language, gestures (Graham & Hobaiter, 2023). Additionally, this similarity may enhance our empathetic attitudes towards primates (Miralles et al., 2019), which can subsequently influence how we judge their emotions. On the other hand, due to the high degree of expressive variation and the homologous nature of some traits between primates, correctly identifying and recognising these expressions may be a challenge for the general public, compared to primate experts (Foley, 1935; Waller et al., 2007). Although welfare assessments carried out by the general public could be an informative asset (Freire et al., 2021), some level of experience with the species is expected to be necessary for the reliable use of QBA in non-human primates.

The current study aimed to explore the development and use of a QBA for bonobos, a great ape species with a high level of emotional expressivity which also plays a pivotal role in regulating their social dynamics. For example, distinct facial expressions and vocalisations are produced during positive and negative social interactions (e.g., play or bared-teeth faces (de Waal, 1988; Demuru et al., 2015)) which signal information about the sender's emotional state and can increase the success of the interaction (Palagi et al., 2020). Other behaviours, such as certain self-directed behaviours, have been shown to be reliable indicators of negative emotional arousal in bonobos (Laméris et al., 2022c). These are highly salient visual stimuli within bonobo societies and bonobos developed attentional mechanisms for the rapid detection of such signals (Kret et al., 2016; Laméris et al., 2022b; van Berlo et al., 2023). This makes bonobos an interesting study subject for QBA.

We completed two studies. In Study 1, we applied Free Choice Profiling (FCP) to examine the terminology used by experts and non-experts to describe bonobo emotional expressivity. In Study 2, we examined the validity of the most commonly used, and reliable terms from Study 1 to develop a list of fixed-terms that can be further used to assess emotional states in bonobos. For both studies, we additionally sought to investigate if a) observers, who differed in their level of experience with bonobos, scored the expressivity of bonobos differently; b) animal-directed empathy levels of observers influenced their QBA scoring; and c) observers perceive differences in the bonobos' expressivity based on contextual or individual factors related to the bonobos. As a specific contextual factor we considered housing condition, as we recorded videos during a period before and after the bonobos moved to a new enclosure within a zoo. The individual factors of the bonobos that we examined were sex and age class.

Methods

Ethics

This study was reviewed by an independent ethical committee, the Social Sciences and Humanities Ethics Advisory Committee (EA SHW) of the University of Antwerp, who issued a favourable opinion on 07-03-2022 (#SHW_22_026). All human participants received an information and consent sheet and provided written consent. The recording of the video footage of the bonobos was approved by the Twycross Zoo Research Committee in May 2021. The bonobos were housed in an EAZA-accredited institution and managed according to the Bonobo Best Practice Guidelines (Stevens, 2020).

Animals and housing conditions

Ten bonobos were selected from a group of twelve individuals, housed in Twycross Zoo (UK). Subjects were selected with the aim to cover both sexes and different age categories in a balanced way as best as possible. As such, four adult females, four adult males and two juvenile males (< 7 years old) were the subjects of the study. Subjects ranged in ages from 5.6 to 36.3 years old at the time of filming (mean = 19.1, sd = 8.2). The bonobos were housed in two subgroups whereby the individuals within the groups were changed regularly in accordance to the needs of the animals and their fission-fusion societal management system. They received regular provision of targeted and group scatter feeds throughout the day, had access to water ad libitum and were daily provided with enrichment and browse. Between 14-22 September 2021, the bonobos moved to a new enclosure. The original enclosure consisted of two separate areas of the same building and were similar in size (2x 52.8m^2). The two enclosures could be connected to each other by opening automatic sliding doors. Indoor areas contained large permanent climbing structures, with wooden beams, softer webbing material, nesting platforms and off-show bed areas. There was a single shared outdoor space (547m^2), with access for each group rotated every 24 hours. The outdoor area included further climbing structures, hiding areas and a drinking pond with fresh running water, and was visible to the public. The new enclosure, though larger in size (2x 54.3m^2), provided a very similar environment with the same husbandry procedures as the pre-move enclosure. The main distinction was that both groups now had full access to an outdoor area at all times (433m^2 and 211m^2), instead of access alternating between groups every 24 hours.

Video footage

Video footage was recorded during two periods: the first period spanned five days between July and September 2021 in the old bonobo enclosure. After the bonobos moved into their new enclosure, we conducted another set of recordings over four days in November 2021. The videos were captured multiple times per day randomly between 9:00 and 16:00 using mobile phones (iPhone, Samsung) or handheld cameras (Canon Legria HF R88). During each recording moment, we aimed to collect footage of each focal animal, unless they were out of sight. We filtered out low-quality videos, or when bonobos did not stay at least 30 seconds in view. In total, we retained 227 videos, ranging from 30 to 120 seconds in length, resulting in approximately 270 minutes of footage. From these videos, we selected the first or last 30 seconds in which one of the ten focal animals was fully visible (mean = 27.8, range = 19-45) to create a library of random snapshots of the focal's demeanour. The focal animal was later identified in each video using a white arrow to simplify identification for the group of raters that were unfamiliar with the individuals.

Survey and animal empathy scale

Prior to participating in the QBA sessions, we asked the participants of Study 1 (n= 26) and Study 2 (n = 49) to fill out a survey consisting of two parts. The first part focused on demographic information, such as age, previous/current pet ownership, how often they visited zoos, and previous/current experience working with animals, and if this was specifically with primates. The distribution of this is presented in Table S6.1. The second part of the survey aimed to establish a level of empathy with animals for each of the participants. We asked the participants in both studies to complete the Animal Empathy Scale (Paul, 2000). This survey contains statements regarding the way people feel about animals and asks participants to score each statement on a 9-point Likert scale (ranging from 'Strongly disagree' to 'Strongly agree'). Six observers from the Students group (Study 1: n = 1; Study 2: n = 5) did not fully complete the survey and were therefore not included in the empathy analysis.

Following the methodology of Cornish et al. (2018), we conducted a Ward's Hierarchical Clustering analysis using Euclidian distance to investigate how participants' responses to the statements of the Animal Empathy Scale clustered together in both Study 1 and Study 2. These analyses revealed two distinct clusters, classifying the statements as either 'empathic' and 'apathic' (see Table S6.2). Based on these clusters, we calculated empathy ratio scores for individual observers by dividing the average of the scores of the statements within the ‘empathic’ cluster by the average of the scores of the statements in the ‘apathic’ cluster. Values above 1 indicate that participants agreed more with ‘empathic’ statements, while values below 1 indicate a higher agreement with ‘apathic’ statements. These empathy ratio scores were subsequently used to investigate the relationship between empathy for animals in Study 1 and 2 and how observers scored along the constructed dimensions.

Study 1: Free Choice Profiling

Observers

In Study 1, two groups of observers participated. The first group consisted of 17 students (age range: 18-35) who were enrolled in a behavioural biology course at a university college and had some prior experience with QBA. The second group comprised nine animal experts (age range: 28-64) who had actively worked on topics like animal welfare or bonobo behaviour in the past years. To accommodate logistics, we organised two sessions in April 2022. The first session involved all the students and five experts, while the remaining four experts participated in a separate session. During both sessions, the observers were seated behind a computer or laptop. Each session began with an instructional period lasting approximately 45 minutes. During this instruction, we first explained what QBA is, and how this is used. We secondly explained that the objective of this study was to explore if QBA can be used to assess the welfare of zoo-housed bonobos. We lastly explained Phase 1 and 2 (described below) with a practice video. Specifically, the observers were instructed to focus on the bodily expressions of the focal animal, without receiving additional information about bonobo behaviour. We did not instruct the participants to pay attention to differences between housing conditions, sexes, or age classes, which could potentially be inferred from visual cues. Furthermore, we explained to the observers that there were no ‘correct’ or ‘incorrect’ answers and explicitly instructed them to complete the QBA on their own. Throughout the sessions we asked the observers not to discuss their terminology nor the videos.

Phase 1 – Term generation

The goal of Phase 1 is for the observers to generate their own terminology that describes the range of bonobo emotional expressivity. We applied FCP for the initial term generation which is an integrative methodology that allows observers to independently generate their own descriptive terminology that, in their opinion, best describes the animal's emotional expressivity (Wemelsfelder et al., 2001). FCP consists of two phases. In Phase 1, the observers viewed 20 x 30-s video clips of bonobos on a computer or laptop. These videos were selected to cover a wide range of behavioural expressions (Table S6.3). After each clip, they had 2-min to write down the adjectives that described the expressive qualities of the bonobos on a paper form. They were instructed to generate as many descriptors as they could come up with and were allowed to re-use terms for subsequent videos. Observers were allowed to write down terms in their native language (i.e., Dutch). After all the clips were viewed, the observers were instructed to create a list of unique terms that they had used. Two researchers (DWL and JMGS) then checked these lists and deleted terms that described what the animals were doing (e.g. walking, feeding), as well as terms that were given both in their positive and negative form, by keeping only the positive form (e.g. only keep 'happy' out of 'unhappy' and 'happy'). For this publication, terms were translated to English and two independent people, fluent in English and Dutch, translated these back to Dutch as double control.

Phase 2 – Rating procedure

After a break, the observers received their checked, final list of terms and continued with Phase 2. The purpose of Phase 2 is for the observers to use their own terminology on a quantitative basis to score bonobo expressivity. In contrast to previous studies who recorded ratings on paper scoring sheets, we implemented a web-based visual analogue scale (VAS) for efficient and more reliable data processing (Couper et al., 2006). The observers were provided with a link to a Qualtrics survey (Qualtrics, Provo, UT, USA), where they were asked to transfer their final list of terms. In this phase, a new set of 20 video clips was presented to the observers, which were randomly selected from our video dataset to cover one video for each of the ten individuals in the old and new enclosure. However, due to an error, for one individual we selected two clips in the new enclosure, resulting in a total of 9 clips from the old enclosure and 11 clips from the new enclosure. The video presentation was integrated within Qualtrics, and we configured the settings to automatically associate each term from the personal list with a VAS to cover a range of 0 to 100 points. The VAS had anchors labelled as 'minimum' and 'maximum', with the left end of the scale (i.e., 'minimum') meaning that the expressive quality indicated by the term was completely absent, and the right end of the scale (i.e., 'maximum') indicating that the term was fully expressed. Through a slider bar, the observers could click a point on the VAS to give a score for each term for each of the 20 videos. We set no default location of the slider and the slider only became visible until the rater clicked somewhere on the VAS. We furthermore set no number of points along the visual analogue slider, nor gave numeric reference of the score, in an attempt to resemble analogue VAS as much as possible.

Statistical analysis

The 26 observers individually assigned quantitative scores to their own terms for each of the 20 videos in Phase 2. Data were analysed separately for the Students and Experts using multiple factor analysis (MFA), which is an extension of principal component analysis (PCA) designed to analyse multiple datasets with different variables collected from the same set of observations. MFA belongs to the family of multi-table methods and is similar to the widely used generalised Procrustes analysis (GPA) (Wemelsfelder et al., 2000). Both procedures are freely accessible in the *FactoMineR* package (Lê et al., 2008) in RStudio (R Core Team, 2020), however, MFA has the statistical advantage over GPA of being an eigendecomposition technique that does not require multiple iterations to reach a consensus.

A detailed review of MFA is provided by Abdi et al. (2013), but in brief, MFA aims to: 1) analyse multiple data sets with different variables on the same observations; 2) provide a set of compromise factor scores; and lastly 3) project the original data onto the compromise, which is a common representation of the observations (similar to the ‘consensus profile’ in GPA) that allows you to analyse communalities and discrepancies between observations. To achieve this, MFA first standardises each of the data tables so that the first principal component of each table has a similar length, which is measured by the first singular value. Next, a non-normalised PCA is performed on the sequence of normalised data tables to obtain common representation of the observations, referred to as the compromise. This compromise consists of a set of principal components (or dimensions), which can be ordered by the amount of variance that each dimension explains. The observations can be plotted along these dimensions, and their respective location can be expressed in their coordinates (i.e., factor scores). The distance between the observations within this compromise expresses the similarities between the observations. This can be further broken down to the observations of each individual data table, which are referred to as partial factor scores.

MFA additionally calculates a similarity matrix between each possible pair of observers. We performed a Principal Coordinate Analysis (PCoA) on these similarity values to estimate the centre of distribution for each of the observers and calculate 95% confidence regions. Observers outside these regions are considered potential outliers. The observer plots depicting these regions can be found in Figure S6.1, revealing three potential outliers in the Student group. However, we decided to retain these observers as we had no discernible reason to believe that their ratings were invalid. To assess whether the results of the MFA truly reflected patterns in the detection of emotional expressions of bonobos or if they were merely statistical artifacts, we ran a permutation test on the eigenvalues of the first dimensions. By running the MFA 500 times, using permuted datasets, we were able to calculate 95% confidence intervals for these ‘random’ eigenvalues. Observed eigenvalues for dimensions from our true dataset that were above these confidence intervals would indicate that the variance explained by the compromise was a meaningful feature of the dataset, and not a statistical artifact. Intraclass correlations among the final dimensions were furthermore assessed using a two-way mixed model and a consistency definition.

MFA transformed the different configurations into one multidimensional compromise profile which is purely defined in terms of its geometrical properties without any semantic connotations. To assign semantic meaning to the dimensions of the compromise profile, we examined the correlations between all the terms generated by the observers and the principal dimensions. Here, the stronger a term correlates with a dimension, the more that term can be considered a representative descriptor of that dimension. For dimension 1, we used terms with correlations lower than -0.7 and higher than 0.7. For dimension 2, we kept terms with correlations lower than -0.4 and higher than 0.4. We then counted how many times each descriptor was above and below the dimension-specific threshold, and used those terms that occurred most frequently to describe the two dimensions.

We were additionally interested if observers perceived differences in the emotional expressions of the bonobos depending on contextual [housing condition (old enclosure or new enclosure)] or focal animal factors [age class (subadult or adult), sex (female or male)]. We analysed the location of the coordinates per observer per video clip along the dimensions in separate linear mixed models against housing condition, age class and sex as predictor variables. Each model included a random intercept for observer ID and video clip. Focal animal ID was considered as additional random intercept, but decreased the model fit. In an additional linear mixed model, we tested the partial coordinates against the observers’ animal empathy scores as predictor variable, separately for the Student and Expert group.

MFA was performed using the *FactoMineR* package (Lê et al., 2008), and linear mixed models were performed using the *lme4* package (Bates et al., 2015) in RStudio version 1.3.1073 (R Core Team, 2020).

Study 2: Fixed List procedure

Observers

For Study 2, we invited 44 new students (age range: 18-44) from the same course as the students from Study 1 and reinvited the experts who also participated in Study 1. Four experts (age range: 25-44) were able to participate in Study 2, and one additional expert, who did not participate in Study 1, rated the videos.

Rating procedure

We randomly selected 40 x 30-s videoclips from our video library that were equally divided across the ten bonobos and the old and new enclosure. Each observer viewed and rated four clips per individual bonobo, two for each housing condition.

Study 2 was carried out online through a live connection. Before starting the assessment, the observers received a ±45 min long instruction in which the goal of the study and QBA process were explained, including a practice video. The terms and their definitions were furthermore explained and discussed.

Selection of terms

The observers in Study 1 came up with 170 unique terms that were then subjected to MFA, resulting in two dimensions which we will describe in more detail in the Results section. From these 170 terms, we selected 21 terms that were most occurrent, showed high positive and negative correlations in the two dimensions and covered a range of expressive qualities. We furthermore added ‘Lethargic’, ‘Positively engaged’ and ‘Indifferent’ based on the existing literature and author discussions (Table 6.1).

Statistical analysis

Prior to running our statistical analyses, we examined if our data were suited for factor analysis by means of the Kaiser-Meyer-Olkin (KMO) test. In brief, the KMO test measures the proportion of variance among variables that might be shared. Here, lower values indicate shared correlations which are undesired for factor analysis. We handled a threshold of > 0.6 for including descriptors in our analysis. We employed dual multiple factor analysis (DMFA), which is an extension of MFA suitable when the same variables are measured, but allows for the partitioning of observers in groups, i.e., Students and

Experts. The key benefit of DMFA over the commonly applied PCA, is its ability to handle multiple datasets (i.e., individual observer datasets) and to standardise the entered data per group (i.e., Students and Experts) (Lê & Pagés, 2010). This standardisation enables direct comparison of the way the different observer groups use the fixed terms, and hence perceived the bonobos' emotional expressivity. Given our interest in identifying and examining these potential differences, we considered DMFA more suitable than PCA. DMFA was performed using the *FactoMineR* package (Lê et al., 2008). As in Study 1, we used linear mixed models (Bates et al., 2015) to test the effect of contextual [housing condition (old enclosure or new enclosure)], focal animal factors [age class (subadult or adult), sex (female or male)] and animal-directed empathy.

Table 6.1: Final list of terms and their characterisations

Term	Description
Active	Bonobo radiates energy and strength, in a lively and excited manner.
Agitated	The bonobo appears restless and nervous.
Anxious	The bonobo appears worried, unable to respond well to its surroundings, afraid.
Bored	The bonobo appears disinterested, passive, tired. May be looking to do something, in an unmotivated way.
Calm	The bonobo appears peaceful, without worries, and behaves relaxed and carefree.
Curious	The bonobo appears exploratory and pro-active in searching its environment.
Excited	Positively restless in response to external stimuli, euphoric, exuberant, enthusiastic.
Focused	Bonobo appears concentrated on an action and pays attention to it.
Frustrated	Bonobo seems to lack fulfilment/satisfaction, is unable to achieve a goal.
Happy	The bonobo looks cheerful, unconcerned and shows joy.
Indifferent[a]	The bonobo does not appear to be concerned with other factors around it.
Irritated	The bonobo appears irritable and reacts negatively to a peer or environment, possibly with rejection.
Lethargic[a]	The bonobo looks tired and sluggish. Lacking strength and energy, it shows little movement, and every movement is slow and laborious.
Lively	The bonobo seems active, enthusiastic, full of life and energy. Regardless of physical activity, the bonobo shows positive energy and strength.
Nervous	The bonobo appears anxious, highly reactive, and excited. They are alert and can be restless.
Playful	The bonobo makes lively movements, together or alone for fun, expressing pleasure, happiness, and amusement.
Positively engaged[a]	The bonobo performs activities in a focused, constructive manner. The bonobo does not seem distracted by others or the environment.
Quiet	Peaceful and carefree. The bonobo behaves unconcerned.
Relaxed	At rest, without tension. They seem unconcerned and at ease.
Sad	Bonobo appears cheerless and gloomy.
Satisfied	The bonobo appears happy and content.
Self-confident	Bonobo shows assertiveness and behaves like this towards other animals in the environment.
Social	Bonobo interacts actively with others, is prepared to interact, and shows social behaviour.
Stressed	The bonobo appears tense, overstrained and nervous.

[a] Terms that have been added from the literature.

Results

Animal-directed empathy

Across both studies, participants (N = 65) had an average empathy ratio score of 2.76 (SD = 1.19, range = 1.19 – 6.93), meaning that all participants had some level of empathy for animals. There was no difference in empathy scores between the Students (M = 2.71, SE = 0.15) and Experts (M = 3.02, SE = 0.0.50; $\chi^2 = 0.544$, df = 1, $P = 0.461$). We did not further explore differences between Students and Experts based on pet ownership and professional experience working with animals, as there was little variation within these variables.

Study 1: Free Choice Profiling

Interpretation of the consensus profile

The 26 observers collectively collected a total of 640 (170 unique) terms to describe the expressive qualities of the bonobos, with an average of 24.6 terms (ranging 14-30) per observer. For the two groups specifically, the Students came up with an average of 23.1 terms (ranging 14-30) and the Experts came up with an average of 27.6 terms (ranging 14-30).

Based on the analysis of the permuted confidence intervals, we identified that the first two dimensions explained a statistically relevant proportion of the variance in the compromise profile, which corresponds to 32.8% in the Student compromise (dimension 1: 22.2%, dimension 2: 10.6%), and 38.8% in the Expert compromise (dimension 1: 25.6%, dimension 2: 13.1%). Intraclass correlations were higher for dimension 1 compared to dimension 2, and slightly higher for Experts (0.75 and 0.50, respectively) than for Students (0.73 and 0.42, respectively).

In Table 6.2, we list the strongest loading terms on dimension 1 and 2. Based on the frequency in which these terms have been used across the observers, we described the dimensions for the different observer groups. For the Students, dimension 1 was described as ranging from ‘quiet/calm’ to ‘angry/active’, and dimension 2 as ‘sad/anxious to ‘happy/loving’. For the Expert group, dimension 1 was described as ranging from ‘quiet/relaxed’ to ‘nervous/alert’, and dimension 2 from ‘nervous/bored’ to ‘playful/happy’.

Table 6.2: Terms with strong loadings used by the observers on the MFA dimensions. Terms with loadings >0.7 and <-0.7 are displayed for dimension 1, and for dimension 2, those with loadings >0.4 and <-0.4. Figures in brackets give the number of times these terms met the beforementioned criterium

	Negative correlation	Positive correlation
Students		
Dimension 1	Quiet (8), Calm (6), Relaxed (2), Bored, Withdrawn, Unimpressed, Carefree	Angry (8), Active (8), Frustrated (6), Irritated (4), Stressed (2), Restless (2), Playful (2), Tense, Panicky, Panicking, Noisy, Nervous, Hunted, Hostile, Fierce, Explosive, Excited, Dominant, Defensive, Curious, Busy, Anxious, Alert, Agitated, Aggressive, Afraid, Alert
Dimension 2	Sad (8), Anxious (7), Nervous (7), Bored (5), Stressed (3), Insecure (3), Frustrated (2), Lonely (2), Restless (2), Afraid (2), Worried (2), Compulsive, Attentive, Unhappy, Concerned, Tense, Irritated, Panicky, Evasive, Submissive, Confused, Withdrawn, Shy, Curious, Uncomfortable, Reluctant, Intimidated, Absent, Happy, Playful, Comfortable, Observant, Suspicious, Excluded, Content	Happy (5), Loving (3), Greedy (2), Relaxed (2), Inattentive, Caring, Playful, Protective, Helping, Loyal, Content, Sweet
Experts		
Dimension 1	Quiet (5), Relaxed (4), Calm (3), Satisfied	Nervous (4), Alert (3), Excited (2), Active (2), Intense (2), Playful (2), Frustrated (2), Attention-seeking, Agitated, Curious, Stressed, Tense, Altered, Challenging, Adventurous, Exploring boundaries, Brusque, Reckless, Insecure, Enthusiastic, Mobile, Impulsive, Worried, Annoyed
Dimension 2	Nervous (8), Bored (4), Anxious (3), Stressed (3), Tense (2), Frustrated, Upset, Timid, Dissatisfied, Difficult, Undecided, Angry, Shocked, Worried, Agitated, Afraid, Drowsy, Submissive, Attentive, Concerned, Waiting, Curious, Uncomfortable, Insecure	Playful (6), Happy (5), Challenging (3), Jealous (2), Content (2), Self-confident, Needy, In good spirits, Enthusiastic, Evasive, Driven, Curious, Relaxed, Frustrated, Teasing, Pushy, Quiet, Social, Bullying, Satisfied, Sad, Excited

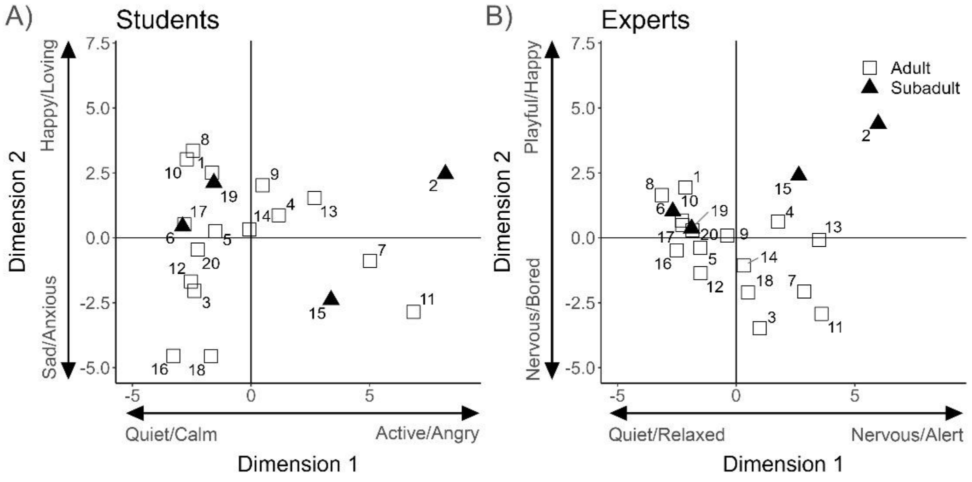


Figure 6.1: MFA compromise scores for the 20 video clips along the two dimensions for the A) Student and B) Expert group. White squares indicate video clips with adults and black triangles with juveniles. The most common, highly correlated descriptors are used to label the two dimensions

Differences in QBA scores between Housing condition, Age class or Sex

Neither the Student or Expert group perceived any differences in the expressive qualities of the bonobos between the old enclosure and new enclosure on dimension 1 (Students: $\chi^2 = 0.236$, df = 1, $P = 0.627$; Experts: $\chi^2 = 0.036$, df = 1, $P = 0.850$), nor dimension 2 (Students: $\chi^2 = 0.126$, df = 1, $P = 0.723$; Experts: $\chi^2 = 0.591$, df = 1, $P = 0.442$).

For age class, again neither the Students or Experts perceived differences between subadults and adults on dimension 1 (Students: $\chi^2 = 1.350$, df = 1, $P = 0.245$; Experts: $\chi^2 = 0.744$, df = 1, P = 0.388). Additionally, the Students did not perceive a difference in the expressive qualities between the age classes on dimension 2 ($\chi^2 = 0.365$, df = 1, $P = 0.546$), whereas the Experts did ($\chi^2 = 8.217$, df = 1, $P = 0.004$). Specifically, Experts scored subadult bonobos as more playful/happy than adults (Figure 6.1: $t_{18} = 2.866$, $P = 0.010$).

For sex, we found no perceived differences for Students nor Experts on dimension 1 (Students: $\chi^2 = 2.149$, df = 1, $P = 0.143$; Experts: $\chi^2 = 1.119$, df = 1, $P = 0.290$) and dimension 2 (Students: $\chi^2 = 2.131$, df = 1, $P = 0.144$; Experts: $\chi^2 = 0.007$, df = 1, $P = 0.933$).

Effects of animal-directed empathy scores

The level of empathy for animals had no influence on the representation of Students and Experts on dimension 1 (Students: $F_{1,14} = 2.565$, $P = 0.132$; Experts: $F_{1,7} = 0.080$, $P = 0.786$) or dimension 2 (Students: $F_{1,14} = 0.050$, $P = 0.827$; Experts: $F_{1,7} = 0.062$, $P = 0.811$).

Study 2: Fixed List procedure

Inter-observer reliability

The KMO test indicated that the descriptors were suitable for the analysis, with an overall value of 0.90 for the Students and 0.87 for the Experts. Descriptor-specific KMO values are presented in Table S6.4.

The first two dimensions of the compromise profile explained 48.7% of the variance (dimension 1 = 26.0%, dimension 2 = 22.7%). By selecting the two terms that have the highest and lowest correlations on the two dimensions, we characterise dimensions. For the Students, dimension 1 ranged from 'quiet/calm to 'agitated/frustrated', and dimension 2 from 'sad/stressed' to 'happy/positively engaged'. For the Experts, dimension 1 ranged from 'quiet/calm to 'active/excited', and dimension 2 from 'sad/bored to 'happy/positively engaged'. Observer agreement across groups was furthermore good for the first dimension for Students (0.717) and Experts (0.764). The second dimension achieved a poor agreement for Students (0.359) and moderate agreement for Experts (0.586). Figure 6.2 shows the correlation plot of the different terms among the two dimensions for the two observer groups separately.

Intra-class correlation analyses for separate terms were all significantly different from random expectation (Table 6.3: $P < 0.001$), of which Students achieved poor agreement on 20 terms (ICC < 0.50; Agitated, Anxious, Bored, Content, Curious, Excited, Focused, Frustrated, Happy, Indifferent, Irritated, Lethargic, Lively, Nervous, Playful, Positively engaged, Relaxed, Sad, Self-confident and Stressed), and moderate agreement on four terms (ICC = 0.50-0.75; Active, Calm, Quiet, Social). Experts achieved poor agreement on 13 terms (Agitated, Anxious, Content, Curious, Focused, Frustrated, Irritated, Lethargic, Nervous, Relaxed, Sad, Self-confident and Stressed), moderate agreement on eight terms (Bored, Calm, Happy, Indifferent, Lively, Positively engaged, Quiet and Social) and good agreement on three terms (ICC = 0.75-0.90; Active, Excited and Playful).

