The Lateralisation of Emotion
in Social Mammals

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Contents

Declaration

I declare that the work undertaken and reported within this thesis is my own and has not been submitted in consideration of any other degree or award.

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Publications & Presentations

Publications

Milligan ADS, Vick SJ, Glickman SE (in prep.) Evidence of emotional laterality in the spotted hyaena, *Crocuta crocuta*.

Milligan ADS, Vick SJ, Meguerditchian A, Paukner A, Suomi SJ (in prep.) Comparing peripheral and central visual field use in social mammals: a new model.

Milligan ADS, Vick SJ, Elwood, RW (in prep.) A study of handedness in three species of lutung.

Presentations

Milligan ADS, Vick SJ, Anderson JA (2014) The lateralisation of emotion in social mammals. Invited talk, University of York, York, UK.

Milligan ADS, Vick SJ (2014) Comparing the use of peripheral and central visual fields by social mammals: a new model. Contributed poster, ASAB Spring Conference, Sheffield, UK.

Milligan ADS, Vick SJ, Anderson JA (2013) The lateralisation of emotion in social mammals. Invited talk, University of Utrecht, Utrecht, The Netherlands.

Milligan ADS, Vick SJ, Glickman SE (2013) The lateralisation of emotion in the spotted hyaena, *Crocuta crocuta*. Contributed talk, Behaviour 2013 Conference ASAB/IEC, Newcastle, UK.

Milligan ADS, Vick SJ, Anderson JA (2013) The lateralisation of emotion in social mammals. Invited talk, CNRS Centre de Recherche Cerveau et Cognition, Toulouse, France

Milligan ADS, Vick SJ, Anderson JA, Glickman SE, Weldele, M (2011) The influence of emotion upon visual field preferences during conspecific interactions in the spotted hyaena. Invited talk, University of California, FSBR, Berkeley, USA.

Milligan ADS, Vick SJ, Anderson JA, Glickman SE, Weldele, M (2010) An Introduction to the Spotted Hyaena. Contributed talk, Behaviour & Evolution Research Group meeting, Stirling, UK.

Milligan ADS, Vick SJ, Anderson JA (2010) Lateralisation of emotion in social mammals. Contributed poster, Primate Society of Great Britain Spring Conference, Dundee, UK.

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Abstract

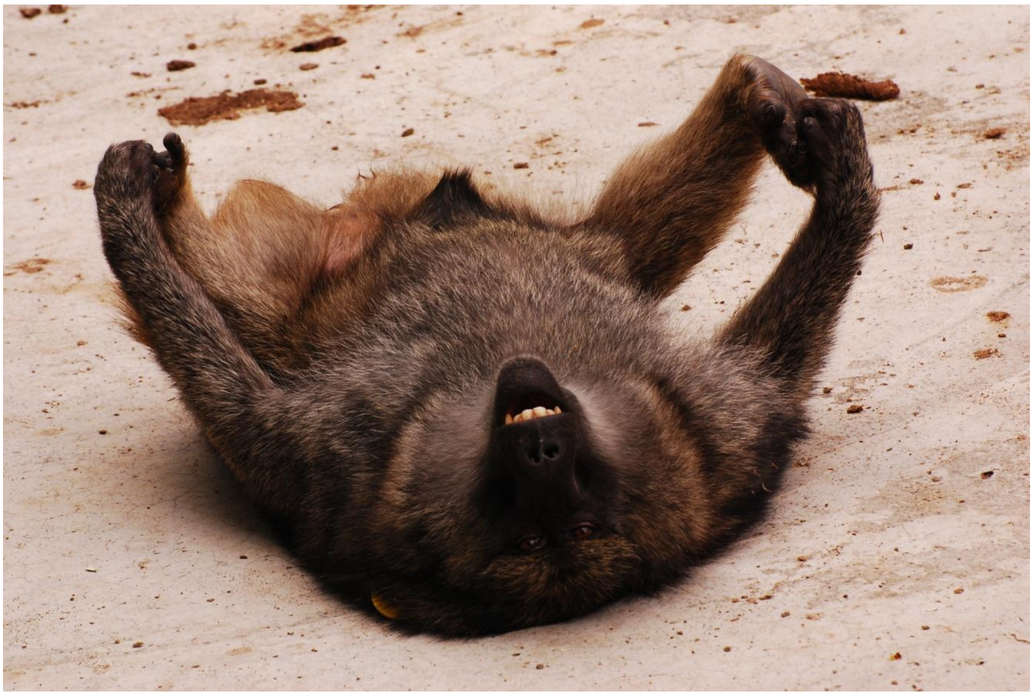
The Lateralisation of Emotion in Social Mammals

The study of lateralisation has taken several forms ranging from investigating morphological asymmetries to research on lateralised motor and perceptual functions with many studies successfully evidencing lateralisation in a variety of species. This study, featuring three species (olive baboons, rhesus macaques, and spotted hyaenas) investigated visual field biases with the aim of determining whether emotional valence underpins these biases whilst also considering the influence of a number of other factors such as emotional intensity, age, sex, rank, and, for the first time, oestrus cycles (olive baboons only). This study aimed to establish whether Campbell's (1982) Right Hemisphere Hypothesis or Silberman & Weingartner's (1986) Valence Hypothesis offered the more valid theory for the lateralisation of emotion by considering interactions across the full spectrum of emotion – a question the almost exclusive investigation of negatively affective scenarios by previous studies has been unable to answer. Furthermore, this study provided a new methodology for investigating behavioural lateralisation by suggesting that separating the visual spectrum into five fields (extreme left, mid left, centre, mid right and extreme right) allows a more accurate insight into the lateralisation of visual perception than the traditional hemifield model. Finally, a more conservative method is proposed for analysing behavioural data in future studies from this field and suggests that these methods provide a more accurate representation of the lateralisation of emotion than those previously employed.

A population-level left side bias was found for the spotted hyaenas, thus providing the first evidence of significantly lateralised behaviour in a large carnivore and, for this species at least, lending some support to Campbell's (1982) Right Hemisphere hypothesis but as population-level biases were not found for either of the other species it may be premature to suggest this support is unequivocal. Significant age effects were found in two species as adult olive baboons and spotted hyaenas were both found to express significant left side biases. Spotted hyaenas were also found to express significant left side biases for females, dominant individuals, high intensity interactions, and sexual valence interactions whilst olive baboons expressed a significant left side bias during negative valence behaviours but no significant lateral biases were found in any context for rhesus macaques. In olive baboons behaviours performed by males and those of a low intensity were found to occur more frequently in the mid and central visual fields and neutral valence behaviours were less occurrent in the extreme visual fields whilst in spotted hyaenas sexual, positive and negative valence behaviours were significantly less centralised than neutral valence behaviours.

Non-oestrus adult female olive baboons were significantly more strongly lateralised than in-oestrus females, thus suggesting an influence of sex hormones upon lateralisation that may also have been apparent from the hyaena data, particularly regarding the significant lateral biases observed for females and dominant individuals.

Finally, this thesis discusses a number of methodological issues that were encountered during this study and provides recommendations for future research in this field. Namely, this thesis provides an updated method for calculating laterality bias that is much more suitable for species with binocular vision and details a novel method of assessing visual field preferences by considering central and peripheral visual fields as separate entities. Furthermore, this thesis suggests that the weighted method designed and implemented for this study provides a much more accurate methodological foundation for analyses which avoids the caveats that may have affected previous research and thus provides a considerably more robust template that should be encouraged for any similar subsequent studies.



An olive baboon at the CNRS Station de Primatologie, Rousset, Bouches-du-Rhône, France

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Chapter 1 | General Introduction

1.1 | Background to Emotion

Emotion can be broadly described as the manifestation of physiological, neurological, behavioural, and cognitive factors that have evolved to deal with recurrent adaptive challenges (Panksepp, 2000). Emotions are involuntary and brief in duration, serving to narrow the behavioural repertoire into a functional, rapid response to stimuli or events, at least for negative emotions (Fredrikson, 1998). However, since James (1884) the difficulty of positing an explicit definition for ‘emotion’ has remained an issue of contention and there are many different theoretical approaches to the study of emotion (MacLean, 1952; Kleinginna & Kleinginna, 1981; LeDoux, 1998; Rolls, 1999; Izard, 2010; Dixon, 2012).

A key contention in emotion research has been the issue of consciousness, leading several theorists to try and differentiate between automatic responses and the subjective feeling of an emotion. Damasio (1999) proposed that ‘emotion’ be used to refer only to the unconscious experience and ‘affect’ for the corresponding conscious experience. In contrast, Panksepp (2000) terms the unconscious component of emotion as ‘emotional affect’ and used ‘emotion’ as an all-inclusive definition to refer to all aspects of this phenomenon. However, most authors (*e.g.* Davidson, 2003) have made no distinction between these terms and have used ‘emotion’ and ‘affect’ interchangeably without any reference to consciousness; a paradigm that is perhaps well suited for animal studies and shall be applied throughout this thesis.

Particularly with regards to non-human species, emotions have commonly been defined in terms of their associated externally observable behaviours. For example, Charles Darwin’s (1872/1998) *The Expression of the Emotions in Man and Animals* proposed that vocal and nonverbal emotional behaviour was adaptive and served both a communicative and motivational function. Darwin also offered examples of human emotional behaviour comparable to those seen in animals to support his thesis that these shared common evolutionary origins, for example teeth baring during agonism (Darwin, 1872/1998).

As an illustration of the adaptive function of emotional expression, Darwin (1872/1998) provided as an example the widening of the eyes that occurs when an individual experiences fear and implied that this offered the individual an increased field of vision and enhanced their ability to monitor their surroundings. More recent work confirms many of Darwin's observations that expressions of emotion are adaptive (e.g. Ekman 1992; Sharriff and Tracy, 2011); for example, the reduction of sensory intake evident in disgust across species or primates (Steiner *et al.*, 2001) although strong counterarguments have been made (e.g. Barrett, 2011). For example, the behavioural ecology approach (Fridlund, 1994) proposes a primarily social causation for emotional expressions, rather than these being veridical indicators of internal states. However, for gregarious species, emotional responses are predominantly evident in response to social challenges or events, making a distinction between emotion and social dimensions redundant (Parkinson, 1996). The social dimension of emotions can be seen in phenomena such as social referencing in human and non-human species. Again using disgust as an example, the expression of this emotion upon the face of one individual after tasting a foodstuff provides a warning to others that it may not be good to consume (Rozin *et al.*, 1993). Similarly, a fearful response to snakes in a mother rhesus macaque, *Macaca mulatta*, elicits a fearful response in their infant (Mineka & Cook, 1993).

While the functions of emotion in human and non-human species were proposed by Darwin (1872/1998) over 130 years ago, the study of emotion in the greater Animal Kingdom outwith *Homo sapiens* was largely impeded in the early 20th century by concerns arising from proponents of behaviourism and fears of anthropomorphism (Ekman, 2006; Panksepp, 2000). As such, comparative animal studies have only relatively recently been able to contribute to the burgeoning discipline of affective neuroscience. What is now apparent is that the brain structures implicated in human emotions are evident in a diverse range of species, and that emotional processes are central to both cognition and behaviour (MacLean, 1952; Panksepp, 2000; Rolls, 1999).

Paul Broca’s (1878) pioneering neuroanatomy research on the human brain included the identification of the limbic lobe and speculation that it was involved in emotional processing, whilst James Papez (1937) provided a detailed delineation of the neural circuitry of emotion and identified the importance of the hypothalamus, cingulate gyrus and hippocampus, now collectively known as the Papez circuit, in emotional processes. Building upon the work of Papez, MacLean (1952) also recognised the role of the amygdala in the control of emotion and included it with the Papez circuit in what he termed the ‘limbic system’ to describe the combination of these brain structures.

1.2| Background to Emotional Laterality

An early pioneer in emotion research, Broca (1861) also laid the foundations for research into hemispheric specialisation and the field of laterality. After observing the inability of several individuals to articulate sentences or even words after head trauma, and later performing post-mortem neuroanatomical studies on these same individuals, Broca discovered that this affliction appeared associated with lesions to the inferior frontal gyrus. Furthermore, Broca remarked that this expressive aphasia was only observed in individuals where lesions had occurred in the left hemisphere and that identical damage to the right hemisphere did not appear to elicit an identical effect.

John Hughlings-Jackson (1878, 1879) distinguished between *intellectual* speech and *emotional* speech through further investigation of hemispheric lesions and found that individuals, such as those studied by Broca, which had been unable to articulate informational content in speech with words had still been able to convey the residual emotional content through intonation; indicating that the left hemisphere controlled cognitive verbal expression while the undamaged right hemisphere mediated the emotional content of verbal expression.

Although Hughlings-Jackson (1878, 1879) had alluded to the lateralisation of emotion it was almost a century before this topic became the subject of active investigation with Campbell (1982) the first to explicitly postulate right hemispheric specialisation in the perception and expression of affective information. This *Right Hemisphere Hypothesis* was based upon a review of the literature, focusing upon the effect of unilateral brain lesions, and examined the evidence that emotional processes were affected by right hemisphere damage. Campbell concluded that there was significantly robust evidence that the right hemisphere was responsible for the interpretation and expression of emotion. Campbell further noted that evidence for the right hemisphere controlling negative emotion was particularly pronounced but reiterated that the right hemisphere was also dominant for positive emotion.

Silberman & Weingartner (1986) also reviewed the literature and also reported a distinction between positive and negative emotions but reached a different conclusion, suggesting that although the right hemisphere controlled negative emotions, positive emotions appeared to be modulated by the left hemisphere: a pattern that became known as the *Valence Hypothesis*. Silberman & Weingartner further suggested that the varied methodologies of previous research made it difficult for direct comparisons between studies. For example, for verbal tasks, the enhanced involvement of the left hemisphere in language processes may bias apparent hemispheric activation during studies of emotional lateralisation. In addition, variance in the position of brain lesions was also highlighted as a possible factor to explain inconsistent findings between studies. Silberman & Weingartner concluded from these studies that hemispheric specialisation for the control of emotion appeared more pronounced in anterior loci of the brain while posterior regions showed no or marginally reversed emotional asymmetry.

A third theory, the *Approach-Withdrawal Hypothesis*, was proposed by Davidson (1984) and also argued that emotion was functionally divided between the hemispheres but according to this theory the dichotomy was between behaviours that served to increase or decrease proximity between interactants. For example, affiliative behaviours, such as play, were considered approach emotions and identified as left hemisphere processes, while fear was identified as a withdrawal emotion that was controlled by the right hemisphere. However, as Davidson *et al.* (1990) have subsequently conceded, not all approach emotions, such as joy or excitement, contain an approach element, leading others including Ekman (1992) to conclude that the Approach-Withdrawal model is untenable. Furthermore, and particularly applicable to animal studies, the emotion of fear is recognised for its elicitation of the ‘fight or flight’ response (Cannon, 1932) and though ‘flight’ behaviour can be considered withdrawal, ‘fight’ behaviour conversely involves an approach, thereby highlighting a further limitation of the Approach-Withdrawal Hypothesis.

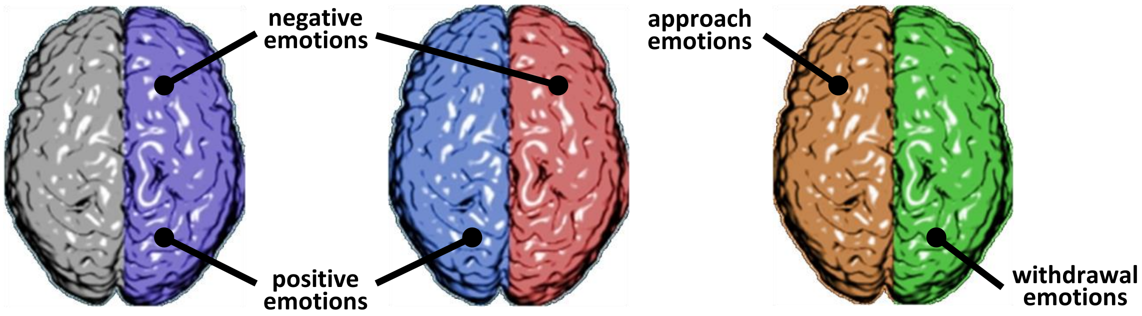

Figure 1.1 | Comparing the Right Hemisphere Hypothesis (L), Valence Hypothesis (C) & Approach-Withdrawal Hypothesis (R) and how each hypothesis proposes emotion is controlled in the brain.

The studies reviewed by Campbell (1982) and Silberman & Weingartner (1986; the differences/similarities between these theories have been contrasted in Table 1.2) were largely based upon post-mortem neurological examinations of individuals with noted atypical behaviours as a consequence of head trauma, wherein particular behaviours were correlated with particular brain lesions. Such methods were therefore highly reliant upon finding individuals that met specific brain injury criteria and as the studies could not be completed until after the natural death of these individuals, it is likely that data were acquired slowly and in small volumes. Consequently, it was understandable that methods which increased sample sizes and considerably reduced time expenditure came to the fore of emotional laterality research and in this respect comparative animal models are particularly advantageous, especially given the additional evolutionary perspective on *Homo sapiens* that was offered by studying closely related species.

theory	emotional valence of interactions	side of subject on which they are predicted to occur
Right Hemisphere Hypothesis (Campbell, 1982)	negative	left
	positive	left
Valence Hypothesis (Silberman & Weingartner, 1986)	negative	left
	positive	right

Table 1.2 | Summarising the predictions that the two key theories for the lateralisation of emotion make regarding how behavioural interactions of a positive or negative emotional valence are more likely to occur on one or other side of the subject

1.3 | Emotional Laterality in Animals

The first to investigate emotional laterality in a non-human study was Rogers (1980) on the domestic chick, *Gallus domesticus*, and involved the injection of a protein biosynthesis inhibitor (cycloheximide) into either the left or right hemisphere to impair its functionality. Rogers found that when the left hemisphere was immobilised chicks expressed elevated levels of agonistic and sexual behaviour but when the right hemisphere was impaired no similar effects were observed. The results of this study thereby provided some of the first evidence that emotion was lateralised in non-human species. The interpretation of these results were however open to ambiguity, as it was unclear whether the right hemisphere was directly responsible for the interpretation and expression of negative and sexual behaviour or whether the left hemisphere moderated and suppressed these behaviours.

Using less invasive methods, Andrew & Brennan (1983) were able to simulate impaired hemispheric functioning by temporarily restricting visual input to one or other cerebral hemisphere in domestic chicks. Due to the complete decussation of optic fibres in avian species, whereby the optic fibres from the left eye project only to the contralateral right hemisphere and the right eye projects only to the left hemisphere (Weidner *et al.*, 1985), eye patches were used to temporarily blind chicks in one eye during testing and the responses of the chicks to the presentation of internally illuminated coloured beads were then observed. Andrew & Brennan reported a significantly stronger reaction from chicks that viewed these novel stimuli with their left eye than those that viewed the bead with their right eye; results which therefore indicated that novel, fear-inducing stimuli were more closely assessed with the right hemisphere.

Using a similar paradigm, domestic chicks were observed on a daily basis for the first two weeks from hatching and presented with visual stimuli (Dharmaretnam & Andrew, 1994). Rather than enforcing eye preferences upon subjects and looking for differences in consequent reactions, unconditioned chicks were observed as they inspected three separate stimuli (a novel light source, a rat or an adult hen) and any naturally occurring eye preferences were noted. The rat was not found to elicit any significant lateral biases but strong eye preferences were observed for each of the other two stimuli. Presentation of an adult hen elicited a right eye bias while the light stimulus elicited a left eye bias but it was also observed that around the eighth day the light stimulus instead elicited a strong right eye bias. Previous observations also indicate a change in eye preferences of chicks approximately nine days after hatching (Rogers & Ehrlich, 1983; Andrew, 1988; Workman & Andrew, 1989) and suggested that although a right eye bias was initially observed in response to the light stimulus, the change was representative of the left and right eyes beginning to function as a coupled system rather than independent units. Dharmaretnam & Andrew further suggested that the development of strong left eye preferences after day 11 implied that lateralisation was an ontogenic process similar to that observed in humans (Thatcher *et al.*, 1987) and that this left eye preference was indicative of the right hemisphere exerting dominant control over this system for assessing novel stimuli. However, as the subjects in Dharmaretnam & Andrew's study had been equally naive to all three stimuli (rat, hen and light) interpreting the difference in results with respect to novelty appears inconsistent and a further contextual difference between the stimuli must therefore exist.

Evans *et al.* (1993) had also presented a novel stimulus to adult hens by simulating a predator (hawk) flying over the test enclosure. Ambiguity regarding this stimulus was reduced as the visual stimulus was preceded by playback of a pre-recorded ‘aerial alarm’ vocalisation (from males from the same population) and it was observed that a significant left eye preference was expressed when hens responsively looked upwards for a predator, thereby demonstrating right hemisphere control for a negative stimulus. Use of a simulated predator was further employed by Cantalupo *et al.* (1995) who presented this stimulus to immature and adult poeciliid fish, *Girardinus falcatus*, and observed their turn escape responses. Similar to birds, fish also have complete decussation at the optic chiasma wherein each eye projects solely to the contralateral hemisphere (Sovrano *et al.*, 1999) and Cantalupo *et al.* found that initial trials elicited right turn escape responses wherein the fish visually attended to the fear-inducing stimuli with their left eye which thereby corresponded with a right hemisphere control of this behaviour. However, with continued trials the right turn bias decreased and became a strong left turn bias; thereby suggesting that as subjects became habituated to the stimulus the emotional context of the scenario changed. The results of the initial trials appear consistent with right hemisphere control for affectively negative scenarios but whether the subsequent change in emotional context can be considered a shift to an affectively positive scenario is unclear, so these data do not provide clear support for either right hemisphere or valence model of emotion (Campbell, 1982; Silberman & Weingartner, 1986). Furthermore, it is possible that if habituation to the stimulus suppressed the subjects’ instinctive turn escape reflex it may then have permitted the subjects to express the right eye monitoring behaviour that had been previously reported in several similar species of poeciliid fishes (Dugatkin, 1991; Bisazza *et al.*, 1997b).

1.4| Observations from Natural Behaviours

While the use of a simulated predator by Cantalupo *et al.* (1995) demonstrated success in initial trials the apparent habituation of the subjects suggested that the lack of genuine danger from this visual stimulus may soon have been realised. However, by investigating interactions between two live conspecifics unpredictability is ensured and therefore habituation is unlikely. The first study to employ this method was also the first example of emotional laterality research in a free-ranging species in a population of gelada baboons (*Theropithecus gelada*, Casperd & Dunbar, 1996). Based upon video footage taken of a large troop of gelada in Ethiopia's Simien Mountains, Casperd & Dunbar observed naturally occurring interactions between adult males and investigated lateral biases before, during and after conflict behaviour. By observing naturally elicited interactions, behaviour could be recognised and accurately interpreted in terms of their emotional contexts, thereby avoiding the ambiguity that may have affected interpretation of previous experimental paradigms (e.g. Dharmaretnam & Andrew, 1994; Cantalupo *et al.*, 1995).

A further contrast between Casperd & Dunbar's (1996) study and the early experimental work in this field described above (Rogers, 1980; Dharmaretnam & Andrew 1983; Cantalupo *et al.* 1995) was the difference in visual systems between the species studied. In most birds and fish the laterally positioned eyes result in almost completely distinct left and right monocular visual fields and due to the complete decussation of optic fibres, determining the controlling hemisphere during a particular behaviour is straightforward. Gelada and many other mammalian species however possess forward facing eyes resulting in a considerable binocular overlap between the visual fields of the left and right eyes. In addition, the optic fibres of these mammalian species have only partial decussation, meaning that each eye projects to both hemispheres with the nasal half of the retina (that closest to the facial midline) projecting to the contralateral hemisphere and the opposite temporal half of the retina projecting to the ipsilateral hemisphere.

Bearing in mind that the image is inverted as it passes through the lens of the eye, for visual targets positioned non-centrally with regards to the facial midline the main projection of that image is still to the contralateral hemisphere and thus assumptions can still be made as to which hemisphere controls visual processing during a particular task or behaviour. However, where the attention of a subject with binocular vision is directed centrally it is unlikely that one hemisphere can be considered to dominate in the processing of the perceptual information. Casperd & Dunbar (1996) attempted to address this concern by eliminating centrally occurring interactions from their analyses entirely, although this method may therefore lead to an overestimation of lateral bias.

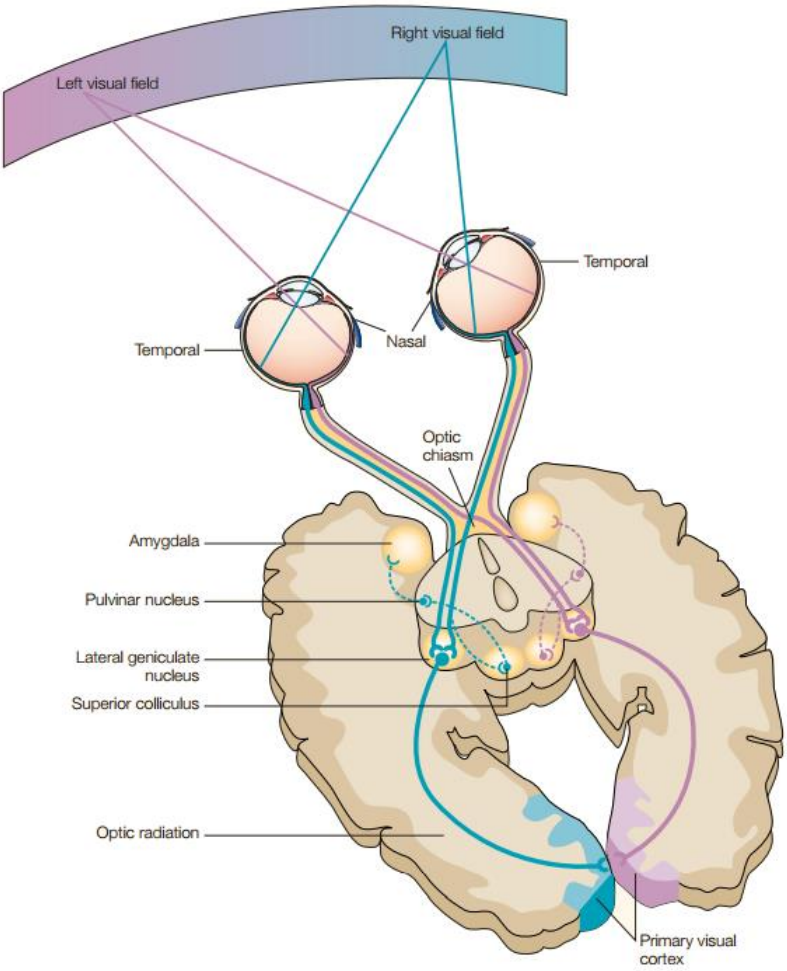

Figure 1.3 | Illustrating the degrees of perception for each eye in eutherian mammals depending upon the position of a visual target and the subsequent projections of each eye to both hemispheres. Reproduced from Hannula *et al.* (2005).

Casperd & Dunbar (1996) reported that a significant left visual field bias existed during agonistic interactions and they suggested that this was evidence of right hemisphere dominance in the control of emotional processing. In another study on patterns of injuries in yellow baboons, *Papio cynocephalus*, injuries had been inflicted significantly more frequently on the right side of the head and body than the left (Drews, 1996). However, Casperd & Dunbar observed no significant asymmetrical distribution of injuries in geladas. Drews' observations could indicate a corresponding right side lateral bias in agonistic interactions, as it might be expected that a lateral bias for physical interaction also followed from a similar lateral bias in the elicitation of the interaction. Indeed, Casperd & Dunbar predicted that a left side bias for visual field preferences would correspond to a left side bias for facial injuries. The lack of lateral bias in injuries reported may have been due to the fast nature of physical conflict, whereby it was difficult for individuals involved in such agonistic encounters to position themselves in the most advantageous way. Alternatively, they postulated that injuries may only have been inflicted upon individuals that positioned themselves poorly during conflict; however, the significantly asymmetrical distribution of injuries reported by Drews appears to challenge these suggestions.

Casperd & Dunbar had predicted that highly aggressive encounters would cause stronger left side biases than those with lower levels of arousal, based upon a similar continuum in humans (Campbell, 1978), but there were more profound left side biases for both high and low arousal interactions than those of an intermediate intensity. The strong bias for low intensity interactions was explained as likely being due to the uncertainty of the subject being approached as to the behavioural intentions of the approacher. In this context, Casperd & Dunbar explained that while interactions of an intermediate intensity, such as threats, immediately conveyed the intentions of one individual to another and thereby reduced vigilance behaviour, the lack of cues provided by unheralded approaches may have necessitated elevated vigilance behaviour similar to that observed for high intensity interactions.

Subsequent studies have also investigated lateral biases during agonistic interactions and Vallortigara *et al.* (1998) and Robins & Rogers (2006) reported similar left eye biases in male toads (*Bufo bufo* and *Bufo marinus*) and green tree frogs (*Litoria caerulea*) respectively. Overall, there is good evidence for right hemisphere control for negative emotion. However, as this is consistent with both the Right Hemisphere Hypothesis (Campbell, 1982) and the Valence Hypothesis (Silberman & Weingartner, 1986) investigation of other emotional contexts is required before determining which of these theories is valid. Preferential use of the right eye during predatory behaviour has also been observed in male toads and green tree frogs (Vallortigara *et al.*, 1998; Robins & Rogers, 2006), in the ornate dragon lizard, (*Ctenophorus ornatus* , Robins *et al.*, 2005), the common wall lizard, (*Podarcis muralis*, Bonati *et al.*, 2008) and the black winged stilt, (*Himantopus himantopus*, Ventolini *et al.*, 2005) with the latter study additionally observing a left eye preference for sexually directed behaviours in the same species. Gülbetekin *et al.* (2007) also observed left eye dominance for sexually guided behaviour in Japanese quail (*Coturnix coturnix japonica*).

However the interpretation of the results from predatory and sexual behaviours with regards to the conventional categories or valences of emotion is difficult. If these observations were to be considered within Silberman & Weingartner's (1986) Valence Hypothesis, the right eye bias found for predatory behaviour would therefore suggest it is categorised as affectively positive, but all other behaviours within the positive valence category serve a distinctly affiliative purpose. Furthermore, if the end purpose of predatory behaviour is ignored (*i.e.* that it serves to provide food for the predator or its offspring) then the physical act of one individual preying upon another is arguably analogous to an intensely aggressive behaviour which would therefore imply that a right eye and thus left hemisphere bias for predatory behaviour was at odds with both Campbell's and Silberman & Weingartner's hypotheses. In this instance, Davidson's (1984) Approach-Withdrawal Hypothesis may explain the right eye bias for predatory behaviour observed in some bird, amphibian and reptile species (Vallortigara *et al.,* 1998; Robins *et al*., 2005; Ventolini *et al.,* 2005; Robins & Rogers, 2006; Bonati *et al.*, 2008) as it includes an approach element. However, as this model is primarily based upon humans, a species with no comparable examples of direct animal-on-animal predatory behaviour, reconciling such behaviour with this model may be difficult. Other issues arise when applying the Approach-Withdrawal hypothesis to other emotional contexts as not all positive valence behaviours include an approach element and the fear response can be expressed through fight (approach) or flight (withdrawal) behaviour but is strongly associated with right hemisphere control (Davidson *et al.,* 1990; Ekman, 1992; Campbell, 1982; Silberman & Weingartner, 1986; Rogers, 2000). Overall, the Approach-Withdrawal hypothesis does not seem to accommodate research findings adequately.

There is also the possibility that the right eye bias for predatory behaviour is similar to the right eye bias for monitoring behaviour exhibited by several species of fishes (Dugatkin, 1991; Bisazza *et al.*, 1997a) and that predatory behaviour, like monitoring behaviour, expresses right hemisphere dominance due to inherent cognitive rather than emotional processes. As such, it appears that the Approach-Withdrawal hypothesis has limitations when applied to animal studies and, furthermore, although the lateralisation of predatory behaviour certainly merits further research, it may not provide the best model for investigating the lateralisation of emotion, which may be better facilitated through the observation of conspecific interactions for which the emotional contexts are comparatively unambiguous.

1.5 | Positive Emotions

Although the chief distinction between the two contrasting theories of emotional lateralisation centres upon which hemisphere is specialised for the control of positive emotions, only a small number of studies have actively investigated how these behaviours are lateralised. Campbell’s Right Hemisphere Hypothesis (1982) states that all emotions are controlled in the same hemisphere whilst Silberman & Weingartner's (1986) Valence Hypothesis proposes that the right hemisphere controls only negative emotion and the left hemisphere is instead responsible for the interpretation and expression of positive emotions. It is therefore clear that the investigation of affectively positive contexts may considerably contribute to our understanding of the lateralisation of emotion yet this valence category is comparatively under-researched.

A number of studies, such as Rogers *et al.* (1994; small-eared bushbaby, *Otolemur garnetti*), Hook-Costigan & Rogers (1998b; common marmosets, *Callithrix jacchus*) and De Latude *et al.* (2009; red-capped mangabeys, *Cercocebus torquatus*) have attempted to elicit affectively positive contexts by presenting subjects with high value food items. By placing these food items in apparatuses which ensure they can only be seen into monocularly, eye preferences for each stimulus could then be tested. Based upon observations from this paradigm, Rogers *et al.* and De Latude *et al.* both evidenced a left eye bias although Hook-Costigan & Rogers observed a right eye bias. Closer consideration of the methods revealed that in the latter study, the subjects were rewarded with the high value food item they had viewed upon completing each viewing task while Rogers *et al.* and De Latude *et al.* instead rewarded subjects with a food item of lower value. The contrast in results between these studies may represent the elicitation of different emotional contexts, due to an inability to obtain higher value food items in some paradigms (Hopkins & Leavens, 1998; De Latude *et al.*, 2009). Furthermore, the influence of hunger (Hook-Costigan & Rogers, 1995) or activity in nearby enclosures (De Latude *et al.,* 2009) may also have influenced results, thereby suggesting that this method may not offer the best paradigm for controlling and analysing emotional contexts.

Studies based upon facial asymmetries, however, appear to avoid most of this contextual ambiguity and this method has been employed to investigate a range of emotional contexts and species. Hauser (1993) performed the first such study in rhesus macaques by comparing measurements of asymmetry from the left and right sides of the face during agonistic interactions. The left side of the face was found to express emotions more intensely and more rapidly than the right side of the face, and this suggests right hemisphere specialisation for the control of emotion. This method was subsequently used by Hook-Costigan & Rogers (1998a) in a study on the common marmoset during fear expressions and social contact calls. Fear expressions elicited a larger left 'hemimouth' area while the social contact calls elicited the opposite effect and a larger right 'hemimouth' area. The observation of exaggerated expressions on the left side of the face for negative emotions (Hauser 1993; Hook-Costigan & Rogers 1998a), is consistent with both theories for the lateralisation of emotional processes. However Hook-Costigan & Rogers stated that the social contact call was not necessarily representative of a positive emotional context and instead suggested that the Right Hemisphere Hypothesis (Campbell, 1982) remained a more appropriate explanation for the lateralisation of emotion than the Valence Hypothesis (Silberman & Weingartner, 1986). Hauser & Akre (2001) and Fernández-Carriba *et al.* (2002) provided further support for Campbell's Right Hemisphere Hypothesis through their studies of facial asymmetry in rhesus macaques and chimpanzees, *Pan troglodytes*, respectively. Both these studies included negative and positive facial expressions and evidenced exaggerated left side biases for both emotional contexts. A more recent study by Wallez & Vauclair (2011) on olive baboons, *Papio anubis*, also measured facial asymmetries for several positive and negative emotional contexts but reported significant asymmetry (a larger left hemimouth) for the affectively negative screeching behaviour alone.

The support for the Right Hemisphere Hypothesis (Campbell, 1982) demonstrated by these studies illustrates the effectiveness of the facial asymmetry model for analysing the lateralisation of emotion, however, a significant caveat of this model is the difficulty of applying it to non-primate species. The ability of primates to convey their intentions or emotional state through facial expressions is unrivalled in the Animal Kingdom (Waller &

Micheletta, 2013) and though several species can express a number of emotions through facial expression, such as brown bears, *Ursus arctos* (Egbert & Stokes, 1976), fur seals, *Arctocephalus forsteri*, (Miller, 1975) walruses, *Odobenus rosmarus* (Miller, 1975), and several species of canid (Fox, 1970; grey wolf, *Canis lupus*; coyote, *Canis latrans*; grey fox, *Urocyon cinereoargenteus*; red fox, *Vulpes vulpes*; Arctic fox, *Vulpes lagopus*) the lack of facial dexterity in other species and non-mammals in particular (Diogo *et al.*, 2009), impairs the use of this model for cross species comparison. Additionally, though there are some examples of other species capable of measurable facial expressions the comparatively flat facial morphology of primates is considerably more conducive to measuring facial asymmetry than any other species, again limiting the application of this model.

As our understanding of the evolution of lateralisation is greatly enhanced through comparative research Casperd & Dunbar's (1996) observation of naturally occurring interactions remains the best paradigm for cross-species comparison. This paradigm also avoids the ambiguity about emotional context that may have affected previous studies (*e.g.* Rogers, 1980; Dharmaretnam & Andrew, 1994; Ventolini *et al.*, 2005) and provides an opportunity to observe and interpret the full spectrum of emotional interactions in almost any animal species irrespective of morphology.

Prior to the three studies detailed in this thesis, only Baraud *et al.* (2009) had used natural interactions as a method to examine both positive as well as negative emotional contexts. In their study, Baraud *et al.* observed naturally occurring positive, negative and neutral valence interactions within small populations of red-capped mangabeys and grey-cheeked mangabeys, *Lophocebus albigena*, and noted any visual field preferences during these interactions. There was no significant influence of emotional valence for either species, but an overall left side bias during interactions was observed for grey-cheeked mangabeys which supports Campbell's (1982) Right Hemisphere Hypothesis. However, Baraud *et al.* found that red-capped mangabeys expressed a right side bias during interactions. The interpretation of this latter result is not as clear as it contrasts with both Campbell's and Silberman & Weingartner's (1986) theories although it highlights that closely related species do not necessarily express similarly lateralised behaviour. It could indicate a difference in motivation for each species similar to that seen in fish (Dugatkin, 1991; Bisazza *et al.* 1997) but may be a result of small sample sizes in both species. Moreover, Baraud *et al.* did not control for the binocular vision of their study species and determined all observed interactions to have

Behaviour	Left Hemisphere Control	Right Hemisphere Control
Negative	gelada baboons: Drews (1996) red-capped mangabeys: Baraud *et al.* (2009)	**CAMPBELL (1982);** **SILBERMAN & WEINGARTNER (1986);** domestic chickens: Rogers (1980) Andrew & Brennan (1983) Evans *et al.* (1993) poeciliid fish: Cantalupo *et al.* (1995) Vallortigara *et al.* (1998) gelada baboons: Casperd & Dunbar (1996) common marmosets: Hook-Costigan & Rogers (1998a) rhesus macaques: Hauser & Akre (2001) chimpanzees: Fernández-Carriba *et al.* (2002) green tree frog: Robins & Rogers (2006) grey-cheeked mangabeys: Baraud *et al.* (2009) olive baboons: Wallez & Vauclair (2011)
Positive	**SILBERMAN & WEINGARTNER (1986),** common marmoset: Hook-Costigan & Rogers (1998b) red-capped mangabeys: Baraud *et al.* (2009)	**CAMPBELL (1982),** small-eared bushbaby: Rogers et al. (1994) rhesus macaques: Hauser & Akre (2001) chimpanzees: Fernández-Carriba et al. (2002) red-capped mangabeys: De Latude et al. (2009) grey-cheeked mangabeys: Baraud *et al.* (2009)
Sexual	-	domestic chickens: Rogers (1980) black-winged stilts: Ventolini *et al.* (2005), Japanese quail: Gülbetekin et al. (2007)
Neutral	-	red-capped mangabeys & grey-cheeked mangabeys: Baraud *et al.* (2009)
Predatory	poeciliid fish: Vallortigara *et al.* (1998) ornate dragon lizard: Robins *et al.* (2005) black-winged stilt: Ventolini *et al.* (2005) green tree frog: Robins & Rogers (2006) common wall lizard: Bonati *et al.* (2008)	-
Monitoring	poeciliid fish: Cantalupo *et al.* (1995), Dugatkin (1991), Bisazza *et al.* (1997)	-

Table 1.4 | Summarising the studies reviewed in the introduction which reported a significant lateral bias; arranged by behavioural context/emotional valence and hemispheric dominance.

occurred in a left or right visual hemifield, based upon the position of these interactions relative to the subject's facial midline. It is therefore possible that some of Baraud *et al.*'s data which had been determined as laterally biased may in fact have occurred centrally, with no single eye or hemisphere exerting dominance; therefore influencing their conclusions.

As can be seen from Table 1.4 there is limited evidence to dispute Campbell (1982) and Silberman & Weingartner's (1986) agreed assertion that the right hemisphere dominates in the perception and expression of negative valence behaviour. However, determining the lateralisation of position emotion continues to lack the same level of consensus. The variation in results between the small number of studies to have investigated positive emotion, allied to the methodological issues regarding how these positive emotions were elicited in these studies, indicates that further research is needed to identify whether the Right Hemisphere Hypothesis or the Valence Hypothesis is more valid and this shall serve as the primary aim of this thesis. In parallel with an assessment of lateralisation for positive and negative emotional contexts this thesis shall also consider behaviours of sexual and neutral emotional contexts. Baraud *et al.* (2009) remains the only study thus far to define low arousal interactions with no clear context as neutral and this may be an important emotional context to consider as it could identify whether an individual subject or group demonstrates behavioural lateralisation in scenarios without strong positive or negative emotional arousal. The inclusion of a sexual emotional context permits further examination of the right hemisphere biases observed by Rogers (1980), Ventolini *et al.* (2005) and Gülbetekin et al. (2007) during such behaviours and allows comparison of the presence, or absence, of lateralisation between sexual and other emotional contexts.

As to the research model that shall be employed by this thesis, there is a compelling rationale for replicating the paradigm proposed by Casperd & Dunbar (1996) and subsequently expanded by Baraud *et al.* (2009) whereby only naturally occurring social interactions are recorded and analysed. Given the potential ambiguity of artificially elicited positive emotional contexts (*e.g.* Rogers *et al.*, 1994; Hook-Costigan & Rogers, 1998b; De Latude *et al.*, 2009) it was felt that naturally occurring behaviours provided the most accurate method for observing each emotional context whilst also permitting observation of the full range of behavioural interactions that a study species may perform.

1.6 | Other Factors

Although the primary aim of this thesis is to investigate how emotion is lateralised, a number of additional factors have been identified that have previously been found to influence lateral biases and thus they shall also be considered.

1.6.1—Age

Ontogenic factors have been identified in a number of studies on lateralisation with some highlighting that lateral biases can be influenced at the earliest stages of development. Rogers & Bolden (1991) and Rogers (2000) found that the direction of light upon unhatched eggs profoundly influenced the subsequent direction of lateral bias after hatching and Dharmaretnam & Andrew (1994) have reported that significant lateralisation in chicks is established as soon as the second week after hatching. In a study of common marmosets, Hook & Rogers (2000) found that infants did not express hand preferences at one or two months old but that significant hand preferences became apparent in the same individuals by five to eight months. Several studies have also compared differences between age categories within the same population with adult rhesus macaques (Lehman, 1970; 1978) and chimpanzees (Hopkins, 1994) both found to demonstrate significant handedness at the individual level whilst subadults did not. Tufted capuchins, *Cebus apella*, (Westergaard & Suomi, 1993) and olive baboons (Vauclair & Fagot, 1987; Vauclair *et al.*, 2005) have been found to express significant right hand biases at the group level in adults that were not apparent in the subadults. In addition, Hauser & Andersson (1994) studied turn biases in response to acoustic stimuli in rhesus macaques and also reported a significant orientation asymmetry in adults that subadults did not express.

These studies appear to suggest that age influences the strength of lateral bias but that the direction of this early lateral bias is not always consistent within the population or species. It may therefore be expected that similar observations will be made by the present study whereby adults should express stronger lateralisation than subadults.

1.6.2—Sex

The observation of sex differences has been recorded in a broad range of species and studies within the field of laterality beginning with one of the key studies upon which the present study is based. Silberman & Weingartner (1986) reported in their Valence Hypothesis paper that human males were significantly more likely to express affectively positive behaviour whilst females tended towards negative emotional behaviour, which, by extension of the Valence hypothesis, may imply that females express left side biases and that males are more right side biased. There appear to have been no similar observations in the animal literature for visual field preferences, although handedness studies offer numerous examples of sex effects.

Significant left hand/paw preferences have been reported in male but not female tufted capuchins (Westergaard & Suomi, 1993), dogs, *Canis lupus familaris* (Wells, 2003), rats, *Rattus norvegicus* (Camp *et al.*, 1984), chimpanzees (Corp & Byrne, 2004), and six species of lemur: ring-tailed lemur, *Lemur catta*, crowned lemur, *L. coronatus*, black lemur, *L. macaco*, mongoose lemur*, L. mongoz*, ruby-bellied lemur, *L. rubriventer*, and the common brown lemur, *L. fulvus* (of which five subspecies were also included: *L. f. albifrons, L. f. collaris, L. f. fulvus, L. f. rufus,* and *L. f. sanfordi*; Ward *et al.*, 1990). Significant right hand preferences have been observed for female ring-tailed lemurs (Milliken *et al.*, 1989) and for siamang, *Symphalangus syndactylus*, white-handed gibbon, *Hylobates lar*, and black-crested gibbon, *Nomascus concolor* (Stafford *et al.*, 1990).

The cause of these sex differences are unclear although Milliken *et al.* (1989) and Ward *et al.* (1990) have speculated that it may be due to the effect of testosterone in the womb during prenatal development. Elevated levels of testosterone may impair the development of the left hemisphere in males and thus lead to the manifestation of a right hemisphere/left hand dominance. Indeed, the influence of testosterone upon hemispheric development *in utero* has been suggested by human studies as a cause of left handedness in males (Geschwind & Galaburda, 1985). Further examples from the human literature include studies of females with Congenital Adrenal Hyperplasia, whereby the adrenal glands produce abnormally high levels of testosterone, and who were found to demonstrate an increased incidence of left handedness (Nass *et al.*, 1987; Smith & Hines, 2000). A key distinction between these findings is that whilst they propose that testosterone prenatally influences lateralisation, Nass *et al.* and Smith & Hines suggest that testosterone exerts an on-going influence of lateralisation that persists from (before) birth into adulthood.

Although the results of these studies are suggestive of sex differences in lateralisation in human and non-human species, further evidence is lacking. Indeed, Hopkins' (2006) extensive review of the handedness literature in non-human great apes found no significant male-female differences. However, due to the lack of studies to have explicitly investigated the influence of sex upon behavioural lateralisation and, more specifically, visual field preferences, it remains an intriguing factor for consideration.

1.6.3—Rank

The social rank of an individual has been given little consideration as a factor that may influence lateralisation. Baraud *et al.* (2009) remain the only study to actively investigate its effect upon lateral bias.

High ranked red-capped mangabeys engaged in more negative behaviour when a group member was positioned on their right whilst high ranked grey-cheeked mangabeys conversely interacted more positively with conspecifics positioned on their left. A positive correlation between strength of lateralisation and rank was also found in grey-cheeked mangabeys with higher ranked individuals expressing stronger lateral biases. However, Baraud *et al.* offered no explanation as to why these effects of rank were observed in either species.

It is possible that the stronger lateralisation observed in higher ranking individuals may have been related to vigilance behaviour whereby lower ranked mangabeys performed social monitoring over a wider visual range and thus expressed less pronounced visual field biases. Research by Keverne *et al.* (1978) in talapoin monkeys, *Miopithecus talapoin*, and by Alberts (1994) in yellow baboons had previously found that lower ranked individuals performed more frequent vigilance glances at conspecifics than their higher ranking counterparts. Although the studies by Keverne *et al.* and Alberts did not consider the direction of these vigilance glances the existence of a relationship between rank and monitoring behaviour may also explain the results found by Baraud *et al.* (2009); particularly regarding the correlation between rank and strength of lateralisation observed in the grey-cheeked mangabeys. Further research is therefore required to determine whether support exists for Baraud *et al.*'s suggestion that rank influences visual field biases as this study included only five individuals from each species of mangabey as research based upon a larger population size may also assist in determining the overall influence of rank.

1.6.4—Emotional Intensity

An additional factor that may influence lateral bias during emotional behaviour is the level of arousal or intensity of that behaviour. In their study of agonistic interactions in gelada baboons Casperd & Dunbar (1996) observed that low and high arousal behavioural interactions elicited stronger left side preferences than those of medium arousal. As mentioned in section 1.4, Casperd & Dunbar suggested that the existence of a strong lateral bias for high intensity interactions was not unexpected; previous research on the lateralisation of emotion in humans had proposed that a positive relationship existed between emotional intensity and the strength of lateralisation (Campbell, 1978). However, the reason for the strong left side bias also observed for low intensity interactions was less clear but may have been due to the inability of the individual observing the approach of another to accurately determine the intentions of the approacher, causing heightened arousal in the individual being approached and a stronger lateral bias (Casperd & Dunbar, 1996).

In addition, Wallez & Vauclair (2011) reported an influence of emotional intensity upon oro-facial asymmetry in olive baboons during a variety of non-physical interactions. In their study, Wallez & Vauclair observed olive baboons during affiliative (positive) and agonistic (negative) encounters and reported that only high intensity agonistic interactions elicited a significant left-biased oro-facial asymmetry and other behaviours did not. Furthermore, as Casperd & Dunbar included only negative valence behaviours and Wallez & Vauclair observed only four types of behaviour (two positive and two negative) it is hoped that the proposed study, by observing all types of behavioural interaction, will provide a more detailed assessment of the influence of emotional intensity upon lateralisation.

1.7 | Choice of Species & Locations

1.7.1—Preference for Captive Populations

Based upon the author’s previous experiences of conducting observational research it was decided that captive research facilities offered a more efficient opportunity for data collection than wild, field-based study sites without compromising the validity of the study. By their very nature, captive populations are confined to a limited range over which they can forage or travel and it is therefore not necessary to expend time fully habituating the study population or locating them each day, as may be the case in the wild, that might otherwise be spent observing the subjects. Secondly, whilst captive populations may be housed in naturalistic enclosures such environments rarely contain as much physical enrichment as the species' natural environment, particularly in terms of flora, that may obscure the observation of these species, therefore it is likely that direct observation of captive populations is more easily facilitated than in the wild. Finally, although great care is generally taken to ensure that captive populations can express behaviour that might be considered normal for a wild population, confinement to an enclosure limits the expression of several behaviours and especially those associated with isolation or separation. Social segregation within a population is often related to rank and, whether self-imposed or driven by other members of the group, reduces the level of agonistic interaction within the population and is an important avoidance behaviour for lower ranked individuals (Maynard Smith, 1974; Conradt, 2005). It is obviously not desirable that this behaviour cannot be expressed by captive populations and it is hoped that, should scenarios of intense and sustained aggression between individuals within a captive population arise, one or more parties would be temporarily or permanently relocated. However, the outcome of this is that captive populations may express an elevated occurrence of behavioural interactions than might be expected in the wild, thus providing the opportunity for a higher frequency of interactions to be observed.

1.7.2—Selecting Species

An aim of the proposed study is to perform a cross-species comparison and as the focus of this study is upon behavioural interactions, species that inhabit large groups are considered preferable to those normally found in smaller populations or that live solitarily as it is likely that groups containing a large number of individuals will provide a higher occurrence of behavioural interactions within a shorter timescale. Similarly, it is expected that species which live in dynamic multi-male/multi-female societies where access to resources is influenced by inter-individual encounters may also enable the observation of a greater frequency of behavioural interactions than in species where age or physical attributes are the chief determinants of rank status (Fredrickson & Sackett, 1984; Noë & Sluijter, 1990; Chase *et al.*, 2002).

From a comparative perspective, non-human primates offer a valuable insight into the evolutionary precursors of hemispheric specialisation in humans and the similarities of human and non-human visual systems, as identified by section 1.4, allow further comparisons to be made regarding lateralised visual field biases in the expression of emotional behaviour that may not be possible through studies of birds or fish.

The phylogenetic relatedness of humans to great apes and Old World monkeys in particular has made species from these taxa especially popular for numerous studies of hemispheric specialisation. Access to large populations of socially housed great apes is limited whereas a number of Old World monkey species are housed in large populations in a variety of behavioural research sites and two such species, olive baboons and rhesus macaques, were thus selected for the present study. In addition, a third non-primate species was selected as an out-group to increase the scope of the proposed research and to enable comparison across taxa.

1.7.2.1 Olive baboons

So called for their greenish grey coat, olive baboons are one of the largest and the most wide-ranging baboon species occurring across much of equatorial Africa (see Figure 1.5) in a variety of habitats including desert, savannah, evergreen montane forest, and rocky kopjes (Dunbar & Dunbar, 1974; Barton &Whiten, 1993). They are generalists and have a varied omnivorous diet that mainly includes roots, fruit, leaves, insects, and small vertebrates, but have also garnered a reputation for crop-raiding where their home range overlaps with farmland (Dunbar & Dunbar, 1974; Nowak, 1999). The home range sizes for olive baboons have been recorded as varying from 745m^2 (Dunbar & Dunbar, 1974) to as much as 43.8km^2 (Barton *et al.*, 1992) with the significant contrast in area due to differences in a number of factors such as habitat, season, troop size and availability of resources.

Troops number between 15-150 individuals and are multi-male/multi-female societies composed mainly of females and subadult males born into the group and adult males that emigrated from their own natal groups after reaching sexual maturity (Dunbar & Dunbar, 1974; Ray & Sapolsky, 1992). Sexual maturity is reached in male and female olive baboons between four and six years of age and males are approximately twice as large as the females at full adult size (Packer, 1979; Smuts, 1985). Olive baboon troops are made up of a strict matrilineal dominance hierarchy in which most females maintain association with the same troop from birth and inherit the rank of their mother, leading to several closely related subgroups within each troop (Smuts, 1985; Ray & Sapolsky, 1992; Barton &Whiten 1993). Females within these matrilines regularly exchange affiliative behaviours such as grooming but also provide mutual support during agonistic encounters with other conspecifics or matrilineal sub-groups. Conversely, rank in male olive baboons is established and consolidated through primarily agonistic interactions with almost daily contests used to determine an individual’s access to females and other resources (Smuts, 1985). Males have also been observed forming coalitions with older males in particular grouping together to displace younger adult males, which are often higher ranked due to their better physical condition, from potential mates (Smuts & Watanabe, 1990). Agonistic interactions between individuals vary in level of arousal from low intensity behaviours, such as displacement, to highly intense aggressive physical bouts that commonly result in injury to one or both parties (Sapolsky & Share, 2004), but there are also a number of affiliative behaviours that play an important role in defining social status in olive baboons. Between males, ritualised greeting ceremonies occur frequently and often in socially neutral scenarios when there is no direct competition for resources, whereby one male may approach another and express a number of non-contact affiliative behaviours, such as lip-smacking, which the other male may reciprocate or reject (Smuts & Watanabe, 1990). Post conflict behaviour is also common in olive baboons and is highly affiliative with reconciliation often occurring between both of the individuals engaged in the bout (Castles & Whiten, 1998a; 1998b). Additionally, these individuals frequently reconcile with the kin of their opponent as well as their own supporters and are also more likely to engage in post conflict reconciliation if their opponent is valuable, such as a female with a young infant (Altmann, 1980; Castles & Whiten, 1998a; 1998b).

Sexual behaviour in olive baboons is polygamous and both males and females have multiple mates, although mating consortships occasionally occur and can last up to two weeks in length during which one male and one sexually receptive female attempt to mate exclusively (Bercovitch, 1983; 1991; Packer, 1979). Females are polyoestrus with cycles lasting approximately 37 days and occurring throughout the year (Bercovitch, 1991). The oestrus cycle of female baboons is characterised by significant sexual swelling of the anogenital region which lasts approximately 18 days and the size of tumescence is considered representative of fitness (Domb & Pagel, 2001). Ovulation occurs during the final week of the oestrus cycle when the swelling is also at its largest and which has been found to elicit elevated competition between males (Domb & Pagel, 2001). Gestation lasts about 180 days with interbirth intervals of approximately two years and the infants are weaned between 10-12 months (Smuts & Nicolson, 1989; Nash, 1978). Olive baboons have a lifespan of approximately 25 years in the wild but have been observed to live considerably longer in captivity (Nowak, 1999).

Olive baboons, along with other members of the genus *Papio*, are a popular species for behavioural and cognitive research owing to their known intelligence and demonstrable understanding of the complex social hierarchies in which they live (Cheney & Seyfarth, 2007). Dunbar’s (1998) Social Brain Hypothesis has postulated that living in large social groups necessitates a large brain and enhanced cognitive ability and for anthropoid primates in particular a quantitative relationship has been identified between group size and brain size (Dunbar, 2009). In brain size alone, olive baboons boast one of the largest brains in the Primate order outwith the great apes at approximately 201g (Montgomery *et al.*, 2010) but as

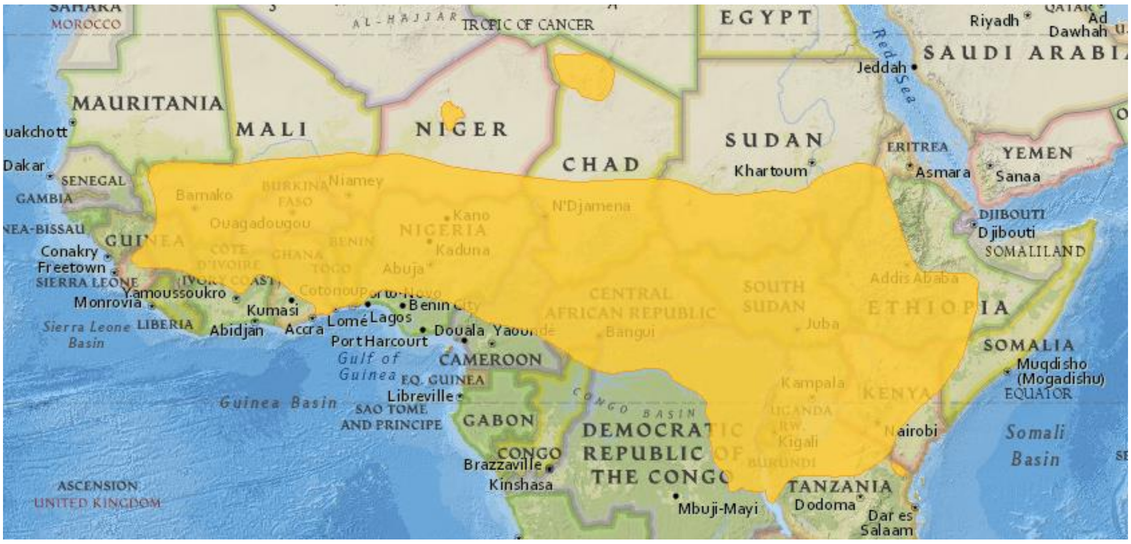

Figure 1.5 | A map of equatorial Africa highlighting the range of olive baboons. ©IUCN

such measurements are often heavily influenced by overall body size a neocortex to brain size ratio has become the preferred standard (Barton & Dunbar, 1997; Dunbar, 1998). In this instance olive baboons are no less impressive with a neocortex ratio (NCR) of 2.76 that is much closer to chimpanzees (NCR=3.22) than prosimian species such as the ring-tailed lemur (NCR=1.18) which have been found to perform less successfully on cognitive tasks than monkeys or apes (Roth & Dicke, 2005; all NCR values from Kudo & Dunbar, 2001).

Olive baboons have also featured prominently in the research of lateralisation with handedness in particular being the subject of much study in this species (*e.g.* Vauclair & Fagot, 1987; Westergaard, 1993; Vauclair *et al.*, 2005; Meguerditchian & Vauclair, 2006; Vauclair & Meguerditchian, 2007). As such, the pedigree of olive baboons in laterality research coupled with their varied range of behaviours and the lack of previous studies[1] to specifically investigate the lateralisation of emotion in this species makes olive baboons ideal for the proposed study.

The Station de Primatologie in Rousset, France is a research facility maintained by the Centre National de la Recherche Scientifique (CNRS) that houses several groups of olive

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[1] When this research was initially proposed in 2009 there was no existing literature regarding the lateralisation of emotion in olive baboons as Wallez & Vauclair's (2011, 2012) publications were subsequent to the research for this thesis.

baboons in large outdoor enclosures for observational research and, coupled with the additional incentive of working alongside some of the leading researchers in the field of laterality, provides a highly suitable location for observing this species.

The Station de Primatologie also houses a number of other species on site (guinea baboons, *Papio papio*, rhesus macaques, and squirrel monkeys, *Saimiri sciureus*) but the enclosures for these species are much smaller and as the dependent variable for the proposed study is the visual field used by subjects during behavioural interactions the size of these smaller enclosures would strongly influence visual field preference due to the proximity of enclosure walls or other physical obstructions within the enclosure.

1.7.2.2 Rhesus macaques

Due to their high intelligence, anatomical and physiological similarities to humans, and the comparative ease with which they can be bred and maintained in captivity, rhesus macaques are the single most studied non-human primate species (Mitruka 1976). Based upon Barton & Dunbar’s (1997) and Dunbar’s (1998) suggestion that a correlation exists between neocortex size and cognitive ability the neocortex ratio of 2.39 for rhesus macaques further demonstrates their intelligence as it compares favourably with other species known for their cognitive ability.

Aside from humans, rhesus macaques have the broadest geographical distribution of any primate species and the six recorded subspecies *(M. m. brevicauda, M. m. lasiota, M. m. mulatta, M. m. sanctijohannis, M. m. vestita, M. m. villosa)* are found across much of South, Central and Southeast Asia (Nowak, 1991; Southwick *et al.*, 1996; see Figure 1.6). Rhesus macaques are well adapted to coexisting in or near human settlements where they thrive in both urban and agricultural settings and have been found in much higher densities around such settlements than in the forest areas that make up their natural habitat (Richard *et al.*, 1989). Additionally, their home range size and diet also appear modulated by proximity to human settlements. The natural diet of macaques inhabiting regions with little or no human disturbance is mainly leaves, fruit, seeds and insects, whereas those closer to human settlements avail of cultivated fruit, vegetables and other foodstuffs through crop-raiding and foraging in bins (Richard *et al.*, 1989), or from hand-outs and offerings as rhesus macaques are often fed as a form of worship by local people (Wolfe, 2002). Likely due to the relative abundance of food, rhesus found near human settlements have a much smaller home-range than normally expected with some temple troops in India having a range as small as $10m^2$ whilst macaques in a natural habitat undisturbed by humans can have a range of up to $22km^2$ in some mountainous regions of China (Seth & Seth, 1986; Southwick *et al.*, 1996).