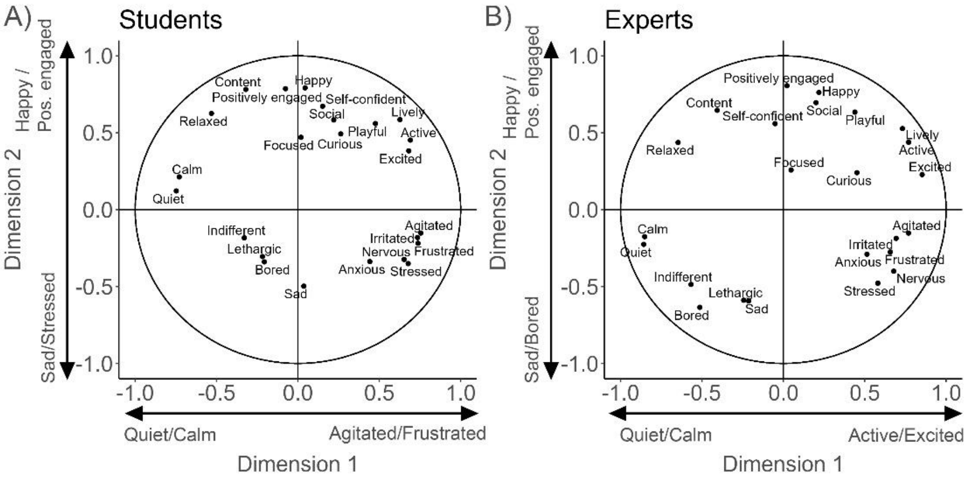


Figure 6.2: Correlation plot with the distribution of the different descriptors for A) Students and B) Experts alongside the two dimensions.

Table 6.3: Inter-observer reliability on the two dimensions and the individual descriptors for the two observer groups

	Students				Experts			
	ICC	95% CI	*F* value (39, 1677)	*P* value	ICC	95% CI	*F* value (39, 156)	*P* value
Dimension 1	0.717	(0.627-0.808)	112.0	< 0.001	0.764	(0.662-0.851)	17.2	< 0.001
Dimension 2	0.359	(0.268-0.485)	25.6	< 0.001	0.586	(0.449-0.720)	8.08	< 0.001
Active	0.602	(0.500-0.716)	67.5	< 0.001	0.805	(0.716-0.879)	21.7	< 0.001
Agitated	0.385	(0.235-0.443)	28.6	< 0.001	0.329	(0.113-0.409)	3.5	< 0.001
Anxious	0.321	(0.183-0.370)	21.9	< 0.001	0.242	(0.440-0.713)	2.6	< 0.001
Bored	0.295	(0.361-0.589)	19.5	< 0.001	0.630	(0.225-0.533)	9.5	< 0.001
Calm	0.546	(0.317-0.543)	54.0	< 0.001	0.686	(0.672-0.856)	11.9	< 0.001
Content	0.305	(0.484-0.702)	20.3	< 0.001	0.356	(0.636-0.837)	3.8	< 0.001
Curious	0.224	(0.306-0.530)	13.7	< 0.001	0.406	(0.228-0.536)	4.4	< 0.001
Excited	0.414	(0.156-0.330)	32.1	< 0.001	0.771	(0.262-0.568)	17.9	< 0.001
Focused	0.240	(0.179-0.364)	14.9	< 0.001	0.386	(0.076-0.363)	4.1	< 0.001
Frustrated	0.402	(0.231-0.438)	30.5	< 0.001	0.371	(0.136-0.437)	4.0	< 0.001
Happy	0.257	(0.222-0.426)	16.2	< 0.001	0.577	(0.214-0.522)	7.8	< 0.001
Indifferent	0.220	(0.443-0.668)	13.4	< 0.001	0.546	(0.565-0.796)	7.0	< 0.001
Irritated	0.462	(0.291-0.513)	38.7	< 0.001	0.367	(0.190-0.497)	3.9	< 0.001
Lethargic	0.217	(0.178-0.363)	13.2	< 0.001	0.384	(0.181-0.487)	4.1	< 0.001
Lively	0.486	(0.169-0.350)	42.5	< 0.001	0.688	(0.243-0.550)	12.0	< 0.001
Nervous	0.274	(0.412-0.640)	17.6	< 0.001	0.383	(0.640-0.839)	4.1	< 0.001
Playful	0.464	(0.153-0.325)	39.0	< 0.001	0.812	(0.405-0.688)	22.6	< 0.001
Positively engaged	0.278	(0.151-0.322)	18.0	< 0.001	0.502	(0.241-0.548)	6.0	< 0.001
Quiet	0.586	(0.287-0.508)	63.3	< 0.001	0.744	(0.221-0.529)	15.5	< 0.001
Relaxed	0.381	(0.383-0.612)	28.1	< 0.001	0.363	(0.567-0.797)	3.9	< 0.001
Sad	0.251	(0.196-0.390)	15.8	< 0.001	0.320	(0.240-0.547)	3.4	< 0.001
Self-confident	0.252	(0.200-0.395)	15.8	< 0.001	0.199	(0.359-0.652)	2.4	< 0.001
Social	0.515	(0.214-0.415)	47.8	< 0.001	0.747	(0.499-0.754)	15.7	< 0.001
Stressed	0.316	(0.362-0.591)	21.3	< 0.001	0.270	(0.725-0.883)	2.9	< 0.001

Differences in QBA scores between Housing condition, Age class and Sex

Students' QBA scores did not show a difference between housing conditions on dimension 1 ($\chi^2 = 1.684$, df = 1, $P = 0.194$) or dimension 2 ($\chi^2 = 2.38$, df = 1, $P = 0.123$). For the Expert observer group, there was a significant effect of housing condition on the bonobos' scores on dimension 1 ($\chi^2 = 4.580$, df = 1, $P = 0.032$), where Experts scored the bonobos more 'active/excited' in the post-move condition compared to the pre-move condition ($t_{38} = 2.140$, $P = 0.039$). There was no difference in how the Experts scored the bonobos on dimension 2 between the two housing conditions ($\chi^2 = 0.841$, df = 1, $P = 0.359$).

Additionally, for the Student observer group, there was a significant effect of the bonobo's age class on the scores on dimension 1 ($\chi^2 = 6.216$, df = 1, $P = 0.013$), with Students scoring adults more 'calm/quiet' than subadults ($t_{38} = -2.493$, $P = 0.017$). No age effect was found in the Students' scores on dimension 2 ($\chi^2 = 1.346$, df = 1, $P = 0.246$). For the Expert group, no significant effect was found of the bonobo's age class on the ExpertsExperts' scores on dimension 1 ($\chi^2 = 0.882$, df = 1, $P = 0.348$), but did so on dimension 2 ($\chi^2 = 20.879$, df = 1, $P < 0.001$). That is, Experts scored subadults more 'happy/positively engaged' than adults ($t_{38} = 4.569$, $P < 0.001$).

No significant effect of the bonobo's sex was found for either the Student nor the Expert group on dimension 1 (Students; $\chi^2 = 0.022$, df = 1, $P = 0.883$; Experts: $\chi^2 = 1.430$, df = 1, $P = 0.232$) or dimension 2 (Students: $\chi^2 = 1.424$, df = 1, $P = 0.233$; Experts: $\chi^2 = 0.158$, df = 1, $P = 0.691$).

Effects of Animal-related empathy scores

A main significant effect of empathy scores was found on dimension 1 ($\chi^2 = 7.185$, df = 1, $P = 0.007$), with a negative association between animal-directed empathy scores and scores on dimension 1 ($t_{39} = -2.116$, $P = 0.041$). No such effect of empathy scores was found for dimension 2 ($\chi^2 = 0.639$, df = 1, $P = 0.424$).

Discussion

Study 1: Free Choice Profiling

In Study 1 we aimed to assess how bonobo experts and students perceived the emotional expressions of zoo-housed bonobos. Using web-based VAS and open-access novel statistics, we aimed to introduce a different approach to conduct the FCP procedure that has statistical advantages and is more publicly accessible than previously used GPA statistics (Wemelsfelder et al., 2001). Dai et al., (2022) used a similar approach using digital QBA recording for horses. Both experts and students identified two dimensions which were roughly similar in terms of their labelling. Students described dimension 1 as ranging from ‘angry/active’ to ‘quiet/calm’, and dimension 2 as ‘sad/anxious to ‘happy/loving’, whereas Experts described dimension 1 from ‘nervous/alert’ to ‘quiet/relaxed’, and dimension 2 from ‘nervous/bored’ to ‘playful/happy’. Inter-observer reliability was adequate for both dimensions within the two groups. The use of these dimensions was furthermore independent of animal-directed empathy levels of the observers, suggesting that variation in such empathy levels was no concern for the application of QBA on bonobos by the current observers. We furthermore aimed to examine if observers perceived differences in these expressions based on contextual (i.e., old enclosure and new enclosure) and individual (age class, sex) factors. Observers did not perceive differences in the emotional expressions based on housing condition or between the sexes, yet experts considered subadult bonobos as more ‘playful’ and ‘happy’ than adults.

Study 2: Fixed List procedure

In Study 2, we built upon the knowledge gained from Study 1 to develop a list of 24 fixed descriptors. Through a combined analysis of student and expert QBA scoring, we identified two dimensions that accounted for almost 50% of the variation. The Student group characterised dimension 1 from ‘quiet/calm’ to ‘agitated/frustrated’, and dimension 2 from ‘sad/stressed’ to ‘happy/positively engaged’. The Expert group characterised dimension 1 from ‘quiet/calm’ to ‘active/excited’, and dimension 2 from ‘sad/bored’ to ‘happy/positively engaged’. The correlation patterns of these 24 descriptors were convergent between the students and experts. Reliability in using these dimensions was generally good for both observer groups in relation to dimension 1, but lower for dimension 2. Notably, the expert group showed a higher agreement regarding dimension 2 compared to the students group, consistent with our findings from Study 1.

Examining the reliability of individual descriptors, we observed overall low agreement, although the level was relatively higher among the experts. Animal-directed empathy influenced observers' scores on dimension 1, regardless of their expertise levels, with more empathic observers assigning lower scores on dimension 1. We furthermore identified that observers scored the emotional expressions of the bonobos differently based on contextual or individual factors. Both students and experts rated subadults and adults differently, although the former group allocated these differences on their respective dimension 1 and the latter on their dimension 2. Specifically, students scored adults as more 'quiet' and 'calm' compared to subadults, while experts scored subadults higher on 'happy' and 'positively engaged' than adult bonobos. Consistent with Study 1, neither observer group perceived differences between male and female bonobos. Experts also rated bonobos in the new enclosure higher on 'active' and 'excited' compared to their old enclosure, suggesting a change in the bonobos' expressivity on this dimension linked to their novel housing condition.

General discussion

Despite still being limited, the application of QBA in non-domesticated species is growing, especially in zoo- and sanctuary settings (Patel et al., 2019; Pollastri et al., 2021; Skovlund et al., 2023; Stagni et al., 2022; Warner et al., 2022). Primates have thus far been underrepresented (Gartland et al., 2022) despite the need for quick and reliable animal-based, rather than resource-based, welfare assessments in this taxon. This paper aimed to examine how human raters describe and perceive emotional expressions in bonobos. In Study 1, observers had to use their own terminology to describe bonobo expressivity and in Study 2 we applied the insights from Study 1 to develop a list of fixed descriptors. In both studies, analyses on the patterns in which the observers scored and used the descriptors revealed two dimensions that can be loosely interpreted as dimensions of arousal and valence. The recognition of these dimensions in bonobo expressivity appeared regardless of expertise level, as bonobo experts and students (without experience with bonobos) came up with convergent terminologies (Study 1) and used fixed terms in a similar fashion (Study 2). This is an important finding as arousal and valence are often considered as the two main dimensions of affective states in animals (Mendl et al., 2010).

In both studies, students and experts showed good agreement on the first dimension, but agreement was lower when scoring the second dimension. This can be partly due to the statistical analyses, which aim to explain the majority of the variation in the first dimension. Alternatively, the terms linked to dimension 1 and 2 more or less reflect concepts of arousal and valence, respectively. It is possible that human observers show lower agreement in describing and assigning emotional valence to bonobos. Recognising valence components of primate emotional expressions has proven to be difficult in other studies using static images (Kret & van Berlo, 2021; Maréchal et al., 2017), whereas the recognition of emotional arousal might be more widely shared among mammalian species (Greenall et al., 2022). The expression of emotions is highly dependent on the context (Kret et al., 2020), and the recognition of emotional expressions is therefore rarely reliable on isolated cues (Ngo & Isaacowitz, 2015). Although the holistic nature of QBA allows such contextual cues to be incorporated in the perception by human observers, and is therefore more inclusive than for example still-images, the correct interpretation of how an animal experiences certain events or stimuli requires knowledge of the species. This is likely to explain why experts showed a higher agreement on the ‘valence’ dimensions than students, especially when using fixed descriptors. We purposefully gave no information regarding bonobos to the student group as we were interested in examining whether the level of experience had an effect on the development of this QBA. Agreement between the students would possibly increase when given more information as exposure to a species enhances the recognition of expressions (Maréchal et al., 2017) and reliability in using fixed list descriptors (Minero et al., 2016).

Arousal is typically characterised by levels of activation, or the intensity of the expression, which is visibly discernible and could explain why both students and experts reached good agreement on the dimension that resembles arousal. Valence, on the contrary, refers to the positivity or negativity of the emotion and requires knowledge of the species to recognise. Experience with the species have previously been shown to facilitate more accurate emotion recognition (Duijvesteijn et al., 2014; Greenall et al., 2022; Menchetti et al., 2019), and the higher degree of similarity in terms of experience with bonobos among the experts likely facilitated more consistent QBA scoring on the dimensions. We should also acknowledge that our observer groups present a rather homogenous group, in the sense that they represent a W.E.I.R.D. (Western, educated, industrialised, rich and democratic) sample (Henrich et al., 2010), meaning that the implications of our results are limited to our sample. Even then, agreement on the individual descriptors remained rather low. We argue this can be explained by the fact that emotions, and their establishment in an animal's 'body language', are the product of previous events or stimuli which are unique to an individual. Although the experts had knowledge about the bonobo as a species, and therefore recognised and agreed on the valence of their expressions to a certain degree, they did not directly work with the bonobos used in the videos in the current study. We predict that people who work regularly with the individual bonobos, such as care staff, will reach a higher agreement on the second dimension of the bonobos' emotional expressivity as they are likely able to identify minor changes in the body language of the animals over various periods of time.

While expertise plays a role in the application of QBA, our study also revealed that levels of animal-directed empathy were associated with variations in QBA usage. Individuals with higher levels of empathy for animals tended to score bonobos lower on dimension 1, irrespective of their level of expertise. Or, in other words, observers with less empathy for animals scored the bonobos higher on 'quiet' and 'calm'. However, the literature on the influence of empathy on human perception of animal emotions presents conflicting findings. Some studies suggest that participants with higher empathic scores perceive emotional expressions as more intense (Allen-Walker & Beaton, 2015; Westbury & Neumann, 2008), whereas other do not (Kujala et al., 2017), although this may be further modulated by experience with the species depicted (Meyer et al., 2014). The reason for the current observed negative correlation between empathy and scores on dimension 1 in bonobos is not clear, but since the correlation is rather weak, other factors, that were currently not addressed, may play a larger role. Further investigation is warranted to explore these modulating factors.

We found that housing condition and age class, but not sex, had an influence on how humans scored bonobo expressivity, but these were specific to the observer group. Namely, experts, across both studies, gave subadult bonobos higher scores on the second dimension (i.e., more 'playful/happy' in Study 1, and more 'happy/positively engaged' in Study 2) than adults. Students instead scored adult bonobos lower on dimension 1 (i.e., more 'quiet/calm') than subadults. This could be explained by age-related differences in the behavioural repertoire of bonobos. For example, despite that adult bonobos still engage in social play activities (Palagi & Paoli, 2007) for regulating social dynamics, this behaviour is more common in subadult individuals. QBA dimensions correlate with performed behaviours at the time of rating (Pollastri et al., 2021; Warner et al., 2022), and age-specific behavioural patterns may therefore influence the outcomes of QBA ratings. Although we did not directly correlate behaviours with the QBA scores, it is possible that these differences in behavioural patterns between adult and subadult bonobos were perceived by the observers, but that they attributed these to different emotional concepts (e.g., arousal and valence). People that have experience with bonobos (keepers or researchers) are typically better than the general public in distinguishing positive and negative bonobo facial expressions (Laméris, unpublished data). Hence, the knowledge of bonobos by the expert group could have facilitated the recognition of behaviours as emotionally positive or negative for the animals, whereas the student group noticed levels of activity.

Observers furthermore perceived changes in the expressivity of the bonobos based on their housing condition. Experts in Study 2, scored the bonobos as more 'active' and 'excited' in the new enclosure as compared to the old enclosure. The indoor housing conditions were more or less similar in the old and new enclosure, and the main difference in the new enclosure was the presence of two outdoor areas, instead of one. Hence, whereas the two bonobo groups previously had to alternate for outdoor access, in the new enclosure they could simultaneously access their own outdoor area. Outdoor access has previously been proven to be beneficial for the behaviour and welfare of zoo-housed primates (Honess & Marin, 2006; Kurtycz et al., 2014; Laméris et al., 2021b; Pines et al., 2007; Videan et al., 2005), and this could explain why differences in the expressivity of the bonobos was observed. This provides valuable information regarding possible welfare implications of changing zoo enclosures.

Conclusions

In conclusion, human observers with varying levels of expertise perceived different aspects of emotional expressivity in bonobos. The reliability of these dimensions, however, increased with experience, especially when scoring differences in valence. Experience furthermore allowed for more nuanced perceived differences in the emotional expressivity based on contextual and individual factors. We recommend including the knowledge of people who are familiar with the individual animals and work regularly with them, such as care staff who are able to notice subtle changes in the emotional expressivity of the animals over time. No single indicator can be considered exhaustive to evaluate the welfare of animal, and QBA is no exception. Welfare is a complex, multifaceted concept that requires multiple indicators for accurate assessment. The QBA developed and tested in the current study could potentially be incorporated into welfare assessment protocols if further (cross-)validation against other well-established welfare measures proves its value.

7

Affective responses and behavioural strategies to social fusion events in zoo-housed bonobos

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Abstract

Species with fission-fusion dynamics may face heightened social tension during fusion events due to relationship insecurity and competition over resources. Affective consequences of such events are important determinants for behavioural responses, yet remain poorly understood. To evaluate the affective consequences of fusion events, we studied cognitive bias responses and changes in the behaviour of zoo-housed bonobos following managed fission-fusion dynamics. Eight bonobos completed a response slowing task on touchscreens, in which individuals with negative affect typically show longer latencies when a mildly threatening stimulus is displayed. We tested the bonobos on days before, during and after fusion events and simultaneously observed their behaviour. Agonistic and socio-sexual behaviours increased during fusions. The bonobos showed response slowing during trials with mildly threatening stimuli during fusion events, indicating a shift towards negative affect. Post hoc analyses furthermore showed arousal-related response speeding during control trials. Independent of testing condition, response slowing was negatively associated with socio-sexual behaviour, and positively associated with social play behaviour, highlighting affective correlates of these behaviours. Our findings provide insights into the affective responses to fusion events in bonobos, suggesting short-lasting shifts towards negative affect. Nonetheless, changes in behavioural strategies presumably function to limit the escalation of conflict and facilitate successful fusions.

Introduction

Species with fission-fusion dynamics are characterised by a social system in which individuals temporarily disperse into smaller subparties (fission) and later reunite to larger groups (fusion). This phenomenon is observed in a wide range of animals, including primates (Aureli et al., 2008), cetaceans (Parra et al., 2011), ungulates (Carter et al., 2013), bats (Patriquin et al., 2016), and birds (Silk et al., 2014), and enables reduced food competition (Ramos-Fernández et al., 2006) and optimised information exchange (Fishlock & Lee, 2013). However, the frequency and patterns of spatial and temporal separations in societies with high degrees of fission-fusion dynamics may also lead to uncertainty in social relationships upon fusion (Aureli & Schaffner, 2007; Barrett et al., 2003; East et al., 1993) and trigger competition over resources or conflicts over coordinated activities (Aureli et al., 2008). Members of fission-fusion societies must therefore adapt strategies to evaluate and re-establish relationships and resolve uncertainties to avoid escalation of social tension into conflict. This spans from elaborate displays in societies with low fission-fusion degrees to more simple behaviours in societies with high degree fission-fusion (Aureli et al., 2008). In primates, for example, greeting behaviours have been observed upon fusions (Okamoto et al., 2001; Schaffner & Aureli, 2005).

Social interactions are accompanied by affective states (Aureli & Schaffner, 2002; Aureli & Whiten, 2003; de Waal, 2011), and affective experiences play a strong role in social group living by improving bonds, cooperation and communication (de Waal, 2008; Špinka, 2012; Spoor & Kelly, 2004). Objectively assessing affective states in animals, however, is challenging as commonly used behavioural or physiological measures are species/individual/context-specific (Paul et al., 2005). Many of these indicators furthermore measure emotional arousal, but do not necessarily distinguish between emotional valence, i.e., whether the affective state is positive/pleasant/rewarding or negative/unpleasant/aversive (hereafter positive and negative, respectively). Cognitive biases, i.e., changes in cognitive processing modulated by underlying affective states, are a promising novel measure for changes in emotional valence (Harding et al., 2004). Cognitive biases can be adaptive in that they promote memory storage and/or reconsolidation of relevant events (Cahill & McGaugh, 1998), flexible behavioural responses when met with risk or uncertainty (Bateson, 2016), or by promoting attention for relevant stimuli (Anderson, 2005; Pourtois et al., 2013; Schupp et al., 2003). Studying cognitive components of affective correlates with social events and behaviours is therefore an important step in understanding the proximate mechanisms and motivations of social interactions.

Only few studies studied the relationships between cognitive measures of affective states and social behaviours. Receiving more grooming, for example, is linked with heightened optimism in tufted capuchins (*Sapajus* sp.) during a judgement bias task (Schino et al., 2016). In bottlenose dolphins (*Tursiops truncatus*) synchronous swimming, an important affiliative behaviour, is associated with more optimistic judgements for ambiguous cues (Clegg et al., 2017). These studies focused on biases in decision-making during ambiguous situations, whereas attention bias is another class of cognitive biases which is especially relevant in social interactions. Attention, as a limited cognitive resource, selectively processes information which facilitates enhanced attention for relevant stimuli while ignoring irrelevant distractors (Compton, 2003). Affect-driven attention bias has been studied only in a few animal species using a limited number of paradigms (reviewed by Crump et al., 2018). Bethell et al. (2016) introduced a response slowing task to evaluate changes in social information processing that are modulated by affective states in rhesus macaques (*Macaca mulatta*). This paradigm is based on human psychological research on the freeze response. Whereas the freeze response is adaptive to threats (LeDoux, 2012a), and facilitates processing of the threat (Bradley, 2009), this response is typically dysregulated in individuals with negative affect (Buss et al., 2004; Kalin et al., 1998). Here, individuals with negative affect exhibit subtle cognitive freezing in inappropriate situations, e.g., when presented with non-threat or mildly threatening stimuli (Bar-Haim et al., 2007; Mogg & Bradley, 2016). The response slowing task, as introduced by Bethell et al. (2016), assesses shifts in emotional responses towards negative valence. It accomplishes this by investigating the dysregulated freeze response in individuals when confronted with mildly threatening social cues, such as a direct gaze from unfamiliar individuals, in comparison to neutral social cues, like an averted gaze. This affective shift is reflected through a subtle cognitive freezing effect, quantified by delayed reaction times, which is referred to as ‘response slowing’. This paradigm has now been applied in a number of non-human primates studies, and identified changes in affective states (Bethell et al., 2016; Cronin et al., 2018; McGuire & Vonk, 2020), yet has never been linked to social interactions or events. Given that affect-driven attention biases play an integral role in shaping social interactions (Bethell et al., 2012b; Yiend, 2010), and allow for behavioural flexibility (Aureli & Whiten, 2003), furthering our understanding of the relationship between affect, attention and behavioural strategies in the context of social events is crucial to better understand animal behaviour.

In the current study we investigate the behavioural and cognitive affective responses to social fusion events in a highly social primate species, the bonobo (*Pan paniscus*). Bonobos live in multi-male/multi-female communities of 10 to 63 individuals (Furuichi & Thompson, 2008; Kano, 1992; Stevens, 2020) with a high degree of fission-fusion dynamics (Hohmann & Fruth, 2002). Aggregation patterns of bonobos are distinct, yet fluid, and vary considerably among bonobo populations and communities (Samuni et al., 2022). Even rates of fission-fusion events differ among populations (Fruth, 1995; Furuichi, 1989; Hohmann & Fruth, 2002; Kano, 1992). Intra-community relationships are highly flexible and complex in nature (Samuni et al., 2022) and inter-community encounters are characterised varying from behaviours to reinforce affiliative relationships, over non-agonistic displays of social status, to dominance relations that are enforced by agonistic displays (Furuichi, 2011; Hohmann & Fruth, 2000; Parish, 1994).

One study on the behavioural and physiological responses in female zoo-housed bonobos found that social fusions were relatively peaceful with little agonistic interactions, and increased levels of sexual solicitations (Moscovice et al., 2015). Socio-sexual behaviours, such as non-copulatory mounts and genital contact (de Waal, 1987), play an important role in regulating bonobo society, including reducing tension during feeding competition (Hohmann & Fruth, 2000; Paoli et al., 2007; Parish, 1994), reconciliation and consolation after conflict (Clay & De Waal, 2015; Hohmann & Fruth, 2000), and social bonding (Moscovice et al., 2019; Parish, 1994; Wrangham, 1993). While socio-sexual behaviour has received most attention in bonobos, other behavioural mechanisms may also be important to regulate tensions associated with fusions. Social play has been suggested to be a mechanism for bonobos to reduce tension, and adult-adult play may be a mechanism to cope with tension and re-evaluate relationships also during fusion events (Palagi et al., 2006; Pellis & Iwaniuk, 2000). While grooming is considered a mechanism among many primate species to re-establish social relationships (De Waal, 2000), Sakamaki (2013), suggested that in wild bonobos grooming is less important during social gatherings, because bonobos form more stable groups with less fission-fusion than chimpanzees (Sakamaki, 2013). Similarly, Moscovice et al. (2015) also found no increase in grooming during fusion events in zoo-housed female bonobos (Moscovice et al., 2015). While there is ample evidence that these behaviours may function to reduce social tension, it is currently unknown how these behaviours actually link to affective states.

The first aim of this study is to compare behaviour as coping mechanisms during the fusion events. Based on theoretical and empirical evidence, suggesting that fusion events can create tension (Aureli et al., 2008; Aureli & Schaffner, 2007; Barrett et al., 2003; East et al., 1993), we created the following predictions. If fusion events present situations of increased social insecurity and tension, (1) we expect an increase in aggressive behaviours during fusions compared to baseline conditions. Additionally, by means of mitigating such social tension, (2) we expect to find an increase of socio-sexual behaviour, (3) and an increase in play interactions compared to baseline condition, (4) but no changes in grooming activities.

The second aim is to evaluate changes in the cognitive components of affective states during fusion events, using touchscreen computers to test the response slowing task (Bethell et al., 2016). If fusions induce social tension, (5) we hypothesise to find relative shifts towards negative affective states of the bonobos during fusions, which should lead to more pronounced response slowing towards ambiguous social stimuli (i.e., direct gaze stimuli) compared to neutral social stimuli (i.e., averted gaze stimuli).

Our last aim is to examine the affective correlates of different behaviours to see how affective states are related to behavioural patterns during fusion events. If the behavioural changes under the first aim result from increases in social tension on days with fusion events, (6) we expect to find a positive association between aggressive behaviours and response slowing. Furthermore, if socio-sexual and play behaviours are indeed coping mechanisms to reduce tension, (7) we expect to find a negative correlation between the response slowing effect and socio-sexual behaviour during fusion days, but not during baseline days, and (8) similarly for social play behaviour. Lastly, (9) we expect no clear correlation between grooming and response slowing.

Methods

Subjects and housing conditions

Eight bonobos (three females and five males; mean age = 15.8 years, range = 7-27 years), at Zoo Planckendael (Belgium) participated in the current study (Table 1). The bonobos were housed in an indoor enclosure (total surface 422 m^2) consisting of ten enclosures of which four main enclosures were visible for zoo visitors. When temperatures allowed, the bonobos had access to an outdoor enclosure (3000 m^2). Fresh vegetables, fruits, browse, and primate chow was provided four times per day and the bonobos had access to water *ad libitum*.