Rhesus macaques generally live in groups that number between 10-80 individuals but in several habitats, particularly where humans directly or indirectly provide food to support larger groups, these groups may contain several hundred macaques (Seth & Seth, 1986; Southwick *et al.*, 1996). Similar to olive baboons, rhesus macaques exhibit female philopatry and male dispersal whereby females rarely leave their natal groups whilst males emigrate from group to group in search of potential mates, perhaps several times in their lifetimes, but unlike olive baboons they often depart their natal group before rather than after reaching sexual maturity (Melnick *et al.*, 1984; Southwick *et al.*, 1996; Fooden, 2000). Males and females are sexually dimorphic with males larger than females when fully grown and males also take a year longer to reach sexual maturity than females; which do so around age three (Rawlins & Kessler, 1986).

For female rhesus macaques, social structure is matrilineal as they inherit their rank from their mother and rank between offspring is determined by age with the youngest ranked higher than their elder siblings: an inverse relationship between age and rank that is known as ‘youngest ascendency’ (Missakian, 1972; Seth, 2000). As such, rank amongst females remains largely stable across generations but this is not the case for males which also inherit their mother’s rank from birth but only maintain this rank whilst they remain with their natal group

Figure 1.6 | A map of central & southern Asia highlighting the range of Macaca mulatta. ©IUCN

(Berard, 1999). Upon transferring to a new group, male macaques must establish their rank through agonistic bouts and often form coalitions with other males to attempt to usurp the dominant individuals in the group (Missakian, 1972) with dominants sustaining their high status for an average of two years before being displaced themselves (Bercovitch, 1997). Post-conflict reconciliation is also an important behaviour in rhesus macaques although this behaviour has been noted to occur less frequently in this species than others of the same genus (de Waal & Ren, 1988; Higham & Maestripieri, 2010). Additionally, de Waal & Yoshihara (1983) have identified that the likelihood of individuals to engage in post-conflict behaviour is determined by the strength of the relationship between these individuals prior to the bout, whereby matrilineal relatives are more likely to engage each other in affiliative reconciliation than non kin.

As with olive baboons and several other species, aggression between male rhesus macaques has been found to increase in intensity when females are sexually receptive (Rowell, 1963; Smuts & Smuts, 1993). Female rhesus are seasonally polyoestrus and October – December are the usual months in which they are sexually receptive although some populations have been found in oestrus outwith this time period (Lindburg, 1971; Chapais, 1986). The ovarian cycle lasts for 28 days with oestrus lasting approximately 10 days of this cycle which is also accompanied by visible darkening of the face and anogenital region (Catchpole & van Wagenen, 1975; Waitt *et al.*, 2006). Ovulation occurs approximately at the midpoint of oestrus and this is indicated by the secondary sexual colourations when the face and anogenital regions are at their reddest (Waitt *et al.*, 2006). Whilst these sexual colourations serve to highlight the sexual receptiveness of the female, a similar observation has been made of male rhesus which have also been found to undergo a hormonally induced change in the colouration of the face and anogenital region during the mating season that may serve as a cue for mate quality (Waitt *et al.*, 2003). Gestation lasts approximately 164 days with an interbirth interval of between 12-24 months and infants are weaned after around 4 months (Fooden, 2000). Rhesus macaques have a life-span of approximately 25 years but have been observed living in captivity up to 40 years of age (Colman *et al.*, 2009).

The National Institutes of Health (NIH)-operated Animal Center in Poolesville, Maryland, USA contains an outdoor field station and houses a large, dynamic breeding colony of rhesus macaques that would provide considerable opportunity for behavioural observation. The exceptionally large and highly naturalistic environment provided for the rhesus macaques suggests they can express as close to natural behaviour as may be possible in captivity which therefore offers a unique opportunity for behavioural observation, making this a highly suitable location for conducting the proposed research.

1.7.2.3 Spotted hyaena

The spotted hyaena is Africa's most abundant predator and is found in much of Sub-Saharan Africa (see Figure 1.7), having the second widest range of the four hyenidae species after the striped hyaena, *Hyaena hyaena*, (Kruuk, 1972). Spotted hyaenas live in multi-male/multi-female clans of between 10-90 individuals and display fission-fusion social behaviour whereby the clan often fractures into smaller groups to locate food and/or hunt but reforms into a larger single unit to sleep in or near a communal den (Kruuk, 1972). The territory of a spotted hyaena clan may vary considerably in area depending upon the abundance of food and competition for other resources: ranging from less than 40km^2 in the Ngorongoro Crater to over 1,000km^2 in the Kalahari. Spotted hyaenas are opportunistic omnivores and, contrary to common knowledge, not merely scavengers but adept predators that frequently employ cooperative hunting strategies to pursue prey (Drea & Carter, 2009). In some habitats the spotted hyaena has displaced the lion, *Panthera leo*, as the apex predator with the latter observed to assume the role of scavenger from hyaena kills despite the fact that the lion is the only carnivore on the continent larger than the spotted hyaena (Kruuk, 1972; Carbone & Gittleman, 2002).

Spotted hyaenas adhere to a strict matrilineal hierarchy but unlike the primate species, and unusually amongst large mammalian carnivores, female spotted hyaenas exert complete dominance over their male counterparts and even the highest ranking male is subordinate to the lowest ranking female with the females also larger than the males at full sexual maturity (Frank, 1986). Female spotted hyaenas form multiple matrilineal kin groups with rank transferred from mother to progeny, whilst the males are mostly immigrants from other clans and are ranked according to a ‘queuing system’ whereby the sequence of arrival in the group determines seniority (Smale *et al.*, 1995).

Spotted hyaenas reach sexual maturity at around three years although the pattern of oestrus cycles remains largely unknown (M. L. Weldele, personal communication). It is understood that the females are polyoestrus with an oestrus period of approximately two weeks (Kruuk, 1972) but there appears to be no apparent regularity to the onset of oestrus as it is neither seasonal nor continuous, although it has been observed in captivity that should the dominant female come into oestrus the other females in the clan typically follow suit (M. L. Weldele, personal communication). Gestation periods last 110 days and cubs are weaned around 12-16 months (Kruuk, 1972) with spotted hyaena milk having the highest protein content of any terrestrial carnivore and the third highest fat content of any animal (Mills & Mills, 2011). Sexual maturity is reached at different ages in spotted hyaenas with males doing so at approximately age two whilst the females are a year later (Kruuk, 1972). Spotted hyaenas have a life expectancy of around 20 years but have been known to live as long as 41 years in captivity (Nowak, 1999).

As with many social carnivores, spotted hyaenas display a balance of agonistic and affiliative behaviours. Females in particular engage in competitive bouts over food and other resources and males have been observed to form coalitions to counter the dominance of females (Szykman *et al.*, 2003). Similar to olive baboons and rhesus macaques, aggression in male spotted hyaenas has also been observed to increase when females are sexually receptive (Szykman *et al.*, 2003) but unlike both of these monkey species hyaenas are more likely to engage in post-conflict reconciliation behaviour with non-kin than kin (Wahaj *et al.*, 2001). One affiliative behaviour in particular, a ritualised greeting ceremony, plays a highly significant role in spotted hyaena social behaviour and often occurs between two or more individuals during first meetings, following separation or immediately preceding mating (Kruuk, 1972). Depending upon the relative ranks of the individuals engaged in a greeting the level of arousal or emotional intensity of that greeting can vary considerably (Theis *et al.*, 2007) and in females the greeting ceremony has been observed to occur more frequently between kin and coalition partners than between other individuals (Smith *et al.*, 2011).

The behavioural synchrony demonstrated by spotted hyaenas during hunts has been suggested as evidence of a highly developed brain with two recent studies further supporting this claim (Drea & Carter, 2009; Benson-Amram & Holekamp, 2012). Drea & Carter's captive-based study challenged two hyaenas to work together to solve a food reward task and the results demonstrated a level of efficiency in cooperative problem solving similar to that of the great apes (Drea & Carter, 2009). More recently, Benson-Amram & Holekamp (2012) demonstrated the innovative problem-solving abilities of wild spotted hyaenas when faced

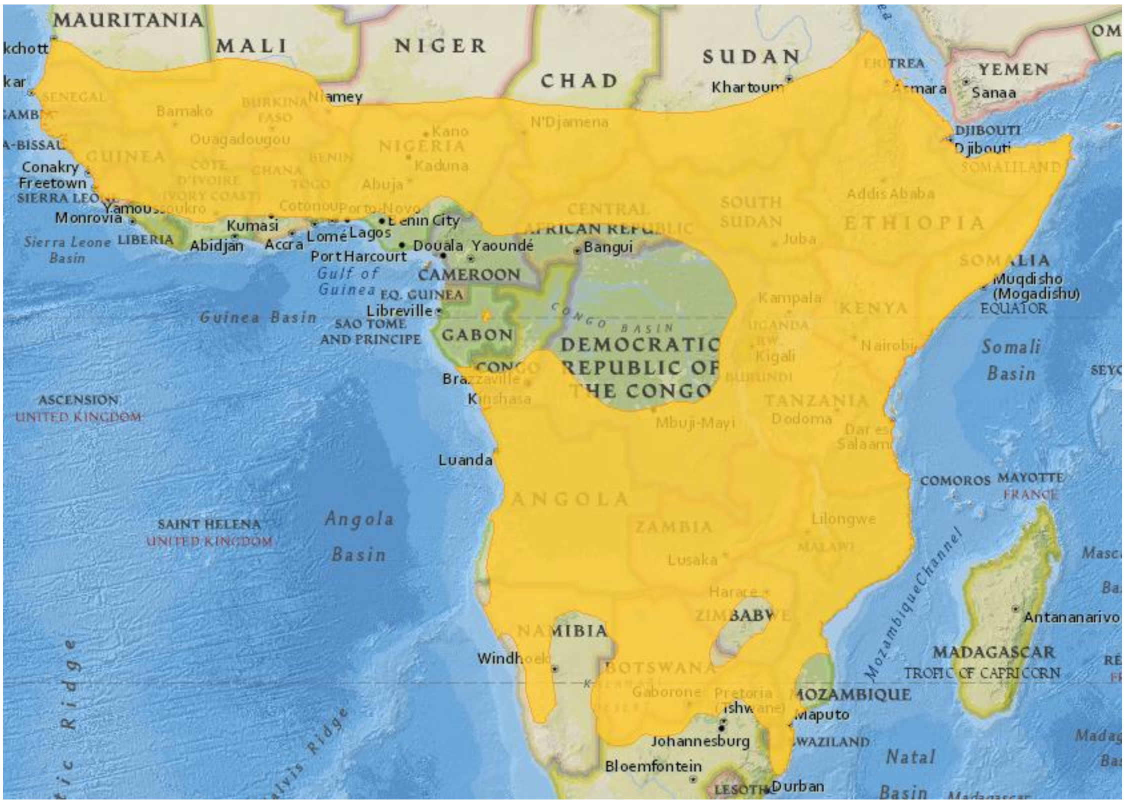
Figure 1.7 | A map of sub-Saharan Africa highlighting the range of Crocuta crocuta. ©IUCN

with a specially constructed puzzle box although neophobia appeared to impair the overall success rates. Benson-Amram & Holekamp suggested that successful problem-solving of man-made tasks in other species appeared to be related to a species' prior familiarity with man-made objects and should be considered when interpreting the results from their study or any subsequent research with wild subjects (Benson-Amram & Holekamp, 2012). The neocortex ratio of 1.94 for spotted hyaenas (Kudo & Dunbar, 2001) does not initially appear to suggest a highly intelligent social species but Holekamp *et al.* (2007) have suggested that this may be due to differences in brain structure between primates and other taxa that subsequently affect the calculation of the neocortex ratio. Holekamp *et al.* highlight that whilst the neocortex has received most of the focus when considering social cognition (Barton & Dunbar, 1997; Dunbar, 1998), it is specifically the frontal cortex that is most closely correlated with complex social behaviour (Adolphs, 2001; Amodio & Frith, 2006). In primates, the neocortex contributes disproportionately to the frontal cortex, thereby validating Barton & Dunbar

(1997) and Dunbar's (1998) social complexity hypothesis in these species, but in non-primates the structure of the frontal cortex is markedly different and the neocortex ratio does not therefore control for this (Holekamp *et al.*, 2006).

The close resemblance of spotted hyaena social behaviour to that of many primates, particularly cercopithecines, offers an excellent model for comparative research in a large predator and that this species has been largely overlooked for cognitive and behavioural study only serves to further emphasise why it should be included in the proposed research. As an out-group, spotted hyaenas may provide a valuable insight into the convergent evolution of hemispheric specialisation and social cognition whilst also addressing the dearth of literature available on lateralisation in predators and large mammals outwith the Primate order.

The Field Station for Behavioral Research, maintained by the University of California at Berkeley, USA, is the only research facility in the world that houses a large colony of spotted hyaenas and is therefore the only location to observe this species in captivity. However, it is also a highly suitable location as the FSBR provides large enclosures for naturalistic observation and the opportunity to learn from some of the world's leading hyaena experts.

1.8 | Thesis Aims

[1] Outline a new methodology for assessing visual field preferences which addresses the caveats of the existing methods, especially when applied to binocular species, and that can be used as a template for subsequent research in any species: thus allowing for valid cross-species comparison.

[2] Investigate the influence of emotional valence, emotional intensity, age, sex, and social rank upon visual field preferences.

[3] Determine whether the Right Hemisphere Hypothesis (Campbell, 1982) or the Valence Hypothesis (Silberman & Weingartner, 1986) provides the most valid model for understanding the lateralisation of emotion.

Chapter two provides an overview of the methodology designed for the proposed study of emotional lateralisation in species with binocular vision. Several studies (Casperd & Dunbar, 1996; Baraud *et al.*, 2009) have investigated visual field preferences in species with considerable binocular overlap by employing a method designed for species with almost completely monocular vision and as such have not addressed the differences in visual information processing between eutherian mammals and birds, fish, reptiles and amphibians identified in section 1.4. This chapter not only outlines a new method of coding visual field preferences but also provides a new method of calculating lateralisation by adapting Hopkins' (1994) Handedness Index to provide a Lateralisation Index suitable for binocular species.

Chapters three, four and five employ the method outlined in chapter two with a view to investigating the influence of emotion upon visual field preferences in three different species: olive baboons (3), rhesus macaques (4), and spotted (5) and also consider the effects of additional cross-study or species-specific factors upon visual field preferences.

Chapter six presents conclusions based upon all three studies and considers whether there is sufficient evidence to determine which of the two competing theories for the lateralisation of emotion is valid whilst also providing further suggestions for future research.


Field Station for Behavioural Research, University of California, Berkeley, CA, USA

2

Chapter 2 | General Methods

2.1 | Overview of Methods

A key aim of this thesis was to implement a single research template that could be applied to each of the three species studied within this thesis as well as any future studies irrespective of species; therein eliminating methodological issues that may confound meaningful cross-species comparisons.

As detailed by the introduction, the study species selected for this thesis inhabited large dynamic multi-male/multi-female groups and were housed in captive research sites but it should be emphasised that this is not a strict requirement for replicating the study method outlined in this chapter. Any species inhabiting any wild or captive habitat are potentially suitable for the method outlined by this study, but an important consideration when identifying suitable species and locations for this thesis was to maximise the potential for observing behavioural interactions within the available timeframe for research in a PhD programme.

2.2 | Study sites & periods

2.2.1—Station de Primatologie du CNRS, Rousset, Bouches-du-Rhône, France

May 2009 – August 2009

Olive baboons, *Papio anubis*

The Station de Primatologie is one of the main research sites operated by the Centre National de la Recherche Scientifique (CNRS) in France. The facility in the Bouches-du-Rhône département of the Provence-Alpes-Côte d'Azur region was established in 1991 on an 18 hectare site for the purpose of animal husbandry and research and currently hosts approximately 700 monkeys from three species: olive baboons, Guinea baboons and squirrel monkeys. The region has a subtropical Mediterranean climate with mild, humid winters, when the average temperatures is 12°C during the day and 4°C at night (December – February), and summers that are hot and dry with July/August temperatures averaging 30°C/19°C (day/night; data from Wunderground.com (a)).

For the present study, the subjects were members of a troop of olive baboons (n=42) ranging in age from <1-26 years and were a mix of wild-caught and captive born. They were kept in a pair of fenced concrete enclosures (enclosures B4-B5, area≈700m^2; see Figure 2.1) connected by a covered walkway and with continual access to indoor sleeping accommodation (area≈42m^2). Observations were performed in the outdoor enclosure only. Subjects were routinely scatter fed an assortment of fruit, vegetables, grain, and commercial primate pellets.

Figure 2.1 | A satellite image of the facility in Rousset with the studied enclosure outlined in orange. ©GoogleMaps

2.2.2—NIH Animal Center, Poolesville, Maryland, USA

September 2009 – December 2010

Rhesus macaques, *Macaca mulatta*

Maintained by the National Institutes of Health (NIH) since 1965, the Animal Center is a large multi-disciplinary facility covering over 207 hectares of farmland near Poolesville in Montgomery County, Maryland. The facility carries out both behavioural and veterinary research as well as animal husbandry and quarantine, and hosts a variety of farming livestock and exotic species. The region has a humid subtropical climate characterised by hot, humid summers averaging 30°C in July and August and cold winters with freezing conditions, frequently accompanied by snow, occurring from December to February (data from Wunderground.com (b)).

Figure 2.2 | A satellite image of the NIH rhesus macaque field site with the enclosure outlined. ©Bing Maps

A multi-male/multi-female group of 48[2] captive-born rhesus macaques ranging in age from six months to 21 years old was studied at this location. These macaques were housed in

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[2] An additional seven adult males were removed unexpectedly from the enclosure during the first month, necessitating all data associated with these individuals be discarded but leaving only a single adult male for observation.

a very large outdoor enclosure (~25,500m^2, see Figure 2.2) that offered an entirely grass/earth substrate with extensive natural and artificial enrichment as well as access to indoor housing (~160m^2) where the macaques were provided bedding materials and fed. Aside from what could be foraged from within this enclosure, they were provided with a diet of assorted fruit, vegetables, grain, popcorn, and primate pellets.

2.2.3—FSBR, University of California, Berkeley, California, USA

June 2010 – September 2010

Spotted hyaena, *Crocuta crocuta*

The Field Station for Behavioral Research (FSBR) was created by the University of California at Berkeley in 1984 to provide a local facility with which to host a number of separate research projects. Most prominent amongst these is the Berkeley Hyaena Project which was established in 1985 by Professors Lawrence G. Frank and Stephen E. Glickman for the purpose of physiological, anatomical and behavioural research and from its inception until the present study the colony has supported a population of 20-30 hyaenas at any one time.

Berkeley has a cool summer Mediterranean climate typified by dry summers and wet winters with the warmest month being September and averaging between 13-22°C whilst January is both the coldest (6-14°C) and wettest month, usually including ⅕th of the annual rainfall (based on data from Wunderground.com(c)).

Unlike the primates, where all individuals were kept together in a single enclosure, the colony of 25 hyaenas was housed in 11 dyads and one triad as this was necessary to reduce intra-individual aggression (Jenks *et al.*, 1995), although the proximity of the enclosures allowed for normal communication and permitted individuals to perform greeting ceremonies, an important social behaviour (Smith *et al.*, 2011), across separating fences. These pairings were changed periodically and under close supervision to facilitate additional interactions and mating [observed by author].

Figure 2.3 | A highlighted satellite image of the hyaena enclosures at UC Berkeley FSBR. ©Bing Maps

The size of hyaena enclosures on-site varied, ranging from smaller indoor enclosures (100m^2) with concrete substrate for animals requiring closer supervision, to large outdoor enclosures with natural substrate and grass, bushes and trees (1200m^2; see Figure 2.3). All individuals housed outdoors were able to access indoor housing and nesting material was available in every enclosure; indoor and outdoor. Additionally, each enclosure included a large water pool for hyaenas to bathe in. Each morning the individuals were fed pork bones and a commercially available carnivore zoo diet (Nebraska Brand Feline Food; Central Nebraska Packing, Inc., North Platte, NE).

2.3 | Ethical considerations

The data collection methods employed by this study were entirely observational and non-invasive. At the CNRS and UC Berkeley study sites, observation of the animal subjects was performed from a viewing position outside of the animal enclosures with no interaction between subject and observer. The researcher adhered to all on-site observation protocols. At the rhesus study site (NIH), the observer was permitted to observe from within the animal enclosure once several weeks of appropriate training and a risk assessment had been completed. Additionally, care was taken to prevent the communication of diseases from the researcher to the animal subjects (and vice-versa) by requiring the researcher to pass a medical examination prior to commencing research and to wear full protective clothing (scrubs, gloves, facemask, goggles, hairnet) at all times whilst inside the enclosure. Whilst the presence of the researcher inside the enclosure at NIH did provide the opportunity for physical interaction with the subjects, such interactions were rare and never initiated by the researcher. Responses appropriate to these interactions were taken by the researcher in accordance with training guidelines.

All research methods and procedures were approved by the University of Stirling's Ethical Committee prior to commencing research and were designed in accordance with the Association for the Study of Animal Behaviour (ASAB) guidelines (Hare, 2012) pertaining to animal research. Approval was sought and obtained from each individual research site prior to arrival: Centre National de la Recherche Scientifique, National Institutes of Health, and the University of California at Berkeley.

2.4 | Procedure

2.4.1—Pilot Study

A pilot study was conducted at Belfast Zoo, Northern Ireland from December 2007-

January 2008 involving a variety of species (primate and non-primate) to test procedural methods and equipment and it was found that video-recorded focal sampling provided the best method for data collection.

The focus of the proposed study is upon behavioural interactions which are often highly transient. In addition to recording the type of behavioural interaction it is crucial that the relative position of two (or more) individuals prior to each interaction is accurately observed. By video-recording each interaction it is possible to observe the full time-course of each interaction from elicitation to separation of subject and interacting conspecific(s), therefore enabling a more accurate assessment of which visual field a behaviour was elicited in. Focal sampling (Altmann, 1974) was found to be the preferred sampling method as it ensures each subject can receive a similar total time-period of observation. Additionally, by performing focal samples the focal subjects can be accurately identified prior to commencing each period of observation which can greatly improve the efficiency of coding data from large populations of individuals. Furthermore, focal sampling is preferable to scan sampling as the latter is dependent upon interactions coinciding with predetermined time intervals and may therefore increase the likelihood of brief interactions being missed. Behavioural sampling was also considered to be inappropriate as there were no particular types of interactions of specific importance to the proposed study and behavioural sampling may therefore lead to the disproportionate representation of some types of interactions in analyses that may occur more/less frequently in the course of normal behaviour.

A 15 minute observation period per focal was found to be an optimal duration as it reduced the frequency of discarded focals (from subjects retiring out of view) whilst permitting adequate time to observe a higher frequency of interactions per focal subject (Kleiman *et al.*, 2010). The use of a tripod was also found to greatly enhance the quality of the recorded video focals.

2.4.2—Focal Individual Sampling

Each focal subject was selected pseudorandomly and continuously observed for a 15 minute period with the entire focal filmed using Sony DCR-SR52E HD HDD video recorder mounted on a Velbon CX-440 video tripod. Video coding also allowed intra and inter observer reliability to be ensured. If it was known to the observer that an individual had already been selected less than two hours prior, twice that day, or four times that week, another individual was then selected for the focal to ensure that each individual was subject to approximately an equal number of focals.

During each focal observation, all interactions between the focal subject and other individuals were recorded, noting the specific behavioural interaction and the position of the other individual in the visual field of the subject. Where the subject was involved in an interaction with more than one individual, or if the interaction took place whereby it was unclear which individual the subject was interacting with, such interactions were discounted from analyses. If the subject was out of view for more than 10% of the focal, *i.e.* more than 90 seconds, the focal was discounted from analyses.

If interactions took place within 2m[3] of a large physical obstruction that may have significantly impaired the subject's field of view such interactions were discounted from analyses as the obstruction may have constrained the interaction by eliminating a particular visual field preference from the subject's overall visual spectrum or by forcing a particular visual field preference upon the subject.

2.4.3—Definition of an Interaction

An interaction was determined to have occurred when a focal subject approached or was approached by a conspecific and engaged that conspecific through eye contact and/or

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[3] At each study site, 2m was measured out and compared to other items within the enclosure for scale, thus allowing this distance to be approximated during focals.

physical contact. Physical contact was not necessary as some behaviours, such as threats, did not involve direct physical engagement but to ensure accurate interpretation of these non-physical behaviours the subject and conspecific were required to be within a 2m proximity. The interaction was considered terminated when one or both parties moved more than 2m apart. Where more than one behaviour was observed to occur before the subject and conspecific separated, only the initial behaviour during the interaction was recorded and included in analyses. All recorded observations involved a social interaction between two conspecifics and any behaviours where a subject interacted with objects or heterospecifics, such as nearby keepers, or exhibited behaviours performed alone were excluded from the main analyses.

2.4.4—Coding

Upon completion of each period of data collection, video files were downloaded from the video camera. Once data collection had been completed at all three sites all video focals were reviewed by the author. Video focals were watched using VLC media player, which permitted video footage to be slowed or paused and thus permitted accurate coding of each interaction, and all information was entered into a Microsoft Excel spreadsheet noting the date, subject ID, behaviour, visual field, and any additional information or observations that may have been of relevance.

2.4.5—Visual Fields

Studies of visual field preferences vary in their methodology. In species such as fish or birds (non-raptors) where there is no or very little binocular overlap (Andrew & Brennan, 1983; Evans *et al.*, 1993; Dharmaretnam & Andrew, 1994; Cantalupo *et al.*, 1995) monocular visual fields can be easily determined based on the position of a visual target object relative to the subject's facial midline. However, in species with a broad binocular overlap, such as primates or mammalian predators, the delineation of each visual field is less straightforward.

Casperd & Dunbar (1996) acknowledged that their study species, the gelada baboon, had binocular vision and noted that when an interaction was elicited directly in front of a subject that there was no obvious lateral bias. They consequently created three visual fields (left, central and right) to describe where an interaction occurred in the overall visual spectrum of their subjects however centrally occurring interactions were then excluded from their analyses; thereby increasing the likelihood of reporting a lateral bias.

Baraud *et al.*'s (2009) method is also problematic as it did not acknowledge the binocular vision of their mangabey subjects and divided the overall visual spectrum into two equal hemifields either side of the subject's facial midline with the result that all interactions were determined as either left or right side biased. This approach may therefore have reported centrally-occurring interactions as being lateralised when it is likely that in such circumstances neither cerebral hemisphere was dominant for processing the visual information; again increasing the likelihood of reporting a lateral bias.

The present study therefore proposes a new model for assessing visual field preferences that is suitable for species with binocular vision but can also be applied to any species. Additionally, the left and right visual fields were each further divided into mid and extreme visual fields (relating to distance from facial midline; see Figure 2.4) leading to a total of five visual fields (extreme left, mid left, centre, mid right, extreme right) and enabling a more detailed analysis of the position in a subject's overall visual spectrum that each interaction occurred.

Interactions which take place directly in front of a subject, and are therefore projected equally to both hemispheres, are determined to have occurred in the central visual field (Figure 2.4, A). Interactions occurring either side of the central visual field and up to the approximate point at which one eye is obscured from visually fixating upon an individual/object, approximately 60° from the subject's midline (Burian & Von Noorden, 1974;

Sarmiento, 1975), are determined to have occurred in the mid visual fields (Figure 2.4, B). It is worth noting that interactions occurring in either of the mid visual fields still project to both hemispheres for binocular species (see Figure 1.3) but the non-central position of the visual target means its image is projected to one hemisphere more than the other and the hemisphere receiving the most visual information is therefore considered to dominate in the interpretation of this information. The extreme visual fields (Figure 2.4, C) cover the occurrence of an interaction beyond the periphery of the binocular mid visual field whereby visual input is monocular and therefore entirely processed by one hemisphere.

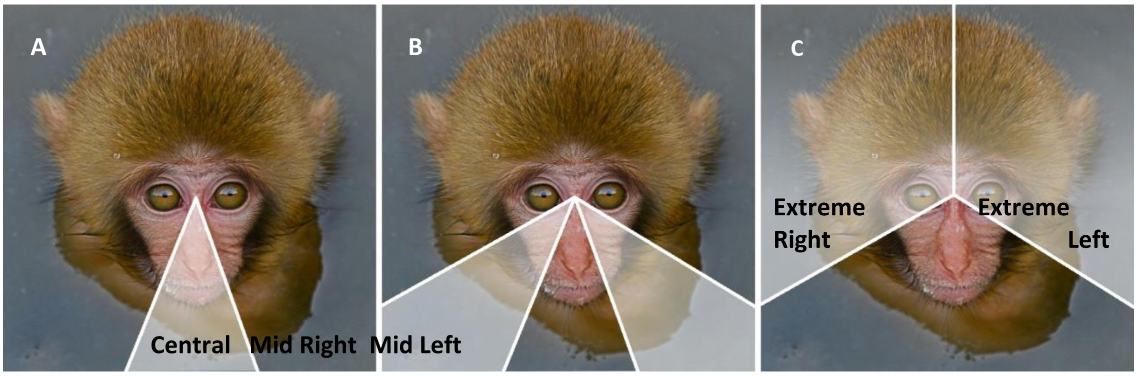


Figure 2.4 | Illustrating the approximate boundaries of the five visual fields used in this study. NB – the sides are labelled from the perspective of the subject.

Valence	Baboon	Macaque	Hyaena
Neutral	Approach	Approach	Approach
	Follow	Follow	Follow
Positive	Beg	Beg	-
	Groom	Groom	Lick
	Lip Smack	Lip Smack	-
	Feed Infant	Feed Infant	-
	Play	Play	Play
	Reach Out	Reach out	-
	Huddle	Huddle	Nuzzle
	Cradle infant	Cradle infant	-
Negative	Aggressive Contact	Aggressive Contact	-
	Avoid	Avoid	Avoid
	Bite	Bite	Bite
	Chase	Chase	Chase
	Displace	Displace	Displace
	Threaten	Threaten	Threaten
	Bared Teeth Display	Bared Teeth Display	Open Mouth Appease
	Simultaneous Assess	-	-
Sexual	Inspect	Inspect	Inspect
	Mount	Mount	Mount
	Present	Present	Present
	-	Post-coital glance	-
	-	-	Greet

Table 2.5 | Briefly detailing only the behaviours included in analyses for each species alongside any comparable behaviours observed in the other study species. Detailed ethograms are provided in each chapter.

2.4.6—Behavioural Interactions

Prior to data collection, a review of the relevant literature on the behavioural repertoire and social dynamics of each species was conducted to inform hypotheses and data collection methods. Upon arrival at each study site the experimenter also consulted with an experienced on-site researcher familiar with the study species to compile a detailed ethogram clearly defining all species-specific behaviours and the level of emotional arousal or intensity of these interactions. The experimenter then performed a brief pilot study at each site under the guidance of the on-site researcher to verify the experimenter was able to accurately identify each behaviour of interest and revise any inconsistencies in the definitions of behaviours. To ensure consistency across the three species only natural, spontaneously occurring conspecific interactions were considered for this study and all other interactions directed at heterospecific individuals (such as the researcher) were disregarded from the main analyses.

A brief overview of the behaviours included in analyses has been given in Table 2.5, also noting their cross-species analogues, with more detailed species-specific ethograms provided in each chapter.

2.4.7—Assessing Valence & Intensity

Once the ethogram had been compiled the valence and intensity of each behavioural interaction included within this ethogram was then determined in collaboration with researchers at each facility; olive baboons/CNRS: A. Meguerditchian, J. Gullstrand, C. Wallez; rhesus macaques/NIH: P. Wagner; spotted hyaena/Berkeley: M. Weldele, S. Glickman, M. Gardner.

Behaviours were classified as belonging to one of four valence categories: positive, negative, sexual or neutral. All interactions that served an agonistic function were classified as negative valence behaviours whilst interactions of an affiliative function were classified as positive valence behaviours. Neutral valence behaviours were those of a low level of arousal (Casperd & Dunbar, 1996; Baraud *et al.*, 2009) that did not involve physical contact and where the individuals involved in these behaviours did not physically communicate (as sudden movements, displacement, avoidance or threats might suggest an agonistic, negative valence). Sexual behaviours were included as a separate category based upon the author’s observation that they appeared to vary in context from acquiescent affiliative acts, often between individuals of similar social rank, to highly agonistic encounters, usually when there was notable disparity between the rank of the individuals involved, thus the use of a specific 'sexual' behaviour category allowed for these behaviours to be accurately separated from the other behavioural categories. Several studies have specifically investigated the lateralisation of sexual behaviour (Rogers, 1980; Ventolini *et al.*, 2005; Gülbetekin et al., 2007) but in the method of Baraud *et al.* all behaviours were classified as being of a positive, negative or neutral valence. As Baraud *et al.* did not report that sexual behaviours were discounted from their analyses it is assumed that they must have been included within one of the three valence categories that they used.

The inclusion of two categories of behavioural intensity was modelled on Casperd & Dunbar (1996) which observed an effect of the intensity of interactions upon the observed lateral bias and all interactions in the present study were consequently classified as either high or low intensity based upon recommendation from experts at each facility.

2.4.8—Assessing Social Factors

Aside from investigating the influence of valence upon visual field preference, a number of additional social factors were considered as variables in the analyses.

2.4.8.1—Age & Sex

Each study-site provided biological data on each individual, thereby allowing age and sex to be easily identified. For the present study all individuals were classified into one of two age categories, subadult and adult, with these categories determined by consulting the relevant literature regarding the approximate point at which each species reached sexual maturity. In olive baboons sexual maturity is reached at five years (Packer, 1979; Smuts, 1985), in rhesus macaques females mature at three years old whilst males do so a year later at age four (Rawlins & Kessler, 1986) and in the spotted hyaenas a sex difference is also observed but with males maturing sooner at around two years of age whilst the females reach maturity a year later (Kruuk, 1972).

2.4.8.2—Rank

Each study site also provided the social rank of each individual, based upon matrilineal dominance hierarchies established in each of the three species and dominance indexes based upon agonistic behavioural interactions (Zumpe & Michael, 1986), although further observations by the author backed up these rankings. For both monkey studies, the subjects were categorised into one of four ranks: high, mid high, mid low and low, and all interactions were then analysed in light of this. For the hyaena study, which had a smaller sample population, the social rank of the focal subject was compared with that of any individual it interacted with and for each interaction it was noted whether the focal subject was the dominant or subordinate individual.

2.4.8.3—Species Specific Considerations

In addition to age, sex, and rank, the influence of oestrus cycling was included as a factor in the olive baboon study. This factor could only be investigated in olive baboons as they are polyoestrus and cycle throughout the year (Bercovitch, 1991), whilst rhesus macaques only ovulate for a single season each year (Lindburg, 1971; Chapais, 1986) and the pattern of oestrus for spotted hyaenas is entirely unknown (M. L. Weldele, personal communication), therefore it was only possible to compare in-oestrus and non-oestrus female individuals during the period of observation for olive baboons.

During observation of the spotted hyaena population a number of additional lateralised behaviours were observed by the author that did not involve a conspecific but as they may relate to the lateralisation of individuals within this population such data were included. Shoulder rolls are frequently performed by spotted hyaenas upon discovering an odoriferous substance whereby the hyaena attempts to roll in the substance so that it may transfer it onto its body; a behaviour found to be socially beneficial in spotted hyaenas as it increases the level of attraction and attention such subjects receive (Drea *et al.*, 2002). In each circumstance where a hyaena performed this behaviour the shoulder roll was elicited on one side or the other and this was therefore recorded. Additionally, as part of their courtship ritual male spotted hyaenas cross their forelegs – the purpose of which is unknown (M.L. Weldele, personal communication) – whereby one foreleg is lifted off the ground and rested upon the other forelimb, and whether the left or right foreleg was lifted has been recorded. Finally, as some of the older spotted hyaenas had been hand reared they occasionally expressed affiliative behaviour towards keepers and other familiar humans by approaching the fence in their enclosures and presenting a side of their head or body to be scratched (which was done using a wooden stick approximately 60cm in length) and thus the lateral bias expressed during this behaviour was also recorded.

Further rationale for these factors has been provided in the relative species-study chapters.

2.4.8.4—Inter-Observer Reliability

In order to ensure the method employed by the author was evenly applied throughout the study and free from bias, 15 focal videos (five from each species) were coded by a naive, independent individual with results from these focals compared with those of the author (see appendix A1 for IOR form used by naive observer; results of IOR found in appendix A2-4). An IOR percentage agreement of 86.1% was achieved for the categorisation of visual fields with a 100% agreement also achieved for the categorisation of behaviours.

2.5 | Calculating Lateralisation

A key aim of this thesis is to establish a new method that can be replicated in any subsequent studies and central to this new method is the calculation of lateralisation and three different measures of lateralisation were calculated in this thesis.

Following Hopkins' (1994) study of handedness in chimpanzees his simple but effective 'Handedness Index' has served as the model for calculating lateralisation in most subsequent studies of limb, eye or ear preferences amongst others, however its application to research on visual field preferences should be limited to species that do not possess a binocular visual field. The reason being that, unlike other examples where lateral bias is a simple left versus right dichotomy, the visual spectrum of binocular species ranges from complete left eye bias to complete right eye bias but contains a large central binocular field where neither eye dominates (see Figure 1.2). As has been detailed in section 2.4.5, for the present study the overall visual spectrum has been split into five visual fields (extreme left, mid left, centre, mid right, extreme right) or three visual fields (by combining mid and extreme visual fields from each direction, thus resulting in left, centre and right) with the inclusion of the central visual field of critical importance to ensuring that individuals are not incorrectly identified as lateralised, as may have been the case in Casperd & Dunbar (1996) and Baraud *et al.* (2009).

2.5.1 | Binocular Laterality Index

The first measure of lateralisation is a modification of Hopkins' (1994) Handedness Index formula that has been adapted for calculations of lateralisation in binocular species. This calculation necessitated combining the extreme left and mid left visual fields to create a single left visual field with the same being done to the extreme right and mid right visual fields to create a single right visual field. The frequency of interactions occurring in these left (L) and right (R) visual fields along with the frequency of interactions occurring in the central (C) visual field can then be inputted into the following formula to calculate each individual's BLI value.

$$\boldsymbol{BLI = \left(\frac{R-L}{R+L}\right) \times \left(\frac{R+L}{R+L+C}\right)}$$

This formula retains the simplicity of Hopkins' (1994) formula and the left set of brackets may be recognisable as the formula for the Hopkins' Handedness Index. The set of brackets on the right of this BLI formula, however, act as a modifier and enable this formula to be applied to species with or without binocular vision. In species with a central binocular visual field, the frequency of centrally occurring interactions will be inputted for value 'C' whereby the value for the modifier shall be the percentage of the total number of interactions that were lateralised. In species without a binocular overlap where the value of 'C' is zero the value of the modifier will consequently be equal to one and will not therefore affect the overall calculation.

As a result, the value of the BLI shall fall anywhere between -1.000 (complete left visual field preference) and +1.000 (complete right visual field preference) thus indicating the degree of lateralisation for each individual.

2.5.2.1—Worked example

To demonstrate the effect of the BLI formula the data from a hypothetical focal subject have been provided: 100 interactions were observed in total, 23 were elicited in the left visual field, 66 in the central visual field, and 11 in the right visual field. These data have then been used to calculate LI and BLI figures for the same individual.

Using the original **LI** formula:

$$\boldsymbol{LI = \left(\frac{11-23}{11+23}\right) = -0.353}$$

Using the modified **BLI** formula:

$$\boldsymbol{BLI = \left(\frac{11-23}{11+23}\right) \times \left(\frac{11+23}{11+23+66}\right) = -0.120}$$

As can be seen, the addition of the modifier leads to a considerably lower BLI value (and thus reports a weaker bias) than had been calculated as an LI value. However, this difference is important as it illustrates how ignoring the centrally occurring interactions could lead to a considerable misrepresentation of the data and of the strength of lateral bias that an individual may express; a potential caveat of the method employed by Casperd & Dunbar (1996) and Baraud *et al.* (2009).

2.5.2 | Absolute Laterality Score

Once BLI values have been calculated for each individual, the Absolute Laterality Score (ABS; Hopkins, 1994) can then be calculated by disregarding the positive or negative direction of the BLI value and considering only its magnitude or absolute value.

At the individual level, this calculation does not provide much additional information but by calculating the mean ABS value for several individuals it may be possible to compare the strength of lateralisation for a given population or context within a population.

2.5.3 | Visual Field Proportions

The aim of calculating Visual Field Proportions (VFP) is to enable a more detailed assessment of the overall visual attention of individuals prior to their interactions with conspecifics. By calculating BLI values it is possible to determine whether an individual is lateralised but the nature of these calculations may disguise specific information regarding which visual field an interaction is most frequently elicited from. For example, Keverne *et al.* (1978) and Alberts (1994) have reported that lower ranked individuals performed more vigilance behaviour than higher ranked individuals and so by calculating VFP values for each individual it may be possible to see whether there is also a rank effect upon the range of vigilance behaviour and whether lower ranked individuals also visually monitored a wider area.

VFP values were calculated for each individual subject by dividing the number of interactions recorded within each visual field by the total number of interactions observed for each subject. Therefore, each VFP value will be a percentage of that individual’s overall total of behavioural interactions and thus all five VFP values should add up to a value of one.

2.6 | Data Analysis

Data were analysed using SPSS Statistics (v.19) and R (v.3.01). Probabilities were two-tailed and the level of significance (α) was set at $p \leq 0.05$ except for post-hoc tests where it has been specified that a Holm-Bonferroni correction (Holm, 1979) was applied to adjust the level of significance.

2.6.1 | Preparation of Data for Analysis

All data were assessed for normality with the Kolmogorov-Smirnov test. Normal data were then analysed using parametric methods whilst non-normal data were analysed using non-parametric methods as transformations of the data (Log_{10}, Square Root, Arcsine) had no effect upon the normality of the data.

2.6.2 | Effect Sizes, Sample Sizes & Power

A review of the literature on behavioural lateralisation reveals that there is no consensus on minimum sample sizes either in terms of events per individual or individuals per population. Large sample sizes are certainly preferable due to their greater statistical power (Hopkins *et al.*, 2001; Hopkins *et al.*, 2005; Hopkins 2006; McGrew & Marchant, 1997) although it has been argued in the handedness literature that even very small sample sizes can prove representative of an underlying pattern that may exist in a larger sample (de Vleeschouwer *et al.*, 1995) with some studies reporting no significant effect of sample size upon lateral bias (Hopkins, 1994; Westergaard & Suomi, 1996; Westergaard *et al.*, 1997; Vauclair *et al.*, 2005). Particularly in the observation of naturally occurring behaviours the number of data points recorded is often limited and therefore setting minimum sample size thresholds (in events per individual) must be balanced between eliminating too many data points and/or individuals and ensuring enough data points for statistical analyses. A number of handedness studies have set six events per individual (*n*=6) as the minimum threshold for inclusion in analyses (Chapelain *et al.*, 2006; Fletcher 2006; Meguerditchian & Vauclair, 2006; Chapelain, 2010) with this minimum criterion applied as it was the lowest number of data points with which binomial tests could be performed. Indeed, the key studies upon which this thesis was based, Casperd & Dunbar (1996) and Baraud *et al.* (2009), did not set a minimum criterion and included all interactions from all individuals in their analyses. Baraud *et al.* included binomial tests in their method, on individuals with at least six interactions, but their calculations at the group level included all observed interactions whilst Casperd & Dunbar specifically stated that a maximum of four events per individual were used and that most individuals within their study contributed only a single data point each. Furthermore, as the present study does not use binomial tests (due to the inclusion of a third, central visual field) it can be suggested that this minimum criterion of six is therefore no longer a constraint. As one-sample t-tests were the basic method of analysis used in this study and as they can be performed with a sample size as small as four (Student, 1908) this could potentially be used as a guideline for the absolute minimum sample size per individual although such a small number naturally raises issues regarding representativeness and statistical power. The reduced power associated with a small sample size, however, does not increase the likelihood of a type I error but instead may increase the probability of encountering a type II error by failing to reject the null hypothesis.

For the purposes of this thesis a minimum sample size of seven behavioural interactions per individual (*n*≥7) was set for the inclusion of each individual in between-subjects analyses. In the analyses of within-subjects factors, such as emotional intensity or rank, the data for each individual were split and this minimum criterion was again employed whereby individuals included in such analyses were required to have at least seven interactions for each subcategory (*e.g.* low or high intensity) that their data were included although individual subjects were not required to have data from all subcategories for inclusion in analyses (due to the use of mixed models; see section 2.6.3).

As the analysis of lateralisation was calculated based upon the occurrence of interactions in one of three visual fields a minimum of seven interactions ensured that more than two interactions occurred in at least one visual field. This criterion ($n \geq 7$) avoids overly reducing the total number of individuals included in analyses however this therefore permits the inclusion of small data samples for some individuals and the power of any analyses may be reduced as a consequence. Therefore, with a view to increasing power, in the subsequent chapters the data for each individual have been randomly sampled with replacement (bootstrapped) using 5,000 bootstrap replications (recommended value from Adams & Anthony, 1996). In order to do this, an individual's data were recoded so that each data point corresponded with a number between one and five whereby '1' represented the extreme left visual field, '2' the mid left, '3' the centre, '4' the mid right and '5' the extreme right visual . As the data were also split by emotional context/intensity it was necessary to perform a bootstrap on the data for each individual within each of these contexts by random sample with replacement using 5,000 replications. It is important to highlight that when the data were bootstrapped for emotional context or intensity that the original data for each individual were used and not the data from previous bootstraps.

For one-sample t-tests, Wilcoxon signed-rank tests and Mann-Whitney U-tests effect sizes have been reported as Pearson' Correlation Coefficient (r) values, for one-way ANOVAs effect sizes are provided using eta squared (η^2), and for Friedman's tests effect sizes are given using Kendall's W. For linear mixed models and generalised linear mixed models the fixed coefficient (FC) and its significance value (p) report whether a fixed factor had a significant effect upon the overall model whilst the intraclass correlation coefficient (ICC) reports the influence of the random factor (individual ID) upon the overall model.

2.6.3 | Statistical Tests

In many previous studies of laterality (*e.g.* Hopkins, 1995; Casperd & Dunbar, 1996; Meguerditchian & Vauclair, 2006; Baraud *et al.*, 2009) binomial tests and z-tests have been used at the individual level to analyse whether or not subjects were lateralised, but for the present study neither of these tests were appropriate. As many individuals included in the present study were observed for fewer than 30 behavioural interactions t-tests are recommended in place of z-tests (Urdan, 2010). Additionally, as the present study calculated lateralisation based upon the occurrence of behavioural interactions in one of three visual fields, rather than two visual fields or limbs, binomial tests were also not suitable.

Additional to the more commonly used statistical tests in assessments of lateralisation the present study also uses linear and non-linear mixed model analyses for a number of calculations. As has been stated in section 2.6.2 small sample sizes are a potential issue in each of the three studies and in particular where the data set was split for within-subjects measures (such as emotional intensity and valence) as this could potentially require the data sample to be further reduced. However, by using a general linear mixed model it is possible to perform analyses without any further reduction of sample size. Furthermore, generalised linear mixed models (GLMM) have been used in each chapter as confirmatory models as they allow for the consideration of all factors (age, sex, rank, emotional intensity and emotional valence) within a single calculation. However, unlike the general linear models which are performed on quantitative data (BLI values), due to the qualitative nature of the overall data set, whereby each data point is coded by visual field and the independent variables of age, sex, rank, emotional intensity and valence, and how GLMMs handle this data it is not possible to use these mixed models as a complete replacement for the smaller tests. As an example, although a GLMM may calculate that an effect of (e.g.) sex exists and that males are more left sided than females, it cannot determine if this is due to males having a left side bias that does not exist in females or if it is because females have a right side bias that does not exist in males. As such, the GLMMs provide a valuable confirmatory model but cannot provide the same detail as the fine grained analyses that constitute most of the data chapter calculations.

2.6.3.1—Analysis of Binocular Laterality Indexes

Once the data had been bootstrapped, and using the formula given in section 2.5.1 above, BLI values were calculated for each individual and assessed for normality; BLI values were normally distributed for all three species. Mean BLI values were calculated for the overall population and also for each context, *i.e.* age, sex, rank, emotional intensity and emotional valence, and then compared to an expected value of zero (no lateral bias) using a one-sample t-test.

Comparisons between age (subadult *vs*. adult) and sex (female *vs.* male) subcategories were performed using an independent samples t-test and as the social rank category contained four between-subjects subcategories (high, mid high, mid low, low) a one-way ANOVA was performed to determine whether an overall effect existed for rank with an independent samples t-test used post-hoc to perform pairwise comparisons of rank categories wherein the level of significance (α) was then adjusted according to the Holm-Bonferroni method (Holm 1979). For spotted hyaenas, however, the data were analysed according to the rank of the focal subject relevant to that of the individual with which it was interacting (rather than the social rank of the subject within the population as a whole). As such, rank for this species was both a within-subjects and a between-subjects measure, as it varied between interactions, therefore a linear mixed model (LMM) was used to compare rank in this instance. An LMM was chosen in preference to a standard regression model as it permitted the inclusion of individual ID as a random effect. For baboons, oestrus-cycling was a within-subjects measure and was therefore analysed using a paired-samples t-test. As the categories of emotional intensity and emotional valence were within-subjects measures and between-subjects measures they were also analysed using LMMs.

2.6.3.2—Analysis of Absolute Laterality Scores

Once BLI values had been calculated these could then be converted into ABS values for each individual assessed for normality. The ABS values for all three species were not normally distributed and therefore a median value was calculated for the overall population which served as the expected value for all subsequent analyses. Median ABS values were then calculated for each context subcategory and compared with the overall population median ABS value using a Wilcoxon signed-rank test.

Comparisons within age and sex categories were performed using Mann-Whitney U-tests. As rank was a between-subjects calculation and there were more than two sub-categories (olive baboons and rhesus macaques only) a Kruskal-Wallis H-test was used to investigate the influence of rank. For olive baboons, oestrus cycling was a within-subjects measure and calculated using a Wilcoxon signed-rank test. The ABS data for emotional intensity and emotional valence (and rank in spotted hyaenas) were assessed using a generalised linear mixed model (GLMM) in preference to an LMM as a GLMM is robust when analysing non-normal data and subject ID was set as the random effect.

2.6.3.3— Analysis of Visual Field Proportions

VFP values were calculated for each individual and although these values were assessed for the overall population and found to be normally distributed, when the data set was split for each of the context subcategories the data were no longer normally distributed therefore comparisons of VFP values were assessed non-parametrically. Median VFP values were calculated for all subcategories and compared to the overall population median VFP values using a Wilcoxon signed-rank test.

Independent samples Mann-Whitney tests were used to compare VFP between sex and age categories and a Kruskal-Wallis test was used to compare the four rank categories for an overall effect of rank (olive baboons and rhesus macaques only). Where rank was found to have a significant effect a Mann-Whitney test was used post-hoc to compare rank categories pairwise with the level of significance adjusted according to the Holm-Bonferroni method. For olive baboons oestrus cycling was a within-subjects measure and calculated using a Wilcoxon signed-rank test

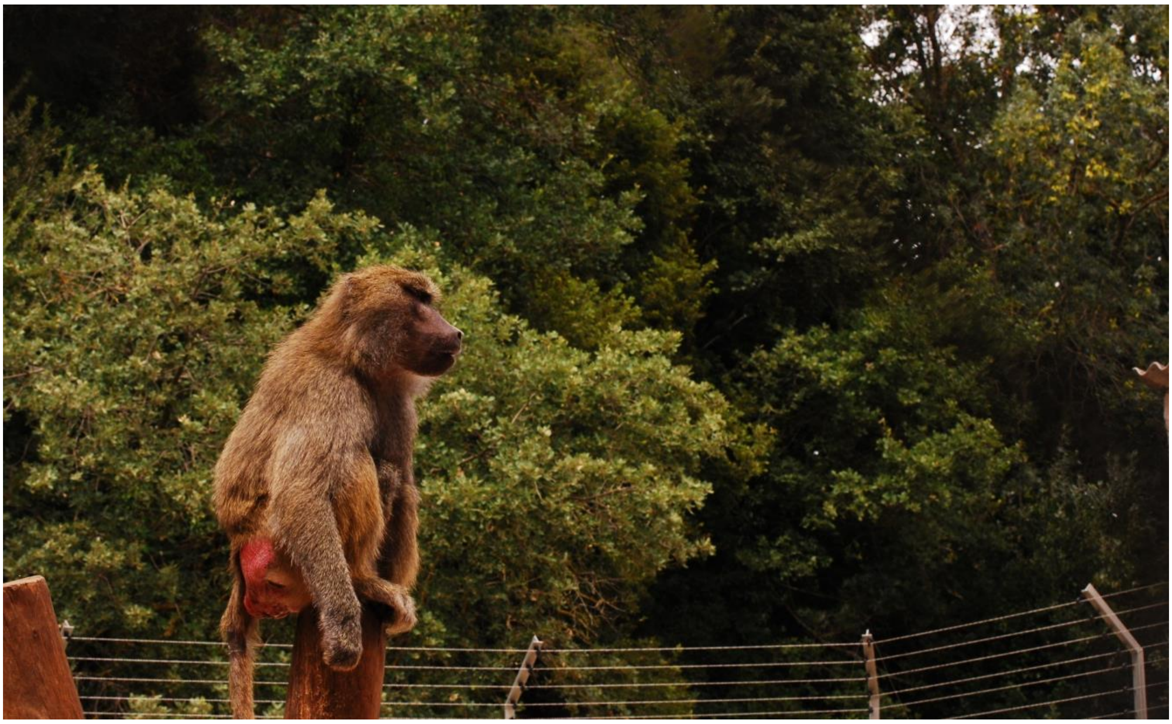
The VFP values for each category of emotional intensity and emotional valence (and rank in spotted hyaenas) were each tested using generalised linear mixed models with ID set as the random effect.

2.6.3.4— Overall Mixed Models

In comparison with the previous analyses which were performed upon the mean or median BLI, ABS and VFP values calculated for each individual or context, it was possible to analyse the overall data set wherein each separate interaction was included using a GLMM. A GLMM was used in preference to an LMM as the dependent variable was categorical (visual field: left, centre, right) and an LMM is not suitable in this circumstance. Interactions were each coded referring to the biological data of the subject (age, sex, rank) as well as their emotional intensity and emotional valence. As the dependent variable of each interaction was categorical (left, central or right visual field) and the GLMM method requires that a reference category is selected within the dependent variable it was necessary to create two models. The first compared the occurrence of behaviours in the central visual field to the left and right visual fields whilst the second model contrasted the occurrence of behaviours in the left and right visual fields and the results from the second model were interpreted in light of the first model. This latter point is important as interpreting the second model independently may result in lateral biases being reported in scenarios when the main bias of behaviours was in fact in the central visual field.

For all of these analyses subject ID was set as the random effect to ensure that the data were appropriately weighted. For factors which contained more than two categories, *i.e.*

rank (in olive baboons and rhesus macaques) and emotional valence, it was necessary, as per the GLMM method, to select one of these categories as a reference category. For emotional valence the neutral valence category was selected as the reference as it was felt that this would therefore permit any underlying lateral biases expressed in low arousal neutral contexts to be controlled for, whilst for the four rank categories the highest rank category was selected as the reference category as, in lieu of a specific reason for selecting a reference category, the GLMM model recommends choosing the reference category with the highest number of data points and these individuals accounted for more interactions than any other rank categories in all three species.



A female olive baboon at the CNRS Station de Primatologie, Rousset, Bouches-du-Rhône, France

3

Chapter 3 | *Papio anubis*

The Lateralisation of Emotion in Olive Baboons

3.1 | Abstract

This chapter investigates the lateralisation of social behaviour in the olive baboon, *Papio anubis* (*n*= 34), by considering whether the emotional context of an interaction influences the direction or strength of lateralised behaviour at the individual or population level and it is hoped that the results of this study shall permit the evaluation of the competing theories for the lateralisation of emotion: the Right Hemisphere Hypothesis (Campbell, 1982) and the Valence Hypothesis (Silberman & Weingartner, 1986). In addition, this study looks at whether specific visual fields are preferred during the elicitation of social interactions of varying emotional context and if additional factors (age, sex, rank, emotional intensity, and, for the first time, oestrus cycling) also influence lateralised behaviour in baboons.

No overall population-level directional bias was found but a significant left side bias was observed for negative valence behaviours as well as a significant left side bias for adults. Males were found to be significantly more active than females in their central and mid visual fields with low intensity interactions also occurring significantly more frequently in the central and mid visual fields than high intensity interactions and a significantly low proportion of neutral valence behaviours occurred in the extreme visual fields. Non-oestrus females were also found to express significantly stronger lateral biases than in-oestrus females

Overall, the results of this study provide no conclusive support for either of the two theories on the lateralisation of emotion, although the significant left side bias for negative valence behaviours is similar to previous studies and raises the suggestion that some valence categories may be more likely to elicit behavioural lateralisation than others. In addition, this study provides the first evidence that oestrus may impact strength of bias.

3.2 | Introduction

The two competing theories for the lateralisation of emotion, the Right Hemisphere Hypothesis (Campbell, 1982) and the Valence Hypothesis (Silberman & Weingartner, 1986), are differentiated by how they each perceive behaviours of a positive emotional valence to be lateralised. Both hypotheses agree that negative emotion is processed by the right hemisphere but whilst Campbell's theory suggests that positive emotional behaviour is also controlled by the right hemisphere Silberman & Weingartner have posited that the left hemisphere is instead the seat of positive emotion. As such, only by observing whether behaviours of a positive valence are lateralised can these competing theories be objectively contrasted.

Several members of the tribe Papionini have featured prominently in studies on the lateralisation of emotion and indeed laterality research as a whole with Guinea baboons and olive baboons the subjects of a number of studies on handedness in particular. One of the first studies to investigate manual laterality through behavioural observation and without brain lesions was performed by Vauclair & Fagot (1987) who observed a population of 18 captive Guinea baboons during spontaneous behaviour and reported a general right hand preference for the group, though also finding that this right hand preference was significant and more pronounced in adults whilst subadults appeared moderately left handed and non-significantly so. Following this, Fagot & Vauclair (1988) devised a series of manual tasks with varying degrees of visuo-spatial coordination for the same troop and observed that higher complexity tasks elicited a strong left hand preference that was not evident for the simpler tasks. This latter point contributed significantly to Fagot & Vauclair's (1991) hypothesis that handedness and laterality were dictated by the level of motor and cognitive involvement in a given task or behaviour which, along with MacNeilage *et al.* (1987), can arguably be attributed with stimulating the now substantial field of research in non-human laterality (Vauclair & Meguerditchian, 2007). One of the subsequent studies of unimanual and bimanual preferences was performed in olive baboons but in this instance a different effect was observed with Vauclair *et al.* (2005) finding that a unimanual (and therefore low complexity) task elicited no bias whilst a bimanual task elicited a strong right hand preference; thereby suggesting that lateralisation may not be consistent across closely related species.

Additional to laterality being investigated for low arousal behaviours, lateral biases have also been identified in less affectively neutral contexts and Damerose & Hopkins (2002) studied lateral biases during mother-infant interactions in olive baboons; observing a strong left side bias for maternal cradling and carrying. This left arm bias for infant cradling/carrying may be analogous to the observations of Vauclair *et al.* (2005) who found that olive baboons regularly employed the left hand for anchoring or holding objects during bimanual tasks whilst the more dextrous right hand was used for intricate manipulation. It is possible that this left side bias may also be representative of a right hemisphere dominance in the processing of emotional stimuli whereby the mother may have held her infant in such a position so as to visually attend to them with the side that is most affectively attuned. This suggestion is however dependent upon whether the mother expresses an eye bias by tilting her head sideways to look at her infant with one eye in particular, or leans her head forward to look at her infant with both eyes equally. Due to the lack of complete decussation of the optic fibres in primates (see Figure 1.2), visual targets appearing in an individual's central visual field are projected to both hemsipheres whilst visual targets outside of this central binocular field are processed by one hemisphere more than the other with the dominant hemisphere in each instance being on the contralateral side to the visual target. Therefore, if the mother tilted her head to the side and expressed a left eye preference when looking at her infant it might be possible that this was representative of a right hemisphere dominance in the processing of emotional stimuli. If this were the case it would offer support to Campbell's (1982) Right Hemisphere Hypothesis in preference to Silberman & Weingartner's (1986) Valence Hypothesis as the mother-infant interaction is highly affiliative and therefore affectively positive; which Silberman & Weingartner's theory would instead expect to be expressed on an individual’s right side. However, as Damerose & Hopkins did not state whether an eye preference or head tilt was observed the suggestion of a link between the lateralisation of cradling biases and emotional processing remains speculative.

One of the first studies in a non-human primate to contribute to our understanding of the lateralisation of emotion was that of Drews (1996) which investigated the asymmetrical distribution of injuries on wild yellow baboons and found that they occurred significantly more frequently on the right side of the head and body. These results suggest a right side bias during agonistic behaviour but as this correlates with a left hemisphere bias in the processing of negative valence behaviours the results of Drews’ study are not therefore compatible with the Right Hemisphere Hypothesis or the Valence Hypothesis and so the interpretation of this study is unclear.

Casperd & Dunbar (1996) performed a similar study on a troop of free-ranging gelada baboons in the Simien Mountains of Ethiopia by investigating lateral biases during agonistic encounters between males and found a significant left side bias for this population. A left side bias was also observed in a more recent study in olive baboons by Wallez & Vauclair (2011) who observed oro-facial asymmetry during four different emotional behaviours (screeching, lip-smacking, eyebrow-raising and copulation calls) and found significantly more magnified expressions on the left half of the face than the right for the screeching behaviour but not for the other three. Wallez & Vauclair attributed this difference to level of arousal and suggested that screeching behaviour was of a comparatively higher level of arousal than the other three behaviours and which therefore resulted in its more pronounced lateralisation. However, Wallez & Vauclair’s study included only four examples of emotional behaviour and thus the observation of a more expansive repertoire of behaviours may permit a more detailed consideration of how these behaviours are lateralised.

Casperd & Dunbar (1996) and Wallez & Vauclair (2011) both provided evidence that the right hemisphere appeared specialised for the control of negative emotion but as the contrast between Campbell's (1982) Right Hemisphere Hypothesis and Silberman & Weingartner's (1986) Valence hypothesis lies in the perceived control of positive emotion the research of Casperd & Dunbar and Wallez & Vauclair was unable to shed any further light on this issue. In fact, prior to the present study only Baraud *et al.* (2009) had investigated the lateralisation of both negative and positive emotion and its effect upon visual field preferences during behavioural interactions.