The full group in Zoo Planckendael consisted of 20 individuals (13 females and 7 males) of varying ages (range = 0 – 43 years) and was managed in two subgroups, for controlled breeding and for conflict management. All individuals had been housed together prior to the study. The two subgroups could not physically interact with each other, but had limited visual contact in some parts of the building and could vocally communicate. The EAZA Best Practice Guidelines recommend simulated fission-fusion dynamics in such cases to mimic natural patterns and facilitate the maintenance of social relationships between subgroup members (Stevens, 2020). In practice, this means that typically one or multiple family units (i.e., females with their dependent offspring or independent sons) were transferred between the subgroups. These transfers were furthermore informed by the breeding program, based on within-subgroup tension, or to facilitate the maintenance of social relationships. Changes in the group compositions were made in the morning after which we tested the bonobos. Due to time constraints, we only focus on the individuals who completed training for the touchscreen task, and who transferred (i.e., transferees) and the individuals in the group to which the bonobos transferred (i.e., residents).

Table 7.1: Subject information

Subject	Sex	Age	Parents	Previous touchscreen experience	Number of transferred
Busira	Female	16.9	Birogu x Eja	Yes	2
Habari	Male	15.0	Vifijo x Djanoa	Yes	1
Kianga	Female	15.5	Diwani x Kombote	No	4
Kikongo	Male	6.9	Bolombo x Hortense	No	1
Mokonzi	Male	7.9	Luo x Banya	Yes	0
Nayembi	Female	14.8	Mobikisi x Liboso	No	3
Vifijo	Male	26.5	Kidogo II x Hortense	No	1
Zamba	Male	22.8	Kidogo II x Hortense	Yes	1

Behavioural observations

An integrated camera system continuously recorded, and saved, footage of the bonobos. Using these recordings, we coded the behaviour of the participating animals on days of cognitive testing. Behavioural coding was performed by one researcher (CG-C) after extensive training on our ethogram and reaching sufficient inter-rater reliability (κ = 0.78). By means of 30-min continuous focal sampling, we recorded all agonistic, socio-sexual and affiliative interactions given or received by the focal using a standardised ethogram (Table S7.1, Stevens et al. 2023) in The Observer (Noldus version XT 10, the

Netherlands). Timing of the behavioural observations was determined by the onset of the fusion events, and were completed before cognitive testing commenced. During the fusion condition, observations started from the moment when the doors opened and the group and transferees could interact with the residents. Observations during the post-fusion started at matched times to those of the fusion condition. Pre-fusion observations started during the average starting times of the fusion and post-fusion condition observations, while ensuring that no husbandry procedures, such as cleaning or feeding, were performed.

Touchscreen setup

Touchscreen sessions were conducted on a 22'' Viewsonic TD2220 touch-sensitive monitor (1920 x 1080 resolution). The researcher (DWL) controlled the sessions on a computer connected to the touchscreen and a second monitor enabled the researcher to view the subject's responses in real-time. The touchscreen setup was mounted on an adjustable cart, placed outside an off-exhibit enclosure. The touchscreen was placed parallel to the enclosure mesh, allowing the bonobos to work on the touchscreen through the mesh. Training and testing tasks were designed using *OpenSesame* (Mathôt et al., 2012).

Training and control stimuli consisted of grey rectangular frames (RGB 151, 151, 151) measuring 254 mm x 254 mm. Social content for the stimulus either comprised images of a profile view face picture with a neutral expression (i.e., an averted gaze), or a frontal face picture with a neutral expression (i.e., a direct gaze), see Figure 7.1. Here, the averted stimulus serves as a social control, whereas the direct stimulus serves as a mildly threatening stimulus. Social content was collected from a personal photo library (JMGS) and only included images of unknown adult bonobos. We collected a total of 26 direct and 26 averted gaze pictures and trimmed these images so that only the bonobo's face was visible. They were then superimposed on the grey rectangular frame, and checked for luminosity and contrast values (Table S7.2). Stimulus preparation was done in Adobe Photoshop version 21.2.2.

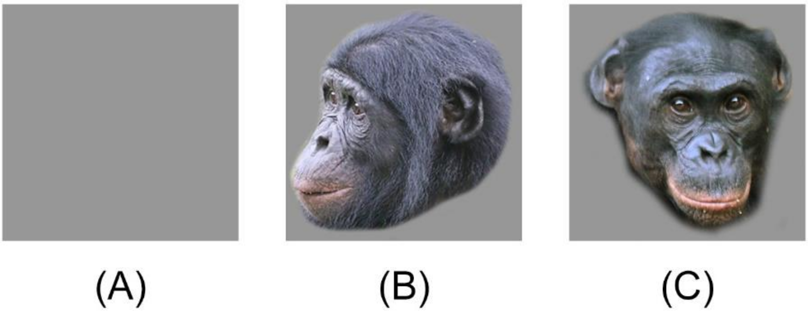

Figure 7.1: Examples of (A) control, (B) averted, and (C) direct stimuli.

Procedure

We trained the bonobos on the response slowing task between December 2020 and February 2021. Four of the bonobos had previous experience working on a touchscreen (Laméris et al., 2022b), and the remaining four bonobos were first trained to touch a small target when it appeared on the screen. Participation in these touchscreen sessions were conducted in social groups between 12:00 and 15:00, four to five times per week. Training and testing sessions were always voluntary, meaning that individuals were not separated from group members for this study. We invited the individuals by calling their name when they were not involved in social interactions, and participants were previously trained to complete touchscreen sessions individually. Sessions were paused if other bonobos distracted the subject.

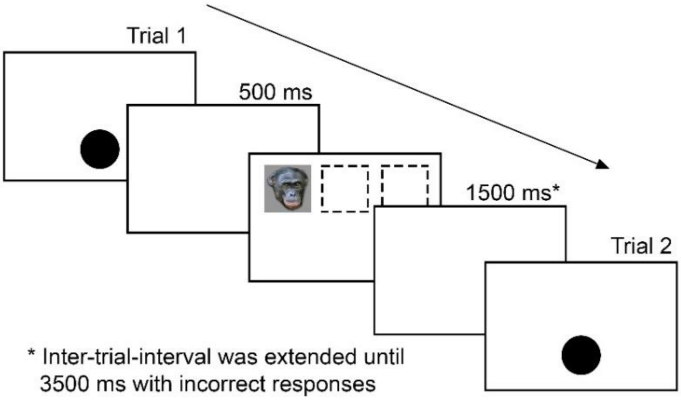

Figure 7.2: Trial outline of the response slowing task. The dashed squares indicate the other possible target locations

We employed the response slowing task, designed by Bethell et al. (2016), but made a slight adaptation by including an initiation button (Figure 7.2). This was done in order to ensure that the bonobos were attending to the screen. On each trial, bonobos were presented with an initiation button, which was located at the lower centre of the screen. Once this initiation button was touched, a 500 ms delay followed, after which the stimulus became visible at one of three locations (upper left, centre or right). The stimulus remained on the screen until the bonobo touched it. Each response was followed by a 1500 ms inter-trial interval (ITI). In case the bonobo made an incorrect response (i.e., the bonobos did not accurately touch the target), no reinforcement was provided and the trial was followed by an extended ITI of 3500 ms in total. The apes were rewarded on correct responses with automatic delivery of a DK Zoological Trainings Biscuit (small) triggered by a custom-made pellet dispenser. A secondary reinforcing tone was played via two speakers behind the touchscreen. Primary and secondary reinforcers were delivered with every correct response (i.e., a 100% fixed reinforcement ratio). Additionally, we manually provided a raisin through a PVC tube on every fifth correct response to maintain the bonobo's interest. If an individual finished all trials within a session, (s)he received three peanuts.

During the training phase, the stimuli consisted solely of the grey squares. During test sessions, the trial types included a control stimulus (grey square), averted gaze stimulus, or direct gaze stimulus. Each session consisted of 33 trials and started with 3 practice trials in which the control stimuli were presented once at each of the three locations. Then, the bonobos were presented with 30 test trials: 12 averted gaze trials, 12 direct gaze trials and 6 control trials. The order of the trial type was randomised and the location of the target was counterbalanced. We made ten different versions in order to avoid order-effects.

We tested the bonobos on the response slowing task during three conditions: a pre-fusion condition; during days with fusion events; and a post-fusion condition. Pre-fusion cognitive data were collected during periods when the group composition remained stable for at least three weeks and collection was completed once an individual finished 10 sessions. For the majority of the subjects this took place between January and February 2021, and subjects completed this between two and eight days. For two additional subjects we completed the pre-fusion data collection in March and July 2021. Preferably, we collected pre-fusion data on the day prior to fission-fusion events but it was not always predictable which individuals would switch between subgroups, neither was the day of this event. Fusion cognitive data were collected on days during which group composition changed, within two hours after the fusion event to allow the bonobos to interact with each other. Post-fusion data were collected on the subsequent day after the fusion events at matched times. On days with fusion events, and post-fusion days, each bonobo was limited to two sessions in order to collect cognitive data from all involved subjects.

We recorded all of the test sessions using a Canon Legria HF R88. These recordings were later coded to exclude outlier trials (e.g., a bonobo other than the subject touching the screen, not attending the screen, the screen did not immediately register the response).

Statistical analyses

All analyses were done in RStudio version 1.3.1073 (R Core Team, 2020). For the behavioural analyses, we created six behavioural variables to correlate to the cognitive data (Table 7.2). We calculated frequencies as events per minute for the different behavioural variables for each 30-min observation point. We then tested the difference in frequency for each variable among the conditions, using generalised linear mixed models with a negative binomial distribution, using the package '*glmmTMB*' (Brooks et al., 2017). Behavioural events were included as dependent variable and observation time as offset. Condition was included as independent variable and subject ID as random intercept.

Table 7.2: List of behavioural variables and included behaviours

Behavioural variables	Individual behaviours
Grooming given	Grooming given
Grooming received	Grooming received
Social play	Calm and rough social play
Socio-sexual	Copulation, non-copulatory mount
Aggression given	Long/short charge given, aggressive intention given, directed display given
Agonistic response	Long/short charge received, aggressive intention received, directed display received, flee, flinch, displace, grin

Prior to the analyses of the cognitive testing, we removed the first three practice trials (544 trials), outlier trials, as determined by the video coding (1103 trials), and trials where the bonobos made incorrect responses (522 trials), resulting in the removal of 2169 trials out of 6306 collected in total. We furthermore filtered our data on extreme values (RT < 250 ms) and detected individual RT outliers that were geater than 2.5 standard deviations from the individual's mean (Berger & Kiefer, 2021), while controlling for target location and subject. This removed an additional 97 trials. Given that human studies typically find that high arousal, negative affective states result in a combination of arousal-related response speeding across conditions (Aston-Jones & Cohen, 2005; Fox et al., 2001), and valence-related response slowing for mildly threatening stimuli (Bar-Haim et al., 2007; Mogg & Bradley, 2016), we followed the human literature and calculated arousal-controlled response ratio scores (Bradley et al., 1998; Ly et al., 2014; McKenna & Sharma, 2004). This was done by dividing the mean of direct/averted trials by the mean of the control trials per testing day, while controlling for target location. Values greater than 1 reveal slowing of responses towards the direct trials relative to the control trials, whereas values lower than 1 reveal response speeding. Hence, the response ratio scores represent an arousal-controlled measure for response slowing while simultaneously controlling for inter-individual variation in reaction times.

We fitted two linear mixed models to examine the response ratio scores for direct and averted trials. The first model included the predictors stimulus type (levels: averted, direct), condition (levels: pre-fusion, fusion, post-fusion) and sex (levels: female, male), and a three-way interaction, and we included target location (levels: left, central, right) as a control variable. The second model was similar to the first model, but instead of a three-way interaction with sex, we included status (levels: transferee, resident). Non-significant interaction terms were excluded from the models. Both models included a random intercept for subject ID with a random slope for condition and a random intercept for stimulus ID. Post-hoc analyses were performed using the *emmeans* package (Lenth, 2023) using a Tukey correction for multiple comparisons.

To examine associations between outcomes of the response slowing task and behavioural variables, we separately tested each behavioural variable against the corresponding daily response ratio scores using linear mixed models. Because a substantial proportion of the behavioural datapoints contained zeros, we included a binary indicator whether the behaviour was performed, or not. The inclusion of this binary indicator variable allows a separate estimation of the effect of zero and non-zero values of the behavioural covariate (Robertson et al., 1994). All models included a control variable for target location and a random intercept for subject ID.

Additionally, we post-hoc tested the absolute reaction time data to check whether response speeding, typical for stress-related arousal, occurred. As such, we fitted a generalised linear mixed model with a Gamma distribution and log link function to assess whether the absolute reaction times of the bonobos were influenced by stimulus type and depending on the condition. Fixed factors included an interaction term between stimulus type (levels: control, averted, direct), condition (levels: pre-fusion, fusion, post-fusion), and a control variable for target location (levels: left, central, right). Non-significant interaction terms were excluded from the model. Our model included a random intercept for subject ID with a random slope for condition and a random intercept for stimulus ID. Post-hoc analyses were performed using the *multcomp* package (Hothorn et al., 2008) using a Tukey correction for multiple comparisons.

Diagnostic plots (residuals vs fitted and QQ plots) were used to examine assumptions of normality and homogeneity of variances and we additionally tested uniformity and dispersion of the residuals using the *DHARMa* package (Hartig, 2020).

Results

Between February and July 2021, seven fission-fusion events occurred, of which six were followed-up with cognitive testing (Table S7.3). Behavioural data were collected across 33 days. Between the eight participating bonobos, this resulted in 113 datapoints in total, of which 48 in the pre-fusion condition, 33 in the fusion condition, and 33 in the post-fusion condition. Subgroups consisted of a mean of 10 individuals (SD = 1.63) and units that transferred between subgroups typically consisted of 3-4 (M = 3.6, SD = 1.44) transferees. The eight bonobos participating in this study completed a combined total of 4040 trials that were included in the analysis (range: 296-738 trials per individual), of which 1635 trials during the pre-fusion condition (range: 154-258 trials per individual), 1177 trials during the fusion condition (range: 44-245 trials per individual), and 1228 trials during the post-fusion condition (range: 35-235 trials per individual).

Behavioural patterns across conditions

We tested for differences in the six behavioural variables of interest among the three testing conditions. The frequencies of aggression given (Figure 7.3A; $\chi^2 = 6.826$, df = 2, $P = 0.033$), socio-sexual behaviour (Figure 7.3B; $\chi^2 = 20.327$, df = 2, $P < 0.001$) differed between conditions. Namely, aggression given was more frequent during the fusion condition compared to the pre-fusion (ratio = 5.670, $z = 2.434$, $P = 0.039$). Socio-sexual behaviour was also more frequent during the fusion condition compared to the pre-fusion (ratio = 8.208, $z = 3.934$, $P < 0.001$) and post-fusion (ratio = 2.539, $z = 3.023$, $P = 0.007$).

Frequencies of the other behavioural variables (grooming given/received, play and agonistic response) did not differ among conditions (*P* > 0.05, see Table S7.4).

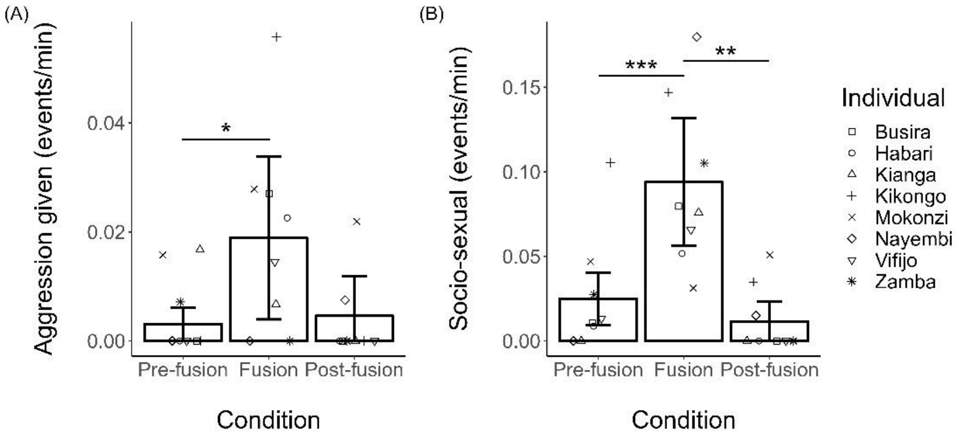

Figure 7.3: Average rates (events/minute) (± 95% confidence intervals) for (A) aggression given, (B) socio-sexual behaviour in the three testing conditions. The symbols indicate the average scores per individual. *** $P < 0.001$, ** $P < 0.01$,
* $P < 0.05$.

Response slowing

Based on the analyses on response ratio scores, we found no three-way interaction between condition, stimulus type, and sex $\chi^2 = 0.620$, df = 2, $P = 0.955$), nor did sex show a significant two-way interaction with condition ($\chi^2 = 2.439$, df = 2, $P = 0.295$) or with stimulus type ($\chi^2 = 0.353$, df = 2, $P = 0.552$). Sex also did not show a significant main effect ($\chi^2 = 1.542$, df = 1, $P = 0.214$). Status neither showed a three-way interaction with condition and stimulus type ($\chi^2 = 0.819$, df = 1, $P = 0.365$), nor did status show a significant two-way interaction with condition ($\chi^2 = 1.876$, df = 1, $P = 0.171$) or with stimulus type ($\chi^2 = 1.573$, df = 1, $P = 0.210$). Status likewise did not show a significant main effect ($\chi^2 = 2.827$, df = 1, $P = 0.098$). Hence we removed sex and status as fixed factor from the models.

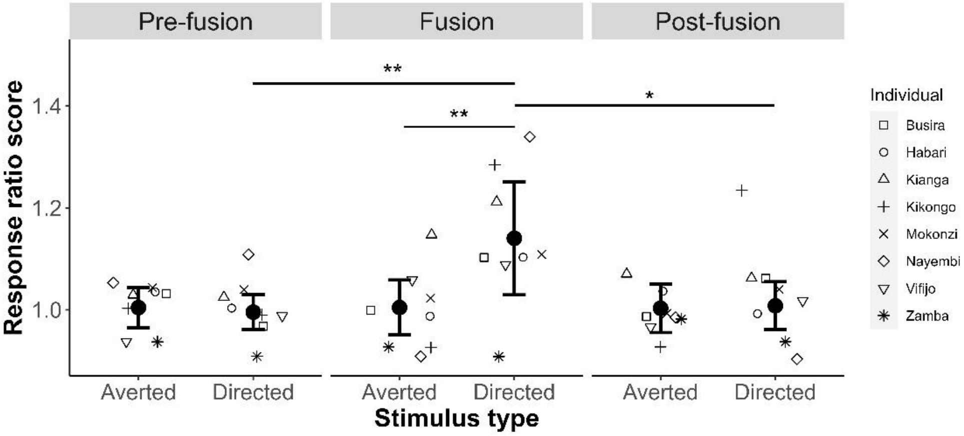

Figure 7.4: Daily ratio scores (± 95% confidence intervals) for direct trials, controlled for stimulus location, as function of (A) socio sexual rates, and (B) play rates. Ratio scores greater than one indicate response slowing

The final model revealed a two-way interaction between condition and stimulus type (Figure 7.4; $\chi^2 = 7.642$, df = 2, $P = 0.022$). Pairwise comparison, using condition as contrast, indicated that response ratio scores for during direct trials were higher than during averted trials during the fusion condition ($t_{527} = 3.159$, $P = 0.002$), but not during the pre-fusion ($t_{526} = -0.360$, $P = 0.719$) or post-fusion condition ($t_{527} = 0.192$, $P = 0.848$). Between conditions, response ratio scores for direct trials were also higher during the fusion condition compared to the pre-fusion ($t_{17.7} = 3.501$, $P = 0.007$) and post-fusion condition ($t_{17.4} = 2.886$, $P = 0.026$). Ratio scores for the averted trials did not differ between conditions ($P > 0.05$, see Table S7.5).

Behavioural associations with response slowing

We found no interaction effects between condition and any of the behavioural variables on response slowing. However, we did find that daily response ratio scores were significantly correlated with frequencies of socio-sexual behaviour (Figure 7.5A; $\chi^2 = 9.132$, df = 1, $P = 0.003$) and social play behaviour (Figure 7.5B; $\chi^2 = 6.147$, df = 1, $P = 0.013$). At times when bonobos engaged more in socio-sexual interactions, they showed lower ratio scores ($\beta = -0.801$, SE = 0.265, $P = 0.003$). Contrary, when bonobos engaged more frequently in social play interactions, they had higher ratio scores on those days ($\beta = 0.388$, SE = 0.157, $P = 0.014$). Other behavioural measures were not significantly correlated with the ratio scores (see Table S7.6).

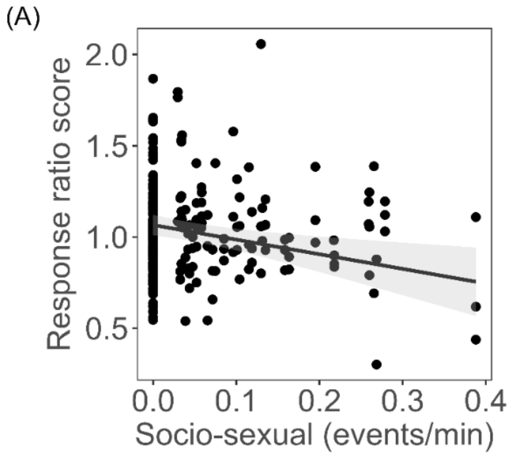

Figure 7.5: Daily ratio scores (± 95% confidence intervals) for direct trials, controlled for stimulus location, as function of (A) socio sexual rates, and (B) play rates. Ratio scores greater than one indicate response slowing

Post-hoc test: Stress-related arousal

We ran similar models as for the response ratio score analyses, but instead with absolute reaction times as dependent variable. Our final model revealed a significant interaction effect between condition and stimulus type (Figure S7.1; $\chi^2 = 14.314$, df = 4, $P = 0.006$). Pairwise comparison, using stimulus type as contrast, revealed that reaction times for control trials were faster during fusion days compared to pre-fusion days ($t_{4021} = 2.943$, $P = 0.009$) and post-fusion days ($t_{4021} = 2.294$, $P = 0.047$). The bonobos were also faster to touch the averted gaze trials during fusion days compared to pre-fusion days ($t_{4021} = 3.683$, $P < 0.001$), but not compared to post-fusion days ($t_{4021} = 1.860$, $P = 0.151$).Additionally, using condition as contrast, pairwise comparison indicated that response times were slower on fusion days during trials showing directed gaze stimuli compared to control trials ($t_{4021} = 3.331$, $P = 0.002$), and to averted gaze trials ($t_{4021} = 3.769$, $P < 0.001$). Reaction times did not differ among stimulus types during pre- and post-fusion days ($P > 0.05$, see Table S7.7).

Discussion

This study aimed to evaluate changes in the behavioural and cognitive components of affective states in zoo-housed bonobos in response to managed social fusion events. We found that both agonistic and socio-sexual behaviour increased during fusions, but not grooming or social play. On days with fusions, bonobos showed a subtle cognitive freeze (i.e., longer reaction times) for mildly threatening stimuli, compared to non-threatening social stimuli and control trials, suggesting a shift towards more negative affect. On days after these events, this response slowing effect was no longer present, indicating that the effect was short lasting. Response slowing was negatively associated with socio-sexual behaviour, and positively associated with social play behaviour.

Following the idea that fusion events can induce social tension, we indeed observed that aggression was more frequent during fusions than during pre-fusion days. The observed increase in aggression and socio-sexual behaviour is similar to that reported in a previous study with female bonobos (Moscovice et al., 2015). The lack of an increase in grooming may be due to the less specialised function of grooming in bonobos compared to chimpanzees (Nakamura, 2003; Sakamaki, 2013). The increase in socio-sexual behaviour appears to fit the hypothesised function that this behaviour reduces social tension in bonobos (de Waal, 1987, 1990; Furuichi, 1989; Hohmann & Fruth, 2000). The simultaneous increase in aggressive behaviours could alternatively suggest that (part of) the increase in socio-sexual interactions were a response to the aggression, and functioned to facilitate reconciliation (Clay & De Waal, 2015).

As for the results of the response slowing task, we found changes in the cognitive processing related with negative affect, independent of the sex of the bonobo. These findings support previous studies reporting response slowing during putative stressful events (Bethell et al., 2016; Cronin et al., 2018). Interestingly, although we observed response slowing in the fusion condition when presented with a mildly threatening stimulus, post-hoc analyses revealed that this effect was combined with faster responses for the control and non-threatening social control trials, suggesting a case of response speeding. Such response speeding is typical of stress-related arousal, and often reported in human studies studying associations between anxiety, arousal and response speeding (Aston-Jones & Cohen, 2005; Fox et al., 2001). The original study by Bethell et al. (2016) likewise described response speeding. Using response ratio scores allowed us to control for these arousal-related changes, and the arousal-controlled response slowing effect therefore reflects a shift in affective valence. Importantly, if only changes in arousal would have occurred, we would expect to also find response speeding for direct trials in the fusion condition, which was not the case as proven by our post-hoc analyses on the absolute reaction times. Additionally, because no arousal-controlled response slowing was observed in pre- and post-fusion conditions, the response slowing within the fusion condition can be attributed to the condition which caused changes in the cognitive processing for mildly threatening stimuli. Nonetheless, the observed response speeding for control trials should be acknowledge and are necessary to fully understand changes in both valence and arousal. The combination of within-condition response slowing for mildly threatening stimuli during fusions and the between-condition response speeding for control trials thus suggests changes in both valence and arousal, respectively. By implementing a post-fusion condition we were moreover able to detect that the observed changes in affective states were only short-term, as reaction times returned to pre-fusion levels.

While previous studies have linked affiliative behaviours to heightened positive affect in bottlenose dolphins (Clegg et al., 2017) and tufted capuchins (Schino et al., 2016), the affective correlates to socio-sexual behaviours have not yet been studied and our results can likely be explained by bonobo socio-ecology. Supporting our predictions regarding potential affective correlates of behavioural patterns, we found that heightened rates of socio-sexual behaviour were associated with reduced negative affect. This suggests that affective correlates of socio-sexual behaviour are general across these contexts, and could hint at a common stress-alleviating effect. Other studies examining physiological associations with socio-sexual behaviours found inconclusive relationships. Cortisol, both salivary and urinary levels, were not linked to the frequency of socio-sexual interactions (Hohmann et al., 2009; Moscovice et al., 2015), whereas a positive link has been found between bonobo female same-sex interactions and urinary oxytocin (Moscovice et al., 2019), a neuropeptide that is thought to, amongst other things, play an anxiolytic role in the stress response in social contexts (Kumsta & Heinrichs, 2013). However, how peripheral levels of oxytocin approximate central levels is currently debated (Crockford et al., 2014; Valstad et al., 2017) which limits further extrapolations to our findings.

While frequencies of play did not differ significantly between fusion days and baselines, we did find that social play behaviour showed a positive association with response slowing, independent of the testing condition. This contradicts our prediction where we expected to find a negative relation between play and response slowing. Play is often linked with positive affective states (Boissy et al., 2007; Held & Špinka, 2011), for which most compelling evidence exists that sub-optimal conditions, that are thought to cause negative affect, suppress play (Oliveira et al., 2010) and some studies have reported links between situations associated with positive affect and increases in play (Ahloy-Dallaire et al., 2018). However, the relationship between play and affect is not as straightforward as proposed, and may depend on the species, sub-type of play and age (Ahloy-Dallaire et al., 2018; Marley et al., 2022; Palagi, 2023). For example, play behaviour in adult animals has been suggested to have an affiliative function to promote social bonds (Enomoto, 1990; Palagi & Paoli, 2007), or to reduce tension during food competition (Asensio et al., 2022; Norscia & Palagi, 2011; Palagi et al., 2006; Yamanashi et al., 2018), social insecurity (Antonacci et al., 2010) or social crowding (Crast et al., 2015; Tacconi & Palagi, 2009), and therefore facilitate social tolerance (Palagi, 2023). Others have suggested that play behaviour can occur as displacement during stressful events (Kortmulder, 1998). Adult social play has a prominent role in some species to regulate tension and social assessment, especially in species with a high degree of fission-fusion dynamics like bonobos (Pellis & Iwaniuk, 2000), and may fulfil a role similar to socio-sexual behaviour in mitigating social tension. Interestingly, we found an opposite association between affect with play and socio-sexual behaviour, which suggests different affective consequences. One major disparity, that may explain differences in the affective correlates found here, is that play as means of tension regulation or social assessment is accompanied by competitive components which changes the nature of the interaction (Palagi, 2006; Rooney et al., 2000). Bonobos may overcome such uncertainty by communicating their intention using facial expressions which may reassure their play mate (Demuru et al., 2015). Unfortunately, the quality of the camera footage did not enable for such detailed analyses. Additionally, while we coded calm play separately from rough play, we pooled these behaviours together for analysis. Many theories have been proposed to explain the function of play, and depending on different variables, the affective experience of such interactions may either be positive or negative. Importantly, for the behavioural associations with the response slowing effect, we cannot disentangle correlation from causation. Hence, it is at this point unclear if the changes in affective states were a result of the behavioural patterns, or vice versa. Future studies could incorporate these details to better understand the affective correlates between different types of play.