In their study, Baraud *et al.* (2009) observed all naturally occurring interactions within two populations of mangabeys thus providing an opportunity to study the full inventory of emotional behaviours and Baraud *et al.* noted the emotional context (positive, negative or neutral) of each interaction and the visual field of the subject in which these interactions took place. Baraud *et al.* found that in grey-cheeked mangabeys subjects were approached significantly more frequently in their left visual field whilst red-capped mangabeys expressed a right visual bias during all interactions, although there was no difference in results between emotional valence categories for either species. The results of Baraud *et al.* therefore highlighted that contrasts in lateralisation existed between closely related genera but although Baraud *et al.'s* results for grey-cheeked mangabeys (and the observations of Damerose & Hopkins, 2002) appeared to support Campbell's (1982) Right Hemisphere Hypothesis, the right side bias of red-capped mangabeys for all emotional contexts was at odds with both Campbell's and Silberman & Weingartner's (1986) theories for the lateralisation of emotion. As such, the lack of clarity on the lateralisation of emotion suggests that further investigation of these competing theories is merited.

The primary objective of the present study is to assess the influence of affective states upon visual field preferences but this study also aims to investigate the effect of several additional factors, namely: age, sex, rank and emotional intensity. Vauclair & Fagot (1987) and Vauclair *et al.* (2005) provided evidence of the ontogenic ritualisation of lateralisation and observed contrasting hand preferences between subadult and adult olive baboons with significant right hand biases observed for adults alone whilst subadults expressed no significant preference. In terms of sex differences, Meunier *et al.* (2011) observed that the strength of bias changed during a reaching task in olive baboons as a consequence of the position of a target item in relation to the subject's midline and the sex of that subject. Meunier *et al.* found that females expressed stronger right hand biases when the target item was approximately 60° from the subject's midline whilst the strength bias of males was most pronounced when the target item was 30° from the midline. Meunier *et al.* posited that sexual dimorphism, rather than any other characteristic, may have caused the observed greater mobility of the females during the test procedure as the females were physically smaller than the males and had to adjust their position to reach the item which may have caused the contrasting results. A review of additional handedness literature on the influence of sex reveals contrasting results between males and females. Significant left handedness was observed for male lemurs but not females (Ward *et al.*, 1990) and significant right handedness was found for female tufted capuchin monkeys but not males (Westergaard & Suomi, 1993) whilst Milliken *et al.* (1989) found similar results within a single species and reported left-handedness in males but right handedness in female ring-tailed lemur. Similar to Meunier *et al's* comparison of strength differences, Stafford *et al.* (1990) found stronger biases in female gibbons than males whilst Spinozzi & Truppa (1999) made the contrasting observation that stronger manual preferences were expressed by male tufted capuchins than females of the same species. As such, the evidence for an overall effect of sex upon lateral bias appears inconclusive but the existence of distinct differences within these studies suggests that the influence of sex should be further considered.

As well as proposing sexual dimorphism as a contributing factor to the different results between males and females, Meunier *et al.* (2011) also suggested that these results may be related to social rank. Meunier *et al.* determined that the mean rank of female subjects observed in this study was lower than that of their male counterparts and that the associated increase in social pressure on the females may have contributed to the difference in results. Baboons live within multi-male/multi-female groups where an individual's rank position within the group hierarchy dictates their access to food and resources and significantly influences their reproductive success (Barton & Whiten, 1993). The dynamic nature of this hierarchy means that individuals regularly challenge and are challenged for a higher position within the group and its associated benefits although the social pressures vary throughout the hierarchy (Sapolsky, 2005). Meunier *et al.* (2011) alluded to this by suggesting that the elevated social pressures the female baboons were subject to, in comparison with males from the same group, influenced the emotional scenario of the reach task. Baraud *et al.* (2009) considered rank as a factor in their study on two mangabey species and found a positive correlation between an increase in the strength of bias and an increase in rank for grey-cheeked mangabeys but no similar effect in red-capped mangabeys. Additionally, Baraud *et al.* observed that a higher frequency of positive valence behaviours occurred in the left visual field of high ranked grey-cheeked mangabeys whilst a higher frequency of negative behaviours was observed in the right visual field of high ranked red-capped mangabeys; however the cause of this difference between emotional valences in different species is unclear. It is possible that the contrast between two closely related species may reflect differences in motivation for each species and emotional context but due to the small number of subjects included in each study (grey-cheeked mangabey *n*=5[4]; red-capped mangabey *n*=5[5]) the observed results may be an effect of such small sample sizes.

Casperd & Dunbar (1995), along with Wallez & Vauclair (2011), suggested that a correlation between the intensity of behaviours and strength of bias may exist as both studies compared low and high arousal behaviours and reported strong left side lateralisation for the

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[4] Baraud *et al.* (2009) state that although the observed population of grey-cheeked mangabeys numbered six, one of these was an infant and was not considered in analyses.

[5] Baraud *et al.* (2009) further stated that two of the red-capped mangabeys died during testing, thereby reducing the observed population of this species to five from seven.

latter category. With this in mind, all interactions observed during the present study have been categorised according to their perceived level of arousal. Furthermore, with the aim of testing Silberman & Weingartner's (1986) Valence hypothesis all behaviours have been additionally categorised by emotional context with each interaction classified as positive, negative, neutral or sexual. Sexual behaviours were included as a separate valence category because it was felt that the underlying emotional context of such behaviours varied and did not consistently match any of the other valence categories. Furthermore, several studies in birds have found sexually guided behaviour to occur significantly more frequently in the left visual field (Bullock & Rogers, 1986; Ventolini *et al.*, 2005; Gülbetekin *et al.*, 2007) therefore it may be interesting to investigate whether the same right hemisphere dominance for sexual valence behaviours exists in a primate species.

The final consideration for the current study focuses upon whether the oestrus cycle of adult females influences lateralisation. Gangestad *et al.* (2007) had observed that women's mate preferences changed at different points in the ovulatory cycle, thereby prompting the author to consider whether lateral preferences were also susceptible to change. A review of the laterality literature found that only one previous study had investigated the influence of oestrus cycles upon lateralisation whereby Rizhova & Vershinina (2000) had observed Wistar albino rats (an outbred lab strain of the brown rat) perform a T-maze test and reported that proestrus rats expressed a significantly higher left turn preference than rats in any other stage of the cycle. In olive baboons each oestrus cycle typically lasts 30-40 days and is characterised by a highly visible sexual swelling of the anogenital region and the swelling is at its largest during the final week of the cycle when the female is in oestrus (Hendrickx & Kraemer, 1969; Bercovitch 1991). It may therefore be possible to observe each adult female over the course of the cycle and, using the size of swelling as a reference, record whether there is an effect of oestrus upon visual field preferences. The base level of arousal for in-oestrus females is also likely to be elevated in comparison with the non-oestrus stages of the cycle therefore, based upon Casperd & Dunbar (1995) and Wallez & Vauclair's (2011) suggestions, it may be possible to predict stronger lateral biases for in-oestrus females. Additionally, several recent studies have highlighted that in-oestrus females are more likely to be subject to aggression from other females (Huchard & Cowlishaw, 2011; Cheney *et al.*, 2012; Clutton-Brock & Huchard, 2013) which may also lead to more frequent high intensity interactions.

3.3 | Hypotheses

H_1 All emotion is controlled by the right hemisphere therefore behaviours in all emotional contexts should be lateralised to the left visual hemifield at the group level; thus supporting Campbell's (1982) Right Hemisphere Hypothesis

H_2 Adults should express a stronger left side bias than subadults.

H_3 Males should express a more pronounced left side bias than females.

H_4 Stronger left side lateral biases should be found in higher ranked individuals than low ranked individuals.

H_5 Interactions with high emotional arousal should elicit stronger left side lateral biases than low arousal interactions.

H_6 In-oestrus females should display stronger left side biases than non-oestrus females.

3.4 | Methods

3.4.1—Observation

All observations were performed from outside the enclosure but as all sides of the enclosure were accessible visual contact could be maintained with the subjects at all times. Observation took place between 7am – 7pm, Monday – Saturday over a period of 12 weeks from May to August 2009.

Subjects were selected at random but with care taken to ensure no individual was observed more than twice per day or four times within a week. All subjects were housed within the same large enclosure with indoor accommodation and a large outdoor 'yard' with data collection only performed from the latter. No change was made to the general methodology given in section 2.4, with subjects selected and video-recorded for 15 minute focals and all behavioural interactions subsequently observed and noted during coding.

3.4.2—Preparation of Data Set for Analyses

Completion of coding revealed that a total of 849 interactions had been observed from a total of 42 individuals but when the minimum criterion of seven (*n*=7) behavioural interactions per individual was applied this data set was reduced to a total of 837 interactions from 34 individuals (interactions per individual: mean=23.9, min= 7, max=69; see Appendix A5 for table on number of focals/interactions per individual). As detailed in section 2.6.2 this minimum criterion was also applied when the data from each individual were split for the analyses of emotional intensity, emotional valence and oestrus status, thereby a minimum of seven interactions per subject per subcategory were required, but as a mixed model was used for these analyses if a subject met this criterion for only one subcategory it could still be used in analyses. Once these minimum criteria had been applied it was determined that the small number of data points for some individuals may impact the power of the overall analyses and thus the data for each individual were randomly sampled with replacement using 5,000 bootstrap replications (Adams & Anthony, 1996) as per the method explained in Section 2.6.2.before the analyses were performed.

The number of individual subjects included in analyses for each context has been noted in Table 3.1 with the biological data for all individuals included in analyses reported in Table 3.2. Table 3.3 provides an ethogram of all behaviours included in analyses and how they have been coded for emotional intensity and valence. This ethogram was compiled in collaboration with researchers at the study site (CNRS): A. Meguerditchian, J. Gullstrand, and

Between-Subjects Comparison			Within-Subjects Comparison			Mixed-Model Comparison		
Age	Subadult	11	Cycling Status	Oestrus	10	Intensity	High	24
	Adult	23		Non-oestrus	10		Low	24
Sex	Male	7				Valence	Neutral	5
	Female	27					Negative	12
Rank	High	10					Positive	21
	Mid High	9					Sexual	8
	Mid Low	9						
	Low	6						

Table 3.1 | Reporting the number of individual subjects that met the minimum criterion (n≥7 interactions) for each context subcategory.

ID	Dob	Age	Sex	Rank	ID	Dob	Age	Sex	Rank
106	1.1.83	Adult	F	High	**804**	9.5.02	Adult	F	Mid High
1	1.1.87	Adult	M	High	**968**	15.1.04	Adult	F	Mid High
79	1.1.90	Adult	F	High	**4**	1.1.95	Adult	F	Mid Low
2	1.2.91	Adult	M	High	**437**	11.1.97	Adult	F	Mid Low
355	1.1.92	Adult	F	High	**805**	14.2.99	Adult	F	Mid Low
5	1.4.92	Adult	F	High	**351**	4.12.01	Adult	F	Mid Low
818	1.1.93	Adult	F	High	**1001**	4.2.02	Adult	F	Mid Low
96	17.4.96	Adult	F	High	**989**	12.11.02	Adult	F	Mid Low
816	10.12.01	Adult	M	High	**349**	14.2.03	Adult	F	Mid Low
3	26.4.02	Adult	M	High	**447**	1.10.03	Adult	F	Mid Low
111	1.7.89	Adult	F	Mid High	**988**	27.11.03	Adult	F	Mid Low
119	1.4.90	Adult	F	Mid High	**825**	15.11.05	Subadult	M	Low
105	1.6.90	Adult	F	Mid High	**821**	3.1.06	Subadult	F	Low
6	1.7.90	Adult	F	Mid High	**629**	5.6.06	Subadult	F	Low
83	1.7.91	Adult	F	Mid High	**959**	16.11.07	Subadult	F	Low
1000	1.8.91	Adult	F	Mid High	**985**	21.11.07	Subadult	M	Low
358	1.4.93	Adult	F	Mid High	**960**	28.3.08	Subadult	M	Low

Table 3.2 | Showing the biological data for each subject included in analysis (F=female, M=male).

Behaviour	Description	Intensity	Valence
Beg	subject attempts to take food from mother/another individual, often involving close contact/touching other's mouth/hand(s) with subject's mouth/hand(s)	low	neutral
Follow	subject approaches and walks behind another individual at a slow pace		
Avoid	subject walks/runs away from an approaching individual; submissive behaviour	low	negative
Displace	subject approaches another, stationary, individual causing them to move away		
Fear Grin	subject bares teeth and pulls back the corners of the mouth so their mouth is agape; submissive behaviour		
Aggressive Contact	subject uses hand(s) or mouth to strike, slap, pull hair or bite another individual	high	
Chase	subject runs or trots after another; aggressive behaviour		
Eye Flash	subject glares at another exposing their eyelids; aggressive behaviour		
Head-bob	subject moves their head up and down whilst visually fixating on another individual, often accompanied by eye flash and/or hand slap		
Hand Slap	subject visually fixates on another individual and slaps palm of hand on surface, usually accompanied with a head-bob and/or eye flash; an aggressive behaviour		
Groom	subject uses hands/mouth to pick through the hair/fingers/toes/other of another individual; affiliative behaviour	low	positive
Lip-smack	subject's tongue rapidly touches lips making a smacking sound; affiliative behaviour		
Reach Out	subject reaches out or raises arm(s) toward another individual; affiliative behaviour		
Play	subject, usually infant or subadult, plays with another individual and may be observed as jumping, trotting, rolling around, wrestling	high	
Present	subject presents anogenital area to male or dominant individual	high	sexual
Mount	subject approaches the rear of another and elevates on hind leg(s) to enact or simulate copulatory behaviour		
Inspect	subject closely looks at, smells and/or touches the anogenital area of another		

Table 3.3 | Detailing each behaviour included in analyses, the description of each behaviour and its corresponding valence and intensity

3.4.3—Statistical Analyses

3.4.3.1 Testing for Normality

Prior to each analysis, the distribution of the data was examined for normality using a Kolmogorov-Smironov test. The overall BLI data were normally distributed (D(34)=0.123, p=0.200) and parametric methods were used, whilst for overall ABS values the data were not normally distributed (D(34)=0.192, p=0.003) and therefore all calculations were performed with nonparametric methods. The overall data for VFP values were found to be normally distributed (extreme left: D(34)=0.097, p=0.200; mid left: D(34)=0.111, p=0.200; centre: D(34)=0.116, p=0.200; mid right: D(34)=0.74, p=0.200; extreme right: D(34)=0.095, p=0.200), however, when the data were split between contexts (*e.g.* male and female) non-normal distribution was observed for one or more visual fields and therefore non-parametric analyses were performed as transformations of the data (Log_{10}, Square Root, Arcsine) had no effect.

3.4.3.2 Analysis of Binocular Laterality Indexes

Once BLI values were calculated for each individual the overall mean BLI value for the population, and the mean BLI values for each category, could then be calculated and a one-sample t-test was used to compare the mean BLI values to the hypothetical expected value of zero (no predicted bias) in each context.

Comparisons within age and sex categories were performed using independent t-tests. Rank sub-categories were compared using a one-way ANOVA and where rank was found to exert a significant influence, independent samples t-tests were used post-hoc to perform pairwise comparisons of rank categories and the level of significance was then adjusted according to the Holm-Bonferroni method (Holm 1979). The influence of emotional intensity and oestrus cycling was analysed using paired-samples t-tests and a mixed linear model was used to compare differences between valences.

3.4.3.3 Analysis of Absolute Laterality Scores

Once the BLI values for each individual had been converted into ABS values the median ABS value for the population was then calculated and used as the expected value for all subsequent tests. Median ABS values were then calculated for each category and compared to the population median ABS value using a Wilcoxon signed-rank test.

Comparisons within age and sex categories were performed using Mann-Whitney U-tests. As rank was a between-subjects calculation and there were more than two sub-categories a Kruskal-Wallis H-test was used to investigate the influence of rank. To assess the influence of emotional intensity and the influence of oestrus cycling Wilcoxon signed-rank tests were used to compare both intensity categories and both states of oestrus. The four valence categories were compared using a mixed linear model.

3.4.3.4 Analysis of Visual Field Proportions

For each of the five visual fields median VFP values were calculated for the overall population and these were then used as the predicted values for subsequent comparisons with each context using a Wilcoxon-signed rank test. A Friedman's test was used for each context to compare each set of five VFP values to determine whether the overall difference between these five values was significant.

Independent samples Mann-Whitney tests were used for between-subjects VFP comparisons (age and sex) whilst a Kruskal-Wallis test was used to compare the VFP data for the four rank categories. Where rank was found to have a significant effect a Mann-Whitney test was used post-hoc to compare rank categories pairwise with the level of significance adjusted according to the Holm-Bonferroni method. Emotional intensity and oestrus cycling contexts were compared using a Wilcoxon signed-rank test and a mixed linear model was used to compare all four emotional valence categories.

3.4.3.5 Overall Mixed Model Analysis

Using a generalised linear mixed model it was possible to analyse the entire data set in a single model (only including individual subjects with $n \geq 7$ interactions and setting individual ID as the random effect) and to determine which factors (age, sex, rank, emotional intensity or emotional valence) were the most significant influences upon lateral bias.

3.5 | Results

3.5.1—Binocular Laterality Indexes and Absolute Laterality Scores

The mean LI for this population was -0.078 (SE=0.041). A one-sample t-test confirms that this overall bias was not significantly different from a test value of 0 (no bias): t(33)=-1.886, p=0.068 (Pearson's r=0.312). The median ABS value for the overall population was calculated as 0.133 (IQR=0.053-0.221). Note: this overall population median ABS value was calculated solely to be used as the 'expected' value for comparison with the median VFP values from each category and was not itself analysed.

At the individual level, only four of the 34 subjects were significantly lateralised with three of these individuals expressing a right side bias: ID#968: BLI=+0.203, t(31)=3.304, p=0.002 (Pearson's r=0.510); ID#119: BLI=+0.269, t(12)=5.500, p<0.001 (Pearson's r=0.846); ID#805 BLI=+0.088, t(16)=2.739, p=0.015 (Pearson's r=0.563), and one expressing a left side bias: ID#437: BLI=-1.000, t(7)=0, p<0.001 (Pearson's r=could not be calculated) whilst the remaining subjects were not significantly lateralised (see Table 3.3 for BLI values of all individuals). A chi-square analysis reveals this population was significantly not lateralised $X^2(2)=46.29$, p<0.001 (Pearson's r=0.825). The BLI values for each individual included in analyses have been detailed in Table 3.4 and illustrated in Figure 3.5 whilst Figures 3.6 and 3.8 show the mean BLI and median ABS values respectively for each context included in analyses. As it was not possible to include error bars on these graphs the standard errors for each context BLI and ABS values have been included in Tables 3.7 and 3.9 respectively.

ID	Original	BLI	*p*	*r*	Lateralised
1	0.024	0.012	0.570	-0.089	-
2	-0.150	-0.175	0.095	-0.264	-
3	0.237	0.184	0.057	0.308	-
4	-0.212	-0.221	0.312	-0.142	-
5	-0.133	-0.198	0.751	-0.086	-
6	-0.077	-0.154	0.337	-0.277	-
79	0.333	-0.085	0.347	0.333	-
83	0.000	-0.037	0.327	0.192	-
96	-0.026	-0.039	0.512	0.108	-
105	0.500	0.057	0.171	0.500	-
106	-0.167	-0.250	0.551	-0.183	-
111	0.029	-0.015	0.701	-0.067	-
119	0.462	0.269	0.000	0.846	Right
349	0.019	-0.010	0.335	-0.135	-
351	-0.143	-0.286	0.736	0.143	-
355	0.167	0.083	0.339	0.289	-
358	-0.056	-0.111	0.163	0.333	-
437	-1.000	-1.000	0.000	0.000	Left
447	0.130	0.109	0.609	0.062	-
629	-0.094	-0.109	0.459	-0.134	-
804	0.107	0.071	0.602	0.101	-
805	0.176	0.088	0.015	0.564	Right
816	0.143	0.107	0.646	0.089	-
818	-0.200	-0.233	0.499	0.183	-
821	-0.150	-0.175	0.577	-0.129	-
825	0.000	-0.020	0.129	0.306	-
959	0.071	0.000	0.547	0.169	-
960	-0.571	-0.500	0.200	-0.507	-
968	0.219	0.203	0.002	0.510	Right
985	0.000	-0.033	0.055	-0.488	-
988	0.286	0.214	0.129	0.289	-
989	0.286	0.190	1.000	0.000	-
1000	-0.195	-0.220	0.268	-0.175	-
1001	0.286	-0.357	1.000	0.000	-

Table 3.4 | Reporting the non-bootstrapped BLI values (original), bootstrapped BLI values (BLI), and the significance (p) and effect size (r) for each individual BLI value. The final column notes which individuals were significantly lateralised.

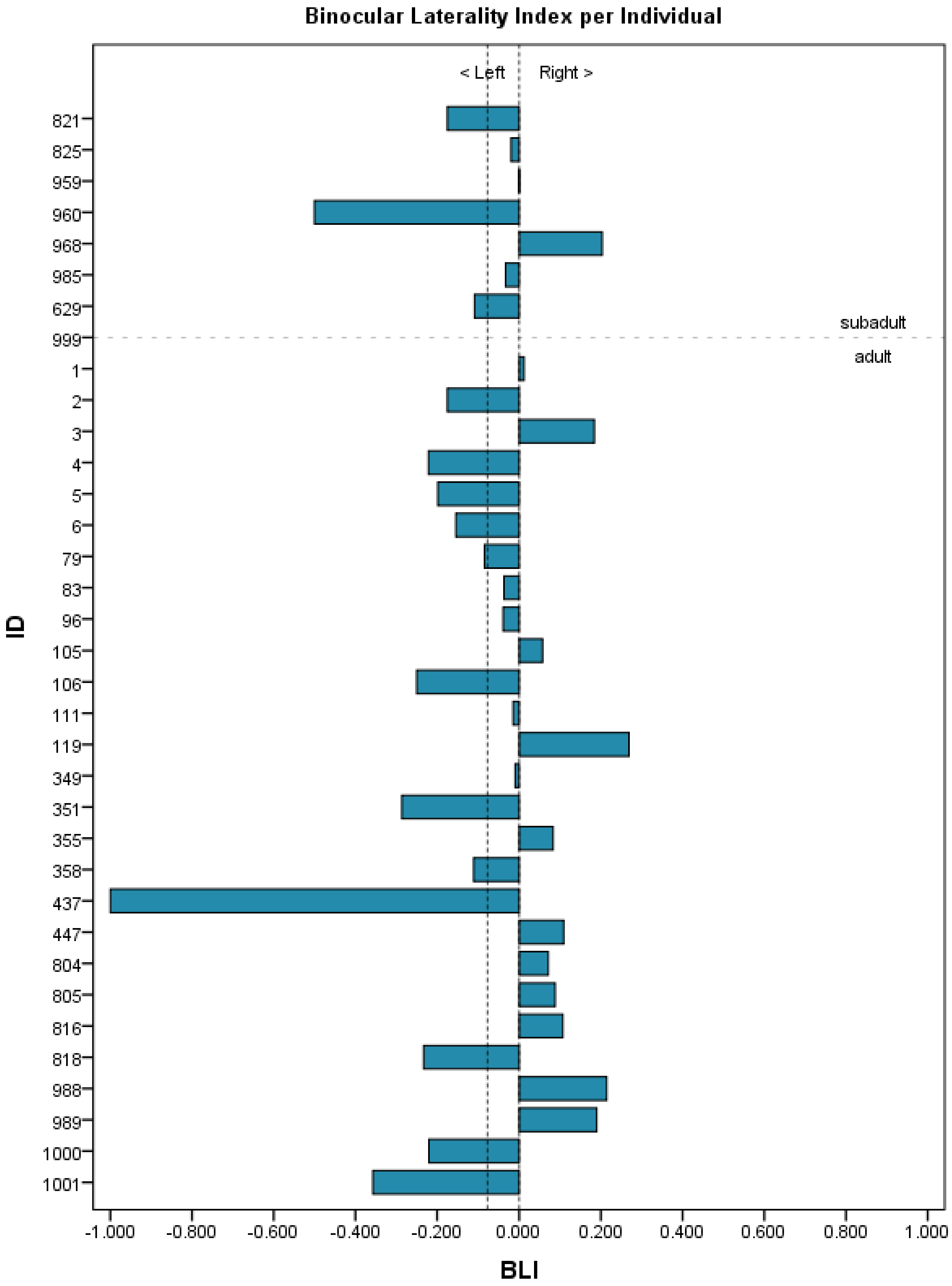

Figure 3.5 | Showing the BLI value for each individual included in analyses. The dashed horizontal line denotes the division between subadults and adults whilst the dashed vertical line illustrates the population mean BLI (-0.078).

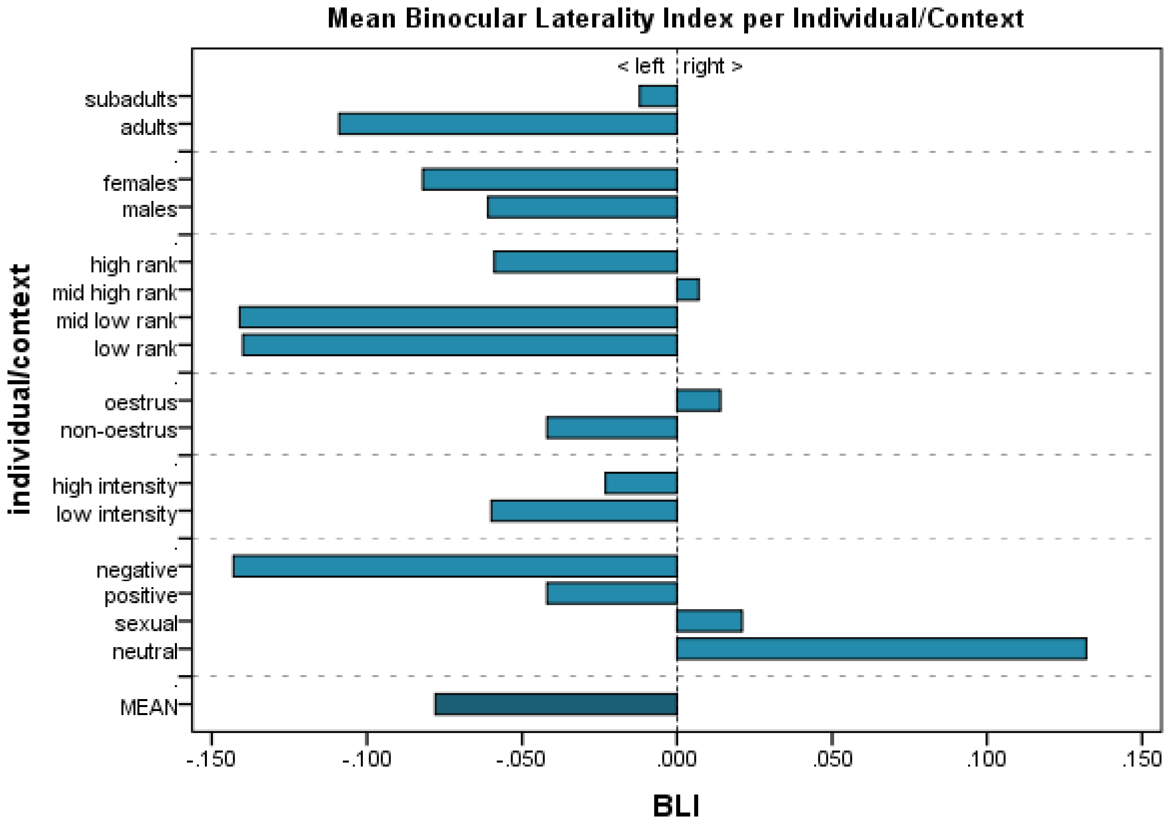

Figure 3.6 | Showing the mean BLI values for each individual/context measured in analyses. The overall population mean has been shown at the bottom.

context		mean	SE	*p*	*r*
age	subadults	-0.012	0.062	0.852	-0.057
	adults	**-0.109**	**0.527**	**0.050**	**-0.396**
sex	females	-0.082	0.048	0.097	-0.319
	males	-0.061	0.085	0.501	-0.281
rank	high	-0.059	0.049	0.253	-0.361
	mid high	0.007	0.054	0.899	0.043
	mid low	-0.141	0.128	0.301	-0.346
	low	-0.140	0.077	0.129	-0.595
cycling	oestrus	0.014	0.041	0.727	0.113
	non-oestrus	-0.042	0.082	0.618	-0.161
intensity	high	-0.023	0.043	0.598	-0.109
	low	-0.060	0.033	0.083	-0.347
valence	neutral	0.132	0.087	0.205	0.561
	negative	**-0.143**	**0.049**	**0.009**	**-0.677**
	positive	-0.042	0.045	0.357	-0.197
	sexual	0.021	0.074	0.789	0.093
overall		-0.078	0.041	0.068	-0.312

Table 3.7 | Showing the mean, standard error (SE), statistical significance (p; significant values in bold font) and effect size (Pearson's r) for each context subcategory. Error bars could not be included in Figure 3.6 as this graph was constructed from separately calculated figures and not directly from the main data set but the inclusion of the SE values provide the corresponding information in more detail.

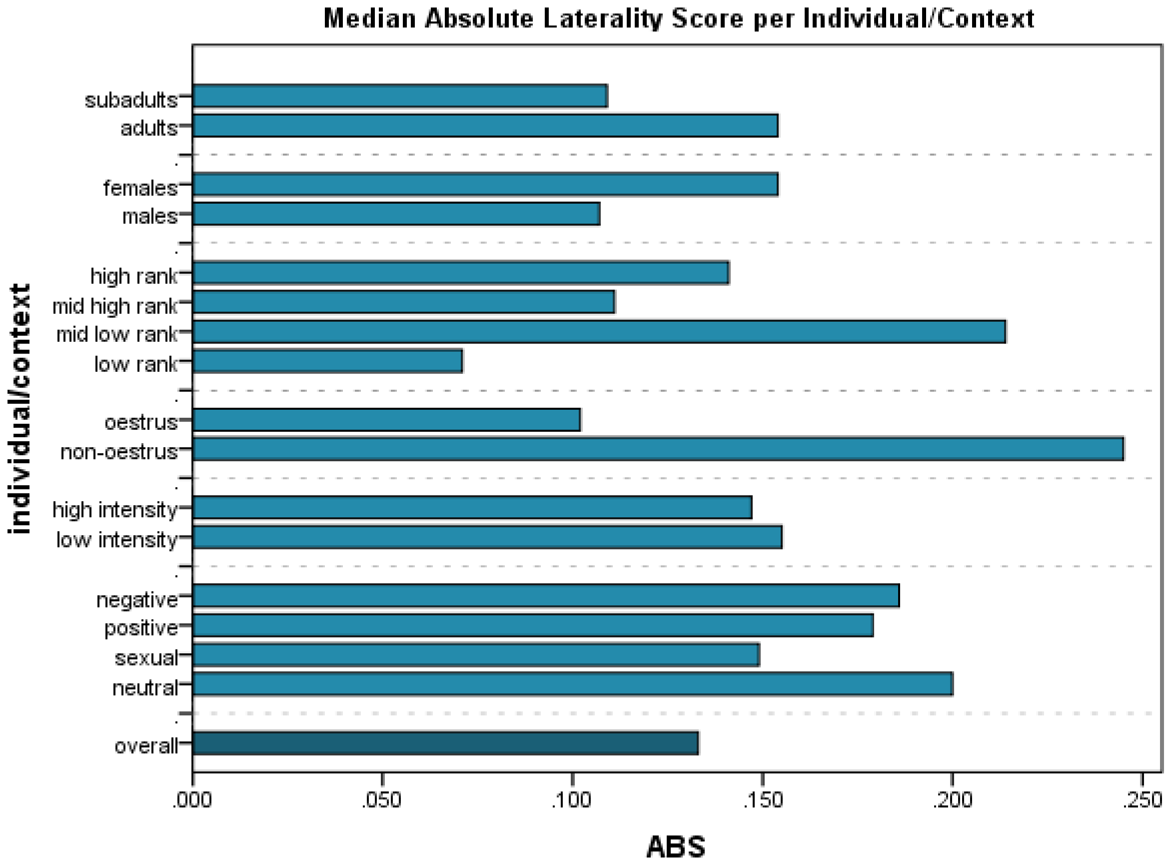

Figure 3.8 | Showing the median ABS values for each individual/context measured in analyses. The overall population median has been shown at the bottom.

		median	IQR		*p*	*r*
age	subadults	0.109	0.020	0.203	0.722	0.107
	adults	0.154	0.071	0.233	0.882	0.190
sex	females	0.154	0.071	0.221	0.865	0.387
	males	0.107	0.020	0.184	0.735	0.128
rank	high	0.141	0.072	0.207	0.799	0.081
	mid high	0.111	0.047	0.212	0.767	0.046
	mid low	0.214	0.099	0.322	0.110	0.533
	low	0.071	0.015	0.256	0.600	0.214
cycling	oestrus	0.102	0.022	0.132	0.169	0.435
	non-oestrus	**0.245**	**0.194**	**0.288**	**0.012**	**0.792**
intensity	high	0.147	0.088	0.212	0.198	0.263
	low	0.155	0.071	0.197	0.343	0.732
valence	neutral	0.200	0.163	0.268	0.078	0.788
	negative	0.186	0.069	0.277	0.158	0.408
	positive	0.179	0.071	0.258	0.170	0.300
	sexual	0.149	0.035	0.235	0.779	0.099
overall		0.133	0.053	0.221	-	

Table 3.9 | Showing the median, interquartile range (IQR), statistical significance (p; significant values in bold font) and effect size (Pearson's r) for each context subcategory. Similar to Figure 3.6 error bars could not be included in Figure 3.8 but SE values have been provided here accordingly.

3.5.1.1 BLI and ABS data by Age

When the BLI data were split by age it was normally distributed for adults: D(23)=0.158, p=0.140 and subadults: D(11)=0.187, p=0.200. A significant left side lateral bias was observed for adults: M=-0.109, SE=0.527, t(23)=-2.070, p=0.050 (Pearson's r=0.396), but no bias was found for subadults: M=-0.012, SE=0.062, t(11)=-0.191, p=0.852 (Pearson's r=0.057). No significant difference was found between these age groups: t(32)=-1.108, p=0.276 (Pearson's r=0.192).

The ABS data were normally distributed for subadults: D(11)=0.218, p=0.152 but not for adults: D(23)=0.221, p=0.005 therefore nonparametric analyses were performed on both to maintain consistency. There was no significant strength bias observed for subadults: MDN=0.109, IQR=0.020-0.203, W(11)=29.0, Z=-0.356, p=0.722 (Pearson's r=0.107), or adults: MDN=0.154, IQR=0.071-0.233, W(23)=167.0, Z=0.882, p=0.378 (Pearson's r=0.190), and no significant difference was observed between the median subadult and adult ABS values: U(32)=102.5, p=0.388 (Pearson's r=0.151).

3.5.1.2 BLI and ABS data by Sex

BLI data were normally distributed for males: D(7)=0.263, p=0.152, and females: D(27)=0.138, p=0.200. There was no significant directional bias was observed for males: M=-0.061, SE=0.085, t(6)=-0.716, p=0.501 (Pearson's r=0.281), or females M=-0.082, SE=0.048, t(26)=-1.719, p=0.097 (Pearson's r=0.319) and there was no significant difference between sexes: t(32)=0.207, p=0.838 (Pearson's r=0.037).

The ABS data were also normally distributed for males: D(7)=0.272, p=0.126 but not for females: D(27)=0.209, p=0.004 therefore nonparametric analyses were performed. No significant strength biases were observed for males: MDN=0.107, IQR=0.020-0.184, W(7)=12.0, Z=-0.338, p=0.735 (Pearson's r=0.128), or females: MDN=0.154, IQR=0.071-0.221, W(27)=225.0, Z=0.865, p=0.387 (Pearson's r=0.166), and no significant difference was observed between sexes: U(32)=73.50, p=0.385 (Pearson's r=0.153).

3.5.1.3 BLI and ABS data by Rank

When the data set was split between ranks, the BLI values for all four ranks were normally distributed; high: D(10)=0.174, p=0.200; mid high: D(9)=0.123, p=0.200; mid low: D(9)=0.189, p=0.200; low: D(6)=0.259, p=0.200. No ranks were significantly lateralised; high: M=-0.059, SE=0.049, t(9)=-1.223, p=0.253 (Pearson's r=0.361); mid high: M=0.007, SE=0.054, t(8)=0.130, p=0.899 (Pearson's r=0.043); mid low: M=-0.141, SE=0.128, t(8)=-1.105, p=0.301 (Pearson's r=0.346); low: M=-0.140, SE=0.077, t(5)=-1.815, p=0.129 (Pearson's r=0.595) and there was no significant difference between these ranks: F(3,30)=0.043, p=0.838 (η^2=0.104).

The ABS data for high: D(10)=0.179, p=0.200; mid high: D(9)=0.176, p=0.200; and low: D(6)=0.259, p=0.200 rank categories were normally distributed but the mid low rank data were non-normal: D(9)=0.278, p=0.043 so nonparametric analyses were performed. No significant strength biases were observed for any rank categories; high: MDN=0.141, IQR=0.072-0.207, W(10)=30.0, Z=0.255, p=0.799 (Pearson's r=0.081); mid high: MDN=0.111, IQR=0.047-0.212, W(9)=20.0, Z=-0.296, p=0.767 (Pearson's r=0.046); mid low: MDN=0.214, IQR=0.099-0.322, W(9)=36.0, Z=1.599, p=0.110 (Pearson's r=0.533); low: MDN=0.071, IQR=0.015-0.256, W(6)=8.00, Z=-0.524, p=0.600 (Pearson's r=0.214). No effect of rank was found: H(3)=3.438, p=0.329 (η^2=0.104).

3.5.4.4 BLI and ABS data by Emotional Intensity

The BLI values for each category of emotional intensity were normally distributed; low intensity: D(24)=0.142, p=0.200; high intensity: D(24)=0.158, p=0.127. No significant lateral biases were found for either intensity category; low intensity: M=-0.060, SE=0.033, t(24)=-1.812, p=0.083 (Pearson's r=-0.347); high intensity: M=-0.023, SE=0.043, t(24)=-0.535, p=0.598 (Pearson's r=-0.109), and no significant difference was observed between these categories:

F(1,46.00)=0.448, p=0.507, ICC=0.00.

The ABS values for low and high intensity interactions were also normally distributed; low intensity: D(24)=0.099, p=0.200; high intensity: D(24)=0.157, p=0.131 but as the overall population ABS data were not normally distributed non-parametric methods were used to compare the ABS values from each intensity to the expected ABS value (population median). No significant strength biases were observed for either intensity category; low intensity: MDN=0.155, IQR=0.071-0.197, W(24)=162.0, Z=0.343, p=0.732 (Pearson's r=0.070); high intensity: MDN=0.147, IQR=0.088-0.212, W(24)=195.0, Z=1.286, p=0.198 (Pearson's r=0.263) and there was no significant difference between these categories: F(1,25.22)=1.298, p=0.265, ICC=0.236).

3.5.4.5 BLI and ABS data by Emotional Valence

The data were normally distributed for BLI in all four valence categories; neutral: D(5)=0.285, p=0.200; negative: D(12)=0.175, p=0.200; positive: D(21)=0.153, p=0.200; and sexual: D(8)=0.182, p=0.200. No significant directional biases were observed for neutral: M=0.132, SE=0.087, t(4)=1.514, p=0.205 (Pearson's r=0.561); positive: M=-0.042, SE=0.045, t(21)=-0.942, p=0.357 (Pearson's r=0.197); or sexual valence: M=0.021, SE=0.074, t(8)=0.279, p=0.789 (Pearson's r=0.093); but a significant left side bias was found for negative valence behaviours: M=-0.143, SE=0.049, t(11)=-3.183, p=0.009 (Pearson's r=0.677). Used a mixed linear model no significant overall effect of valence was found: F(3,37.61)=2.663, p=0.062 (ICC=0.089) and when the neutral valence subcategory was set as the reference category negative valence behaviours were significantly more strongly left-side lateralised than neutral valence behaviours: t(40.12)=-2.665, p=0.011 (Pearson's r=-0.388) but there were no similar effect for positive or sexual valences behaviours; positive: t(39.72)=-1.842, p=0.073 (Pearson's r=-0.281); sexual: t(37.27)=-1.043, p=0.304 (Pearson's r=-0.168).

When the ABS data were split by valence all four categories were found to be normally distributed: neutral: D(5)=0.220, p=0.200; negative(12)=0.163, p=0.200; positive(21)=0.137, p=0.200; sexual(8)=0.204, p=0.200. As the overall population ABS data were not normally distributed each valence ABS value was compared to the population median (the predicted ABS value) using nonparametric methods and none of the valence categories were found to exhibit a significant strength bias; neutral: MDN=0.200, IQR=0.163-0.268, W(5)=14.00, Z=1.761, p=0.078 (Pearson's r=0.788); negative: MDN=0.186, IQR=0.069-0.277, W(12)=57.00, Z=1.412, p=0.158 (Pearson's r=0.408); positive: MDN=0.179, IQR=0.071-0.258, W(21)=155.00, Z=1.373, p=0.170 (Pearson's r=0.300); sexual: MDN=0.149, IQR=0.035-0.235, W(8)=20.00, Z=0.280, p=0.779 (Pearson's r=0.099). No significant overall effect of valence was found: F(3,42.00)=0.300, p=0.825 (ICC=0.00) and, by using the neutral valence category as the reference category in a linear mixed model, none of the valence categories exerted a significant influence upon lateralisation: negative: t(42.00)=-0.558, p=0.580 (Pearson's r=-0.086); positive: t(42.00)=-0.746, p=0.460 (Pearson's r=-0.115); sexual: t(42.00)=-0.924, p=0.361 (Pearson's r=-0.141).

3.5.4.6 BLI and ABS data by Oestrus Cycling

The data for in-oestrus and non-oestrus adult females were normally distributed for both subcategories; in-oestrus: D(10)=0.168, p=0.200; non-oestrus=D(10)=0.257, p=0.060. No significant lateral biases were observed for either in-oestrus: M=0.014, SE= 0.041, t(9)=0.360, p=0.727 (Pearson's r=0.113), or non-oestrus individuals: M=-0.042, SE= 0.082, t(9)=-0.516, p=0.618 (Pearson's r=0.161) and there was no significant difference between these subcategories: t(9)=0.519, p=0.616 (Pearson's r=0.136).

The ABS data were normally distributed for in-oestrus: D(10)=0.187, p=0.200, and non-oestrus: D(10)=0.251, p=0.073 adult females. No significant strength bias was observed for in-oestrus females: MDN=0.102, IQR=0.022-0.132, W=14.00, Z=-1.377, p=0.169 (Pearson's r=0.435), but a significant strength bias was found for non-oestrus females: MDN=0.245, IQR=0.194-0.288, W=52.00, Z=2.504, p=0.012 (Pearson's r=0.792) and a significant difference in strength bias was found between in-oestrus and non-oestrus individuals: Z=-2.803, p=0.005 (Pearson's r= 0.693).

3.5.2—Visual Field Proportions

For the overall data the VFP values were normally distributed and thus mean VFP values could be calculated; extreme left: M=0.173, SE=0.021; mid left: M=0.229, SE=0.023; centre: M=0.204, SE=0.024; mid right: M=0.211, SE=0.017; and extreme right: M= 0.182, SE= 0.024 and no significant overall difference between these values was observed using a repeated measures ANOVA with a Greenhouse-Geisser Correction (Mauchly's Test of Sphericity: $X^2(9)$= 25.108, p=0.003): F(2.925, 96.533)=0.649, p=0.582 (η^2=0.019). However, when VFP values were calculated for each of the subcategories within each context (e.g. for males & females within the sex context) the data were not normally distributed for all visual fields therefore it was necessary to use nonparametric methods for any comparions between the data from each category and the expected VFP values (the overall population median VFP values). The median population VFP values were then calculated for each visual field; extreme left: MDN=0.167, IQR=0.087-0.265; mid left: MDN=0.211, IQR=0.141-0.273; centre: MDN=0.201, IQR=0.113-0.316; mid right: MDN=0.217, IQR=0.151-0.270; extreme right: MDN=0.160, IQR=0.054-0.254 (and these have been plotted in Figure 3.10). No significant overall difference was found between these median VFP values: $X^2(4)$=2.419, p=0.659 (Kendall's W= 0.018).

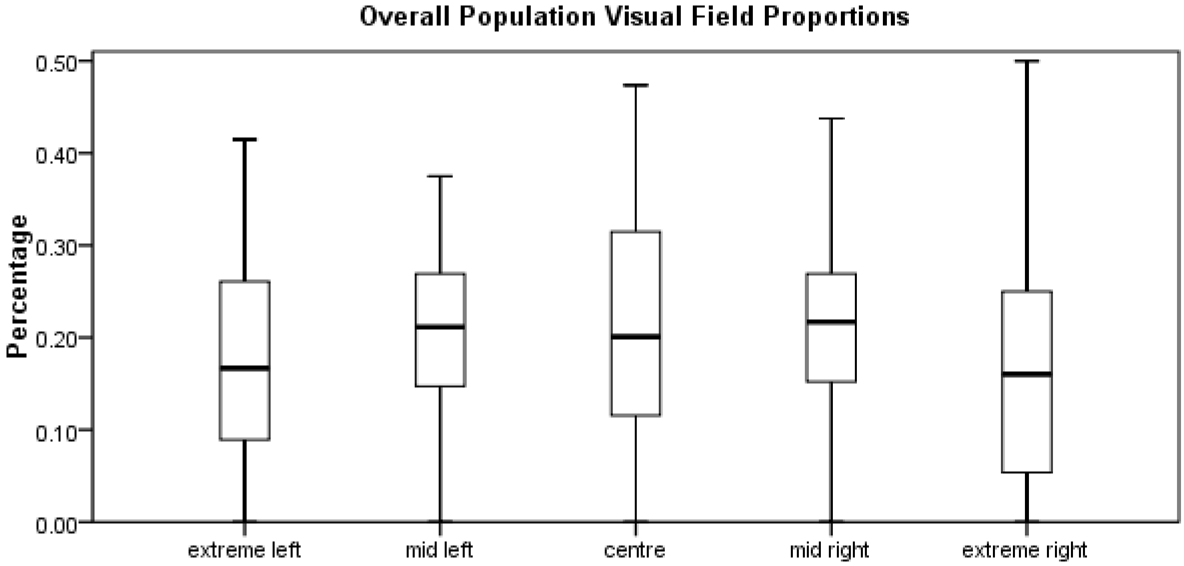

Figure 3.10 | Showing the population median VFP values for the five visual fields based on data from all 34 individuals.

3.5.2.1 Visual Field Proportions by Age

For subadults the VFP data were normally distributed for three five visual fields; mid left: D(11)=0.108, p=0.200; mid right: D(11)=0.213, p=0.177; and extreme right: D(11)=0.129, p=0.200; but were not normally distributed for the extreme left: D(11)=0.252, p=0.050; or central: D(11)=0.263, p=0.032 visual fields. For adults the data were normally distributed for all visual fields; extreme left: D(23)=0.083, p=0.200; mid left: D(23)=0.143, p=0.200; centre: D(23)=0.121, p=0.200; mid right: D(23)=0.135, p=0.200, and extreme right: D(23)=0.121, p=0.200.

There was no significant overall difference between the five VFP values for subadults: $X^2(4)=5.414$, p=0.247 (Kendall's W=0.123) and none of the VFP values differed significantly from the predicted VFP values of the overall group population. Subadults performed the highest proportion of their behaviours in their mid right visual field: MDN=0.250, IQR=0.160-0.269, W=37.00, Z=0.356, p=0.722 (Pearson's r=0.107), and the lowest proportion of behaviours in their extreme left visual field: MDN=0.089, IQR=0.060-0.261, W=25.00, Z=-0.712, p=0.477 (Pearson's r=0.215). The remaining VFP values were calculated as follows: mid left:

MDN=0.219, IQR=0.094-0.340, W=45.00, Z=1.067, p=0.286 (Pearson's r=0.322); centre: MDN=0.214, IQR=0.156-0.225, W=39.50, Z=0.578, p=0.563 (Pearson's r=0.174); extreme right: MDN=0.200, IQR=0.107-0.240, W=41.00, Z=0.712, p=0.477 (Pearson's r=0.215).

For adults there was no significant overall difference between VFP values: $X^2(4)=1.076$, p=0.898 (Kendall's W= 0.012) and none of the observed VFP values were significantly different from the predicted values. Both mid visual fields reported the highest VFP values (mid left: MDN=0.208, IQR=0.161-0.267, W=194.00, Z=1.704, p=0.088 (Pearson's r=0.355); mid right: MDN=0.208, IQR=0.133-0.274, W=114.00, Z=-0.730, p=0.465 (Pearson's r=0.152)) whilst the lowest VFP value was calculated for the extreme right visual field: MDN=0.154, IQR=0.054-0.265, W=143.00, Z=0.152, p=0.879 (Pearson's r=0.032). The VFP values for the extreme left visual field (MDN=0.177, IQR=0.110-0.276, W=170.00, Z=0.974, p=0.330 (Pearson's r=0.203)) and the central visual field (MDN=0.167, IQR=0.083-0.333, W=137.00, Z=-0.030, p=0.976 (Pearson's r=0.006)) were also non-significant. All VFP values for both age categories have been plotted in Figure 3.12.

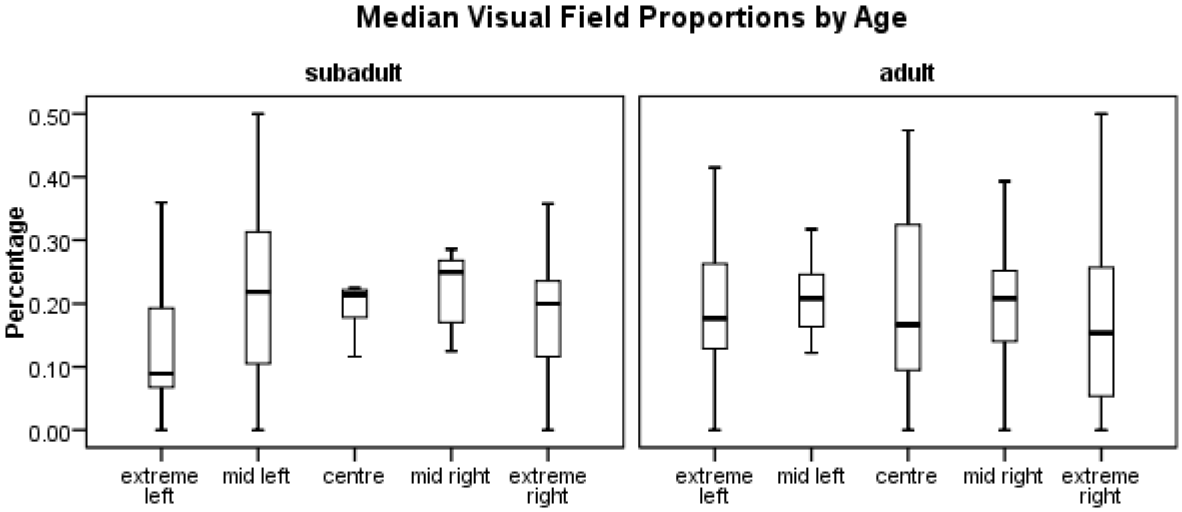

Figure 3.11 | Comparing the VFP values for subadults (n=11) and adults (n=23)

When both age categories were compared no significant contrasts were observed between any of the VFP values for subadults and adults: extreme left: U=82.50, p=0.105 (Pearson's r=0.278); mid left: U=117.50, p=0.740 (Pearson's r=0.057); centre: U=389.50, p=0.632 (Pearson’s r=0.082); mid right: U=379.00, p=0.387 (Pearson’s r=0.148); extreme right: U=192.50, p=1.000 (Pearson’s r=0.000).

3.5.2.2 Visual Field Proportions by Sex

For females the VFP data were normally distributed for all five visual fields; extreme left: D(27)=0.073, p=0.200; mid left: D(27)=0.120, p=0.200; centre: D(27)=0.100, p=0.200; mid right: D(27)=0.100, p=0.200; extreme right: D(27)=0.105, p=0.200 . For males the data were normally distributed for four visual fields; extreme left: D(7)=0.172, p=0.200; mid left: D(7)=0.167, p=0.200; centre: D(7)=0.227, p=0.200; mid right: D(7)=0.228, p=0.200, but were not normally distributed for the extreme right visual field: D(7)=0.379, p=0.003, thereby necessitating nonparametric analyses.

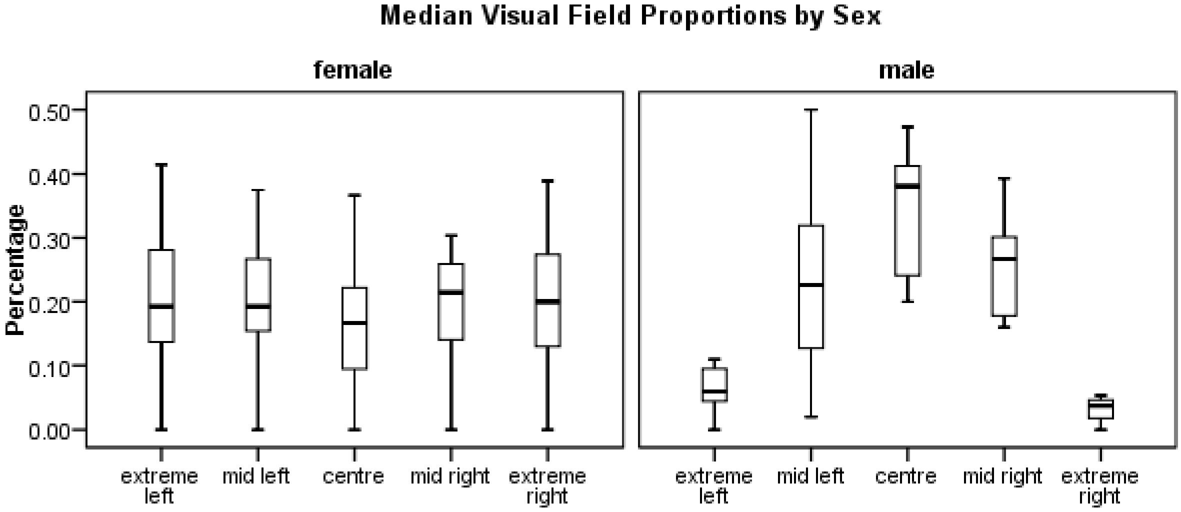

Figure 3.12 | Showing the median VFP values of female (n=27) and male (n=7) subjects

For females, there was no significant overall difference between the five VFP values: $X^2(4)=0.904$, p=0.924 (Kendall’s W=0.008) and none of the VFP values were significantly different from predicted. The highest VFP value was found for the mid right visual field: MDN=0.214, IQR=0.133-0.268, W=150.00, Z=-0.937, p=0.349 (Pearson’s r=0.180), whilst the lowest VFP value was found for the central visual field: MDN=0.167, IQR=0.083-0.225, W=133.50, Z=-1.334, p=0.182 (Pearson’s r=0.257), and the remaining VFP values were: extreme left: MDN=0.192, IQR=0.125-0.286, W=250.00, Z=1.466, p=0.143 (Pearson’s r=0.282), mid left: MDN=0.192, IQR=0.147-0.267, W=162.00, Z=-0.649, p=0.516 (Pearson’s r=0.125), and extreme right: MDN=0.200, IQR=0.125-0.283, W=260.00, Z=1.706, p=0.088 (Pearson’s r=0.328).

There was a significant difference between VFP values for males: $X^2(4)$=0.16.089, p=0.003 (Kendall’s W=0.575) and both of the extreme visual fields returned significantly lower VFP values than predicted: extreme left: MDN=0.060, IQR=0.040-0.100, W=0.00, Z=-2.366, p=0.018 (Pearson’s r=0.894), and extreme right: MDN=0.038, IQR=0.000-0.054, W=1.00, Z=-2.201, p=0.028 (Pearson’s r=0.378). The central visual field returned the highest VFP value and was also significantly different from predicted: MDN=0.381, IQR=0.214-0.425, W=27.00, Z=2.197, p=0.028 (Pearson’s r=0.830) although neither of the mid visual fields reported significant VFP values: mid left: MDN=0.226, IQR=0.040-0.340, W=17.00, Z=0.507, p=0.612 (Pearson’s r=0.192), and mid right: MDN=0.267, IQR=0.175-0.329, W=20.00, Z=1.014, p=0.310 (Pearson’s r=0.383) and the median VFP values for both sexes have been shown in Figure 3.11.

Significant differences between male and female VFP values were observed with males found to perform a significantly higher percentage of their behaviours in their central visual field than females (U=26.50, p=0.004 (Pearson’s r=0.497) and a significantly lower percentage of behaviours in their extreme visual fields (extreme left: U=22.50, p=0.002 (Pearson’s r=0.526); extreme right U=27.50, p=0.004 (Pearson’s r=0.490), but no significant contrast was found for either of the mid visual fields; mid left: U=74.00, p=0.382 (Pearson’s r=0.150), mid right: U=63.00, p=0.180 (Pearson’s r=0.230).

3.5.2.3 Visual Field Proportions by Rank

Data were normally distributed for all visual fields in three of the four rank subcategories with the low rank subcategory the sole exception thereby necessitating nonparametric analyses for these data. For high rank individuals all data were normally distributed: extreme left: D(10)=0.176, p=0.200; mid left: D(10)=0.202, p=0.200; centre: D(10)=0.146, p=0.200; mid right: D(10)=0.157, p=0.200; extreme right: D(10)=0.225, p=0.165. VFP data were also normally distributed for the mid high rank group: extreme left: D(9)=0.222, p=0.200; mid left: D(9)=0.252, p=0.105; centre: D(9)=0.148, p=0.200; mid right: D(9)=0.157, p=0.200; extreme right: D(9)=0.152, p=0.200. For the mid low rank subcategory all data were normally distributed: extreme left: D(9)=0.176, p=0.200; mid left: D(9)=0.147, p=0.200; centre: D(9)=0.183, p=0.200; mid right: D(9)=0.189, p=0.200; extreme right: D(9)=0.149, p=0.200. For individuals in the low rank group data were not normally distributed for the extreme left VFP values but were normally distributed for each of the other visual fields: extreme left: D(6)=0.331, p=0.039; mid left: D(6)=0.203, p=0.200; centre: D(6)=0.288, p=0.132; mid right: D(6)=0.171, p=0.200; extreme right: D(6)=0.203, p=0.200.

There was no significant overall difference between the five VFP values for the high rank subcategory: $X^2(4)=6.324$, p=0.176 (Kendall’s W=0.158), and none of the VFP values differed significantly from the predicted VFP values. The highest VFP value was found for the central visual field: MDN=0.301, IQR=0.167-0.392, W=44.00, Z=1.683, p=0.092 (Pearson’s r=0.532) whilst the lowest VFP value was for the extreme right visual field: extreme right: MDN=0.077, IQR=0.037-0.213, W=17.00, Z=-1.070, p=0.722 (Pearson’s r=0.338) and the remaining VFPs were as follows: extreme left: MDN=0.167, IQR=0.079-0.213, W=19.00, Z=-0.869, p=0.385 (Pearson’s r=0.275); mid left: MDN=0.218, IQR=0.170-0.267, W=33.00, Z=0.561, p=0.575 (Pearson’s r=0.177), mid right: MDN=0.215, IQR=0.165-0.301, W=31.00, Z=0.357, p=0.721 (Pearson’s r=0.113).

For the mid high rank group, there was no significant overall difference between the five VFP values: $X^2(4)=0.655$, p=0.176 (Kendall’s W=0.158) although the mid left VFP value was significantly lower than predicted: MDN=0.167, IQR=0.074-0.206, W=3.00, Z=-2.310, p=0.021 (Pearson’s r=0.770). None of the remaining VFP values were significantly different from predicted: extreme left: MDN=0.154, IQR=0.093-0.249, W=21.00, Z=-0.178, p=0.859 (Pearson's r=0.059), centre: MDN=0.147, IQR=0.078-0.292, W=17.00, Z=-0.652, p=0.515 (Pearson's r=0.217), mid right: MDN=0.219, IQR=0.131-0.277, W=21.00, Z=-0.178, p=0.859 (Pearson's r=0.059), extreme right: MDN=0.203, IQR=0.129-0.322, W=32.00, Z=1.125, p=0.260 (Pearson's r=0.375).

In the mid low ranked subcategory there was no significant overall difference between the VFP values for the five visual fields: $X^2(4)=5.461$, p=0.243 (Kendall's W= 0.152) but the VFP value for the central visual field was significantly lower than predicted: MDN=0.116, IQR=0.036-0.208, W=6.00, Z=-1.958, p=0.050 (Pearson's r=0.653). None of the remaining four visual fields proportions were significantly different from predicted: extreme left: MDN=0.261, IQR=0.173-0.311, W=40.00, Z=2.073, p=0.038 (Pearson's r=0.691), mid left: MDN=0.214, IQR=0.132-0.302, W=25.00, Z=0.296, p=0.767 (Pearson's r=0.099), mid right: MDN=0.214, IQR=0.076-0.269, W=18.00, Z=-0.534, p=0.594 (Pearson's r=0.178), extreme right: MDN=0.232, IQR=0.139-0.343, W=34.00, Z=1.362, p=0.173 (Pearson's r=0.454).

There was no significant difference between VFP values for the lowest rank group: $X^2(4)=6.712$, p=0.152 (Kendall's W=0.280) and none of these VFP values were significantly different from their corresponding predicted values. The highest VFP value was found for the mid left visual field: MDN=0.313, IQR=0.075-0.406, W=14.00, Z=0.734, p=0.463 (Pearson's r=0.300), and the lowest was reported for the extreme left visual field: MDN=0.068, IQR=0.000-0.165, W=6.00, Z=-0.946, p=0.344 (Pearson's r=0.386). The remaining VFP values were as follows: centre: MDN=0.220, IQR=0.189-0.341, W=16.00, Z=-1.153, p=0.249 (Pearson's r=0.471), mid right: MDN=0.208, IQR=0.151-0.271, W=37.00, Z=0.356, p=0.722 (Pearson's r=0.145), extreme right: MDN=0.116, IQR=0.000-0.210, W=9.00, Z=-0.314, p=0.753 (Pearson's r=0.128).