We encountered several (potential) limitations. First, bonobos are known to pay relatively more attention to the eye region compared to chimpanzees (Kano et al., 2015; Mulholland et al., 2020), and one could therefore argue that the stimuli used in this paradigm are prone for such a confounding effect. In that case, we would expect to find a difference in reaction times for the stimuli in baseline conditions, for which we found no evidence. We can therefore suggest that the response slowing task is suitable to detect changes in affective states in bonobos, and that the previously observed bias for eye regions does not influence their performance in baseline conditions. Second, as the participation of the bonobos in the touchscreen sessions was completely voluntarily, we could not control if individuals joined, or not. We can therefore not exclude that individuals who experienced stronger changes in affective states were not sampled, therefore potentially biasing our results. Third, we should acknowledge the temporal discrepancy between our behavioural and cognitive data. We aimed to collect the cognitive data as soon as possible after the fusion events, without disrupting the social interactions of the bonobos, which was typically within two hours after fusions. Yet, our behavioural data was collected within the first 30 minutes after fusion events. Hence, it is possible that in the meantime other events occurred that could have influenced the cognitive data. Fourth, whereas wild bonobos initiate and coordinate social fusion events (Schamberg et al., 2016), in our study zoo staff decided which social units changed between the subgroups. Objective criteria exist to decide who transfers between subgroups (Stevens, 2020), but ultimately this decision remains partly based on subjective factors. Generalisations of results from captive studies to wild populations should therefore be made with care. Additionally, it is likely that individual variables of our participating bonobos, such as inter-individual relations, ontogeny or affective styles, shaped their affective experiences, which draws further caution against generalisations and requires further investigation. Hence, although we report on one specific group of bonobos, the results from the current study provide a unique perspective on the affective consequences of fusion events and behavioural correlates in bonobos.

Finally, our results can have implications for animal welfare and the management of bonobos under human care. Although we found evidence that fusion events were associated with shifts towards negative affect, these were only short-lasting. An increase in aggression was observed, but limited to mild, non-contact aggression, and the increase in socio-sexual behaviour might suggest that the bonobos were able to mitigate the social tension (Moscovice et al., 2015). If zoo-housed bonobo groups are not able to naturally fission and fusion, mimicking natural fission-fusion dynamics is advised for managed populations (Stevens, 2020) and can benefit the bonobos' social dynamics (Classen et al., 2016). The impact on the welfare of the bonobos of the social tension associated with fusion events would be limited if the bonobos are able to cope adaptively with the situation (Englund & Cronin, 2023). In the current study, this appeared to be the case, but requires case-by-case evaluation.

Conclusions

We observed short-lasting shifts towards negative affective states in the bonobos during social fusions. During fusion events the bonobos showed increased rates of mild aggressive and socio-sexual behaviour. The lack of severe contact aggression could indicate a role of socio-sexual behaviour in mitigating this tension. Additionally, the negative association between socio-sexual behaviour and cognitive response slowing could further hint at tension reducing mechanisms. The positive association between response slowing and adult-adult social play, however, raises questions about the affective experience of such playful interactions. However, it is important to note that our study does not investigate the causal relationship between these behaviours and affective states, but we demonstrate that socio-sexual behaviour and social play either induced certain affective states in the bonobos, and/or were induced by them. Further research will enhance our understanding of the affective consequences of social events and the mechanisms and motivations of behavioural strategies.

8

General discussion

Daan W. Laméris

The study of animal emotions is an emerging and rapidly evolving field. Besides advancement in our fundamental knowledge regarding this topic, it also yields practical implications, including those related to animal ethics and welfare (de Waal & Andrews, 2022). Emotions guide daily behaviour, informed by an individual's contextual relationship and shaped by past and present experiences. They enable dynamic responses to rewarding and aversive experiences, being either internal or external, allowing for behavioural flexibility (Faustino et al., 2015). Emotions are triggered by the appraisal of stimuli, which induces numerous neurophysiological, cognitive, and motivational processes. This illustrates the complex nature of emotions, but also shows that emotional episodes are accompanied by different, identifiable components.

Much remains unknown about the emotional lives of animals, and how we can use this to assess their welfare. Following the framework of an emotional episode (Crump et al., 2020), I have attempted to obtain a better understanding of different components of bonobo emotions. Chapters 2 and 3 elaborate on how emotions influence attentional processing in bonobos, providing novel fundamental insights in bonobo emotions, whereas Chapters 4-6 examines behavioural aspects of bonobo emotions that maintain the practical feasibility to be included in regular welfare monitoring. Chapter 7 ultimately integrates different cognitive and behavioural measures and applies this to study a husbandry practice. I will continue by discussing some general methodological considerations of the use of touchscreen and eye-tracking technology in the study of animal emotions. Finally, I will consider future directions that can help us move forward in understanding affective states in animals and conclude by integrating my findings.

Between play and prey: Decoding bonobo emotional responses to diverse stimuli

In **Chapter 2**, I used a pictorial emotional Stroop task (Allritz et al., 2016) to study what emotional information distract the attention of the bonobos while performing on a simple cognitive task (Laméris et al., 2022b). Attention is inherently linked to the process of appraisal, and therefore an important step in shaping emotional responses (Ellsworth & Scherer, 2003). Little is known about what captures the attention of bonobos. The pictorial emotional Stroop task is a relatively simple method to study attentional prioritisation, and has previously tested with different primate species (Allritz et al., 2016; Hopper et al., 2021a; Vonk et al., 2022). In this study, I applied the same pictorial emotional Stroop task as the previous studies but included a wider range of biologically relevant stimuli.

When I tested how environmental stimuli with assumed positive (i.e., preferred food item), negative (i.e., predator), and neutral (i.e., flower) associations interfere with the attention of the bonobos on the Stroop task, I found that accuracy decreased, and reaction times increased for all of the categories. The leopard stimulus elicited the strongest response. Attention for threats is closely tied to survival, and the rapid and implicit detection is rooted in evolutionary old mechanisms (Öhman, 2009). Within the primate literature, compelling evidence exists that primates exhibit heightened attention for snakes (Hopper et al., 2021a; Kawai & Koda, 2016; Masataka et al., 2018; Shibasaki & Kawai, 2009). I initially considered snakes as a negative environmental stimulus but previous work suggests that bonobos actually do not strongly respond to a snake model (Staes et al., 2016). In the wild, bonobos face predation pressure from leopards (Corredor-Ospina et al., 2021; D'Amour et al., 2006), hence why I reasoned that leopards were more salient than snakes. The responses to the leopard images are interesting, as none of the bonobos in my study were born in the wild, and hence had no direct experience with leopards, although some have been exposed to a taxidermied specimen (Staes et al., 2016). This suggests that some attention biases are innate processes shaped by evolutionary pressures. This view is supported by the previous mentioned primate studies that likewise worked with captive-born primates and still found biased attention for snakes. This contrasts my finding for the food-based attention bias, which is likely a case of an acquired bias since the cultivated bananas fed to the bonobos and presented in the stimuli are not naturally occurring in wild bonobo habitat. Bonobos have a strong preference for bananas (Verspeek & Stevens, 2020) and primates recognise food items from pictorial stimuli (Hopper et al., 2019; Huskisson et al., 2020).

I can argue that the Stroop effects for the negative and positive stimuli represent top-down processing, as they are driven by cognitive processes, rather than sensory information (Corbetta & Shulman, 2002). Still, I can discuss that they likely tap into different cognitive mechanisms. I can assume that the leopard was interpreted as a threat, whereas the banana was interpreted as a reward. Although both have their inherent values, the leopard likely triggered instant punishment avoidance systems to effectively respond to immediate threats (Bishop, 2008; Carver, 2001), while the banana triggered reward acquiring systems (Burgdorf & Panksepp, 2006) and therefore reflects value-driven attention processing (Anderson et al., 2011). The two systems are theoretically, and functionally different, but can both result in altered performance in the Stroop task (Krebs et al., 2011; McKenna & Sharma, 2004). It is therefore difficult to disentangle the two mechanisms based on my data.

Surprisingly, the bonobos also showed altered performance for the presumed neutral flower, stimuli. I selected flowers as a neutral stimulus based on previous studies (Shibasaki & Kawai, 2009), and because flowers naturally occur on the bonobo island. The specific flower (*Rudbeckia hirta*), however, does not grow in the outdoor enclosure of the bonobos at Planckendael. The reason to select this specific flower was because it, more or less, matched the colour configurations of those of the leopard and banana. Low-level, sensory features drive attentional processes (Treue, 2003), and careful matching was therefore important. The *Rudbeckia hirta* flower was deemed the best neutral object to match these characteristics, however results suggest that this was actually not the case and perhaps the overall yellow features of the non-social stimuli influenced attention patterns. Although it is possible that we captured a novelty effect with the flowers (Ernst et al., 2020), this is difficult to disentangle without a true neutral stimulus.

In terms of the emotional responses to facial expressions, the bonobos only showed longer reaction times for touching the target with positive facial expressions compared to neutral expressions. Play faces fulfil a significant communicative role (Demuru et al., 2015; Palagi, 2006, 2008), and it is likely that these pressures shaped attentional processes. The enhanced attention to play faces also supports previous findings suggesting that bonobos readily pay more attention to affiliative scenes (Kret et al., 2016). Interestingly, Kret et al. (2016) did not find enhanced attention for play scenes, but for scenes picturing grooming and sexual interactions. A follow-up study found that these attention biases were more pronounced when displayed by unfamiliar animals, compared to familiar ones (van Berlo et al., 2023). I decided not to include familiarity as experimental condition because relationships among bonobos are complex and dynamic (Stevens et al., 2015; Verspeek et al., 2019), and difficult to incorporate at this stage. As such, I only included stimuli of unfamiliar individuals which could have impacted the results. That is, even though bonobo inter-community encounters involve both affiliative and agonistic interactions (Cheng et al., 2021; Hohmann & Fruth, 2002; Lucchesi et al., 2021; Sakamaki et al., 2018; Tokuyama et al., 2019), peaceful and tolerant encounters are more frequent compared to inter-community encounters among chimpanzees (Pisor & Surbeck, 2019). This could enhance the saliency of these play faces in unfamiliar individuals.

In the general introduction of this thesis, I explain that emotions have a relational component, meaning that emotional responses are tailored to the appraised relevance and potential consequences of stimuli or events (Faustino et al., 2015; Smith & Kirby, 2009b). This process of appraisal enables individualised emotional responses based on the individual's set of resources and goals. To investigate possible individual effects, I analysed the data at a subject level. These analyses indeed revealed individual differences in the effect of specific social and non-social stimuli on attention. This may represent a case of attention biases to personally relevant stimuli, which has been previously reported in human Stroop studies (Wingenfeld et al., 2006). For example, while multiple individuals showed longer reaction times to the leopard stimulus, only one bonobo showed lower accuracy scores. Notably, this was the only female who had a dependent infant at the time. This stronger response by this female could have been driven by her current situation in which she was not only responsible for herself, but also for her infant. While these are currently speculations, previous work has shown that primate mothers adapt their responses to predators depending on their infant (Lameira & Call, 2018), which could possibly extent to attentional mechanisms.

Another individual effect I would like to highlight here is that three out of four bonobos had longer reaction times to positive facial stimuli. Other studies on humans found that positive biases to facial stimuli were associated with positive affectivity and heightened optimism (Mauer & Borkenau, 2007), positive emotions (Sanchez & Vazquez, 2014; Strauss & Allen, 2009), higher trait emotional intelligence (Lea et al., 2018) and higher tendencies for prosocial behaviour (Troller-Renfree et al., 2015). These are interesting directions for future research as bonobos are often considered more empathising than chimpanzees (MacLean, 2016). While it is possible that the individual effects can be explained by their own emotional states (Crump et al., 2018), other factors such as age, sex or dominance may also play a role in modulating attention to socio-emotional information (Kret & De Gelder, 2012; Mather & Carstensen, 2003). Unfortunately, my current sample size does not allow to test such factors.

Investigating the effect of emotional priming on attention

In Chapter 2, I found that bonobos show an attention bias for play faces, but that not all participating individuals showed this effect. In **Chapter 3**, I aimed to further test if attention biases can be shaped by current affective states. In order to do so, I designed an eye-tracking paradigm in which I primed emotions using valenced video scenes. Afterwards, I presented the bonobos with competing social information to examine if and how attention biases are influenced by affective states.

In the first part of this study, I aimed to prime affective states using valenced videos, and looked at changes in pupil size as correlate of the autonomic nervous system that explains emotional arousal. Results from these analyses were inconclusive as to whether the videos successfully primed affective states. Based on the percentual change in pupil size, it appeared that pupils generally dilated after observing the bonobo primers, while they constricted after observing the human primers. However, when looking at how the pupils reacted while viewing the primer videos, it becomes clear that, after the initial light reflex, the pupils dilated in all conditions. Remarkably, the initial light reflex for the Positive and Negative Human videos was stronger compared to the Neutral Human and all of the Bonobo videos, albeit not significantly (Figure S3.1). In the discussion of Chapter 3, I discussed multiple possible explanations for this, including differences in luminance (Hess et al., 1975), or emotional content (Snowden et al., 2016), although this did not seem to explain this difference. An alternative approach to look at changes in pupil size would be to disentangle the initial light response from *late* pupil dilation, and separately analyse the two (Henderson et al., 2014). I also proposed that perhaps the guide used as a model for the Neutral Human was not familiar. Great apes have previously shown to exhibit a novelty effect when presented with unfamiliar humans (Leinwand et al., 2022), and it seems likely that this was similarly the case in my study. In retrospect, it would have been better to include a human for the neutral videos that occasionally entered the keepers' corridors but did not interact with the bonobos.

Unfortunately for this study, there were no suitable candidates that met these criteria. In general, I could argue that using human models to prime affective states is perhaps not ideal as the relationships between, for example, caretakers or veterinarians can vary across institutions, and thus do not present a standardised priming method.

When looking at the individual responses to the primer videos, large inter-individual differences were observed. This may inherently be linked to the relational nature of emotions (Faustino et al., 2015), and I could argue that individuals may have different associations with each of the primer videos. For example, seeing individuals play may be perceived differently by subadult bonobos compared to adult ones, as play changes in function with age (Palagi & Cordoni, 2012). Similarly for the veterinarian videos, despite that all bonobos were previously exposed to the veterinarian, not all individuals had the same experiences. For instance, some individuals were anaesthetised and underwent medical procedures, whereas other did not, resulting in different associations with the veterinarian. Previous work has shown that chimpanzees show long-lasting effects on performance during a Stroop task when presented with veterinarian images, and that this effect is stronger with more recent medical interventions (Allritz et al., 2016). This suggests that apes have long-term memory for such events and that this influences the individual’s perception and responses when encountering such stimuli. Anecdotally, this became evident from personal observations during this study. Djanoa, a female bonobo who did not participate in this study, would initially retrieve her infant, Unabii, from the eye-tracking setup when she was observing the veterinary videos. Interestingly, Djanoa also showed similar responses with the guide stimuli, but haltered her response before actually retrieving her infant. Djanoa did, in return, not respond to the caretaker videos at all. Habituation to the veterinary videos occurred for Djanoa during subsequent trials and ultimately let Unabii view the footage. Of course, this resulted in missing data for Unabii during the initial sessions with the veterinary primers. These individual differences become more pronounced with small sample sizes. While such individual variation is often considered as an undesired artefact of small sample sizes, this also provides a wealth of information that is worth investigating. Later in this discussion, I will discuss the added value of individual differences for future directions.

In the second part of the study, I investigated how bonobos attended to competing socio-emotional information, and if this was influenced by observing the primers. For this, I applied a novel modified version of the ‘face in the crowd’ paradigm (Halamová et al., 2022). The original paradigm presents a configuration of different sizes (e.g., 2x2, 3x3, 4x4, etc.) in which one target face, of a certain emotional valence, is contrasted against a crowd of distractor faces, either being neutral or another emotional valence (Öhman et al., 2001). In my modified version, I used a 2x2 configuration, including one positive, one negative and two neutral images. This increases the ecological relevance of the paradigm, and arguably provides more valid results. Despite this more complex configuration, I found that the bonobos preferentially attended to negative facial expressions, that is, bared-teeth facial expressions. This supports previous findings for an attention bias for bared-teeth faces in bonobos in an eye-tracking study (van Berlo, 2022), but contrasts my own results of Chapter 2, where I found an attention bias for play faces. However, as discussed in the discussion of Chapter 3, it is possible that the attention bias for play faces in the Stroop task is driven by implicit attentional processes, whereas the current bias for bared-teeth faces reflects sustained attention, and hence explicit attentional processes. The context in which these facial expressions are exhibited, and the urgency of rapid attention allocation and behavioural response can explain this difference in temporal attentional processing. That is, play faces are typically displayed during playful interactions, in which the quick allocation of these expressions is essential for rapid facial mimicry, which is characteristic among primates (Davila Ross et al., 2008; Mancini et al., 2013; Palagi et al., 2019), and benefits the success of these interactions. Bared-teeth faces, in contrast, are displayed when bonobos are in distress, signalling appeasement or reassurance (de Waal, 1988; Vervaecke et al., 2000; Vlaeyen et al., 2022). The processing of fearful expressions is a deeply rooted mechanism (Pichon et al., 2009), and to a certain degree involuntarily and automatically (Vuilleumier et al., 2001; Williams et al., 2004), while further conscious processing optimises the visual processing and guides threat perception (Furl et al., 2013; Sussman et al., 2016). Such facial expressions therefore provide information about potential threats in the environment to bystanders (de Gelder, 2006). Interestingly, I found that as the session progressed, the attention for bared-teeth faces increased, suggesting that seeing multiple individuals with these expressions enhances attention which could further improve threat processing.

In summary, I did not find strong evidence to support my prediction of affect-congruent attention biases in bonobos. Although there was some evidence that the bonobos responded affectively to the primer videos, at least for the bonobo videos, it is possible that the footage used was not salient enough to induce changes in the affective states that lasted throughout the entire session. Additionally, as the videos were muted, the auditory component of these stimuli was excluded which likely made them less salient. From a methodological perspective, it would require further validation to conclude whether video footage is a successful method to prime affective states. Still, the overall attention bias for negative facial expressions gave some insight in the appraisal and cognitive processes of an emotional episode. This contrasting result with **Chapter 2** may preliminarily suggest that facial expressions are distinctively attended to during different attentional processes, although further detailed research is needed to draw these conclusions.

Anomalies and affect: Abnormal behaviour in zoo-housed bonobos and its welfare significance

The previous studies have shown how bonobos respond to different emotional stimuli, how this emotional content modulates attention and shapes appraisal processes. Ultimately, emotions shape and fine-tune behaviours, and abnormal behaviours have traditionally been proposed as indicators of negative emotions in animals as they arise with poor living conditions, such as early maternal separation (Bellanca & Crockett, 2002; Freeman & Ross, 2014; Turner et al., 1969), inadequate (social) housing (Fontenot et al., 2006; Gottlieb et al., 2013), lack of environmental control (Hosey, 2005), or the inability to perform species-specific behaviours (Browning, 2019; Clubb & Mason, 2007). Abnormal behaviours may serve as coping mechanisms to alleviate stress to some extent (Mason & Latham, 2004; Pomerantz et al., 2012a), but further than that, they serve no obvious purpose or function, and may in fact interfere with normal behavioural activities (Mason & Latham, 2004; Novak et al., 2012). Abnormal behaviours may also be learnt through social transmission (Nash et al., 1999), which could mean that the presence of socially-learned abnormal behaviours is no longer the results of suboptimal conditions. In other words, although abnormal behaviours may provide a valuable source of information regarding the emotional status of an individual, the reliability of the behaviours should be carefully examined.

To overcome the lack of our current knowledge on abnormal behaviours in zoo-housed bonobos, **Chapter 4** conducted a cross-institutional overview of the abnormal behaviours present and aimed to explore what factors influence their occurrence (Laméris et al., 2021a). I documented 13 abnormal behaviours out of the 28 included in the ethogram, which is considerably lower than the 37 abnormal behaviours previously reported in zoo-housed chimpanzees (Birkett & Newton-Fisher, 2011). Four behaviours were habitual, being present in ~50% of the sampled individuals. These behaviours included coprophagy, poke anus, social hair plucking, and regurgitation. Considerable inter-individual variation in the frequency of these behaviours was documented, and I identified multiple factors that can explain this variation. More Sociable and Active individuals, for example, engaged more in coprophagy behaviour, which could be explained by higher levels of boredom experienced by these individuals (Hoff et al., 1994; Martin, 2002). Bonobos who scored higher on Sociability also engaged more in social hair plucking, although this is likely confounded as social hair plucking is embedded in grooming interactions (Brand & Marchant, 2019). Poke anus was more frequent in wild-born individuals, and in females which warrants further investigation. One explanation may be that poke anus is a self-stimulating behaviour for females (Vasey & Duckworth, 2006). Alternatively, poke anus also appears to preside coprophagy (pers. observation), perhaps by means of stimulating defecation. Just like the hand-assisted regurgitation behaviours, which appears a learned behaviour, poke anus could present a behaviour that is tied to coprophagy. No determinants were found for regurgitation, which confirms previous reports that this behaviour is not influenced by these tested factors (Miller & Tobey, 2012).

There are many more factors that may explain the occurrence or modulate the frequency of abnormal behaviours that I have not addressed in **Chapter 4**. One factor that likely influences abnormal appetitive behaviours, such as regurgitation and coprophagy, is the dietary composition and feeding schedule (Hill, 2018). For example, the amount of dietary roughage and presence of fruit in the diet is known to highly influence rates of coprophagy (Fritz et al., 1992; Kollar et al., 1968) and regurgitation (Hill, 2018). Continuous feeding is suggested as a key factor in reducing regurgitation behaviour in zoo-housed great apes (reviewed in Hill, 2018). Wild-living great apes spend the majority of their active hours on foraging behaviours, and this is often difficult to achieve in captive settings (Brando & Buchanan-Smith, 2018). This may lead to under-stimulated levels of satiety (i.e. the feeling or state of being sated) (Coria-Avila et al., 2022), which apes may compensate for by regurgitation or coprophagy behaviour. This can explain why individuals with higher Activity levels engaged more in coprophagy, as they were lacking stimulation in their daily activity. Regurgitation, often followed by reingestion, and coprophagy may therefore indicate a coping strategy performed in response to current environmental deficits.

What can abnormal behaviours tell us about emotions and welfare? This remains a central discussion point around abnormal behaviours. Most abnormal behaviours are indicators of past or current compromises in welfare aspects of an animal. However, as abnormal behaviours are often seen to persist beyond poor welfare conditions they cannot be unconditionally used as signal of compromise at the time of performance. Notably, when animals experience a strong motivation to perform certain behaviours without being able to activate natural satiety mechanisms, they may revert to abnormal or stereotypical behaviours. Despite their abnormal nature, these behaviours may stimulate the release of opioids, which reinforces their repetitive occurrence (Coria-Avila et al., 2022). This raises the question of which animal then has a better welfare status: the one who developed a coping mechanisms within the situation, resulting in some level of reward, or the individual that did not (Mason & Latham, 2004). The fact that some individuals do not engage in certain abnormal behaviours therefore does not distinguish whether they are not coping, or simply are not stressed (Rushen, 1993). This remains a key critique in the study of abnormal behaviours and is currently beyond the scope of this chapter to answer. At this point, the presence of abnormal behaviours could inform us about potential shortcomings in the environment of the animal that can extend to higher levels of animal welfare (Reimert et al., 2023).

In the case of bonobo abnormal behaviour, there is reason to assume that not all behaviours have negative emotional consequences. For some of the most common abnormal behaviours, data exists that these are socially learned (poke anus: Stevens and Staes, unpublished data; social hair pluck: Brand & Marchant, 2019; regurgitation: Stevens & Wind, 2011). There is no data available that confirms whether coprophagy is socially learned in zoo-housed bonobos, although the fact that all individuals in the current sample performed this behaviour suggests that this is likely. If such behaviours are socially learned, this challenges their reliability as emotional indicator, as their presence no longer is the product of negative emotional states. Further validation against physiological or cognitive measures of emotional states could help to enhance our understanding of the emotional consequences of these abnormal behaviours. For example, one study found that coprophagy in chimpanzees actually is more similar to social behaviour rather than other abnormal behaviours (Hopper et al., 2016), and another study in capuchins found that stereotypic head twirls, but not pacing, is linked to higher levels of pessimism (Pomerantz et al., 2012b). These examples indicate that it is worthwhile to individually examine abnormal behaviour against other correlates of affect, to better understand their emotional consequences.

Nonetheless, even if abnormal behaviours have no immediate emotional consequences, this does not exclude other potential welfare implications. Abnormal behaviours that compete with other behaviours that provide positive affective experiences or behaviours that impose health effects still negatively impact an individual's welfare. Hence, abnormal behaviours, regardless of their (in)direct impact on the welfare, should be evaluated and attempts should be made to alleviate their presence. Interventions to mitigate abnormal behaviours have been proposed, and include: (1) adequate social housing, (2) enrichment, (3) increased enclosure size, (4) outdoor housing, (5) positive reinforcement training, or (6) drug therapy (Lutz & Baker, 2023). Interventions should be tailored to the specific abnormal behaviour and its aetiology, and, importantly, also to the individual(s) (Baker et al., 2009). Looking at inter-species comparison of abnormal behaviours can help to understand why certain abnormal behaviours arise within a species. This can subsequently inform possible areas of intervention. For example, comparison among captive carnivores revealed that levels of stereotypy can be explained by the natural ranging behaviour (e.g. home-range size and daily travel distances) of a species in the wild (Clubb & Mason, 2007). An order-wide study on primate abnormal behaviours in zoos is currently lacking, although smaller scale studies did identify for example that primate species with a omnivorous diet show abnormal behaviour more often than folivorous species (Mallapur, 2005), suggesting that diet is a risk factor for certain species in developing abnormal behaviours. Another study on laboratory-housed long-tailed macaques (*Macaca fascicularis*), rhesus macaques (*Macaca mulatta*) and baboons (*Papio hamadryas*) showed that, when singly-housed, both macaque species exhibited higher levels of abnormal behaviours than baboons (Lutz, 2018). This study furthermore found sex by species interactions, and for example found that baboon females were more likely to exhibit abnormal appetitive behaviours than baboon males, whereas the opposite pattern is found for macaques. Another study on stereotypic behaviour in prosimians found that individuals in the genus *Varecia* were more likely to perform stereotypic behaviours than individuals in the genus *Lemur* despite both being frugivores and having similar home ranges (Tarou et al., 2005). Individuals in the genus *Microcebus* were also more likely to engage in stereotypic behaviours, whereas internal factors such as rearing history, age or sex did not predict stereotypic behaviour (Tarou et al., 2005). This suggests that the natural behavioural biology of a species can predict whether individuals perform abnormal behaviours which can inform practitioners to develop interventions.

Looking at the current study, it becomes apparent that abnormal appetitive behaviours (e.g. coprophagy and regurgitation and reingestion) are common among zoo-housed bonobos, which are arguably the result of unsatisfied dietary provisioning, either in the way food is provided or the quality or quantity of food. Interestingly, appropriate nutrition and feeding schedules are not originally included in the list of interventions proposed by Lutz & Baker (2023), but seem promising for bonobos.

In summary, the intricate interplay between abnormal behaviours, emotional states, social learning, and coping mechanisms presents challenges in interpreting their significance. Although risk factors that contribute to the prevalence of abnormal behaviours have been identified, they do not fully explain whether these individuals are predisposed to conditions that trigger these behaviours, or if they are simply more inclined to express such behaviours. In other words, the absence of abnormal behaviours does not necessarily indicate the absence of potential underlying emotional states but does not preclude the presence of other potential welfare concerns. As a result, the welfare implications associated with the most frequently observed abnormal behaviours remain uncertain within the context of this study. It is sensible to exercise caution when drawing conclusions, and future investigations should explore additional welfare-related factors to gain a deeper understanding of the impact of abnormal behaviours on bonobo welfare.