A comparison of all four rank subcategories found a significant effect upon the central visual field: H(3)=9.261, p=0.026 ($\eta^2=0.281$), but for none of the four other visual fields:

extreme left: H(3)=7.540, p=0.057 (η^2=0.228); mid left: H(3)=4.451, p=0.217 (η^2=0.135); mid right: H(3)=0.868, p=0.833 (η^2=0.026); extreme right: H(3)=6.009, p=0.111 (η^2=0.182). Post-hoc Mann-Whitney tests were then performed upon the central visual field data and pairwise comparisons were made between each of the four rank groups with the Holm-Bonferroni method used to adjust the level of significance accordingly but no significant differences were found (reported in order of significance): high vs mid low (α=0.008): U=15.00, p=0.014 (Pearson's r=0.421); mid low vs low (α=0.010): U=7.00, p=0.018 (Pearson's r=0.406); high vs mid high (α=0.013): U=23.00, p=0.072 (Pearson's r=0.308); mid high vs low (α=0.017): U=16.00, p=0.195 (Pearson's r=0.222); mid high vs mid low (α=0.025): U=28.00, p=0.268 (Pearson's r=0.190); high vs low (α=0.050): U=25.50, p=0.625 (Pearson's r=0.084). The median VFP values for each rank have been shown in Figure 3.13.

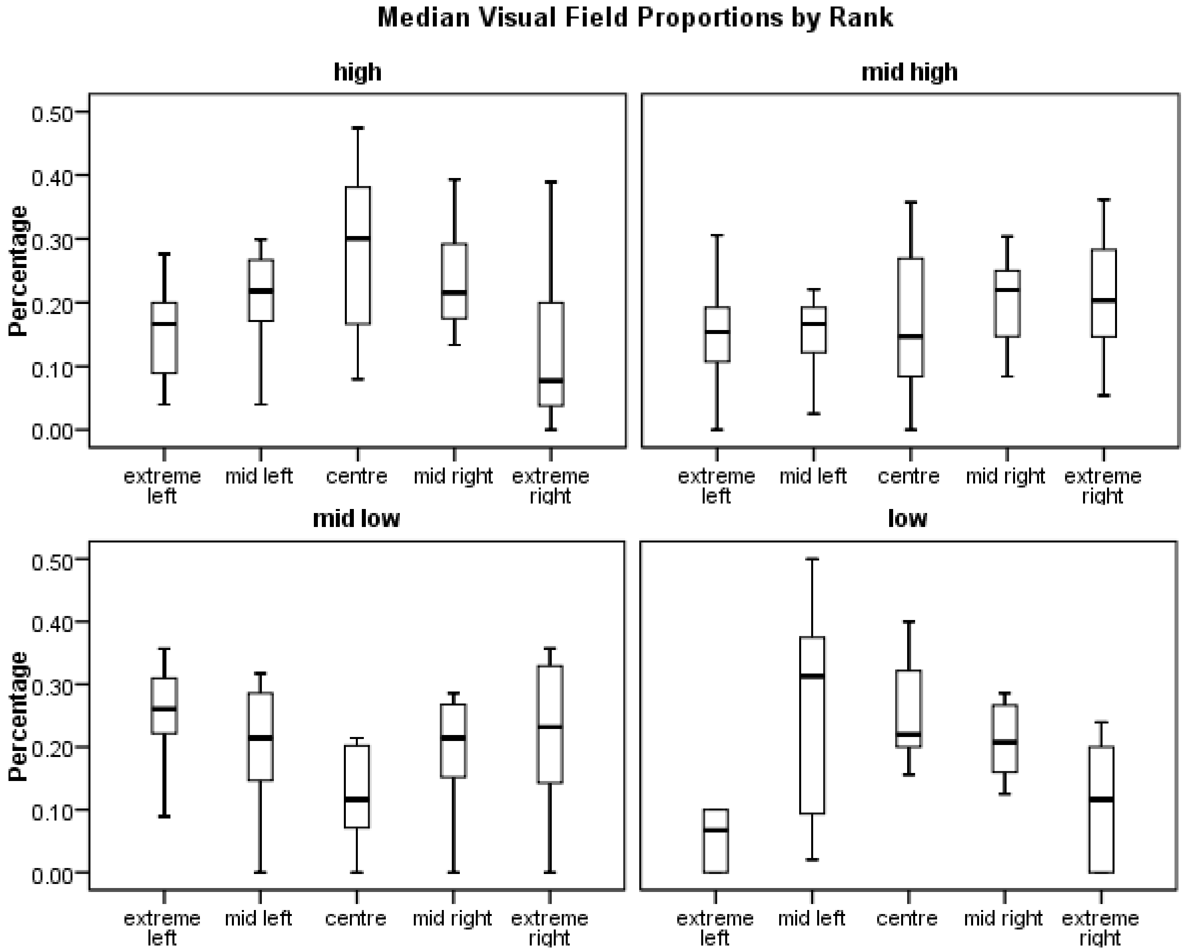

Figure 3.13 | Showing the four rank categories and the median VFP values for each (high n=10, mid high n=9, mid low n=9, low n=6).

3.5.2.4 Visual Field Proportions by Emotional Intensity

Non-normally distributed data were found for both subcategories of emotional intensity. In low emotional intensity contexts the data were not normally distributed in the extreme left visual field: D(24)=0.215, p=0.006, but were normally distributed for the remaining four VFP values: mid left: D(24)=0.147, p=0.192; centre: D(24)=0.120, p=0.200; mid right: D(24)=0.100, p=0.200; extreme right: D(24)=0.132, p=0.200. For the high intensity emotion subcategory data were not normally distributed for the mid left: D(24)=0.184, p=0.034; centre: D(24)=0.198, p=0.016; and extreme right: D(24)=0.193, p=0.021; visual fields but were normally distributed for the extreme left: D(24)=0.118, p=0.200; and mid right: D(24)=0.133, p=0.200; visual fields.

A significant overall difference between the five VFP values for the low intensity emotion category was reported: $X^2(4)=30.330$, p<0.001 (Kendall's W=0.316) and both of the extreme visual fields returned VFP values significantly lower than the corresponding expected values for those visual fields: extreme left: MDN=0.059, IQR=0.000-0.143, W=61.00, Z=-2.565, p=0.010 (Pearson's r=0.475); extreme right: MDN=0.078, IQR=0.012-0.143, W=37.00, Z=-3.237, p=0.001 (Pearson's r=0.666) whilst the VFP value for the mid right visual field was significantly higher than expected: MDN=0.268, IQR=0.195-0.367, W=226.00, Z=2.172, p=0.030 (Pearson's r=0.434), but neither of the remaining categories differed significantly from expected: mid left: MDN=0.267, IQR=0.135-0.306, W=197.00, Z=1.344, p=0.179 (Pearson's r=0.120); centre: MDN=0.268, IQR=0.129-0.484, W=210.00, Z=1.715, p=0.086 (Pearson's r=0.434);

No significant overall difference was observed between the VFP values for high intensity emotion behaviours: $X^2(4)=4.562$, p=0.335 (Kendall's W=0.048). The mid left VFP was significantly lower than predicted: MDN=0.127, IQR=0.060-0.221, W=69.00, Z=-12.316, p=0.021 (Pearson's r=0.300), but no other significant differences were observed: extreme left: MDN=0.200, IQR=0.127-0.300, W=209.00, Z=1.686, p=0.092 (Pearson's r=0.300); centre:

MDN=0.106, IQR=0.057-0.296, W=117.00, Z=-0.943, p=0.346 (Pearson's r=0.300); mid right: MDN=0.164, IQR=0.119-0.287, W=114.00, Z=-1.029, p=0.304 (Pearson's r=0.300); extreme right: MDN=0.176, IQR=0.053-0.490, W=205.00, Z=1.573, p=0.116 (Pearson's r=0.300). The median VFP values for high and low intensity interactions have been shown in Figure 3.14.

Using a generalised linear mixed model to compare the VFP data from low and high intensity interactions within each visual field a significant difference was found in all five visual fields with low intensity behaviours performed significantly less frequently than high intensity interactions in the extreme left (F(1,46)=35.357, p<0.001, ICC=0.909, FC=-0.120, p<0.001) and extreme right (F(1,46)=13.040, p=0.001, ICC=0.188, FC=-0.156, p=0.001) visual fields but significantly more frequently than high intensity interactions in the central visual field (F(1,46)=7.318, p=0.010, ICC=0.385, FC=0.117, p=0.010) mid left (F(1,46)=5.105, p=0.029, ICC=0.00, FC=0.085, p=0.029) and mid right (F(1,46)=5.874, p=0.019, ICC=0.00, FC=0.085, p=0.019) visual fields.

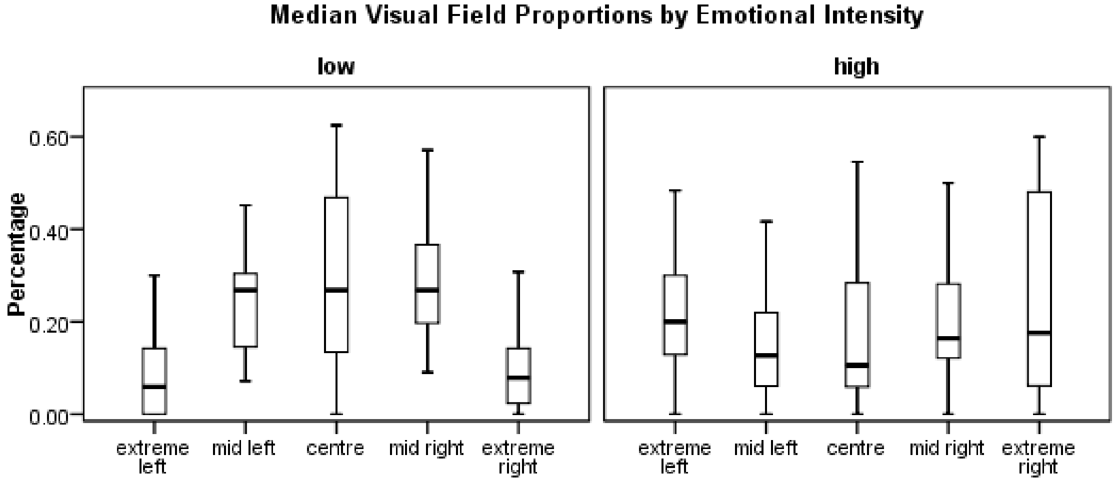

Figure 3.14 | Showing the median VFP values for the categories of high (n=24) and low (n=24) emotional intensity.

3.5.2.5 Visual Field Proportions by Emotional Valence

When the data set was split into the four valence categories non-normally distributed data were reported for all four valences. For the neutral valence subcategory no interactions were observed in the extreme left visual field whilst the data were non-normal for the extreme right visual field: D(5)=0.365, p=0.029, but normally distributed for the remaining three visual fields; mid left: D(5)=0.190, p=0.200; centre: D(5)=0.215, p=0.200; mid right: D(5)=0.185, p=0.200. For negative valence behaviours data were non-normal for the extreme right visual field: D(12)=0.262, p=0.022; but normally distributed for the other four visual fields; extreme left: D(12)=0.188, p=0.200; mid left: D(12)=0.158, p=0.200; centre: D(12)=0.153, p=0.200; and mid right: D(12)=0.230, p=0.080. The data were also non-normal in the central visual field for positive valence behaviours: D(21)=0.278, p<0.001, but normally distributed for each of the other four visual fields; extreme left: D(21)=0.178, p=0.082; mid left: D(21)=0.171, p=0.109; mid right: D(21)=0.181, p=0.069; and extreme right: D(21)=0.139, p=0.200. For sexual behaviours the data were normally distributed for mid left: D(8)=0.194, p=0.200; centre: D(8)=0.183, p=0.200; and mid right: D(8)=0.161, p=0.200; but were not normally distributed for the extreme left: D(8)=0.453, p<0001; and extreme right: D(8)=0.426, p<0.001.

VFP values from each valence were then compared to the median VFP values for the overall population. For neutral valence behaviours significantly lower than predicted VFP values was observed for both extreme visual fields; extreme left: MDN=0.000, IQR=0.000-0.000, W(5)=0.00, Z=-2.236, p=0.025 (Pearson's r=-1.000); Extreme right: MDN=0.000, IQR=0.000-0.127, W(5)=0.00, Z=-2.060, p=0.039 (Pearson's r=0.921), but no significant differences were observed for the other three visual fields; mid left: MDN=0.143, IQR=0.063-0.254, W(5)=4.00, Z=-0.944, p=0.345 (Pearson's r=-0.422); centre: MDN=0.444, IQR=0.188-0.714, W(5)=13.00, Z=1.490, p=0.136 (Pearson's r=0.666); or mid right: MDN=0.286, IQR=0.111-0.607, W(5)=12.00, Z=1.214, p=0.225 (Pearson's r=0.543).

Behaviours of a negative valence corresponded with a significantly higher than predicted VFP value for the mid left visual field: MDN=0.333, IQR=0.222-0.396, W(12)=74.00, Z=2.752, p=0.006 (Pearson's r=-0.794) but there was no significant difference for the remaining visual fields; extreme left: MDN=0.111, IQR=0.025-0.151, W(12)=17.00, Z=-1.732, p=0.083 (Pearson’s r=0.500); centre: MDN=0.171, IQR=0.061-0.243, W(12)=22.00, Z=-1.336, p=0.182 (Pearson’s r=-0.386); mid right: MDN=0.218, IQR=0.119-0.312, W(12)=39.00, Z=0.000, p=1.000 (Pearson’s r=0.000); extreme right: MDN=0.111, IQR=0.111-0.253, W(12)=31.00, Z=-0.632, p=0.527 (Pearson’s r=-0.182).

Positive valence behaviours returned significantly lower VFP values than predicted for both mid visual fields; mid left: MDN=0.133, IQR=0.000-0.191, W(21)=20.00, Z=-3.329, p=0.001 (Pearson’s r=-0.726); mid right: MDN=0.143, IQR=0.106-0.232, W(21)=38.00, Z=-2.696, p=0.007 (Pearson’s r=-0.588); and a significantly higher VFP value for the extreme right visual field: MDN=0.286, IQR=0.143-0.437, W(21)=179.00, Z=2.764, p=0.006 (Pearson’s r=0.603). No significant difference was observed for the extreme left: MDN=0.267, IQR=0.134-0.366, W(21)=168.00, Z=1.826, p=0.068 (Pearson’s r=0.398); or central visual fields: MDN=0.091, IQR=0.000-0.279, W(21)=85.00, Z=-1.065, p=0.287 (Pearson’s r=-0.232).

Finally, for behaviours of a sexual valence a significantly lower than predicted VFP value was observed for the extreme left visual field: extreme left: MDN=0.000, IQR=0.000-0.047, W(8)=0.000, Z=-2.636, p=0.008 (Pearson’s r=-0.932); whilst a significantly higher than predicted value was observed for the mid right visual field: MDN=0.343, IQR=0.359-0.472, W(8)=35.00, Z=2.383, p=0.017 (Pearson’s r=0.843) but no significant differences were reported for the remaining visual fields; mid left: MDN=0.250, IQR=0.135-0.375, W(8)=25.00, Z=0.981, p=0.326 (Pearson’s r=0.347); centre: MDN=0.333, IQR=0.165-0.469, W(8)=28.00, Z=1.402, p=0.161 (Pearson’s r=0.496); extreme right: MDN=0.000, IQR=0.000-0.083, W(8)=8.00, Z=-1.465, p=0.143 (Pearson’s r=-0.404). The median VFP values for each valence have been shown in Figure 3.15.

The median VFP values for each valence were then compared within each visual field using a generalised linear mixed model and significant overall effects of valence were reported for all five visual fields; extreme left: F(3, 42)=11.020, p<0.001, ICC=0.500; mid left: F(3, 42)=10.840, p<0.001, ICC=0.000; centre: F(3, 42)=2.845, p=0.049, ICC=0.026; mid right:

F(3,42)=4.955, p=0.005, ICC=0.000; extreme right: F(3,42)=6.419, p=0.001, ICC=0.008. Using the neutral valence as the reference category, negative valence VFP values were significantly higher in the mid left visual field: FC=0.171, p=0.005, but significantly lower for the central visual field: FC=-0.272, p=0.017. Positive valence VFP values were significantly higher in the extreme left: FC=0.220, p<0.001; and extreme right: FC=0.211, p=0.005, but also significantly lower in the central visual field: FC=-0.249, p=0.019 (Pearson's r=-0.359); and mid right: FC=-0.187, p=0.010, visual fields. Sexual valence behaviours had no significant effect upon VFP values in any visual field.

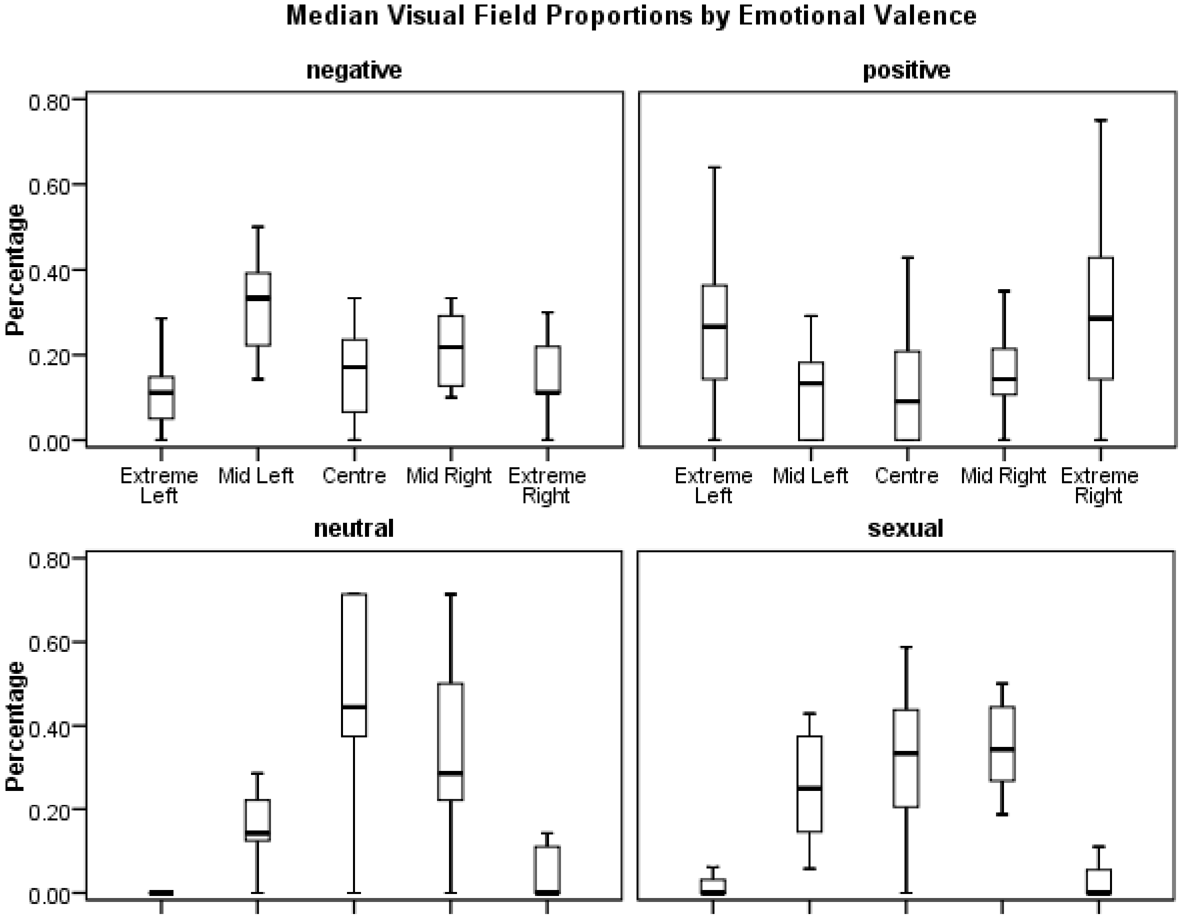

Figure 3.15 | Showing the median VFP values for each of the four valence categories (neutral n=5, negative n=12, positive n=21, sexual n=8).

3.5.2.6 Visual Field Proportions by Oestrus Cycling

For in-oestrus individuals data were normally distributed in four of the visual fields:

mid left: D(10)=0.199, p=0.200; centre: D(10)=0.201, p=0.200; mid right: D(10)=0.111, p=0.200; extreme right: D(10)=0.169, p=0.175; but were not normally distributed for the extreme left visual field: D(10)=0.260, p=0.050. For non-oestrus individuals all data were normally distributed; extreme left: D(10)=0.167, p=0.200; mid left: D(10)=0.165, p=0.200; centre: D(10)=0.238, p=0.115; mid right: D(10)=0.168, p=0.200; and extreme right: D(10)=0.255, p=0.065.

The overall difference between the five VFP values for in-oestrus individuals was not significant: $X^2(4)=1.587$, p=0.811 (Kendall's W=0.040) and none of the VFP values were significantly different from the expected values; extreme left: MDN=0.174, IQR=0.146-0.338, W=37.00, Z=0.968, p=0.333 (Pearson's r=0.475); mid left: MDN=0.174, IQR=0.000-0.248, W=15.00, Z=-1.277, p=0.201 (Pearson's r=0.120); centre: MDN=0.163, IQR=0.120-0.282, W=24.50, Z=-0.306, p=0.760 (Pearson's r=0.434); mid right: MDN=0.172, IQR=0.106-0.229, W=11.00, Z=-1.682, p=0.093 (Pearson's r=0.434); extreme right: MDN=0.188, IQR=0.137-0.381, W=31.00, Z=0.357, p=0.721 (Pearson's r=0.666).

For adult females not in oestrus there was no significant overall difference between the five VFP values: $X^2(4)=7.204$, p=0.125 (Kendall's W=0.180) and four of the five VFP values were not significantly different from predicted: extreme left: MDN=0.278, IQR=0.058-0.418, W=42.00, Z=1.479, p=0.139 (Pearson's r=0.300); mid left VFP: MDN=0.214, IQR=0.058-0.333, W=23.00, Z=-0.460, p=0.646 (Pearson's r=0.300; mid right: MDN=0.222, IQR=0.058-0.328, W=29.00, Z=0.153, p=0.878 (Pearson's r=0.300); extreme right: MDN=0.122, IQR=0.083-0.353, W=24.00, Z=-0.357, p=0.721 (Pearson's r=0.300); although the central visual field was used significantly less frequently than predicted: MDN=0.111, IQR=0.050-0.200, W=8.00, Z=-1.994, p=0.046 (Pearson's r=0.300).

Comparisons between each of the five VFP values for in-oestrus and non-oestrus individuals revealed no significant contrasts for four visual fields: extreme left: Z=-0.153, p=0.878 (Pearson's r=0.048); mid left: Z=-0.764, p=0.445 (Pearson's r=0.242); mid right: Z=-

0.764, p=0.445 (Pearson's r=242); extreme right: Z=-0.255, p=0.846 (Pearson's r=0.081) but a significant contrast was found for the central visual field and non-oestrus individuals performed a lower percentage of their behaviours in this field than when they were in oestrus: Z=-1.988, p=0.047 (Pearson's r=0.629). The median VFP values for individuals in oestrus and not in oestrus have been shown in Figure 3.16.

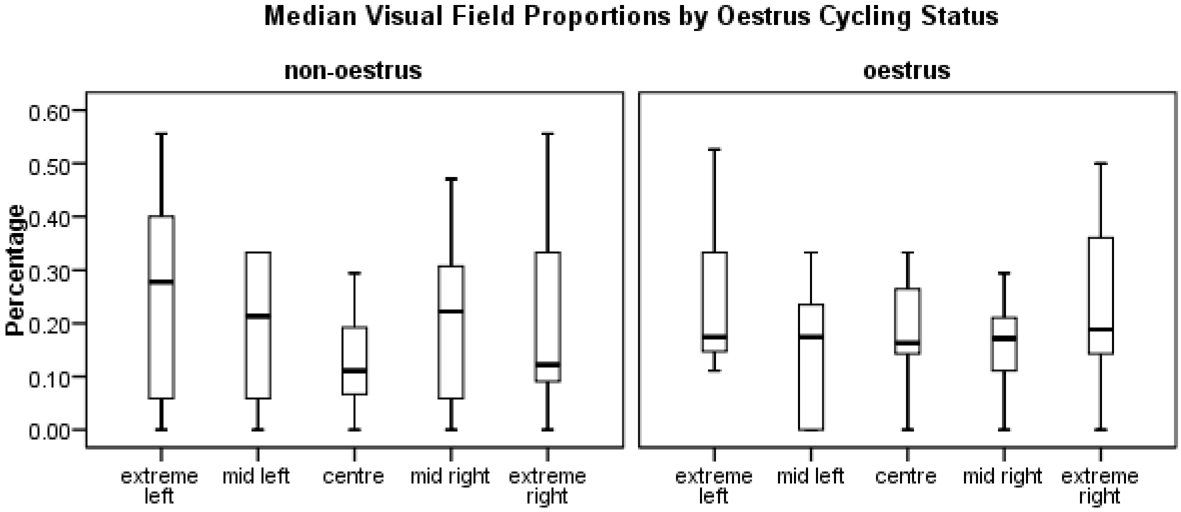

Figure 3.16 | Comparing the VFP values for adult females in oestrus (n=10) with those not in oestrus (n=10).

3.5.3—Overall Mixed Model Comparison

A generalised linear mixed model was used to investigate whether the occurrence of behaviours in one of the three visual fields (left, centre or right) was influenced by the factors of age, sex, rank, emotional intensity or emotional valence with subject ID set as the random effect.

A significant overall effect was reported by the model (F(18,817)=5.543, p<0.001, ICC=0.124) within which the influences of age (F(2,817)=4.428, p=0.012), emotional intensity (F(2,817)=12.062, p<0.001) and emotional valence (F(6,817)=7.352, p<0.001) were found to have a significant effect upon the visual field in which an interaction took place. The mixed model confirmed the influence of age upon lateral bias identified in Section 3.5.1.1 as adults had a significantly greater effect upon left side bias than subadults (FC=0.763, p=0.028) but there was no significant effect of age upon the occurrence of behaviours in the right visual field (FC=0.046, p=0.888). The model also demonstrated that the effect of high intensity emotions was significantly greater than low intensity emotions for both the left (FC=1.168, p<0.001) and right (FC=1.362, p<0.001) visual fields thus supporting the pattern found in Section 3.5.2.4. Positive (FC=1.320, p=0.001) and negative (FC=1.676, p<0.001) valence behaviours had a significantly stronger effect upon left side bias in the overall population than neutral valence behaviours whilst sexual valence behaviours has a significantly weaker effect upon right side bias than neutral valence behaviours (FC=-1.086, p=0.012).

A second mixed model was used to compare the occurrence of behaviours in the left visual field against the occurrence of those in the right and a significant overall effect of this model was found (F(9,644)=2.135, p=0.025, ICC=0.000) and the influences of age (F(1,644)=8.373, p=0.004) and valence (F(3,644)=2.666, p=0.047) were also found to be significant. Adults significantly influenced left side bias in comparison with subadults (FC=0.697, p=0.004) whilst negative (FC=1.080, p=0.006), positive (FC=1.075, p=0.009) and sexual valence behaviours (FC=0.914, p=0.046) significantly influenced left side bias when compared with neutral valence behaviours.

3.6—Discussion

Analysis of the mean BLI values for each context found a significant left side bias for adults and a significant left side bias during negative valence behaviours and these observations were supported by the mixed model analysis but no other significant lateral biases were observed in any other categories. A significant contrast in bias strength was found within the oestrus cycling category as non-oestrus females reported a higher ABS value than oestrus females but none of the remaining categories reported any significant differences in bias strength. The VFP data revealed that low intensity interactions occurred significantly less frequently than high intensity interactions in both extreme visual fields and significantly more frequently than high intensity interactions in the central and mid visual fields and this was again supported by the mixed model analysis. Neutral valence behaviours also occurred significantly less frequently than expected in the extreme visual fields whilst behaviours of a positive valence reported significantly lower VFP values for both mid visual fields and a significantly higher VFP value in the extreme right visual field. There was no population level lateral bias whilst at the individual level only four of the 34 subjects were lateralised: three right-side biased and one left-side biased. In comparison with previous studies of emotional lateralisation the present study does not support the significant population-level lateral biases reported in baboons (Damerose & Hopkins, 2002; Wallez & Vauclair, 2011), gelada (Casperd & Dunbar, 1996) and mangabeys (Baraud *et al.,* 2009).

The similarity of the paradigm employed by Baraud *et al.* (2009) to that of the present study allows for closer comparison as it was the only other study to observe the full emotional spectrum during naturally occurring behavioural interactions. A possible explanation for the lack of lateral bias in the present study compared with Baraud *et al.* may be due to the difference in population sizes between the group used in the present study and those of Baraud *et al.*. As there were six red-capped and seven grey-cheeked mangabeys in each of the populations included in Baraud *et al.*'s study it may have been possible for subjects within these small groups to orient themselves in such a way as to ensure most or all other individuals in their group were maintained within a preferred visual field, thereby resulting in more pronounced lateral biases during social monitoring. By comparison, the present study group contained 42[6] olive baboons therefore such behaviour would have been rendered highly unlikely. In addition, although the observational methods used by Baraud *et al.* mirror those of the present study, the analytical methods used by Baraud *et al.* to determine whether their observed populations of mangabeys were lateralised may also have contributed to their

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[6] This figure of 42 is correct when referring to the total number of individuals within the observed population although only 34 individuals were included in analyses when the minimum criterion of seven interactions was applied, as per the methods.

reported population-level lateral bias. As has been detailed in the methods (section 2.6.3.1) the present study weighted the individual data points from each individual by calculating a BLI value for each subject before using these subject BLI values to calculate means for each category and the overall population. Furthermore, the results of the present study failed to meet the criteria for population-level lateral bias because only four of 34 subjects included in this study were significantly lateralised at the individual level and irrespective of the direction of lateral bias and such a small number of lateralised subjects is not different to that which may be expected by chance. By contrast, Baraud *et al.* appear to have pooled all data points from all individuals when calculating lateralisation for the population (and each context). This method is therefore highly susceptible to being skewed by subjects with a disproportionately large number of data points that also express a strong lateral bias and a review of the data in Baraud *et al.*'s paper suggests that the most strongly and significantly lateralised individuals also accounted for more of the data which may therefore have contributed to the significant population-level bias observed in their study.

An additional reason that the results of the present study do not support those of Baraud *et al.* (2009) may relate to the division of the visual fields used in analyses. As reported in Section 1.4, primates do not possess distinct left and right visual fields but a continuous visual spectrum with a considerable central binocular overlap. The methods of the present study have attempted to control for this binocular overlap by including it as an additional visual field however Baraud *et al.* assigned all centrally occurring interactions to the left or right visual field based upon their position relative to the subject's facial midline. As such, it may be expected that the results of Baraud *et al.* were more likely to report a lateral bias than the results of the present study which permitted interactions to be coded as centrally occurring and therefore without a lateral bias. As Wallez & Vauclair's (2011) study was based upon facial asymmetry rather than visual field preferences their use of the facial midline as a distinction between left and right side biases is more valid. However, it is possible that underlying morphological facial asymmetries may have influenced the observation of facial asymmetries during emotional behaviour and this does not appear to have been controlled for.