Scratching the surface: Examining self-directed behaviours as emotional indicators in bonobos

Another set of behaviours that are commonly used to measure negative emotions are self-directed behaviours (SDBs) (Schino et al., 1991; Troisi, 1999). Similar to abnormal behaviours, SDBs are thought to be beneficial for the individual as it functions as coping mechanisms against stress and reduces the physiological stress response (Koolhaas et al., 1999). Yet, as for abnormal behaviours, not all SDBs are reliable indicators of negative emotions (Aureli & De Waal, 1997; Baker & Aureli, 1997; Leavens et al., 2004), while some may actually be associated with positive emotions (Neal & Caine, 2016). In **Chapter 5**, I set out to evaluate SDBs in bonobos while performing on two touchscreen-based cognitive tasks (Laméris et al., 2022c). These cognitive studies are presented in **Chapters 2** and **7**. Due to the nature of these tasks, I was able to collect data on when and how SDBs occurred in relation to the bonobo's task performance. Across these two experiments, I recorded four SDBs: nose wiping, rough self-scratching, gentle self-scratching, and self-touching. Interestingly, nose wiping was by far the most common

SDB, totalling 75.5% of all recorded SDBs. This contrasts previous studies with chimpanzees, where self-scratching was most common (Yamanashi & Matsuzawa, 2010). So far little is known about nose wiping, and those that report the behaviour suggest a link with edginess (Marchant & McGrew, 1996), or arousal (Kret et al., 2016). The current study provides empirical evidence that nose wiping is linked to emotional arousal as frequencies increased after the bonobos made incorrect responses during the cognitive tasks. I found additional evidence that rough self-scratching, but not gentle self-scratching, is linked to negative emotional arousal. These findings align with studies conducted on chimpanzees (Baker & Aureli, 1997), emphasising that not all SDBs reliably indicate emotional arousal. In addition to this, I found that gentle self-scratching increased when the bonobos made correct responses, which could provide preliminary evidence that gentle self-scratching is associated with positive arousal (Neal & Caine, 2016).

In attempt to better understand the potential link between SDBs and affective states, I examined the asymmetrical production of these behaviours (Leavens et al., 2001, 2004; Wagner et al., 2016). The specialisation of the left and right cerebral hemispheres contributes to differential information processing, perception, and emotional expression in vertebrates (Rogers & Andrew, 2002). Different hypotheses exist that explain this lateralisation of such behaviours. According to the 'right-hemisphere hypothesis', for example, the right hemisphere is superior in processing both negative and positive emotions (Gainotti, 1972; Levy et al., 1983), whereas the 'valence hypothesis' proposes that the right hemisphere is more specialised in processing negative emotions (Baijal & Srinivasan, 2011; Davidson et al., 1987). The 'modified valence hypothesis' proposes the potential complementary nature of the two hypotheses (Prete et al., 2015). Arousal-related hemispace effects were only observed for rough self-scratching, such that rough self-scratches were more directed to the left hemispace when the bonobo made a mistake. This left hemispace bias is consistent with previous work (Hopkins et al., 2006; Leavens et al., 2004) and would support the 'valence hypothesis' proposing that the right hemisphere is dominant for processing arousal, which then has consequences for asymmetries in cutaneous sensation (Leavens et al., 2001).

It is worth noting that there was a considerable difference between how often nose-wiping and rough self-scratching occurred. I have proposed that nose-wiping may be an expression of more low-level arousal, whereas rough self-scratching is expressed with more intense, or cumulative, arousal. This hypothesis requires future investigation, but potentially points in the direction of emotion regulation. Emotion regulation is the ability modify, inhibit, evaluate, and monitor affective states to achieve individual goals (Gross, 2015). As coping mechanism, the performance of SDBs may represent a behavioural manifestation of emotional regulation among primates, including bonobos (Clay & de Waal, 2013a). Humans show remarkable differences in their emotion regulation strategies (Bonanno & Burton, 2013), and this extends to primates (Kalin & Shelton, 2003). I indeed observed individual differences in the performance of nose-wipes and rough self-scratches. However, when I assessed if the behavioural reactivity to negative arousal can be explained by hemispheric lateralisation, I found no correlation.

Does this mean that nose wiping, and rough self-scratching are reliable indicators of negative emotional arousal? My results provide some evidence that these behaviours can be used as indicators of negative arousal, and add to an already existing body of research that find similar evidence in other species (Aureli & De Waal, 1997; Baker & Aureli, 1997; Leavens et al., 2004). However, there is also evidence that these behaviours (mostly self-scratching) may function as gestures and serve a communicative role separate from any affective meaning, as found in other ape studies (Fröhlich et al., 2016, 2019). This has not (yet) been explicitly mentioned in bonobo studies (Graham et al., 2017; Pika et al., 2005), but we should take this into consideration. Self-directed behaviours, like self-scratching, may also communicate information about the expresser’s affective state to bystanders (Laméris et al., 2020; Whitehouse et al., 2016), which can in turn elicit behaviours that benefit the expresser, such as consolation behaviour (Clay & de Waal, 2013b; Palagi & Norscia, 2011). Although these are interesting avenues for future studies, I consider that this was unlikely the case in the current study, as I trained the bonobos to complete touchscreen tests individually. Even if group members could have been in proximity, I coded whether social interactions occurred prior to the performance of self-directed behaviours and, if so, excluded these cases from analyses. It therefore seems likely that, at least in the context of cognitive challenge, nose-wiping and rough self-scratching reliably reflect negative emotional arousal, whereas preliminary evidence suggests that gentle self-scratching may be associated with positive arousal. Potential communicative and social functions can be assessed in future studies.

Evaluating bonobo emotions through human perception: A Qualitative Behavioural Assessment approach

Changes in behaviour provide valuable insights into the emotional states of animals. In **Chapters 4** and **5**, the validity of two commonly used behavioural measures for assessing negative emotions was examined. However, one drawback of behavioural measures remains the extended observation periods to gather sufficient data. To overcome this, **Chapter 6** employed Qualitative Behavioural Assessments (QBA) as an alternative approach to measure emotions in bonobos. QBA is a holistic method that focuses on the expressive qualities of animals, or their body language (Wemelsfelder et al., 2000). It involves assessing how animals respond to their environment using descriptive terms like "angry," "happy," or "agitated" (Wemelsfelder et al., 2001). QBA has been widely applied in farm animal welfare assessment due to its efficiency and validation against other behavioural and physiological indicators of emotions (Carreras et al., 2016a; Skovlund et al., 2023; Stockman et al., 2011; Wickham et al., 2015).

QBA is typically done using either Free Choice Profiling (FCP) or using Fixed List (FL). To develop a bonobo QBA, I considered it important to first examine the terminology used by human observers to describe bonobo expressivity, as this can vary across species. In a first study, I applied FCP, and in a second study I used this information to create a fixed list of descriptors. In the FCP study, I found that experts and non-experts use convergent terminology to describe the bonobos' emotional expressivity. This is perhaps not surprising as humans are limited to their own perception of emotions and the terminology associated with this (Jackson et al., 2019), which is partially driven by cultural backgrounds (Barrett et al., 2007; Mesquita & Boiger, 2014). Both groups perceived differences in emotional expressivity across the age classes (i.e., subadults and adults), although they attributed this to different QBA dimensions. Experts furthermore perceived differences in arousal between the two housing conditions.

These results provide valuable information for the development of a QBA for great apes. While agreement on the dimensions was moderate to good, the agreement on the individual fixed terms was lower. While it is not uncommon that agreement on individual terms is lower (Arena et al., 2019; Bokkers et al., 2012), I still expected higher agreement on more terms. However, this may be explained by several reasons. First, the majority of the studies applied QBA in domesticated species, either farm or pet species, with who humans share a long history with these species (Larson & Fuller, 2014). This co-evolution likely contributes to a heightened sensitivity to emotional cues (Ferretti & Papaleo, 2019; Greenall et al., 2022). Although bonobos are phylogenetically close and are physically similar to humans, and many homologies exist between our emotional expressions (Kavanagh et al., 2022), it appears that accurately recognising their emotional expressivity is challenging (Foley, 1935). I ran an online pilot-study (Laméris unpublished data) in which I asked people to rate facial expressions of bonobos on scales of valence and arousal, similar as I did with bonobo experts in Chapters 2 and 3. Here, I indeed found that people with more experience with bonobos (e.g., caretakers or researchers) are better in categorising positive and negative facial expressions compared to people with no experience (unpublished data). One aspect, which I argue is of significant importance here, is the familiarity with the individual bonobos. In the current study, the bonobo experts did not have (recent) personal experience working with these bonobos. Experts used the QBA more reliably than non-experts, which can be explained by their knowledge of bonobo behaviour. However, their agreement is not sufficient to reliably use all fixed terms in the QBA. I expect that the agreement improves when individuals are involved who directly, and repeatedly work with the bonobos. Researchers who work extensively with the bonobos, or (more importantly) caretakers are suitable candidates for this. Caretakers, for example, are arguably better in noticing subtle changes in the demeanour of the animals who they work with over different time periods. As such, QBA could be an interesting tool for repeated emotional assessment, capturing subtle changes over time which can retrospectively be associated with certain events (e.g., introduction of new individuals, social tension within the group, outdoor access, etc.). To further develop the bonobo QBA, I would therefore recommend caretakers to be included and to schedule routinely assessment.

Several methodological considerations can be considered for future studies. In this study, the video clips were 30 seconds in duration. While this falls within the range of previous research, this is at the shorter end. In making this decision, I had to balance a trade-off between video quantity and duration. I prioritised a larger video count, enabling to explore diverse factors like age class, sex, and housing conditions. For future studies, I recommend extending the length of the video clips. Additionally, although video-based QBAs are commonly done, it important to note that agreement tends to be somewhat lower compared to in-person QBA (Cooke et al., 2022). Therefore, live QBAs would be the preferred option. This approach would simultaneously address my decision to mute the videos in this study. I decided to mute the videos as they were captured within the visitor area, separated from the bonobos by a glass barrier. By muting the videos, I aimed to eliminate human interference, but simultaneously erased bonobo vocalisations as well. Humans are able to recognise emotional cues in primate vocalisations (Debracque et al., 2023), and this may help when completing a QBA. However, due to the glass barrier, softer vocalisations would not have been captured by the cameras, therefore potentially biasing the interpretation of more high arousal vocalisations. Hence, future studies should seek to enable raters to access vocalisations as this likely helps guiding their QBA scores.

I additionally set out to make methodological improvements while applying the QBA. Traditionally, QBA scores are recorded using pen and paper (Wemelsfelder et al., 2001), and consecutive studies have implemented QBAs in a similar fashion. The scores on the paper-based Visual Analogue Scale (VAS) are then manually measured and enter into datasheets. In my case, in the FCP study, the 26 participants collected 640 terms. These 640 terms were used for 20 videos, totalling 12.800 datapoints. In the Fixed List study, I had 44 participants who used 24 fixed terms to rate 40 videos, totalling an additional 42.240 datapoints. Manually measuring and entering these 55.040 datapoints is an extremely time-consuming and labour-intensive task, which is furthermore prone to human errors. A digital VAS is a suitable alternative for paper-based VAS (Couper et al., 2006). I designed a standardised digital VAS in Qualtrics (Qualtrics, Provo, Utah, UT, USA) to overcome this methodological constraint. The digital VAS proofed to be an extremely useful, reliable, and time-effective alternative to paper-based VAS and is highly recommended for future studies. Open access alternatives to Qualtrics would further increase the accessibility of digital VAS.

Another methodological constraint of QBA is the statistical processing of the data. Due to the type of data collected, especially for FCP studies, specialised statistics are needed. Originally applied in sensory studies, the majority of the FCP studies used Generalised Procrustes Analysis (GPA) to find a common structure in the data (Wemelsfelder et al., 2001). However, almost all studies that I consulted used statistical programs that are not openly accessible. Multiple Factor Analysis (MFA) was recommended to me by Dr. Lê and appeared to have statistical advantages over GPA (Abdi et al., 2013) and is freely accessible in RStudio (Lê et al., 2008; R Core Team, 2020)[2]. I have shown that MFA can be applied to analyse QBA data. In addition, in FL studies, scientists typically use PCA analyses to process their data. However, data in FL studies are collected in a k-table structure (participant x video x term), which, to the best of my knowledge, requires averaging of data across either participants or videos to then

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[2] GPA is also available in the same R package *FactoMineR* (Lê et al., 2008).

run a PCA. By doing so, valuable variation in the data is lost, which is ultimately what needs to be analysed. Dual Multi-Factor Analysis is an extension of MFA but allows for the separation of participants in groups (i.e., experts and non-experts). This enables to accommodate potential differences in correlations between these groups (Lê & Pagés, 2010), which is essentially one of the desired testing variable. DMFA therefore allows to analyse the data in its purest form, including all possible variation. The use of MFA and its extensions DMFA is advised for the abovementioned reasons, but also allowed me to have equivalent test statistics after both analyses, eventually leading to more transparent and comparable results.

Altogether, QBA could therefore be a potential interesting tool to assess emotional states in bonobos. The methodological alterations that I have made in this chapter would eventually benefit the field of QBA by making it more accessible and less time demanding. However, people may also be sceptical about the method as QBA remains based on human perception of the emotional state. Even if observers agree on what they perceive, they can collectively be wrong regarding the actual state. Previous studies have shown that QBA scores correlated with physiological and cognitive measures (Carreras et al., 2016b; Skovlund et al., 2023; Stockman et al., 2011; Wickham et al., 2015). Hence, future work on the bonobo QBA should focus on validation against behavioural, physiological and/or cognitive measures. With appropriate validation, QBA can be an important addition to welfare assessments as it provides a measure of the affective domain of an animal’s welfare.

Bonobo dynamics: Exploring affective responses and behavioural strategies during fusion events

The final study, presented in **Chapter 7**, aimed to investigate how emotions influence social information processing, its behavioural correlates and how this changes with naturally occurring events. The managed fission-fusion dynamics that were introduced at the Planckendael group at the time of this study, created the opportunity to study the affective responses of the bonobos to these social events. The response slowing task was particularly suitable in this case as it requires limited training and it only involves participants to reliably touch grey squares on the touchscreen whenever they appear

(Bethell et al., 2016). During testing sessions, low-level threatening (faces with directed gaze) and non-threatening (faces with averted gaze) stimuli were introduced in the grey squares. The idea of this paradigm is that individuals in a negative emotional state show a maladaptive cognitive freeze response to the directed gaze stimuli (measured as longer reaction times), whereas individuals with neutral or positive states disregard these stimuli and interpret it as non-threatening. The response slowing task is a relatively new paradigm (Bethell et al., 2016) and has been replicated in a handful of studies (Cronin et al., 2018; McGuire & Vonk, 2020). I tested eight bonobos during pre-fusion days, where group composition has been stable for 2-3 weeks, roughly two hours after fusion events, and on post-fusion days, one day after the fusion. I simultaneously recorded their behaviour.

The results of this chapter suggest that the managed-fusion events were accompanied by social tension, indicated by increases in agonistic and socio-sexual behaviour. Although not much is reported about the behavioural responses of fusion events in wild bonobo populations, these results align with a previous report in zoo-housed bonobos (Moscovice et al., 2015). It is important to note here that aggression was overall of low intensity, mostly consisting of (un)directed charges while physical aggression was virtually absent. Because I also observed an increase in socio-sexual interactions, it is possible that these strategies alleviated social tension and avoided the escalation of further aggression, or functioned to facilitate reconciliation (Clay & De Waal, 2015; de Waal, 1990). Accumulating evidence suggest that bonobos use socio-sexual behaviours to regulate and reduce tension across contexts (Clay & De Waal, 2015; Hohmann & Fruth, 2000; Paoli et al., 2007; Parish, 1994) and improve social bonding (Moscovice et al., 2019; Parish, 1994; Wrangham, 1993). Result from the cognitive testing further confirm that the bonobos experienced a shift in affective valence as I found response slowing during trials with the directed stimuli, suggestive of negative emotions. This was combined with increased levels of arousal, as indicated by general response speeding. The response slowing effect was relative, meaning that this effect was visible based on within-condition comparisons, but not based on between-condition comparisons. One can therefore question whether the relative response slowing effect truly indicates changes in emotional valence. However, this is why I calculated arousal-controlled ratio scores as a measure of response slowing. On top of that, human studies report associations between anxiety, arousal and response speeding (Aston-Jones & Cohen, 2005; Fox et al., 2001) which can explain why participants show response speeding when stressed. If no changes in emotional valence occurred, I would similarly expect response speeding for direct stimuli during the fusion condition, for which I did not find evidence. Hence, the combination of response slowing and speeding seems a reasonable explanation for the observed effect.

Interestingly, on the day after the fusion events, there was no cognitive or behavioural evidence for negative emotions in the bonobos, suggesting that the emotional consequences of the fusion events were short-lasting. My current behavioural and cognitive measures were collected within roughly two hours after the fusion, which was suitable to measure immediate effects. However, personal observations suggest that social tension lasted shortly, and at the end of the day most bonobos were grooming. It would have been interesting to additionally complete the response slowing task at this moment, to measure the course of the emotional impact. However, this was logistically not possible, and could furthermore intervene too much with the social activities of the bonobos.

As mentioned before, numerous studies suggest that socio-sexual behaviours reduce social tension in bonobos. However, studies regarding the emotional consequences of these behaviours are limited. Studies investigating the physiological correlates of emotions and socio-sexual behaviours find inconclusive whether these behaviours reduce physiological stress (Hohmann et al., 2009; Moscovice et al., 2015, 2019). The current study reports the first evidence of associations between cognitive measures of emotions and socio-sexual behaviours and finds that increased rates of socio-sexual behaviour are indeed linked to lowered negative emotional states (as measured as lower values of response slowing). Response slowing furthermore correlated with daily levels of social play behaviour, albeit in an opposite manner, meaning that daily levels of play behaviour were positively linked with negative emotional states. At first, this may seem surprising as many studies claim that play behaviour is a strong indicator of positive states (Ahloy-Dallaire et al., 2018; Boissy et al., 2007; Held & Špinka, 2011; Oliveira et al., 2010). However, one important detail is that I looked at adult play, for which the function may vary strongly between species (Ahloy-Dallaire et al., 2018; Marley et al., 2022; Palagi, 2023). Within bonobo fission-fusion society, play may fulfil an important role in regulating tension and in social assessment (Pellis & Iwaniuk, 2000), and therefore may include a degree of competition (Pellis & Pellis, 2017). Bonobo social play consists of a rich set of behavioural patterns (Palagi, 2006), and the detailed content of a playful interaction may determine its quality and potential function (Tacconi & Palagi, 2009). Future studies can pay attention to this level of detail to further understand, and distinguish, what types of play may be positive for bonobos, and which may not be so much.

Importantly, however, my current associations between response slowing and socio-sexual and play behaviours cannot indicate causation. Behavioural observations were conducted one to two hours prior to cognitive testing, and this may suggest a causative relationship. Yet, without baseline testing before the interactions it is challenging to examine causality. Hence, future studies should clarify whether the behaviour of the bonobos changed due to their affective state, or whether the behavioural interactions had emotional consequences.

Interestingly, and relevant to the response slowing task, a number of studies administered intranasal oxytocin, aiming to influence central concentrations (Quintana et al., 2018), and found enhanced attention to eye regions in rhesus macaques (Dal Monte et al., 2014; Ebitz et al., 2013), common marmosets (Kotani et al., 2017), and bonobos (Brooks et al., 2021), and reduced social vigilance in rhesus macaques (Ebitz et al., 2013). One study found a trend for enhanced attention in a dot-probe paradigm for direct gaze stimuli compared to averted gaze stimuli after oxytocin administration in chimpanzees (Parr et al., 2013), but another found eye avoidance in this species (Brooks et al., 2021). Circulating levels of oxytocin could therefore be a mediating factor in the affective experience of socio-sexual behaviour. Regardless of the possible modulating effect of oxytocin, bonobos are known to pay relatively more attention to the eyes (Kano et al., 2015; Mulholland et al., 2020), and one could therefore argue that the stimuli used in this paradigm are prone for such a confounding effect. In that case, I would expect to find a difference in reaction times for the stimuli in baseline conditions, for which I found no evidence. I can therefore suggest that the response slowing task is suitable to detect changes in affective states in bonobos, and that the previously observed bias for eye regions does not influence their performance in baseline conditions.

The results of this study suggest that managed fusion events may initially induce social tension. It is possible that the managed nature of these events contributed to this, as the caretakers ultimately decided which animals were switching between the subgroups, and thereby restricting the bonobos in their agency. As agency is considered an important aspect of an animal’s welfare (Englund & Cronin, 2023; Špinka, 2019), this could present an area of compromise. This is why evaluating such husbandry practices is important. I found that that on the day immediately after the fusion event, there was no evidence for negative affect or social tension suggesting that the bonobos were able to cope with the fusion event, implying that they regained part of their agency. Ideally, long-term effects of these managed fission-fusion activities should be assessed as some suggest that it may eventually be socially enriching (Classen et al., 2016; Stevens, 2020).

Methodological considerations

Throughout the chapters I have addressed various methodological limitations of the specific studies. I would additionally like to take the opportunity to discuss the application of touchscreen and eye-tracking technology to study animal emotions. These technologies have received increasing attention in recent years, and enhanced technology have greatly improved their accessibility. The advantages of these techniques include rapid and automated data processing, minimising human errors and enhancing the precision of key variables, such as reaction times. They also allow to record nuanced cognitive processes, that are otherwise not accessible. Furthermore, they present a potential solution to mitigating experimenter effects (Beran, 2012) by being automated.

These research methods, however, also came with potential drawbacks. Due to the voluntary participation of the bonobos during training and testing sessions, it is important to acknowledge the potential influence of a participant bias. At the start of my study, the bonobos at Zoo Planckendael were inexperienced with touchscreen setups, and the process of introducing and training them proved to be both time-consuming and labour intense. Despite a relatively large group of 18 individuals, only four individuals successfully completed training for the first study. This is the average of the number of participants in great ape touchscreen studies (Egelkamp & Ross, 2018), and this number only increased with additional training throughout this PhD project. Yet, it is possible that the four first participants were unknowingly selected for certain traits. Variation in personality among individuals, for example, can lead to different responses to novel objects (Weiss et al., 2015), like the touchscreen setup (Herrelko et al., 2012). At the time, I did not have personality scores for all of the individuals in Zoo Planckendael, and could not test for such effects, but it is possible that individuals with certain personality traits were more prone to participate in training sessions. Once the touchscreen training became more established in their daily routines, more individuals participated in the training and testing sessions, possibly eliminating this bias.

Additionally, touchscreen studies typically require lengthy training periods. This was especially the case for the Planckendael bonobos as they did not have previous experience working on touchscreens. Combined with several unforeseen delays that I have encountered when starting this touchscreen research, such as the move of the bonobos to a new enclosure, and the COVID-19 pandemic, it took >1 year to implement the touchscreen setup, train and test the bonobos for the first study (Chapter 2). Even with this amount of effort, I managed to include only four bonobos. This number gradually increased throughout my project, with eight individuals included in Chapter 7 (which was chronologically the second touchscreen study), and then 12 individuals in Chapter 3. In the final stage of my PhD project, from January to June 2023, I aimed to train the bonobos on a last touchscreen paradigm, being the judgement bias task. For this, I had 13 individuals that showed repeated motivation and skills to operate the touchscreens, but unfortunately none of the bonobos learned the task contingencies within the available time. In this time, I completed almost 10,000 trials across the participants (Laméris unpublished data). The judgement bias paradigm is known to require lengthy training periods, and the number of trials completed by me is not extraordinary (Roelofs et al., 2016). While a separate chapter can be dedicated to discussing why the bonobos did not learn this task, I want to take this opportunity to highlight that, although the judgement bias paradigm is currently one of the most established cognitive measures of affective states, there is still a need for more ecologically relevant, and less training intense paradigms. Similarly, although eye-tracking requires less training, it does require the participants to pay attention to the stimuli shown. While conducting these testing sessions, I aimed to minimise any potential negative impacts on the welfare of the bonobos, meaning that I did not separate the participants from groups members, as this might cause stress, and we did not call animals when they were involved in social interactions, as this would disrupt their normal social dynamics. This inherently means that many distractions were present during the eye-tracking sessions, which may have resulted in unfinished sessions or lower data quality. Nevertheless, the animal’s welfare should always be prioritised over research goals and flaws in the data collection should be acknowledged.

It depends on the research question and aim whether touchscreen and eye-tracking technology are suitable for measuring emotions and welfare in animals. These methods lend themselves for detailed studies on cognitive aspects of emotional states. However, their practicality in assessing emotions across a larger number of individuals remains dependant on the research facilities, species, and group composition. This may particularly be the case for primate studies in zoo settings where group sizes are typically smaller compared to laboratory environments (e.g., Howarth et al., 2021). In this thesis, my primary emphasis with the touchscreen and eye-tracking setups has been on exploring attention as a cognitive bias for investigating emotions. While other cognitive biases, such as memory or decision-making, also offer insights into underlying emotional states, attention bias has emerged as a novel and more easily applicable cognitive bias. Researchers can use biologically relevant stimuli to study attentional processes, which arguably reduces training time (Crump et al., 2018). Attention is able to capture a variety of fundamental aspects of cognition, including interest, motivation, novelty, as well as more subtle components such as emotional states (Wilson et al., 2023). Although attention biases may be more feasible in larger-scale studies, the use of these technologies is not feasible in every context and requires expensive materials that may not be available for every researcher. The scientific community would therefore benefit from analogous paradigms that are sensitive to measure changes in emotions (Bethell et al., 2012b; Howarth et al., 2021). This would additionally be beneficial for comparative studies with species for who touchscreen and eye-tracking technology would not work. Overall, from my perspective, I see touchscreen and eye-tracking paradigms suitable to study the fundamental aspects of animal emotions and would help to validate other more accessible measures such as behaviours, non-invasive physiological measures, or for example QBA.

Another methodological consideration for the studies in this thesis is the selection of socio-emotional stimuli. I selected positive and negative facial expressions that I judged as relevant to bonobos and had the potential to measure affect-congruent attention biases. Of course, there are many more expressions that are worth exploring, that are not limited to the negative versus positive dichotomy or to facial expressions (Kret et al., 2020). Even with the expressions selected for this thesis, it is possible that I misinterpreted the images. The Facial Action Coding System is an objective, standardised observational tool to measure facial movement in animals, which has been developed for chimpanzees (Vick et al., 2007). Nonetheless, facial expressions are dynamic, and using static images means that the static images lack crucial information. Despite that still images have proven to work in primate cognition studies, I could argue that the relevance of the stimuli would improve if short video clips were used. This could further extend to include other modalities, such as vocalisations and whole-body movements.

Scientific and welfare implications

The work presented throughout this thesis has multiple scientific and welfare implications. To start, in the general introduction I describe how emotions are an integral part of an animal's welfare and their daily lives. Emotions are extremely complex and multifaceted processes, and in this thesis I aimed to address different stages of an emotional episode. Obviously, only a select number of indicators have been addressed, and much work remains to be done to assess others. In the beginning of this thesis I advocated for a species-specific, and even an individual-specific approach when measuring animal emotions and welfare. Here in the general discussion, I would like to elaborate on this view. I will limit this reflection to comparisons between primates species, but similar arguments can be raised for comparisons with more distantly related species. Physiological and cognitive systems of emotional responses are to some extend shared across mammals (Beaulieu, 2023; Panksepp, 2011), although there is also large variation in the actual functioning or output of these systems (Browning, 2023; Mormède et al., 2007). While this thesis did not directly compare bonobos with other species, the results can be compared to existing literature. For example, when presented with different facial expressions in eye-tracking studies, both bonobos and orangutans preferentially looked at fear-related facial expressions (Chapter 3 of this thesis; van Berlo, 2022; Pritsch et al., 2017). In contrast, when tested on the dot-probe task, which measures earlier stages of attention, bonobos show an immediate attention bias for affiliative scenes (Kret et al., 2016), whereas orangutans do not (Laméris et al., 2022a), even when presented with similar stimuli. Although the lack of evidence for an implicit attention bias for socio-emotional information in orangutans can be explained by methodological reasons, it can also be explained by their behavioural biology in which rapid, and automatic, attention biases for this type of information is not needed. This is not to say that orangutans lack the neural structures for rapid attention biases, but rather that the presented stimuli did not elicit such biases, which can be specific to the species. This illustrates that appropriate testing designs should be taking into consideration that measure variables which are suitable for inter-species comparisons. Physiological indicators can also vary between species on different aspects, including baseline levels, time lag of response, and amplitude of the response (Behringer & Deschner, 2017; Browning, 2023). Similar arguments can be applied for behavioural indicators as behaviours may be shared, but individuals/species vary in their response and behavioural expressions to the same stimulus (Hill & Broom, 2009). That is, a behaviour can be performed in multiple species, but what is considered as a 'normal' rate of performing this behaviour in one species, or even in one individual (cfr the level of the individual in Figure 1.2), may be considered ‘deviating’ for another. Alternatively, certain behaviours may be performed by multiple species, but performed in different situations, or for different emotional motivations. In Chapters 4 and 5 of this thesis I illustrated that behavioural indicators of emotions or welfare may be specific to the species. Perhaps most notably, in Chapter 5, I identified nose wiping as a potential indicator of negative emotional arousal in bonobos. This behaviour, despite being reported in multiple primate species (Jordan, 1977; Marchant & McGrew, 1996; Meguerditchian & Vauclair, 2009), it is reported not as frequently as in this study (Laméris et al., 2022c).

Similar emotional indicators are frequently being used for different species. There are practical reasons why this is common practice. Nonetheless, to further the field of animal welfare science, we should be cautious with this approach. Indeed, on a theoretical level, interspecies emotion/welfare comparison can be considered problematic. Browning (2023) addresses two sources of variation that may explain why multiple conclusions can be compatible with specific observations, therefore creating a risk of underdetermination. The first source of variation refers to the values of the underlying welfare state, and the second source of variation relates to the association between the measured indicator and the actual welfare state. For example, certain species may be highly reactive to factors influencing their welfare, and show larger changes in the measured emotional indicator, while having minimal impact on the actual welfare whereas other species show the opposite. In one study seven rodent species were observed when placed in a novel environment. Here, guinea pigs (*Cavia procellus*) show high levels of inactivity remaining ‘motionless’, whereas chinchillas (*Chinchilla laniger*) were highly active, while also defecating extensively and biting different objects (Glickman & Hartz, 1964). With the degree of ‘freezing’ typically used as measure of aversion, this could suggest that the guinea pigs responded most aversively. However, the overall behavioural pattern of the chinchillas suggests that they also experienced the novel environment as aversive. This illustrates that response styles may greatly vary among species (Mason, 2010), and that such variation should be taken into consideration when assessing emotional responses.

Species-specific welfare protocols exist for some zoo-housed species and have an advantage over generic protocols as they are more likely to cover a wider range of aspects of animal welfare and are tailored to the biological needs and characteristics of the species (Tallo-Parra et al., 2023). An obvious disadvantage, however, is that developing these protocols for different species is a time-consuming task, and that the information needed is often lacking. As a result, reliable and validated indicators are missing for the majority of zoo-housed species. This is why generic welfare protocols are most commonly applied. Advantages of such generic protocols is that they provide a framework that can be applied to a wide variety which can be applied on a larger scale. This can in return reveal patterns, such as biological roots of welfare issues (Mason, 2010), or identify institutional-level welfare risk factors (Sherwen et al., 2018). Generic protocols are also flexible and allow for adaptation to the species. In other words, generic welfare protocols are currently invaluable to assess the welfare of many species. They can form the basis of a protocol from which they can be developed into more species-specific protocols when sufficient knowledge is available. This approach is increasingly being applied for zoo animals as more information is gathered. For example, Clegg et al. (2015) adapted a well-established farm animal welfare protocol for dolphins based on the biology of the species and the Husbandry Guidelines, as did Salas et al. (2018) for dorcas gazelles (*Gazella dorcas*). This is likely to benefit the welfare of the species as it allows to identify areas of poor/good welfare in more detail.

On top of a more species-specific approach, I make the case that indicators of emotions, and their application for welfare assessment, should take the individual into consideration. Indeed, there are numerous factors that can be attributed to an individual that may influence their emotional responses to events (Frijda, 2009). Some of these internal factors, that received considerable attention include, but are certainly not limited to: brain lateralisation (Leliveld et al., 2013), rearing history (Spinelli et al., 2009), personality (Asher et al., 2016), or trait affect (Polk et al., 2005). Throughout this thesis, I have attempted to address such individual factors where possible. In Chapter 4, on abnormal behaviours, I identified differences based on sex, rearing history, and personality traits. In Chapter 5, on self-directed behaviours, I examined if the behavioural reactivity differed between individual with varying lateral tendencies but found no convincing evidence. In Chapter 6, I saw that humans perceived differences in the bonobos' emotional expressivity depending on their age class. Lastly, in Chapter 2, I found individual differences in the bonobos' responses to emotional stimuli, which may reflect emotional states in itself, or possibly sex differences, whereas in Chapter 7 I did not find sex differences in affective responses to social fusion events. While these are attempts to better understand what drives the emotional experience of an individual, they still rely on the classification, or grouping, based on variance-explaining factors, e.g., mother-reared versus not mother-reared, left- versus right-handed, young versus old. Personality research was a seminal development in studying how individuals differ in their responses to situations and now receives considerable attention in the field of animal welfare science (Richter & Hintze, 2019). This resulted in an important shift towards more individual-focused welfare assessments, and enhanced awareness for unique features of individual animals. However, in practice, experimental studies often still group animals based on their personality traits (e.g., shy versus bold), therefore actually still ignoring much of this possibly important variation. Additionally, although personality measures cover a large variety of inter-individual differences, they arguably do not encompass the flexible and relational nature of emotions. As such, personality research often does not focus on the internal states that originate behavioural outputs that determine an individual's personality trait (Goursot et al., 2021).

Future directions

An individual approach to animal emotions would therefore be beneficial to advance the field of animal emotions and to ensure the individual's welfare, but this is challenged due to their complex and dynamic nature. To implement an individual-specific approach to welfare assessments, more knowledge and know-how is needed. In this regard, I propose a set of tests that measure affective responses of an individual across different contexts, similar to the primate cognitive test battery (Herrmann et al., 2007). The primate cognitive test battery measures various cognitive skills in the physical and social domain, and unravels stable individuals characteristics (Bohn et al., 2023). A series of tests that encapsulate an individual's affective profile would be an interesting and valuable source of information. This is different from affective styles, that are addressed in human research, and refer to consistent individual differences in emotional reactivity and regulation (Davidson, 1992), and is suggested for animal studies (Goursot et al., 2021). The purpose of the proposed 'affective test battery', however, is to capture variation in task performance that can be explained by affective states. Herein, it is important that results from the affective test battery reflect affect-driven variation in negative and positive contexts. The challenge, however, comes with performance during neutral contexts. On the one hand, repeatability is desired across similar situations (although this might then reflect affective styles (Davidson, 1992)). On the other hand, as long-term mood states are present in the background, and occur irrespective of specific stimuli or events, variation may reflect mood states.

For humans, such a neuropsychological test battery has been developed to cover multiple affective domains, predominantly relevant in a range of psychological disorders and evaluates aspects of emotion processing, motivation, impulsivity and social cognition (Bland et al., 2016). Comparable test batteries exist to test affective behaviours in rodents (Blanchard et al., 2003), but are invasive, can be considered unethical, and overall unfeasible with zoo animals. The neuropsychological test battery for humans can be used as a guideline of measures of interest. These can include emotional processing, such as emotional attention bias and memory. For touchscreen trained individuals, this can include the response slowing task (Bethell et al., 2016), or the dot-probe task which has been proven to be sensitive to changes in affective states (Cassidy et al., 2021). Alternatively, to circumvent technologies such as touchscreens, non-digitalised tests for attention can be applied such as looking time tasks (Bethell et al., 2012b). Startle tests are also relatively simple in which subjects are exposed to sudden acoustic or visual stimuli, and in which the degree of attention paid to the stimulus is modulated by affective states (Grillon & Baas, 2003; Roelofs, 2017). Variation in behavioural responses to positive or negative audio sounds in playback experiments may also capture emotional processing (Smit et al., 2019). Attentional scope is suggested as a potential novel indicator of emotional state in animals which can capture positive affect (Hamlaoui et al., 2022). Additionally, positive affect is suggested to allow flexibility and creativity (Fredrickson, 1998, 2003), which can be measured relatively easily in animals with, for example, reversal learning tasks (Dickstein et al., 2010). Any of these measures can be complemented by other behavioural or physiological measures.

However, this still requires extensive testing. How can practitioners already incorporate a more species- or individual-specific approach to assessing the welfare of animals? Starting with a species-specific approach, as mentioned before knowledge of the species will be essential. As proven in previous studies, the natural behavioural biology of a species may determine the degree in which it develops abnormal behaviours (Clubb & Mason, 2007). Knowledge about the biology of the species is crucial for practitioners at different positions. For example, designers and architects responsible for the enclosure design determine the external living conditions of captive animals, nutritionists determine their diet. On a daily base, caretakers are responsible for the care and welfare of their animals. Because of the daily interaction with their animals, caretakers already inadvertently keep track and discuss changes in the welfare or emotional states of their animals. These informal welfare assessments can result in welfare interventions. For instance, when an animal exhibits signs of lethargy or anorexia, adjustments to their diet may be made, and veterinary interventions may take place. Even more subtle daily changes in the demeanour of animal are recognised by caretakers (pers. obs. Laméris). The role of caretakers in welfare assessments is therefore vital, as they are able to identify short- and long-term deviations from the ‘normal’ or baseline status of an animal. As such, caretaker ratings allow for a more individual welfare assessment. The day-to-day knowledge of caretakers about the state of an animal can be a valuable source of information regarding their emotions or welfare, sometimes even more than lengthy behavioural observations (Whitham & Wielebnowski, 2009). Quantifying and validating such assessments is needed to make evidence-based welfare recommendations. Caretaker ratings are increasingly included in welfare assessment protocols (Whitham & Wielebnowski, 2009). Caretaker ratings of bottlenose dolphins’ willingness to participate in positive reinforcement training, for example, showed a significant decrease up to three days before the veterinarian diagnosed a decline in the health status (Clegg et al., 2019). QBA is likewise proving to be a promising tool to assess the emotional state of an animal and is increasingly applied in zoo-settings (e.g., Skovlund et al., 2023). Of course, single indicators cannot encompass the full range of welfare aspects, and emotional indicators should be combined with other well-established indicators. The study of Yon et al. (2019) nicely illustrates how species-specific behavioural indicators can be combined with emotional indicators (i.e., QBA) for elephants. This may be a time- and resource-demanding task to achieve for more species, but one that is needed if we want to ensure the welfare of animals under human care.

Conclusions

To conclude this thesis, I would like to go back to the framework of an emotional episode. Throughout the chapters of this thesis, I have gathered results that contribute to this model and that can be used to inform welfare assessment and practices in bonobos. Appraisal is the first process of an emotional episode in which external or internal stimuli are evaluated, and which is closely linked to attention. Little is known about what drives attention in bonobos, and the efforts of this thesis have contributed to our knowledge by showing that bonobo attention is determined by the relevance of the stimulus (i.e., survival-related information in Chapter 2), but also by outcome probability (i.e., potential social threats in Chapter 7). I also found that social context modulates attention, potentially operating at distinct stages of attention processing (i.e., early processing for play faces in Chapter 2, and late processing for bared-teeth faces in Chapter 3).

Secondly, I was also able to provide novel insights that are linked to the core of an emotion, unveiling that bonobos adapt their social information processing according to their affective state. Negative affect, as demonstrated in Chapter 7, altered how individuals processed potentially threatening information. In Chapter 2, I found individual differences in the degree to which bonobos have biased attention for play faces, which might be driven by their underlying affective states. While investigating affect-congruent attention biases in Chapter 3, I found no substantial impact of emotion priming. Nevertheless, I detected initial indications that viewing valenced scenes induces changes in the autonomic nervous system, evidenced by pupil size changes, and pointing at possible emotional responses.

Finally, I examined potential behavioural manifestations of emotional episodes. While the behavioural outputs of an emotional episode are countless, this thesis focused on the more traditional, and most commonly used behaviours that have been linked with affective states. Although a direct connection between abnormal behaviour and affective states was not established (Chapter 4), my evaluation across multiple zoological institutions introduced nuanced considerations for its use to assess bonobo emotions and welfare. Additionally, in Chapter 5 I identified two previously unvalidated behaviours associated with emotional arousal and showed that these may reflect species-specific patterns. In Chapter 6, I attempted to develop a Qualitative Behavioural Assessment as a promising novel tool to monitor emotional states and welfare in bonobos. This chapter considered the holistic nature of animal behaviour, and therefore did not focus on isolated behavioural events. Finally, in Chapter 7, I found associations between negative affective states and socio-sexual, and play behaviour, possibly tapping into the emotional consequences of these behaviours.

I can also conclude several welfare considerations. While the behavioural output of an emotional episode is arguably most accessible, these measures should also be carefully examined to ensure that they reliably reflect the targeted state. Traditional behavioural welfare indicators did not unconditionally appear suitable to use for bonobos, as illustrated in the case of most abnormal behaviours in Chapter 4. Some self-directed behaviours can be used to assess immediate emotional arousal, and can be included in welfare assessments (Chapter 5). Although the QBA presented in Chapter 6 should be further developed and validated against other behavioural, physiological, or cognitive measures, this approach has potential to regularly monitor the affective welfare state of bonobos under human care. QBA may be especially suitable to assess the affective domain of animal welfare, one that is currently often overlooked. Cognitive measures may also inform about the welfare of bonobos, but are arguably less accessible.

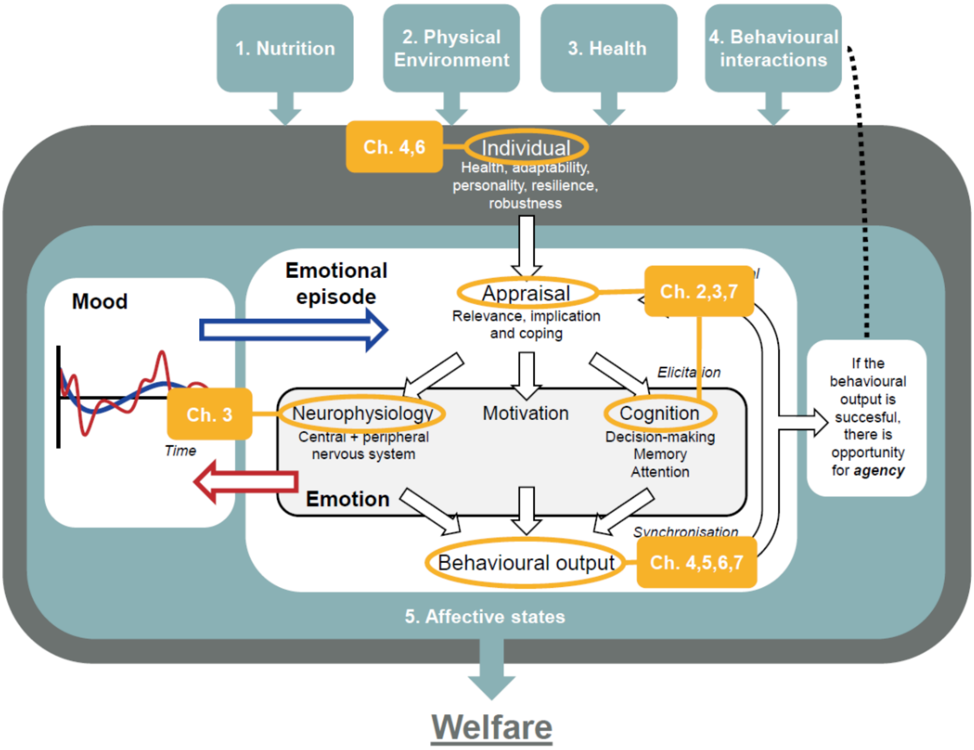
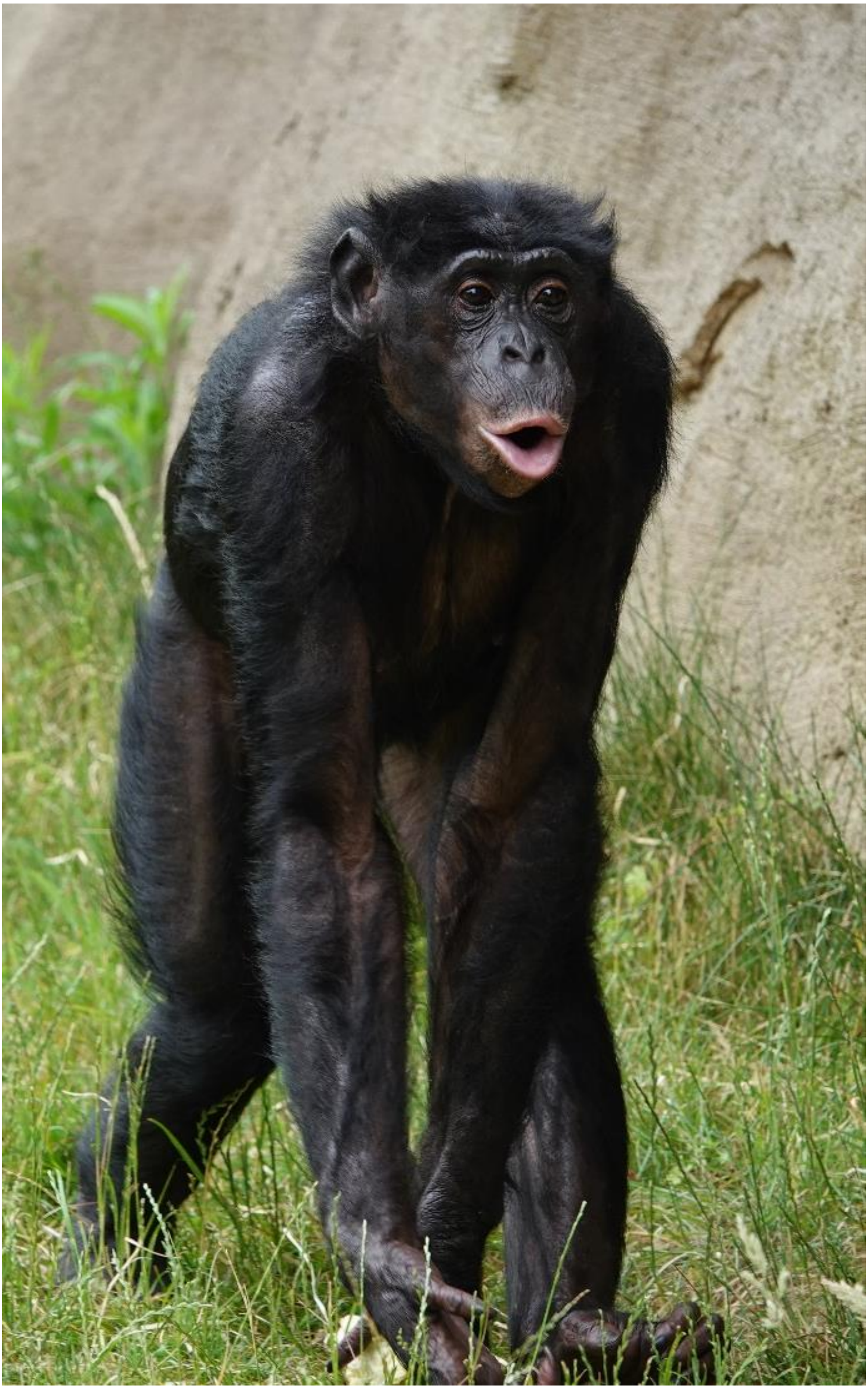


Figure 8.1: An overview of the different chapters of this thesis integrated in an emotional episode and the Five Domains model.

In Chapter 7, I monitored the affective responses of the bonobos to a common husbandry routine for zoo-housed bonobos. This provided valuable grounds to conclude that managed fission-fusion practices do not impair the welfare of the bonobos and could, on the long-term, be enriching by providing opportunities for natural social interactions.

Bonobos are emotionally complex animals and in this thesis I have attempted to provide a glimpse into their emotional lives with the ultimate goal to better understand them as a species and to provide knowledge to guide evidence-based welfare practices. The studies presented here merely scratch the surface of what is to be investigated, and it is my sincerest hope that they provide guidance for future studies to better understand these animals.



Supplements

Chapter 2

Social and non-social stimuli alter the performance of bonobos during a pictorial emotional Stroop task

Methods

Training phase 1: Habituation and shaping

None of the bonobos in this group had previous experience with touchscreen tasks, except for Hortense and Zamba who were exposed to touchscreen before in another zoo, but never participated in training sessions (Kret et al., 2016). Therefore, we first had to train the bonobos to work on the touchscreen. Between July 2019 and March 2020 we habituated the bonobos to the touchscreen setup and shaped their touching behaviour. Initially, we presented a black circle that was either moving or changing in size to attract the attention of the bonobos. At this stage, each response registered by the touchscreen was rewarded as described above. Once a bonobo was conditioned on touching the screen and receiving the reward, we gradually reduced the size of the circle until the bonobo could reliably touch a 2.96 cm x 2.96 cm circle. The smaller targets appeared randomly in one of four locations. We trained subjects on this task until they reached a >70% accuracy score over +20 trials during a day. Correct responses were considered when the bonobos touched the target within a 5000 ms timeframe. Not all responses were immediately registered by the hardware, resulting in the bonobos making multiple touches until the response was registered. As long as the bonobo kept touching the target, and the response was ultimately registered, we included these responses as correct. Since this was their first experience working on touchscreens, we reasoned that this facilitated the learning process of the bonobos.

Training phase 2: Colour discrimination

Eight bonobos showed consistent interest in the touchscreen and completed training phase 1. Between February and August 2020 these bonobos participated in the second training phase which consisted of a colour discrimination task. We presented two stimuli on a white screen which consisted of natural scenes. These stimuli appeared at two out of the four possible locations. The stimuli were always identical within each trial, except for the border colour. One of the stimuli had a blue border (RGB 0, 0, 254) and the other had a red border (RGB 254, 0, 0). We initially pseudo-randomly assigned the subjects to one of the two colours. However, we soon noticed that, because we performed all touchscreen sessions in social settings, individuals would switch between each other within one training session, or that they would look how one bonobo was working on the screen. Even if the researcher could manually switch to the training program with the correct border colour, we reasoned that social learning could interfere with the training. Therefore, we decided to train all bonobos to touch stimuli with a red border, which is from here considered the target. Stimuli with a blue border were considered as the distractor. As the bonobos progressed with their training, they also learned to sit more independently in front of the screen. In March 2020, we paused the training in response to the COVID-19 pandemic. When analysing these training data, we noticed that in the sessions prior to this, the bonobos did not make substantial progress. Therefore, we decided to adapt the stimuli to facilitate the learning process. Mid-June 2020, when we had limited access to the bonobos again, we resumed the training following a COVID-protocol, using full-coloured squares in either red or blue. Note that these were not the same stimuli as used in Experiment 1. We tested each subject until they reached an accuracy score of >70% in 1-2 sessions (i.e., 24-48 trials) per day, over two consecutive days.

Training phase 3: Transfer task

Five of the eight bonobos completed training phase 2 and continued to phase 3. At this stage, we included a start target, which was the black circle on which the bonobos were trained in phase 1. Following Allritz et al. (2016), the start target was followed by a 500 ms delay after which two matched stimuli would appear, again one with a blue and one with a red border. We selected 50 greyscale images of random human objects that were considered neutral to the bonobos. The two stimuli would appear simultaneously on the screen in two, out of four, random locations. At this stage, bonobos were required to achieve an >80% accuracy score in 1-2 sessions (i.e., 24-48 trials) per day, over two consecutive days. One female bonobo was transferred to another zoo before she could complete this training. The remaining four bonobos completed training phase 3 between July 2020 and September 2020.

Figure S2.1: View of the touchscreen as seen from the bonobos' perspective

Results

Training phase 1, 2 and 3

Eight bonobos, three females and five males, completed the habituation and shaping training phase on the touchscreens. On average, it required them 441.3 trials (range = 251-641) to reach the inclusion criterion.

Of these eight bonobos, five bonobos (two females and three males) completed the colour discrimination training within an average of 731.6 trials (range = 446-1176). One juvenile male was excluded because he did not reach the inclusion criterion (373 trials), another adult male was not included because he would not come when other bonobos were around (146 trials), despite efforts to create settings for him to join sessions. The last female that was excluded at this stage lost interest in the training sessions (146 trials).

Of the five bonobos that continued to the training phase 3, four individuals, one female and three males, completed this training in 892.3 trials (range = 587-1516). The one female that did not complete this training transferred to another zoo before she reached the inclusion (134 trials).

Table S2.1: Mean luminance and colour hue values and test statistics

	Luminance [a]		Hue [b]	
	Mean	SD	Mean	SD
Experiment 2				
Negative	93.049	16.527	95.060	16.891
Neutral	101.340	6.071	102.881	7.180
Positive	98.999	12.347	101.118	10.952
Anova statistics	$F_{2, 21} = 0.948$, $P = 0.403$		$F_{2, 21} = 0.884$, $P = 0.428$	
Experiment 3				
Negative	139.945	34.693	142.118	42.729
Neutral	167.223	7.315	133.658	6.734
Positive	151.591	12.951	135.046	13.822
Anova statistics	$F_{2, 21} = 3.155$, $P = 0.063$		$F_{2, 21} = 0.240$, $P = 0.789$	

Luminance and Hue values are taken from Adobe Photoshop version 21.2.2, and are calculated as: [a] the luminous intensity per unit area of light travelling in a given direction, and [b] shift in the colour, respectively.

Table S2.2: The total number of trials completed by all subjects in each experiment and number of trials excluded during data filtering

	Accuracy			**Reaction time [a]**		
	Trials completed	Trials excluded [b]	Trials excluded (%)	Trials completed	Trials excluded [b]	Trials excluded (%)
Experiment 1 (all)	1410	319	22.6%	952	208	21.8%
Busira	*370*	116	37.8%	245	53	21.6%
Habari	*347*	107	33.0%	291	102	35.1%
Mokonzi	*344*	48	15.3%	203	22	10.8%
Zamba	*349*	48	14.5%	213	31	14.6%
Experiment 2 (all)	1741	386	22.2%	1448	427	29.5%
Busira	*451*	134	36.4%	326	110	33.7%
Habari	*441*	145	39.2%	481	180	37.4%
Mokonzi	*430*	43	10.5%	329	64	19.5%
Zamba	*419*	64	16.0%	312	73	23.4%
Experiment 3 (all)	1754	319	18.2%	1375	330	24.0%
Busira	*428*	107	26.9%	311	91	29.3%
Habari	*445*	104	23.5%	431	154	35.7%
Mokonzi	*440*	43	10.3%	358	45	12.6%
Zamba	*441*	65	15.4%	275	40	14.5%

[a] Reaction time data only included correct trials.

[b] This represents the number of trials excluded before analyses, e.g.: not filmed (51 trials for Experiment 2), a bonobo other than the subject touching the screen, not attending the screen, the screen did not immediately register the response, outliers with extreme low reaction times (< 250 ms) and reaction times that exceeded the median plus or minus 2.5 times the median absolute deviation.

Table S2.3: Subject level model output for Experiment 1 (dependent variable: Accuracy)

Busira				**Habari**			
Chi square test	χ^2	df	*P*	*Chi square test*	χ^2	df	*P*
	22.651	2	**< 0.001**		23.432	2	**< 0.001**
Post hoc	*t* value	df	*P*	*Post hoc*	*t* value	df	*P*
Control – Congruent	4.605	249	**< 0.001**	Control – Congruent	4.341	235	**< 0.001**
Control – Incongruent	1.354	249	0.367	Control – Incongruent	2.396	235	**0.046**
Congruent – Incongruent	-2.894	249	**0.012**	Congruent – Incongruent	-3.084	235	**0.007**
Mokonzi				**Zamba**			
Chi square test	χ^2	df	*P*	*Chi square test*	χ^2	df	*P*
	2.890	2	0.236		4.406	2	0.111
Post hoc	*t* value	df	*P*	*Post hoc*	*t* value	df	*P*
Control – Congruent	1.699	291	0.207	Control – Congruent	2.042	296	0.104
Control – Incongruent	0.669	291	0.782	Control – Incongruent	0.432	296	0.902
Congruent – Incongruent	-0.934	291	0.619	Congruent – Incongruent	-1.493	296	0.296

Table S2.4: Subject level model output for Experiment 1 (dependent variable: Reaction time)

Busira				**Habari**			
Chi square test	χ^2	df	*P*	*Chi square test*	χ^2	df	*P*
	1.495	2	0.473		0.800	2	0.670
Post hoc	*t* value	df	*P*	*Post hoc*	*t* value	df	*P*
Control – Congruent	1.222	186	0.442	Control – Congruent	0.888	183	0.649
Control – Incongruent	0.354	186	0.933	Control – Incongruent	0.203	183	0.978
Congruent – Incongruent	-0.785	186	0.713	Congruent – Incongruent	-0.660	183	0.787
Mokonzi				**Zamba**			
Chi square test	χ^2	df	*P*	*Chi square test*	χ^2	df	*P*
	0.815	2	0.665		1.934	2	0.380
Post hoc	*t* value	df	*P*	*Post hoc*	*t* value	df	*P*
Control – Congruent	0.347	175	0.936	Control – Congruent	1.162	176	0.478
Control – Incongruent	0.903	175	0.639	Control – Incongruent	-0.272	176	0.960
Congruent – Incongruent	0.473	175	0.884	Congruent – Incongruent	-1.305	176	0.395

Table S2.5: Subject level model output for Experiment 2 (dependent variable: Accuracy)

	Busira				**Habari**		
Chi square test	χ^2	df	*P*	*Chi square test*	χ^2	df	*P*
	1.307	3	0.727		1.759	3	0.624
Post hoc	*t* value	df	*P*	*Post hoc*	*t* value	df	*P*
Blank – Negative	0.553	311	0.581	Blank – Negative	-0.001	290	1.000
Blank – Neutral	1.141	311	0.255	Blank – Neutral	0.114	290	0.999
Blank – Positive	0.487	311	0.627	Blank – Positive	0.995	290	0.752
Negative – Neutral	0.557	311	0.570	Negative – Neutral	0.001	290	1.000
Negative – Positive	-0.059	311	0.953	Negative – Positive	0.001	290	1.000
Neutral – Positive	-0.613	311	0.541	Neutral – Positive	1.091	290	0.695
	Mokonzi				**Zamba**		
Chi square test	χ^2	df	*P*	*Chi square test*	χ^2	df	*P*
	2.106	3	0.551		4.449	3	0.217
Post hoc	*t* value	df	*P*	*Post hoc*	*t* value	df	*P*
Blank – Negative	0.355	381	0.985	Blank – Negative	1.374	349	0.517
Blank – Neutral	-0.670	381	0.908	Blank – Neutral	1.317	349	0.553
Blank – Positive	0.874	381	0.818	Blank – Positive	2.045	349	0.174
Negative – Neutral	-0.941	381	0.783	Negative – Neutral	-0.046	349	1.000
Negative – Positive	0.477	381	0.964	Negative – Positive	0.638	349	0.920
Neutral – Positive	1.407	381	0.496	Neutral – Positive	0.679	349	0.905

Table S2.6: Subject level model output for Experiment 2 (dependent variable: Reaction time)

	Busira				**Habari**		
Chi square test	χ^2	df	*P*	*Chi square test*	χ^2	df	*P*
	0.649	3	0.885		18.078	3	**< 0.001**
Post hoc	*t* value	df	*P*	*Post hoc*	*t* value	df	*P*
Blank – Negative	0.623	209	0.534	Blank – Negative	-2.347	294	**0.090**
Blank – Neutral	0.151	209	0.880	Blank – Neutral	-1.272	294	0.581
Blank – Positive	0.662	209	0.508	Blank – Positive	-4.116	294	**< 0.001**
Negative – Neutral	-0.432	209	0.666	Negative – Neutral	1.020	294	0.738
Negative – Positive	0.029	209	0.977	Negative – Positive	-1.576	294	0.394
Neutral – Positive	0.462	209	0.645	Neutral – Positive	-2.637	294	**0.043**
	Mokonzi				**Zamba**		
Chi square test	χ^2	df	*P*	*Chi square test*	χ^2	df	*P*
	6.543	3	**0.088**		14.473	3	**0.002**
Post hoc	*t* value	df	*P*	*Post hoc*	*t* value	df	*P*
Blank – Negative	0.333	258	0.987	Blank – Negative	1.504	232	0.437
Blank – Neutral	1.179	258	0.641	Blank – Neutral	3.732	232	**0.001**
Blank – Positive	-0.746	258	0.878	Blank – Positive	0.807	232	0.851
Negative – Neutral	1.099	258	0.690	Negative – Neutral	2.072	232	0.166
Negative – Positive	-1.392	258	0.506	Negative – Positive	-0.592	232	0.935
Neutral – Positive	-2.537	258	**0.057**	Neutral – Positive	-2.613	232	**0.047**

Table S2.7: Subject level model output for Experiment 3 (dependent variable: Accuracy)

	Busira				**Habari**		
Chi square test	χ^2	df	*P*	*Chi square test*	χ^2	df	*P*
	17.014	3	**< 0.001**		8.232	3	**0.041**
Post hoc	*t* value	df	*P*	*Post hoc*	*t* value	df	*P*
Blank – Negative	3.915	315	**0.001**	Blank – Negative	0.373	335	0.982
Blank – Neutral	2.922	315	**0.019**	Blank – Neutral	2.170	335	0.134
Blank – Positive	1.714	315	0.318	Blank – Positive	-0.283	335	0.992
Negative – Neutral	-1.016	315	0.740	Negative – Neutral	1.708	335	0.321
Negative – Positive	-2.321	315	**0.096**	Negative – Positive	-0.588	335	0.936
Neutral – Positive	-1.281	315	0.576	Neutral – Positive	-1.970	335	0.201
	Mokonzi				**Zamba**		
Chi square test	χ^2	df	*P*	*Chi square test*	χ^2	df	*P*
	11.479	3	**0.009**		12.341	3	**0.006**
Post hoc	*t* value	df	*P*	*Post hoc*	*t* value	df	*P*
Blank – Negative	2.207	391	0.123	Blank – Negative	0.432	370	0.973
Blank – Neutral	3.32	391	**< 0.001**	Blank – Neutral	3.090	370	**0.012**
Blank – Positive	2.575	391	**0.050**	Blank – Positive	2.220	370	0.120
Negative – Neutral	1.133	391	0.669	Negative – Neutral	2.489	370	**0.063**
Negative – Positive	0.394	391	0.979	Negative – Positive	1.665	370	0.344
Neutral – Positive	-0.734	391	0.884	Neutral – Positive	-0.875	370	0.818

Table S2.8: Subject level model output for Experiment 3 (dependent variable: Reaction time)

	Busira				**Habari**		
Chi square test	χ^2	df	*P*	*Chi square test*	χ^2	df	*P*
	6.775	3	**0.079**		13.296	3	**0.004**
Post hoc	*t* value	df	*P*	*Post hoc*	*t* value	df	*P*
Blank – Negative	-1.505	213	0.436	Blank – Negative	-2.741	270	**0.033**
Blank – Neutral	-0.552	213	0.946	Blank – Neutral	-3.189	270	**0.009**
Blank – Positive	1.268	213	0.584	Blank – Positive	-2.413	270	**0.077**
Negative – Neutral	0.854	213	0.829	Negative – Neutral	-0.498	270	0.960
Negative – Positive	2.534	213	**0.058**	Negative – Positive	0.277	270	0.993
Neutral – Positive	1.642	213	0.358	Neutral – Positive	0.763	270	0.871
	Mokonzi				**Zamba**		
Chi square test	χ^2	df	*P*	*Chi square test*	χ^2	df	*P*
	17.783	3	**< 0.001**		4.456	3	0.216
Post hoc	*t* value	df	*P*	*Post hoc*	*t* value	df	*P*
Blank – Negative	-3.835	306	**0.001**	Blank – Negative	-2.005	228	0.189
Blank – Neutral	-2.808	306	**0.027**	Blank – Neutral	-1.387	228	0.509
Blank – Positive	-2.694	306	**0.037**	Blank – Positive	-0.929	228	0.789
Negative – Neutral	0.834	306	0.839	Negative – Neutral	0.395	228	0.979
Negative – Positive	1.017	306	0.740	Negative – Positive	0.924	228	0.792
Neutral – Positive	0.158	306	0.999	Neutral – Positive	0.466	228	0.966

Chapter 3

Affect-congruent attention biases in bonobos: Investigating the impact of emotional priming

Table S3.1: Average luminance values (± SD) for the primer videos

	Bonobo	**Human**
Neutral	0.74 (± 0.08)	0.69 (± 0.06)
Positive	0.69 (± 0.03)	0.72 (± 0.06)
Negative	0.64 (± 0.07)	0.72 (± 0.04)

Table S3.2: Average valence and arousal values (± SD) for the facial expression stimuli based on expert ratings

	Valence	**Arousal**
Neutral	4.0 (± 0.00)	1.6 (± 0.15)
Positive	5.8 (± 0.54)	4.9 (± 0.99)
Negative	1.5 (±0.23)	6.0 (± 0.44)

Note: Valence ratings are given on a 7-point Likert scale ranging from 'extremely negative' to 'extremely positive', where a score of 4 equal 'neutral'. Arousal ratings are given on a 7-point Likert scale ranging from 'not intense at all' to 'very intense'

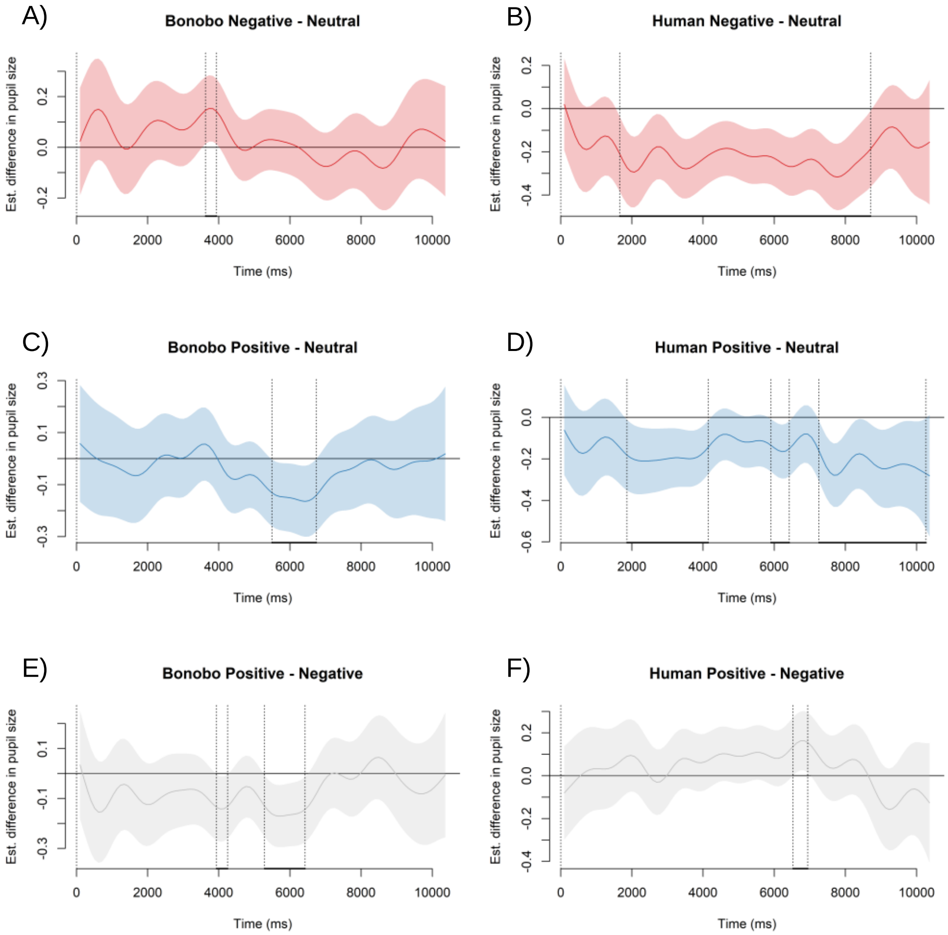


Figure S3.1: Estimated differences in pupil size depending on primer valence and model. Significant differences are indicated between the dotted lines

Table S3.3: Bayesian estimates of the different models assessing attention biases towards emotional stimuli based on primer videos. Effects are highlighted in bold

Model: General emotion bias[1]				
Primer valence	*Primer model*	*Median*	*L-89%*	*U-89%*
Neutral	Bonobo	0.444	0.363	0.525
Negative	**Bonobo**	**0.398**	**0.317**	**0.475**
Positive	**Bonobo**	**0.406**	**0.326**	**0.489**
Neutral	Human	0.428	0.353	0.512
Negative	**Human**	**0.388**	**0.312**	**0.469**
Positive	Human	0.424	0.344	0.510
Model: Negativity bias[2]				
Primer valence	*Primer model*	*Median*	*L-89%*	*U-89%*
Neutral	**Bonobo**	**0.385**	**0.276**	**0.497**
Negative	**Bonobo**	**0.423**	**0.308**	**0.541**
Positive	**Bonobo**	**0.425**	**0.310**	**0.547**
Neutral	**Human**	**0.419**	**0.309**	**0.531**
Negative	**Human**	**0.460**	**0.346**	**0.581**
Positive	**Human**	**0.389**	**0.270**	**0.498**
Model: Positivity bias[2]				
Primer valence	*Primer model*	*Median*	*L-89%*	*U-89%*
Neutral	Bonobo	0.296	0.223	0.362
Negative	Bonobo	0.301	0.237	0.366
Positive	Bonobo	0.293	0.227	0.359
Neutral	Human	0.267	0.205	0.329
Negative	Human	0.251	0.194	0.311
Positive	Human	0.315	0.246	0.382

[1] *Threshold for an emotion bias is if median < 0.5 and 89% CrI does not involve 0.5*

[2] *Threshold for a negativity and positivity bias is if median > 0.25 and 89% CrI does not involve 0.25*

Table S3.4: Summaries for the Bayesian models assessing attention biases. Effects are highlighted in bold

Model: General emotion bias	Estimate	Est. error	L-89%	U-89%	R^	Bulk ESS	Tail ESS	pd
Intercept	-0.08	0.23	-0.46	0.29	1.00	6102	7719	63.93%
Negative [Neutral]	0.12	0.17	-0.14	0.38	1.00	4482	5589	77.78%
Positive [Neutral]	-0.08	0.17	-0.33	0.19	1.00	4625	5334	69.11%
Human	-0.01	0.08	-0.15	0.13	1.00	5874	7958	55.33%
Trial order	**-0.16**	**0.05**	**-0.24**	**-0.08**	**1.00**	**5693**	**7977**	**99.87%**
Data quality primer	0.09	0.21	-0.25	0.43	1.00	7610	8903	65.63%
Negative [Neutral] x Human [Bonobo]	-0.06	0.12	-0.25	0.13	1.00	4877	7174	68.50%
Positive [Neutral] x Human [Bonobo]	-0.03	0.12	-0.22	0.16	1.00	5413	7597	59.12%
Random effects								
Primer ID	0.28	0.13	0.13	0.52	1.00	2635	4375	
Subject	0.19	0.08	0.09	0.33	1.00	2461	2989	
Subject/SessionID	0.08	0.06	0.01	0.19	1.00	1307	2280	
Subject/SessionID/TrialID	0.71	0.04	0.64	0.78	1.00	3448	6205	

Model: Negativity bias	Estimate	Est. error	L-89%	U-89%	R^	Bulk_ESS	Tail_ESS	pd
Intercept	-0.53	0.27	-0.96	-0.11	1.00	5343	7020	97.48%
Negative [Neutral]	-0.10	0.24	-0.49	0.28	1.00	3902	5581	68.28%
Positive [Neutral]	0.05	0.25	-0.34	0.44	1.00	3658	4872	58.46%
Human	0.05	0.09	-0.09	0.18	1.00	5149	7097	71.06%
Trial order	**0.14**	**0.05**	**0.06**	**0.22**	**1.00**	**5228**	**7737**	**99.60%**
Data quality	-0.15	0.22	-0.50	0.19	1.00	5992	8361	75.95%
Negative [Neutral] x Human [Bonobo]	0.09	0.12	-0.10	0.28	1.00	4462	6697	77.62%
Positive [Neutral] x Human [Bonobo]	0.10	0.12	-0.08	0.29	1.00	4364	7254	80.42%
Random effects								
Primer ID	0.48	0.18	0.28	0.80	1.00	4107	5557	
Subject	0.13	0.08	0.02	0.26	1.00	1464	2528	
Subject/SessionID	0.11	0.08	0.01	0.25	1.01	845	1796	
Subject/SessionID/TrialID	0.72	0.04	0.65	0.78	1.00	3149	5552	

Model: Positivity bias	Estimate	Est. error	L-89%	U-89%	R^	Bulk_ESS	Tail_ESS	pd
Intercept	-0.81	0.24	-1.18	-0.43	1.00	5964	7369	99.98%
Negative [Neutral]	-0.00	0.16	-0.25	0.24	1.00	4434	6119	50.48%
Positive [Neutral]	0.02	0.16	-0.22	0.27	1.00	4051	5629	55.48%
Human	-0.10	0.09	-0.24	0.04	1.00	5072	8112	85.89%
Trial order	0.01	0.05	-0.08	0.09	1.00	5193	7251	54.05%
Data quality	-0.09	0.22	-0.44	0.27	1.00	7135	9143	64.40%
Negative [Neutral] x Human [Bonobo]	-0.04	0.12	-0.24	0.15	1.00	4343	7186	62.98%
Positive [Neutral] x Human [Bonobo]	-0.16	0.12	-0.35	0.04	1.00	4415	6944	90.05%
Random effects								
Primer ID	0.26	0.12	0.12	0.49	1.00	2567	3203	
Subject	0.15	0.08	0.03	0.29	1.00	1781	2186	
Subject/SessionID	0.10	0.07	0.01	0.22	1.00	873	1860	
Subject/SessionID/TrialID	0.69	0.04	0.62	0.76	1.00	3181	5409	

Table S3.5: Post hoc contrasts using estimated marginal means for the model testing a general emotion bias

Model: General emotion bias Contrast	Primer model	Median	MAD	89% CrI	pd
Neutral – Negative	Bonobo	0.19	0.25	[-0.26, 0.63]	77.48%
Neutral – Positive	Bonobo	0.16	0.27	[-0.29, 0.61]	72.38%
Negative – Positive	Bonobo	-0.03	0.26	[-0.51, 0.40]	55.23%
Neutral – Negative	Human	0.16	0.25	[-0.30, 0.59]	74.08%
Neutral – Positive	Human	0.02	0.26	[-0.43, 0.47]	52.76%
Negative – Positive	Human	-0.15	0.27	[-0.59, 0.31]	71.38%
Model: Negativity bias Contrast	Primer model	Median	MAD	89% CrI	pd
Neutral – Negative	Bonobo	-0.16	0.39	[-0.83, 0.51]	65.72%
Neutral – Positive	Bonobo	-0.16	0.39	[-0.83, 0.50]	66.22%
Negative – Positive	Bonobo	-0.07	0.39	[-0.69, 0.65]	50.77%
Neutral – Negative	Human	-0.17	0.39	[-0.83, 0.50]	67.26%
Neutral – Positive	Human	0.11	0.38	[-0.51, 0.82]	62.24%
Negative – Positive	Human	0.29	0.69	[-0.36, 0.97]	77.50%
Model: Positivity bias Contrast	Primer model	Median	MAD	89% CrI	pd
Neutral – Negative	Bonobo	-0.03	0.25	[-0.43, 0.40]	54.56%
Neutral – Positive	Bonobo	0.02	0.25	[-0.43, 0.45]	52.38%
Negative – Positive	Bonobo	0.04	0.25	[-0.42, 0.45]	56.48%
Neutral – Negative	Human	0.09	0.25	[-0.33, 0.53]	63.72%
Neutral – Positive	Human	-0.23	0.25	[-0.67, 0.19]	81.97%
Negative – Positive	Human	-0.32	0.25	[-0.76, 0.11]	88.77%

Chapter 4

The influence of sex, rearing history, and personality on abnormal behaviour in zoo-housed bonobos (*Pan paniscus*)

Table S4.1: Variable loadings dimension reduction personality model (from Staes et al., 2016)

	Factor				
Variable	Sociability	Openness	Boldness	Activity	*h²*
Grooming Received	**0.83**	-0.03	-0.03	0.20	0.74
Grooming Density Received	**0.76**	-0.07	-0.12	0.14	0.68
Number of Neighbours	**0.71**	0.13	0.13	-0.04	0.54
Grooming Given	**0.67**	0.18	0.13	0.39	0.69
Latency to Approach Puzzle	**-0.66**	**-0.49**	0.02	0.24	0.79
Grooming Density Given	**0.64**	0.20	0.33	**0.42**	0.84
Latency to Approach Durian	**-0.64**	-0.23	-0.01	0.14	0.47
Grooming Diversity Index	**0.53**	0.12	0.19	0.36	0.67
Autogroom	**-0.48**	0.10	-0.39	0.01	0.46
Puzzle Number of Approaches	0.08	**0.91**	0.13	0.06	0.83
Play	-0.07	**0.70**	0.00	0.22	0.63
Time in Proximity to Puzzle	0.20	**0.68**	-0.31	0.03	0.59
Approach others	0.05	**0.65**	0.35	0.27	0.69
Taste Pasta	0.27	**0.41**	0.20	0.11	0.42
Leopard Number of Approaches	0.02	0.11	**0.82**	0.02	0.67
Leopard Number of Displays	0.21	0.07	**0.62**	-0.01	0.48
Time in Proximity to Leopard	0.10	-0.08	**0.59**	**-0.44**	0.54
Aggression Received	-0.37	0.12	**0.54**	0.31	0.54
Self-scratch	-0.10	-0.17	0.19	**-0.69**	0.66
Activity	0.29	0.30	0.26	**0.53**	0.65
Eigenvalue	5.98	2.85	2.59	1.73	
% variance explained	29.92	14.25	12.93	8.65	

Boldface indicates loadings >|0.40|

Table S4.2: Fixed effects for the diversity of abnormal behaviour

Predictors	Estimates	std. Error	*z* value	*P*
Diversity				
(Intercept)	-1.35	0.10	-14.12	**<0.001**
Rearing [Hand]	0.43	0.22	1.94	0.053
Rearing [Wild]	0.38	0.19	2.04	**0.042**

Reference category for Rearing was set to Mother-reared.

Table S4.3: Fixed effects for the frequency of individual abnormal behaviours

Predictors	Estimates	std. Error	*z* value	*P*
All				
(Intercept)	0.885	0.157	5.625	**<0.001**
Coprophagy				
(Intercept)	-0.215	0.116	-1.858	0.063
Activity score	-0.332	0.116	-2.873	**0.004**
Sociability score	-0.496	0.128	-3.882	**<0.001**
Finger in anus				
(Intercept)	-2.215	0.474	-4.674	**<0.001**
Sex [Male]	-1.627	0.598	-2.722	**0.006**
Rearing [Hand]	1.655	0.783	2.113	**0.035**
Rearing [Wild]	1.720	0.628	2.737	**0.006**
Social hair pluck				
(Intercept)	-1.482	0.287	-5.167	**<0.001**
Sociability score	0.807	0.365	2.210	**0.027**
Regurgitation				
(Intercept)	-0.196	0.373	-0.526	0.599
Head shaking				
(Intercept)	-4.372	0.752	-5.815	**<0.001**
Activity score	-1.300	0.426	-3.053	**0.002**

Reference category for Sex was set to Female and for Rearing to Mother-reared.

Chapter 5

Evaluating self-directed behaviours and their association with emotional arousal across two cognitive tasks in bonobos (*Pan paniscus*)

Table S5.1: Model outputs testing the effects of condition and stimulus type on the rate of SDBs in Study 1

Nose wipe ~ condition + stimulus				Chisq	df	*P*
			Condition	0.554	2	0.758
			Stimulus	3.393	2	0.183
Fixed factor	Contrast	Estimate	SE	df	*t* value	*P*
Stimulus	Averted – Control	0.001	0.002	5864	0.379	1.000
	Averted – Direct	-0.002	0.001	5864	-1.418	0.469
	Control - Direct	-0.003	0.002	5864	-1.698	0.269
Condition	Pre-fusion – Post-fusion	0.0004	0.001	5744	0.236	1.000
	Pre-fusion – Fusion	-0.0008	0.001	5719	-0.554	1.000
	Post-fusion - Fusion	-0.001	0.002	5870	-0.719	1.000

Gentle self-scratch ~ condition + stimulus				Chisq	df	*P*
			Condition	0.746	2	0.689
			Stimulus	6.759	2	0**.034**
Fixed factor	Contrast	Estimate	SE	df	*t* value	*P*
Stimulus	Averted – Control	-0.002	0.0008	5864	-2.392	**0.050**
	Averted – Direct	-0.002	0.0008	5864	-2.016	0.132
	Control - Direct	0.0004	0.0008	5864	0.524	1.000
Condition	Pre-fusion – Post-fusion	-0.0005	0.0008	5710	-0.582	1.000
	Pre-fusion – Fusion	0.0003	0.0008	5679	0.354	1.000
	Post-fusion - Fusion	0.0008	0.0009	5870	0.853	1.000

Rough self-scratch ~ condition + stimulus				Chisq	df	*P*
			Condition	1.349	2	0.510
			Stimulus	1.737	2	0.420
Fixed factor	Contrast	Estimate	SE	df	*t* value	*P*
Stimulus	Averted – Control	0.0007	0.0006	5865	1.179	0.715
	Averted – Direct	0.0006	0.0006	5865	1.070	0.854
	Control - Direct	-0.0001	0.0006	5865	-0.188	1.000
Condition	Pre-fusion – Post-fusion	6.61e-04	0.0006	4384	1.112	0.799
	Pre-fusion – Fusion	8.34e-05	0.0006	4203	0.141	1.000
	Post-fusion - Fusion	-5.77e-04	0.0007	5860	-0.883	1.000

Table S5.2: Model outputs testing the effects of stimulus type on the rate of SDBs in Study 2 – Experiment 1

Nose wipe ~ stimulus				Chisq	df	*P*
			Stimulus	1.027	2	0.599
Fixed factor	Contrast	Estimate	SE	df	*t* value	*P*
Stimulus	Congruent – Control	-0.003	0.004	1217	-0.899	1.000
	Congruent – Incongruent	-0.004	0.004	1217	-0.882	1.000
	Control – Incongruent	-0.0002	0.004	1217	-0.064	1.000
Gentle self-scratch ~ stimulus				Chisq	df	*P*
			Stimulus	1.565	2	0.457
Fixed factor	Contrast	Estimate	SE	df	*t* value	*P*
Stimulus	Congruent – Control	-0.001	0.001	1218	-1.070	0.855
	Congruent – Incongruent	-0.002	0.001	1218	-1.127	0.780
	Control – Incongruent	-0.0002	0.001	1218	-0.160	1.000
Rough self-scratch ~ stimulus				Chisq	df	*P*
			Stimulus	3.083	2	0.214
Fixed factor	Contrast	Estimate	SE	df	*t* value	*P*
Stimulus	Congruent – Control	-0.002	0.001	1218	-1.125	0.782
	Congruent – Incongruent	0.0008	0.001	1218	0.515	1.000
	Control – Incongruent	0.002	0.001	1218	1.687	0.276

Table S5.3: Model outputs testing the effects of stimulus type on the rate of SDBs in Study 2 – Experiment 2

Nose wipe ~ stimulus				Chisq	df	*P*
			Stimulus	8.447	3	**0.034**
Fixed factor	Contrast	Estimate	SE	df	*t* value	*P*
Stimulus	Blank – Negative	0.004	0.004	1817	1.035	1.000
	Blank – Neutral	0.009	0.004	1817	2.108	0.211
	Blank – Positive	0.012	0.004	1817	2.655	**0.048**
	Negative – Neutral	0.005	0.005	1817	0.995	1.000
	Negative – Positive	0.007	0.005	1817	1.504	0.796
	Neutral - Positive	0.002	0.005	1817	0.508	1.000
Gentle self-scratch ~ stimulus				Chisq	df	*P*
			Stimulus	2.006	3	0.571
Fixed factor	Contrast	Estimate	SE	df	*t* value	*P*
Stimulus	Blank – Negative	0.002	0.002	1817	0.957	1.000
	Blank – Neutral	0.002	0.002	1817	0.903	1.000
	Blank – Positive	0.002	0.002	1817	1.315	1.000
	Negative – Neutral	-0.00009	0.002	1817	-0.050	1.000
	Negative – Positive	0.0006	0.002	1817	0.333	1.000
	Neutral - Positive	0.0007	0.002	1817	0.382	1.000
Rough self-scratch ~ stimulus				Chisq	df	*P*
			Stimulus	2.283	3	0.516
Fixed factor	Contrast	Estimate	SE	df	*t* value	*P*
Stimulus	Blank – Negative	-0.002	0.001	1818	-1.419	0.937
	Blank – Neutral	-0.0003	0.001	1818	-0.262	1.000
	Blank – Positive	-0.0002	0.001	1818	-0.172	1.000
	Negative – Neutral	0.001	0.001	1817	1.071	1.000
	Negative – Positive	0.002	0.001	1817	1.153	1.000
	Neutral - Positive	0.0001	0.001	1817	0.083	1.000

Table S5.4: Model outputs testing the effects of stimulus type on the rate of SDBs in Study 2 – Experiment 3

Nose wipe ~ stimulus				Chisq	df	*P*
			Stimulus	5.439	3	0.142
Fixed factor	Contrast	Estimate	SE	df	*t* value	*P*
Stimulus	Blank – Negative	0.001	0.005	1670	0.212	1.000
	Blank – Neutral	-0.010	0.005	1670	-1.996	0.276
	Blank – Positive	-0.001	0.005	1670	-0.249	1.000
	Negative – Neutral	-0.011	0.005	1670	-2.045	0.246
	Negative – Positive	-0.002	0.005	1670	-0.427	1.000
	Neutral - Positive	0.008	0.005	1670	1.620	0.633

Gentle self-scratch ~ stimulus				Chisq	df	*P*
			Stimulus	3.872	3	0.276
Fixed factor	Contrast	Estimate	SE	df	*t* value	*P*
Stimulus	Blank – Negative	-0.001	0.002	1670	-0.715	1.000
	Blank – Neutral	-0.0002	0.002	1670	-0.087	1.000
	Blank – Positive	0.003	0.002	1670	1.341	1.000
	Negative – Neutral	0.001	0.002	1670	0.587	1.000
	Negative – Positive	0.004	0.002	1670	1.905	0.342
	Neutral - Positive	0.003	0.002	1670	1.330	1.000

Rough self-scratch ~ stimulus				Chisq	df	*P*
			Stimulus	3.297	3	0.348
Fixed factor	Contrast	Estimate	SE	df	*t* value	*P*
Stimulus	Blank – Negative	0.0002	0.001	1670	0.197	1.000
	Blank – Neutral	0.001	0.001	1670	1.212	1.000
	Blank – Positive	0.002	0.001	1670	1.553	0.724
	Negative – Neutral	0.001	0.001	1670	0.938	1.000
	Negative – Positive	0.002	0.001	1670	1.255	1.000
	Neutral - Positive	0.0004	0.001	1670	0.324	1.000

Table S5.5: Rates of SDBs per trial per second for the subjects across the two studies

	Busira		**Habari**	
	Study 1	Study 2	Study 1	Study 2
Nose wipe	0.018 ± 0.002	0.036 ± 0.002	0.009 ± 0.001	0.011 ± 0.001
Rough self-scratch	0.0015 ± 0.0006	0.0026 ± 0.0007	0.0016 ± 0.0006	0.0004 ± 0.0002
Gentle self-scratch	0.0051 ± 0.0011	0.0065 ± 0.0012	0.0043 ± 0.001	0.0028 ± 0.00061
	Kianga		**Kikongo**	
	Study 1	Study 2	Study 1	Study 2
Nose wipe	0.017 ± 0.002	NA	0.007 ± 0.002	NA
Rough self-scratch	0.0018 ± 0.0005	NA	0.0001 ± 0.0001	NA
Gentle self-scratch	0.0075 ± 0.0013	NA	0.0043 ± 0.0014	NA
	Mokonzi		**Nayembi**	
	Study 1	Study 2	Study 1	Study 2
Nose wipe	0.008 ± 0.001	0.016 ± 0.002	0.008 ± 0.002	NA
Rough self-scratch	0.0008 ± 0.0004	0.001 ± 0.0004	0.0035 ± 0.0016	NA
Gentle self-scratch	0.0018 ± 0.00057	0.003 ± 0.0007	0.003 ± 0.00094	NA
	Vifijo		**Zamba**	
	Study 1	Study 2	Study 1	Study 2
Nose wipe	0.014 ± 0.002	NA	0.016 ± 0.002	0.029 ± 0.002
Rough self-scratch	0.0016 ± 0.0007	NA	0.0008 ± 0.0004	0.0018 ± 0.0006
Gentle self-scratch	0.0019 ± 0.00074	NA	0.00023 ± 0.00023	0.00039 ± 0.00026

Table S5.6: Post-hoc results of tested predictors in final models testing the effect of trial accuracy and hemispace. Simple contrasts were applied

Study 1						
Nose wipe ~ trial accuracy	Contrast	Estimate	SE	df	*t* value	*P*
	Accuracy: Incorrect - correct	0.007	0.003	5846	2.447	0.014
Gentle self-scratch ~ trial accuracy + hemispace	Contrast	Estimate	SE	df	*t* value	*P*
	Accuracy: Incorrect - correct	-0.014	0.026	220	-0.526	0.600
	Hemispace: left - right	-0.009	0.013	220	-0.747	0.456
Rough self-scratch ~ trial accuracy + hemispace	Contrast	Estimate	SE	df	*t* value	*P*
	Accuracy: Incorrect - correct	-0.021	0.026	217	-0.903	0.367
	Hemispace: left - right	0.023	0.012	220	1.966	0.051
Study 2						
Nose wipe ~ trial accuracy	Contrast	Estimate	SE	df	*t* value	*P*
	Accuracy: Incorrect - correct	0.011	0.002	4696	4.606	< 0.001
Gentle self-scratch ~ trial accuracy + hemispace	Contrast	Estimate	SE	df	*t* value	*P*
	Accuracy: Incorrect - correct	-0.056	0.020	119	-2.886	0.005
	Hemispace: left - right	0.001	0.019	147	0.039	0.969
Rough self-scratch ~ trial accuracy * hemispace	Contrast	Estimate	SE	df	*t* value	*P*
Hemispace: Left	Accuracy: Incorrect - correct	0.107	0.024	123	4.556	< 0.001
Hemispace: Right	Accuracy: Incorrect - correct	0.028	0.021	145	1.311	0.192
Accuracy: Incorrect	Hemispace: left - right	0.056	0.026	135	2.250	0.026
Accuracy: Correct	Hemispace: left - right	-0.022	0.018	141	-1.210	0.228

Table S5.7: Post-hoc results of tested predictors in final models testing the effect of trial accuracy and hemispace based on the subset of subjects that also participated in Study 2. Simple contrasts were applied

Study 1						
Nose wipe ~ trial accuracy	Contrast	Estimate	SE	df	*t* value	*P*
	Accuracy: Incorrect - correct	0.022	0.005	3342	4.009	< 0.001
Gentle self-scratch ~ trial accuracy + hemispace	Contrast	Estimate	SE	df	*t* value	*P*
	Accuracy: Incorrect - correct	-0.016	0.038	100	-0.421	0.675
	Hemispace: left - right	-0.008	0.019	100	-0.438	0.662
Rough self-scratch ~ trial accuracy + hemispace	Contrast	Estimate	SE	df	*t* value	*P*
	Accuracy: Incorrect - correct	-0.003	0.029	100	-0.107	0.915
	Hemispace: left - right	0.023	0.014	100	1.617	0.109

Chapter 6

Human perception of bonobo emotional expressivity using a Qualitative Behavioural Assessment

Table S6.1: Demographics of human participants in Study 1 and Study 2

	Study 1		**Study 2**	
Experience				
Student	17	65.4%	38*	88.4%
Expert	9	34.6%	5	11.6%
Pet ownership				
Yes, present	23	88.5%	39	90.7%
Yes, past	3	11.5%	4	9.3%
No	0	0.0%	0	0.0%
Zoo visits				
0 visits/year	6	23.1%	13	30.2%
1-5 visits/year	12	46.2%	24	55.8%
6-10 visits/year	2	7.7%	1	2.3%
+10 visits/year	6	23.1%	5	11.6%
Work experience (only students)				
Yes, present	12	70.6%	28	73.7%
With primates	1	5.9%	2	5.3%
Yes, past	4	23.5%	6	15.8%
With primates	0	0.0%	0	0.0%
No	0	0.0%	2	5.3%

** 6 Students did not fully complete the survey and were not included here*

Table S6.2: Clustering of Animal Empathy statements based on Ward Hierarchical Clustering analysis

Cluster 1 – ‘Empathic’
5. Sad films about animals often leave me with a lump in my throat.
7. It makes me sad to see an animal on its own in a cage.
9. A friendly purring cat almost always cheers me up.
10. It upsets me when I see helpless old animals.
13. I get very angry when I see animals being ill treated.
15. Pets have a great influence on my moods.
17. I enjoy feeding scraps of food to the birds.
18. Seeing animals in pain upsets me.
21. I would always try to help if I saw a dog or puppy that seemed to be lost.
22. I hate to see birds in cages where there is no room for them to fly about.
23. It upsets me to see farm animals in lorries going to slaughter.
26. The thought of calves being reared in veal crates really makes me feel sad.
27. I hate seeing pictures of animals used in scientific experiments.
Cluster 2 – ‘Apathic’
1. So long as they’re warm and well fed, I don’t think zoo animals mind being kept in cages.
2. Often cats will meow and pester for food even when they are not really hungry.
3. It upsets me to see animals being chased and killed by lions in wildlife programs on TV.
4. I get annoyed by dogs that howl and bark when they are left alone.
6. Animals deserve to be told off when they’re not behaving properly.
8. People who cuddle and kiss their pets in public annoy me.
11. Dogs sometimes whine and whimper for no real reason.
12. Many people are over-affectionate towards their pets.
14. It is silly to become too attached to one’s pets.
16. Sometimes I am amazed how upset people get when an old pet dies.
19. People often make too much of the feelings and sensitivities of animals.
20. I find it irritating when dogs try to greet me by jumping up and licking me.
24. It’s silly to worry about how farm animals feel.
25. People are too concerned about the suffering of laboratory rats and mice.
28. Many people are over affectionate towards their pets.

Table S6.3: Descriptions of the videos used in Phase 1 of the Free Choice Profiling procedure

Video	Short description
01	Bonobo resting
02	Bonobo autogrooming
03	Bonobos A and B vocalising, C charging and hitting glass towards the visitors and scratching
04	Bonobo performing solitary play
05	Bonobo mother interacting with infant
06	Bonobo A approaches B and C and starts displaying
07	Bonobo swinging through flexible structures
08	Bonobos A and B engaging in genito-genital rubbing, C harasses
09	Allogrooming among four bonobos
10	Bonobo hit on glass, then starts feeding on browse
11	Bonobo A grooms B, B embraces A, B leaves and reaches for C
12	Genito-genital rubbing between bonobo A and B, C harasses A, and A and C perform parallel display. D undirected display, and E and F perform short charge
13	Bonobo tries to open a coconut and succeeds
14	Bonobo A follows B, B displaces
15	Four bonobos gentle playing
16	Two bonobos playing with object
17	Bonobo looking through door to other group, sticking fingers through holes
18	Bonobo sits, then moves and rough scratches
19	Bonobo A sits, then vocalises and short charge to B
20	Bonobo A grooming B, A pushes away C. Bonobo D is resting and eating

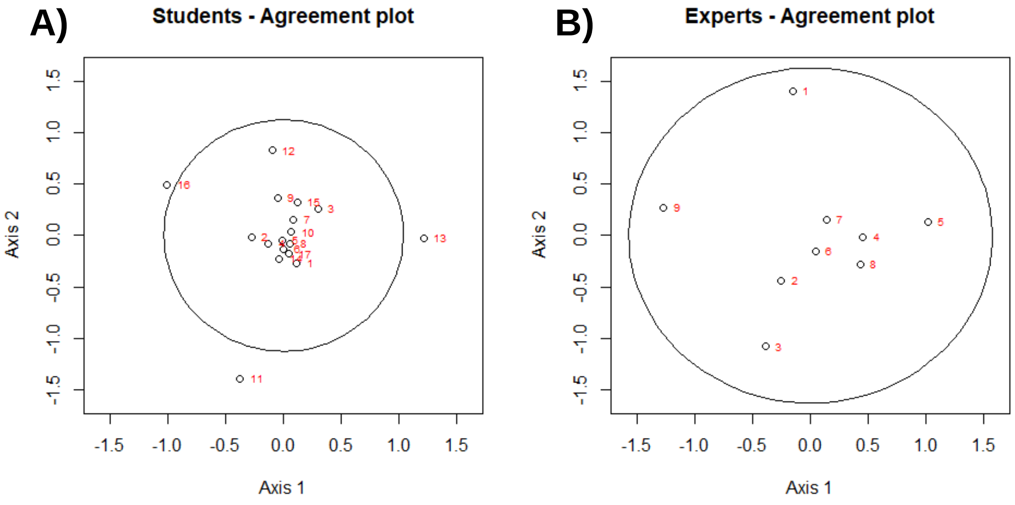


Figure S6.1: Observer plots for A) Students and B) Experts in Study 1. Numbers represent the observers, and the circle represents the 95% confidence ellipse

Table S6.4: Sampling adequacy for Study 2

KMO - Student		**KMO - Expert**	
Overall	0.90	Overall	0.87
Active	0.92	Active	0.90
Anxious	0.85	Anxious	0.86
Happy	0.91	Happy	0.85
Irritated	0.87	Irritated	0.83
Excited	0.95	Excited	0.94
Quiet	0.87	Quiet	0.88
Frustrated	0.88	Frustrated	0.82
Curious	0.88	Curious	0.84
Self-confident	0.93	Self-confident	0.76
Stressed	0.90	Stressed	0.81
Content	0.90	Content	0.86
Calm	0.87	Calm	0.90
Agitated	0.94	Agitated	0.91
Sad	0.85	Sad	0.85
Focused	0.83	Focused	0.66
Social	0.94	Social	0.87
Indifferent	0.86	Indifferent	0.92
Lethargic	0.85	Lethargic	0.82
Relaxed	0.93	Relaxed	0.91
Lively	0.93	Lively	0.90
Nervous	0.92	Nervous	0.88
Positively engaged	0.92	Positively engaged	0.87
Bored	0.81	Bored	0.90
Playful	0.90	Playful	0.87

Chapter 7

Affective responses and behavioural strategies to social fusion events in zoo-housed bonobos

Table S7.1: Ethogram used in this study

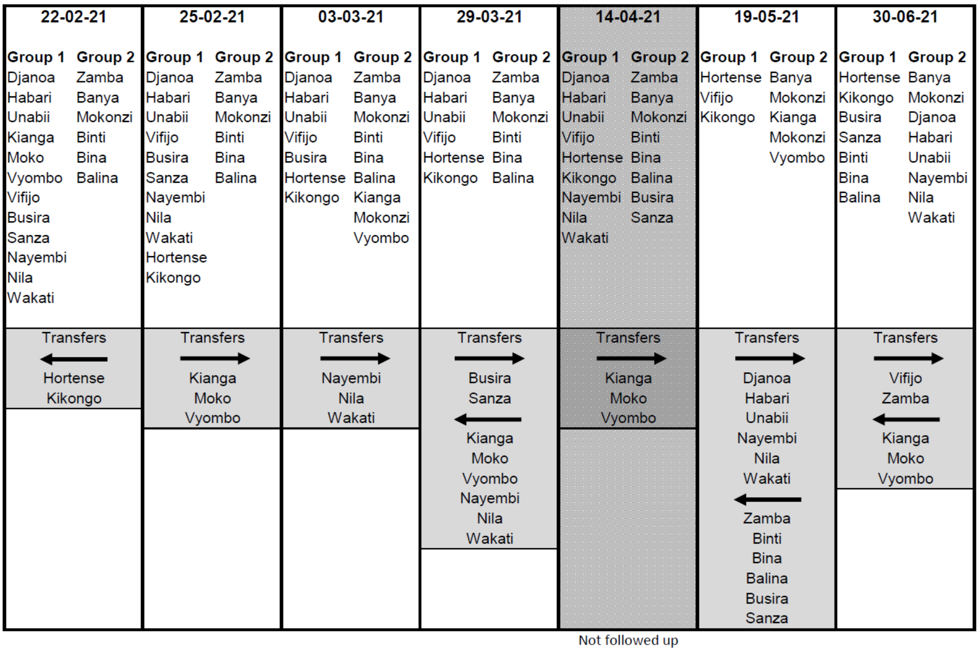
Behaviour	State/Event	Description
Grooming	State	Subject manipulates Receiver's body surface and hair with lips, fingers…
Calm social play	State	Subject and Receiver play socially in a calm way, with play face, exaggerated movements and (occasionally) with laughing sounds.
Rough social play	State	Subject and Receiver play socially in a rough way, with play face, exaggerated movements and (occasionally) with laughing sounds.
Copulation	State	Heterosexual mount accompanied by pelvic thrusts and intromission between two sexually mature partners.
Non-copulatory mount	State	Subject mounts Receiver without intromission of the penis in the vagina, or without thrusting of the pelvis; or any sexual contact between 2 individuals of the same sex; or sexual contact involving immature individuals. Includes GG rubbing between females. Various positions are possible.
Long charge	Event	Subject shows tensed running towards Receiver over a longer distance (more than five steps). Modifiers: hit, kick, bite, wrestle, nothing.
Short charge	Event	Subject shows tensed running towards Receiver over a few meters (or up to five steps). Modifiers: hit, kick, bite, wrestle, nothing.
Aggressive intention	Event	Subject directs a sudden tense hand or body movement in the direction of the Receiver in a non-playful context or hitting, kicking etc. without locomotion. Modifiers: hit, kick, bite, wrestle, nothing.
Directed display	Event	Subject runs tensed in the direction of, parallel to or closely passing by Receiver, often while pushing an object. This can end in a collision or other contact. There is often a clear phase where the display is built up (body swaying). Modifiers: hit, kick, bite, wrestle, nothing.
Flee	Event	Subject moves away after a quick aggressive approach or charge without indication of play, and the fleeing lasts at least until the aggression stops
Flinch	Event	This may vary from a slightly ducking of the head, via more intense withdrawal movements of the upper part of the body to short momentary actual retreat movements, in that Subject takes one or more steps backwards. The retreat may be performed by crouching backwards.
Displace	Event	Subject approaches to within arm's reach of the Receiver, or moves in direction of receiver with attention focused on receiver and Receiver retreats spatially or yields within 30 seconds
Grin	Event	Retraction of the lips resulting in partial or complete exposure of the gums and teeth with the face directed to the partner [a]

[a] Based on (de Waal, 1988)

Table S7.2: Mean luminance and contrast values for the different stimuli used

	Luminance		Contrast	
	Mean	SD	Mean	SD
Direct	0.477	0.008	0.167	0.022
Averted	0.479	0.011	0.169	0.015
Anova statistics	$F_{1,\,50}$ = 0.633, *P* = 0.430		$F_{1,\,50}$ = 0.137, *P* = 0.713	

Table S7.3: Group compositions and social units that transferred between groups throughout the study period.



22-02-21		25-02-21		03-03-21		29-03-21		14-04-21		19-05-21		30-06-21	
Group 1	**Group 2**	**Group 1**	**Group 2**	**Group 1**	**Group 2**	**Group 1**	**Group 2**	**Group 1**	**Group 2**	**Group 1**	**Group 2**	**Group 1**	**Group 2**
Djanoa	Zamba	Djanoa	Zamba	Djanoa	Zamba	Djanoa	Zamba	Djanoa	Zamba	Hortense	Banya	Hortense	Banya
Habari	Banya	Habari	Banya	Habari	Banya	Habari	Banya	Habari	Banya	Vifijo	Mokonzi	Kikongo	Mokonzi
Unabii	Mokonzi	Unabii	Mokonzi	Unabii	Mokonzi	Unabii	Mokonzi	Unabii	Mokonzi	Kikongo	Kianga	Busira	Djanoa
Kianga	Binti	Vifijo	Binti	Vifijo	Binti	Vifijo	Binti	Vifijo	Binti		Mokonzi	Sanza	Habari
Moko	Bina	Busira	Bina	Busira	Bina	Hortense	Bina	Hortense	Bina		Vyombo	Binti	Unabii
Vyombo	Balina	Sanza	Balina	Hortense	Balina	Kikongo	Balina	Kikongo	Balina			Bina	Nayembi
Vifijo		Nayembi		Kikongo	Kianga			Nayembi	Busira			Balina	Nila
Busira		Nila			Mokonzi			Nila	Sanza				Wakati
Sanza		Wakati			Vyombo			Wakati					
Nayembi		Hortense											
Nila		Kikongo											
Wakati													
Transfers ← Hortense Kikongo		Transfers → Kianga Moko Vyombo		Transfers → Nayembi Nila Wakati		Transfers → Busira Sanza ← Kianga Moko Vyombo Nayembi Nila Wakati		Transfers → Kianga Moko Vyombo		Transfers → Djanoa Habari Unabii Nayembi Nila Wakati ← Zamba Binti Bina Balina Busira Sanza		Transfers → Vifijo Zamba ← Kianga Moko Vyombo	

Not followed up

Table S7.4: Model outputs testing the effect of condition on different behavioural categories

Grooming given ~ Condition		Chisq	df	*P*
	Condition	2.876	2	0.237
Grooming received ~ Condition		Chisq	df	*P*
	Condition	2.387	2	0.303
Social play ~ Condition		Chisq	df	*P*
	Condition	3.953	2	0.139
Agonistic response ~ Condition		Chisq	df	*P*
	Condition	1.040	2	0.594
Socio-sexual ~ Condition		Chisq	df	*P*
	Condition	20.327	2	< 0.001
Fixed factor	Ratio	SE	z-value	*P*
Pre-fusion – Fusion	8.208	4.392	3.934	< 0.001
Post-fusion – Fusion	2.539	0.783	3.023	0.007
Pre-fusion – Post-fusion	0.309	0.172	-2.114	0.087
Aggression given ~ Condition		Chisq	df	*P*
	Condition	6.826	2	0.033
Fixed factor	Ratio	SE	z-value	*P*
Pre-fusion – Fusion	3.650	2.770	1.707	0.203
Post-fusion – Fusion	5.670	4.040	2.434	0.039
Pre-fusion – Post-fusion	1.550	1.320	0.519	0.862

Table S7.5: Final model outputs testing the effects of stimulus type and condition on the response ratio scores

Response ratio score ~ Stimulus type * Condition			Chisq	df	*P*
		Stimulus type	2.511	1	0.113
		Condition	6.177	2	0.046
		Target location	3.226	2	0.199
		Stimulus * Condition	7.642	2	0.022
Contrast = Stimulus type	Ratio	SE	df	*t* value	*P*
Averted					
Pre-fusion – Fusion	0.012	0.049	18.1	0.235	0.970
Post-fusion – Fusion	0.011	0.052	17.8	0.216	0.975
Pre-fusion – Post-fusion	-0.0004	0.043	25.0	0.009	1.000
Direct					
Pre-fusion – Fusion	0.172	0.049	17.7	3.501	0.007
Post-fusion – Fusion	0.149	0.052	17.4	2.886	0.026
Pre-fusion – Post-fusion	-0.023	0.043	24.9	0.538	0.854
Contrast = Condition	Ratio	SE	df	*t* value	*P*
Pre-fusion					
Averted – Direct	0.014	0.039	526	0.360	0.719
Fusion					
Averted – Direct	-0.146	0.046	527	-3.159	0.002
Post-fusion					
Averted – Direct	-0.008	0.044	527	-0.192	0.848

Table S7.6: Model outputs testing the effect of condition and behaviour on response ratio scores

Response ratio score ~ (Grooming given + Grooming given binary)*Condition + target location	Chisq	df	*P*
Grooming given	0.160	1	0.689
Grooming given binary	0.078	1	0.780
Condition	8.668	2	0.013
Target location	0.787	1	0.375
Grooming given * Condition	2.264	2	0.322
Grooming given binary * Condition	1.075	2	0.584
Response ratio score ~ (Grooming received + Grooming received binary)*Condition + target location	Chisq	df	*P*
Grooming received	0.688	1	0.407
Grooming received binary	0.072	1	0.789
Condition	8.490	2	0.014
Target location	0.795	1	0.373
Grooming received * Condition	0.498	2	0.779
Grooming received binary * Condition	0.310	2	0.856
Response ratio score ~ (Socio-sexual + Socio-sexual binary)*Condition + target location	Chisq	df	*P*
Socio-sexual	9.132	1	0.003
Socio-sexual binary	0.468	1	0.494
Condition	16.526	2	0.0003
Target location	0.914	1	0.339
Socio-sexual * Condition	3.625	2	0.163
Socio-sexual binary * Condition	5.491	2	0.064
Response ratio score ~ (Social play + Social play binary)*Condition + target location	Chisq	df	*P*
Social play	6.147	1	0.013
Social play binary	2.192	1	0.139
Condition	6.924	2	0.031
Target location	0.695	1	0.404
Social play * Condition	0.952	2	0.621
Social play binary * Condition	0.004	2	0.998
Response ratio score ~ (Aggression given + Aggression given binary)*Condition + target location	Chisq	df	*P*
Aggression given	3.576	1	0.086
Aggression given binary	1.103	1	0.294
Condition	11.095	2	0.004
Target location	0.924	1	0.337
Aggression given * Condition	0.557	2	0.757
Aggression given binary * Condition	0.714	2	0.699
Response ratio score ~ (Agonistic response + Agonistic response binary)*Condition + target location	Chisq	df	*P*
Agonistic response	0.141	1	0.707
Agonistic response binary	0.633	1	0.426
Condition	9.049	2	0.011
Target location	0.799	1	0.371
Agonistic response * Condition	0.850	2	0.654
Agonistic response binary * Condition	2.294	2	0.318

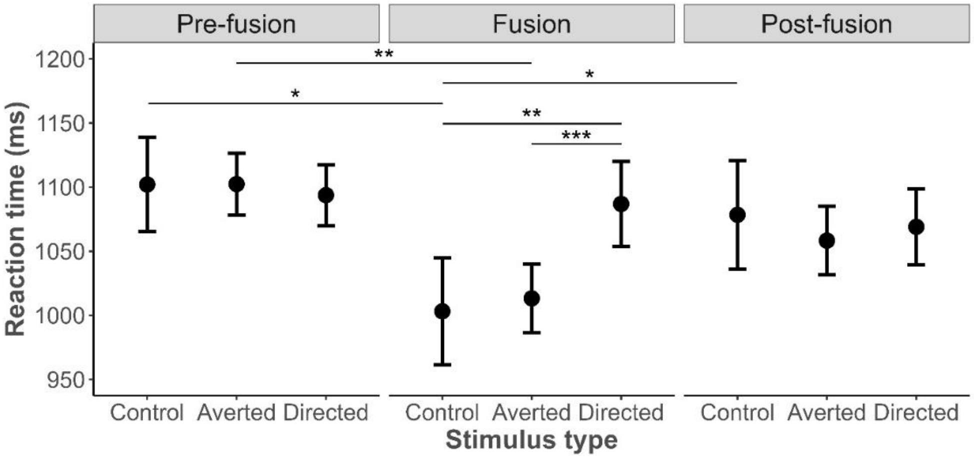


Figure S7.1: Average reaction times (± 95% confidence intervals) for the different stimulus types depending on testing conditions. ***P < 0.001, **P < 0.01, *P < 0.05.

Table S7.7: Final model outputs post-hoc testing the effects of stimulus type and condition on the reaction times to check for arousal-related response speeding

Reaction time ~ Stimulus type * Condition			Chisq	df	*P*
		Stimulus type	4.775	2	0.092
		Condition	9.013	2	0.011
		Target location	33.507	2	< 0.001
		Stimulus * Condition	14.314	4	0.006
Contrast = Stimulus type	**Ratio**	**SE**	**df**	***t* value**	***P***
Control					
Pre-fusion – Fusion	1.079	0.028	4021	2.943	0.009
Post-fusion – Fusion	1.005	0.027	4021	0.186	0.981
Pre-fusion – Post-fusion	0.931	0.029	4021	-2.294	0.047
Averted					
Pre-fusion – Fusion	1.075	0.021	4021	3.683	0.0007
Post-fusion – Fusion	1.025	0.022	4021	1.156	0.479
Pre-fusion – Post-fusion	0.953	0.024	4021	-1.860	0.151
Direct					
Pre-fusion – Fusion	1.000	0.019	4021	0.002	1.000
Post-fusion – Fusion	1.012	0.021	4021	0.567	0.838
Pre-fusion – Post-fusion	1.012	0.026	4021	0.476	0.883
Contrast = Condition	**Ratio**	**SE**	**df**	***t* value**	***P***
Pre-fusion					
Control – Averted	0.997	0.019	4021	-0.141	0.989
Control – Direct	1.003	0.019	4021	0.138	0.990
Averted – Direct	1.005	0.015	4021	0.342	0.938
Fusion					
Control – Averted	0.994	0.022	4021	-0.288	0.955
Control – Direct	0.929	0.021	4021	-3.331	0.003
Averted – Direct	0.935	0.017	4021	-3.769	0.0005
Post-fusion					
Control – Averted	1.017	0.022	4021	0.804	0.701
Control – Direct	1.010	0.021	4021	0.453	0.893
Averted – Direct	0.992	0.018	4021	-0.428	0.903

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