No significant contrasts in BLI values were found within the categories of sex, rank, emotional intensity or oestrus cycling, although significant left side biases were found for adults and negative valence behaviours and negative valence behaviours were also significantly more left side biased than neutral valence behaviours. Whilst no significant overall lateral bias was observed at the population level, the significant left side bias found during negative valence behaviours is particularly interesting when compared to Casperd & Dunbar's (1996) study. As Casperd & Dunbar based their observations solely upon agonistic behaviours the significant left side bias for negative valence behaviours found by the present study therefore supports their results. This also suggests that claiming support for one or other theory for the lateralisation of emotion may be premature if based upon the study of a single valence of emotion but it also raises the question as to whether some valence categories are more likely to elicit a significant lateral bias than others. The reason for a lateral bias in only negative valence interactions is unclear but it may relate to the influence of cognitive processes and the role of monitoring behaviour and its potentially greater importance for negative valence behaviours (and avoiding attritional conflict) than behaviours from a different valence. Whilst Casperd & Dunbar noted a stronger left side bias for high intensity agonistic encounters than for low intensity interactions they also noted that the lateral bias for lower intensity interactions was stronger than expected. Casperd & Dunbar suggested that the uncertainty of a subject, as to the intentions of an approaching individual during a low intensity agonistic interaction, may have resulted in this lateralised monitoring behaviour so that it may be prepared to respond appropriately. Similar observations of left side biased monitoring behaviour have also been observed in birds as Ventolini *et al.* (2005) and Gülbetekin *et al.*'s (2007) studies, in black-winged stilts and Japanese quail respectively, found left side biases when subjects assessed the identity and/or intentions of a conspecific. It is therefore possible that the significant left side bias observed by the present study for negative valence behaviours alone may reflect that a greater cognitive involvement precedes agonistic interactions than any other type of behaviour and the significant contrast found between negative valence and neutral valence behaviours further supports this suggestion. The mixed model analysis did report a significant contrast between positive valence behaviours (as well as negative valence behaviours) and the reference category of neutral valence behaviours but this might be expected based upon the comparison of these BLI values. Whilst neither the positive nor the neutral valence category returned a significant BLI value when compared to zero (no expected bias), a distinct contrast between the left side bias of positive valence behaviours and the right side bias of neutral valence behaviours is evident. It might be suggested that this should therefore lead to a discussion on whether a BLI value of zero or the BLI value for neutral valence behaviours should be used as the reference category when assessing behavioural lateralisation for other valence categories. However, as the underlying aim of research upon the lateralisation of emotion is to determine which of the two cerebral hemispheres controls emotional processes it is likely that the BLI value of zero, suggesting no bias and therefore no emotional lateralisation, provides the natural reference point.

Although the observed right side bias for neutral valence behaviours was not significant the mean BLI value for neutral valence behaviours was high when compared with the other three valences; of which positive and negative valence behaviours were left-sided. The lack of an overtly negative or positive emotional context may therefore remove the potential for emotional lateralisation and instead suggest that an alternative lateralised process may have caused this high BLI value during neutral behaviours. It has already been suggested above that the stronger left side bias found during negative valence behaviours may be related to lateralised monitoring behaviour so this cannot also be an explanation for the right-sided bias in neutral valence behaviours however a possible explanation may be handedness. The same population of olive baboons from the CNRS facility in Rousset, France included in the present study have also been subject to extensive manual laterality studies and have all reported right handedness (Vauclair *et al.*, 2005; Meguerditchian & Vauclair, 2006; 2009; Meguerditchian *et al.*, 2011). As has been reported in fish (Dugatkin, 1991; Bisazza *et al.*, 1997b) in scenarios of elevated arousal the lateralisation of instinctual emotional behaviour appears to take precedence over other behaviours, but when the level of arousal is reduced the lateralisation of other behaviours is more clearly expressed. Therefore, during low arousal/neutral valence behaviours the behavioural lateralisation of olive baboons that results in right handedness in manual tasks may similarly result in a right eye bias during behavioural interactions although as there is no evidence to suggest that identical eye and hand preferences exist in olive baboons, and only limited evidence in other species (common marmosets, Hook-Costigan & Rogers, 1998), this suggestion remains speculative. Nonetheless, as a significant overall left side bias was not found for all emotional valence categories the results of this study do not therefore support the Right Hemisphere Hypothesis or the first hypothesis predicted by this study (H_1)

No significant directional or strength biases were observed for either category of emotional intensity therefore the results of the present study did not support hypothesis five (H_5) or the results of Casperd & Dunbar (1995) or Wallez & Vauclair (2011), which reported a stronger left side bias for high arousal behaviours. Comparison of the VFP data however, revealed a stark contrast between high and low intensity behavioural interactions as there were significant differences between intensity categories in all visual fields. High intensity interactions were significantly more likely to occur in the extreme visual fields than low intensity interactions whilst high intensity interactions were also significantly less likely to occur in the central and mid visual fields. This observation may suggest that behaviours occurring towards the extreme periphery of a subject’s visual field may be more reactionary and consequently of a higher level of arousal than interactions initiated in a subject's central or mid visual fields whereby the subject may have monitored the behaviour of that conspecific prior to initiating the interaction; thus leading to a scenario of lower arousal.

Although there was no significant difference in BLI values between adults and subadults the existence of a significant left side bias for adults may provide some evidence of the ontogenic ritualisation of lateral preferences also reported in the handedness literature (Vauclair & Fagot, 1987; Vauclair *et al.,* 2005) and may further relate to the socio-ecological factors suggested by Meunier *et al.* (2012). Though subadults are generally lower ranked than adults they are also subject to less agonistic behaviour and competition than adults (Cheney, 1978) which may in turn cause them to express less monitoring behaviour than their older group members. As only negative valence behaviours were found to elicit a significant lateral bias for this population it may therefore be expected that subadults expressed a less pronounced overall bias than adults and this observation supports the second hypothesis (H_2).

In terms of sex differences, no significant lateral or strength biases were observed for males or females. Females were found to express a moderately stronger left side bias than males but the small effect size further emphasises the lack of significant contrast between the sexes thus rejecting this study's third hypothesis (H_3) which predicted stronger left side biases for males. However, the significant contrast in all VFP values between males and females is stark. A relationship between sex and the orientation of a subject with respect to a target object/individual had been previously observed by Meunier *et al.* (2012) who suggested that this difference may have been a product of disparities in socio-ecological pressures between the sexes. This may also be true of the present study as the greater use of the extreme visual fields by females may represent differences in monitoring behaviour whereby the females, which tend to be lower ranked than the males, visually attended to a greater area of their surroundings whilst the males did not express the same range of vigilance, possibly due to their comparatively elevated status. The clear difference between the VFP values for males and females, as well as between both categories of emotional intensity, that is not evident from the BLI and ABS data also serves to highlight the benefit of the VFP model for analysing where behaviours occur in the overall visual spectrum field of a subject. The relative symmetry in VFP values between the left and right sides explains why the BLI and ABS values could not identify a difference between the sexes but by analysing VFP values it has been possible to observe a clear difference in the monitoring behaviour of males and females.

The assessment of rank upon lateral bias (BLI) revealed no significant effect and no evidence was found to support Baraud *et al.*'s (2009) correlation of an increase in strength of bias (ABS) with rank therefore hypothesis four (H_4) was not supported. Whilst no significant contrasts were found between rank categories in the VFP data the differences in the pattern of VFP values for each rank supports the suggestion that higher ranked individuals express more centrally focussed monitoring behaviour whilst lower ranking individuals visually attend to a much wider visual spectrum, although this suggestion does not appear to apply to the lowest rank category which shows a more central visual focus than either of the mid ranked categories. As low ranked individuals are subject to a greater frequency of agonistic interactions than higher ranking individuals (Barton *et al.*, 1996) it is possible that the more centrally focused behaviour in low ranking individuals may be due to these individuals having to react to more agonistic approaches thereby permitting them less time to visually monitor a wider spectrum. In addition, Alberts (1994) reported that vigilance behaviour in subadults was influenced by a relationship between rank and sex in wild yellow baboons as the female offspring of low ranking mothers expressed less vigilance behaviour than the offspring of high ranking mothers. Therefore, as the low ranked category included in analyses for this species contained only subadults this may explain the lower VFP values for extreme visual fields.

No significant lateral biases were observed for either category of oestrus cycling but non-oestrus females were found to express a significantly stronger bias and a significantly lower VFP value for the central visual field than females in oestrus. As only one study has previously identified an effect of oestrus upon lateralisation (Rizhova & Vershinina, 2000), finding a stronger left side bias in rats during proestrus than any other stage of the oestrus cycle, it is difficult to interpret the results of the present study and as no significant contrast in lateral biases was found between oestrus categories and no left side bias was observed for the in-oestrus subjects hypothesis six (H_6), and the results of Rizhova & Vershinina, were not supported by this study. It might have been expected that similar results to those already reported, regarding the contrasts in high and low intensity interactions, might have been replicated between in-oestrus and non-oestrus females but this was not the case. Previous observations of in-oestrus females have revealed that they are subject to elevated levels of aggression than those not in oestrus (Huchard & Cowlishaw, 2011; Cheney *et al.*, 2012; Clutton-Brock & Huchard, 2013) therefore it may have been predicted that a more frequent occurrence of aggressive behaviours may have resulted in a more frequent occurrence of high intensity interactions and should thus have led to a greater strength of bias in in-oestrus females. As in-oestrus females also returned a higher VFP value than non-oestrus females for the central visual field this may therefore suggest that in-oestrus females performed a narrower range of monitoring behaviour and were also more likely to interact with another individual if that individual was directly in front of them. In addition, this may suggest a reduced cognitive influence upon interactions during oestrus whereas in periods of non-oestrus adult females were more selective when interacting with others but as oestrogens have been found to increase cognitive functioning in macaques (Lacreuse, 2006) this may be unlikely.


A rhesus macaque at the NIH Animal Center, Poolesville, MD, USA

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Chapter 4 | *Macaca mulatta*

Chapter 4

The Lateralisation of Emotion in Rhesus Macaques *Macaca mulatta*

4.1 | Abstract

This chapter details a study of lateralised social behaviour in a population of rhesus macaques, *Macaca mulatta* (*n*= 29), where the lateralisation of the four emotion valences have been considered at the individual and population level in terms of direction and strength biases and visual field preferences with a view to comparing the two competing theories for the lateralisation of emotion: Campbell’s (1982) Right Hemisphere Hypothesis or Silberman & Weingartner’s (1986) Valence Hypothesis. Additional factors, such as age, sex, rank and emotional intensity, have also been investigated. No overall population level bias was observed in this study and only five of the 29 subjects were significantly lateralised at the individual level. A significant bias strength was observed for high intensity behaviours and a higher proportion of sexual valence behaviours were observed in the extreme visual fields than in neutral valence scenarios but no other significant observations were made. The results of this study were therefore unable to offer support for either the Right Hemisphere Hypothesis or the Valence Hypothesis. As a consequence, this study discusses whether the method employed had a significant impact upon the results of this and previous studies.

4.2 | Introduction

How emotion is lateralised in the brain has been a subject of debate for almost three decades since Silberman & Weingartner's (1986) Valence Hypothesis provided an alternative theory to the earlier Right Hemisphere Hypothesis proposed by Campbell (1982). Both theories agree that negative emotion appears to be controlled by the right hemisphere but the distinction between them lies in the processing of positive emotion which the Valence Hypothesis proposes takes place in the left hemisphere whilst the Right Hemisphere Hypothesis eponymously suggests that the seat of such emotions is the right hemisphere.

Rhesus macaques feature in several studies on the lateralisation of emotion with one of the earliest such studies performed by Ifune *et al.* (1984) which observed the facial expressions of split-brain[7] rhesus macaques in response to video footage of conspecifics and other species. By independently stimulating the left or right hemisphere, Ifune *et al*. found that the right hemisphere, and thus left side of the face, elicited a significantly higher frequency of facial expressions than the left hemisphere. A subsequent but non-invasive study by Hauser (1993) observed naturally elicited interactions between rhesus macaques and also tested for asymmetry in their facial expressions. Hauser observed that the left side of the face displayed more exaggerated expressions for agonistic behaviours (fear and aggression) and did so more rapidly than the right side of the face; thereby supporting the results of Ifune *et al.* and suggested as being indicative of right hemisphere control for the lateralisation of emotion. However, though the right hemisphere appears to be specialised for these examples of negative emotion, as Hauser and Ifune *et al.* did not study positive emotion their studies were therefore unable to compare Campbell (1982) and Silberman & Weingartner's (1986) competing theories. A follow-up study by Hauser & Akre (2001) again reported a left-side biased asymmetry in the intensity of facial expression of emotion in rhesus macaques but in

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[7] Split-brain individuals have been subject to partial or complete ablation of the corpus callosum thereby leading to the isolation of the cerebral hemispheres.

this instance the observed repertoire of emotional behaviours had been expanded to also include those of a positive valence and in doing so provided valid evidence in favour of Campbell's theory. Facial asymmetries in the size of hemimouth area or eye-flashes during behavioural interactions have also been reported in a number of other species (common marmosets: Hook-Costigan & Rogers, 1998a; chimpanzees: Fernández-Carriba *et al.*, 2002; olive baboons: Wallez & Vauclair, 2011, 2012) with each reporting similar observations to those found in rhesus macaques (Hauser, 1993; Hauser & Akre, 2001) and thereby providing further support to the Right Hemisphere Hypothesis.

Rhesus macaques have also been subject to extensive study on the lateralisation of aural function and Hauser & Andersson (1994) performed the first such study based upon observations of a semi-wild troop of rhesus macaques on Cayo Santiago, Puerto Rico. Hauser & Andersson arranged an audio speaker 180° directly behind a food source and upon arrival of a macaque at the food source played a variety of acoustic stimuli (conspecific and heterospecific vocalisations) from the speaker and recorded which direction macaques oriented in response to these stimuli. Hauser & Andersson reported a group-level right-turn bias by macaques in response to conspecific vocalisations but a group-level left-turn bias for heterospecific vocalisations, thereby suggesting that the interpretation of acoustic signals was divided between hemispheres. Furthermore, closer consideration of the methods revealed that emotion was unlikely to have contributed to the contrast in results as the conspecific vocalisations used during this study had included aggressive, fearful (both negative valence) and affiliative (positive valence) calls with no significant difference observed between these categories. Several follow-up studies in rhesus macaques reported similar results (Hauser *et al.*, 1998; Ghazanfar & Hauser, 2001; Ghazanfar *et al.*, 2001) and thereby provided additional evidence that aural lateralisation appeared to be moderated by cognitive rather than emotional function. However a key observation from Hauser & Andersson's study was that although group-level turn biases were observed for both contexts, no turn biases were expressed by infants for either context, therefore suggesting that lateralisation for aural function was subject to ontogenic factors. Much of the subsequent research to use or adapt Hauser & Andersson's method similarly investigated orientational asymmetries in response to conspecific and heterospecific vocalisations and found right turn biases (*e.g.* Palleroni & Hauser, 2003; Böye *et al.*, 2005; Gil-da-Costa & Hauser, 2006) but a study by Siniscalchi *et al.*, (2008) in dogs additionally included a strong fear-inducing stimulus by playing a clap of thunder and observed that although conspecific vocalisations elicited a right-turn bias, the thunder stimulus instead elicited a strong left-turn bias. In comparison with interpreting vocalisations, the level of cognitive processing required to respond to a clap of thunder is profoundly lower which suggests that the observed left-turn response by the dogs to the thunder stimulus was due to the emotional rather than informational content. As such, it could be argued that Hauser & Andersson's paradigm may yet provide a valid method for investigating the lateralisation of emotion. However, a review of the studies to have factored emotional context into their analyses reveals that Siniscalchi *et al.*'s study appears to represent an exceptional example. Furthermore, whilst it may be possible to perform further studies evoking negative emotional contexts through non-vocal fear-inducing stimuli, the elicitation of a positive emotional context with a non-vocal stimulus may prove difficult.

Whilst the above review has identified some of the merits of facial asymmetry (Hauser, 1993) or orientation-asymmetry (Hauser & Andersson, 1994) studies it was decided that the most suitable method for investigating the lateralisation of emotion was based upon the research of Casperd & Dunbar (1996) and expanded by Baraud *et al.* (2009). Casperd & Dunbar's study of emotional lateralisation in gelada baboons was the first such example based solely upon observing naturally elicited interactions whereby the position of competing conspecifics in the left or right visual field of subjects during agonistic interactions was recorded. The results of this study found a significant left side bias during these negative valence behaviours and suggested that this was supportive of Campbell's (1982) Right

Hemisphere Hypothesis for the control of emotion but by not considering positive valence behaviours, Casperd & Dunbar were unable to compare Campbell's hypothesis with Silberman & Weingartner's (1986) Valence Hypothesis. As such, Casperd & Dunbar's method was expanded by Baraud *et al.* for a similar study in grey-cheeked and red-capped mangabeys wherein interactions of negative and positive valence were included in analyses, thereby facilitating the objective comparison of Campbell's and Silberman & Weingartner's competing theories. Further to the three emotional valences (positive, negative and neutral) observed by Baraud *et al.* a fourth valence for sexual behaviours has been included in the present study. Amongst the various rhesus macaque vocalisations studied by Hauser & Akre (2001) for facial asymmetries the ambiguity of the emotional context for 'copulation screams' was noted and Hauser & Akre stated that although sexual behaviours are normally classified as affectively positive, these vocalisations frequently triggered aggressive interactions with conspecifics and so were categorised as negative for their study. However, as the present study aims to reduce ambiguity wherever possible, all sexual behaviours shall be classified as a separate category for this analysis.

In addition to investigating the influence of emotion upon visual field preferences additional factors shall also be included in analyses. In their studies on orientation asymmetries, Hauser & Andersson (1994) evidenced that lateralisation appears to develop with age as significant turn biases were reported for adults but not infants. Similar results have also been identified in the handedness literature, with Lehman (1970; 1978) reporting stronger manual preferences in adult rather than infant rhesus macaques and Vauclair & Fagot (1987) and Vauclair *et al.* (2005) correlating an increase in the strength of manual bias with an increase of age in olive baboons. Stafford *et al.* (1990) also evidenced a similar age effect but in female gibbons only, thereby suggesting that the sex of an individual may also influence their lateralisation. Indeed, Stafford *et al.* also reported that females demonstrated a significantly stronger manual preference than did males whilst Milliken *et al.* (1989) found a left hand preference in male lemurs but a right hand preference in female lemurs, and Camp *et al.* (1984) reported a male left side bias and female right side bias for rats (Sprague Dawley strain) during a number of behavioural measures. It is therefore apparent that sex and age have been found to influence lateralisation in a number of previous studies and species and merit further consideration as potential factors in the development of emotional laterality in rhesus macaques.

For social mammals that live within large multi-male/multi-female groups social rank is particularly important with higher social status associated with better access to food, mates, resources and better overall fitness and this is especially true of rhesus macaques which live in large dynamic troops (Belzung & Anderson, 1986; Huntingford & Turner, 1987; Brennan & Anderson, 1988; Deutsch & Lee, 1991). In their study of emotional laterality, Baraud *et al.* reported that higher ranked mangabeys were engaged in a greater number of interactions on their left side but a detailed study on the influence of rank upon the lateralisation of emotion has yet to be performed. Meunier *et al.* (2011) suggested that the results of a reaching task may have been influenced by socio-ecological pressures, particularly on low-ranking females, although the exact nature of this influence was not detailed, therefore it is hoped that by including rank as a factor it may be possible to further elucidate its influence upon emotional laterality.

Finally, the intensity of interactions shall be recorded with a view to determining their influence upon visual field preferences during emotional interactions. Based upon observations by Casperd & Dunbar (1995) and Wallez & Vauclair (2011) it appears that there is a positive between level of arousal and strength of bias whereby high intensity behaviours generating a more pronounced lateral bias than low intensity behaviours, therefore this shall also be included as a potential factor.

4.3 | Hypotheses

H_1 All emotion is controlled by the right hemisphere therefore behaviours in all emotional contexts should be lateralised to the left visual hemifield at the group level; thus supporting Campbell's (1982) Right Hemisphere Hypothesis

H_2 Adults should express a stronger left side bias than subadults.

H_3 Males should express a more pronounced left side bias than females.

H_4 Stronger left side lateral biases should be found in higher ranked individuals than low ranked individuals.

H_5 Interactions with high emotional arousal should elicit stronger left side lateral biases than low arousal interactions.

4.4 Methods

4.4.1—Observation

The researcher was permitted access to the facility between 8am-4pm, Monday-Friday, over a period of nine weeks from September to December 2009, excluding specific dates designated by the facility (national holidays etc.).

Focal subjects were pseudorandomly selected but care was taken to ensure no individuals were observed more than twice per day or four times within a one week period. All subjects were housed within a large, naturalistic outdoor enclosure (25,500m^2) and observations were performed by the researcher from within this enclosure with no barriers between observer and subjects. No change was made to the general methodology detailed in section 2.4, with subjects selected and video-recorded for 15 minute focals and all behavioural interactions subsequently observed and noted during coding.

4.4.2—Preparation of Data Set for Analyses

Over the entirety of the study period, a total of 529 interactions were observed from 44 individuals. Application of the minimum criterion of seven interactions per individual (n≥7) reduced this data set to 489 interactions from 29 individuals (interactions per individual: mean n=16.2, min n=7, max n= 52; see Appendix A6 for table on number of focals/interactions per individual).

As detailed in section 2.6.2 this minimum criterion was also applied when the data from each individual were split for the analysis of emotional intensity and emotional valence, thereby a minimum of seven interactions per subject per subcategory were required, but as a mixed model was used for these analyses if a subject met this criterion for only one subcategory it was still included in analyses. Upon the application of these minimum criteria it was determined that the small number of data points for some individuals may reduce the power of the overall analyses and thus the data for all individuals were randomly sampled with replacement using 5,000 bootstrap replications (Adams & Anthony, 1996) as per the method explained in Section 2.6.2.before the analyses were performed.

The number of individual subjects included in analyses for each context has been noted in Table 4.1 with the biological data for all individuals included in analyses reported in Table 4.2. Table 4.3 provides an ethogram of all behaviours included in analyses and how they were coded in terms of emotional intensity and valence and this was completed in collaboration with an on-site researcher on site (P. Wagner).

Between-Subjects Comparison			Mixed-Model Comparison		
Age	Subadult	13	Intensity	High	12
	Adult	16		Low	19
Rank	High	8	Valence	Neutral	0
	Mid High	9		Negative	10
	Mid Low	6		Positive	8
	Low	6		Sexual	5
Sex	Male	8			
	Female	21			

Table 4.1 | Reporting the number of individual subjects that met the minimum criterion (n≥7 interactions) for each context subcategory.

ID	Sex	Age	Age Cat.	Rank Grp.	ID	Sex	Age	Age Cat.	Rank Grp.
M05	Female	15	Adult	High	ZE47	Female	3	Adult	Low
R27	Female	14	Adult	High	ZE57	Male	3	Subadult	Low mid
R47	Female	12	Adult	High mid	ZF05	Male	2	Subadult	Low
T27	Female	11	Adult	High mid	ZF14	Male	2	Subadult	Low
X32	Female	9	Adult	Low	ZF15	Female	2	Subadult	High mid
X51	Female	9	Adult	Low mid	ZF27	Female	2	Subadult	High
ZA21	Male	8	Adult	High	ZF34	Female	2	Subadult	High
ZA29	Female	7	Adult	Low mid	ZF37	Female	2	Subadult	Low mid
ZB10	Female	6	Adult	High	ZF39	Female	2	Subadult	High mid
ZB28	Female	6	Adult	Low	ZF41	Male	2	Subadult	High mid
ZC23	Female	5	Adult	High	ZG16	Male	1	Subadult	High
ZC32	Female	5	Adult	High mid	ZG20	Male	1	Subadult	High mid
ZD26	Female	4	Adult	Low mid	ZG39	Female	1	Subadult	Low mid
ZD60	Female	4	Adult	High mid	ZG50	Female	1	Subadult	High mid
ZE16	Female	3	Adult	High	ZG53	Female	1	Subadult	Low mid
ZE19	Male	3	Subadult	Low	ZG59	Female	1	Subadult	High
ZE23	Female	3	Adult	High mid					

Table 4.2 | Providing the biological data for each individual included in analyses.

Behaviour	Description	Intensity	Valence
Approach	subject walks casually toward another stationary individual displaying no signs of aggression	Low	Neutral
Follow	subject casually walks towards and after another non-stationary individual		
Huddle	subject sits close beside one or more individuals, occasionally using forelimbs to hold others closer with fully body contact		
Reach Out	subject extends (fore)limb towards conspecific in non-sudden non-aggressive manner to grasp or physically interact with conspecific		
Avoid	subject walks/runs away from an approaching individual: a submissive behaviour	Low	Negative
Displace	subject approaches another, stationary, individual causing them to move away		
Threat	subject exhibits non-physical aggressive behaviour by dipping or bobbing head, opening mouth and baring teeth	High	
Chase	subject runs or trots after another individual: an aggressive behaviour		
Cradle Infant	subject (often adult female) holds infant in one or both arms close to their body	Low	Positive
Groom	individual licks the head or body of another individual: an affiliative behaviour		
Play	subjects, usually infant, juvenile, or adolescent, interacts with another and may be observed as jumping, trotting, rolling around, or mock fighting	High	
Inspect	subject closely looks at, smells and/or touches the anogenital area of another	Low	Sexual
Mount	subject approaches the rear of another and elevates on hindlegs to enact or simulate copulatory behaviour	High	
Post-Coital Glance	immediately after copulation, subject orients head towards their partner		
Present	subject presents anogenital area to male or dominant individual		

Table 4.3 | Detailing the description, emotional intensity and emotional valence of each behaviour included in analyses.

4.4.3—Statistical Analyses

4.4.3.1 Testing for Normality

Prior to each analysis, a Kolmogorov-Smironov test was performed on the data to examine normality in the distribution. For all BLI analyses the data were normally distributed (D(29)=0.123, p=0.200) and parametric methods were used whilst the data were not normally distributed for ABS (D(29)=0.215, p=0.001) or all VFP values (extreme left: D(29)=0.230, p<0.001; mid left: D(29)=0.128, p=0.200; centre: D(29)=0.105, p=0.200; mid right: D(29)=0.163, p=0.048; extreme right: D=(29)=0.204, p=0.003) and non-parametric methods were used as transformations of the data (Log$_{10}$, Square Root, Arcsine) had no effect.

4.4.3.2 Analysis of Binocular Laterality Indexes

Once BLI values had been calculated for each individual a mean BLI value for the population and for each category could also be calculated, and these mean values were then compared to the predicted value of zero (no lateral bias) using a one-sample t-test.

Between-subjects comparisons (*e.g.* age and sex categories) were performed using independent t-tests. Rank subcategories were compared using a one-way ANOVA and where rank was found to exert a significant influence, independent samples t-tests were used post-hoc to perform pairwise comparisons of rank categories and the level of significance was then adjusted according to the Holm-Bonferroni method (Holm 1979). The influence of emotional intensity and emotional valence were each tested using a linear mixed model.

4.4.3.3 Analysis of Absolute Laterality Scores

Once ABS values had been calculated for each individual the median ABS value for the population could then be calculated and this was used as the expected value for comparison with the median ABS value from each category using a Wilcoxon signed-rank test.

Comparisons within age and sex categories were performed using Mann-Whitney U-tests. As rank was a between-subjects calculation and there were more than two sub-categories a Kruskal-Wallis H-test and where rank was found to have a significant effect pairwise Mann-Whitney tests were used post-hoc to compare rank categories with the level of significance adjusted according to the Holm-Bonferroni method. The influences of emotional intensity and emotional valence were each analysed using a linear mixed model.

4.4.3.4 Analysis of Visual Field Proportions

The median VFP values for each visual field were calculated for the population and these were then used as the predicted values for subsequent comparisons with the median VFP values for each category (*e.g.* sex, age *etc.*) using a Wilcoxon-signed rank test. Comparisons were also made within each set of five VFP values using a Friedman's test to examine whether a significant difference existed between the occurrence of behaviours in these five visual fields.

Independent samples Mann-Whitney tests were used to compare VFP values within the categories of sex and age whilst a Kruskal-Wallis test was used to compare the four rank categories. Where rank was found to have a significant effect pairwise Mann-Whitney tests were used post-hoc to compare rank categories with the level of significance adjusted according to the Holm-Bonferroni method.

The VFP values within each emotional intensity and valence category were tested using a linear mixed effects model.

4.4.3.5 Overall Mixed Model Analysis

Using a generalised linear mixed model the entire data set was analysed in a single model (only including individual subjects with $n \geq 7$ interactions and setting individual ID as the random effect) to determine which factors (age, sex, rank, emotional intensity or emotional valence) were the most significant influences upon lateral bias.

4.5 | Results

4.5.1—Binocular Laterality Indexes and Absolute Laterality Scores

At the group level, the mean BLI was -0.062 (*SE*= 0.047) and a one-sample t-test, *t*(29)= -1.321, *p*= 0.197 (Pearson's r=-0.238) revealed that this was not significantly different from a test value of zero (no bias predicted). The median ABS value for the population was calculated as 0.133 (IQR=0.077-0.223) and this value was then used as the expected value in subsequent tests.

At the individual level, only five of the 29 subjects included in analyses were significantly lateralised with two of these individuals expressing a right side bias: R27: BLI=+0.635, t(51)=6.171, p<0.001 (Pearson's r=0.654); ZF05: BLI=+0.125, t(23)=3.140, p=0.005 (Pearson's r=0.548); and three expressing a left side bias: X32: BLI=-0.600, t(9)=-2.445, p=0.037 (Pearson's r=-0.632); ZE47: BLI=-0.222, t(8)=-3.500, p=0.008 (Pearson's r=-0.778); and ZE59: BLI=-0.479, t(10)=-2.391, p=0.038 (Pearson's r=-0.603) whilst the remaining subjects were not significantly lateralised (see Table 4.3 for BLI values of all individuals). A chi-square analysis reveals this population was significantly not lateralised $X^2(2)=31.93$, p<0.001 (Pearson's r=0.742). The BLI values for each individual included in analyses have been provided in Table 4.4 and have been illustrated in Figure 4.5. Figures 4.6 and 4.8 show the mean BLI and median ABS values respectively for each context included in analyses and the standard errors for each context BLI and ABS values have been included in Tables 4.7 and 4.9 respectively.

ID	Original	BLI	*p*	*r*	Lateralised
M05	-0.125	-0.135	0.871	0.024	-
R27	0.731	0.635	0.000	0.654	Right
R47	0.000	-0.059	0.083	-0.420	-
T27	0.091	0.000	0.441	-0.246	-
X32	-0.500	-0.600	0.037	-0.632	Left
X51	0.200	0.160	0.356	0.189	-
XF41	-0.091	-0.182	0.756	0.100	-
ZA21	0.000	-0.017	0.677	-0.078	-
ZA29	-0.125	-0.156	0.581	-0.144	-
ZB10	0.222	0.056	0.729	-0.126	-
ZB28	0.143	-0.071	0.457	0.309	-
ZC23	0.111	0.056	0.136	0.355	-
ZD26	0.000	-0.111	0.594	-0.192	-
ZD60	0.222	0.111	0.594	0.192	-
ZE16	0.556	0.270	0.195	0.447	-
ZE23	-0.040	-0.100	0.503	-0.138	-
ZE47	-0.111	-0.222	0.008	-0.778	Left
ZE59	-0.364	-0.479	0.038	-0.603	Left
ZF05	0.167	0.125	0.005	0.548	Right
ZF14	-0.083	-0.130	0.755	-0.096	-
ZF27	0.000	-0.111	0.681	-0.149	-
ZF34	0.294	0.224	0.750	0.081	-
ZF37	-0.100	-0.207	0.343	-0.316	-
ZF41	0.222	0.167	0.717	-0.089	-
ZG16	0.000	-0.083	0.054	0.546	-
ZG20	-0.333	-0.333	0.447	-0.272	-
ZG39	0.250	0.063	0.171	0.500	-
ZG50	-0.067	-0.100	0.301	-0.276	-
ZG59	-0.556	-0.556	0.104	-0.544	-

Table 4.4 | Reporting the non-bootstrapped BLI values (original), bootstrapped BLI values (BLI), and the significance (p) and effect size (r) for each individual BLI value. The final column notes which individuals were significantly lateralised.

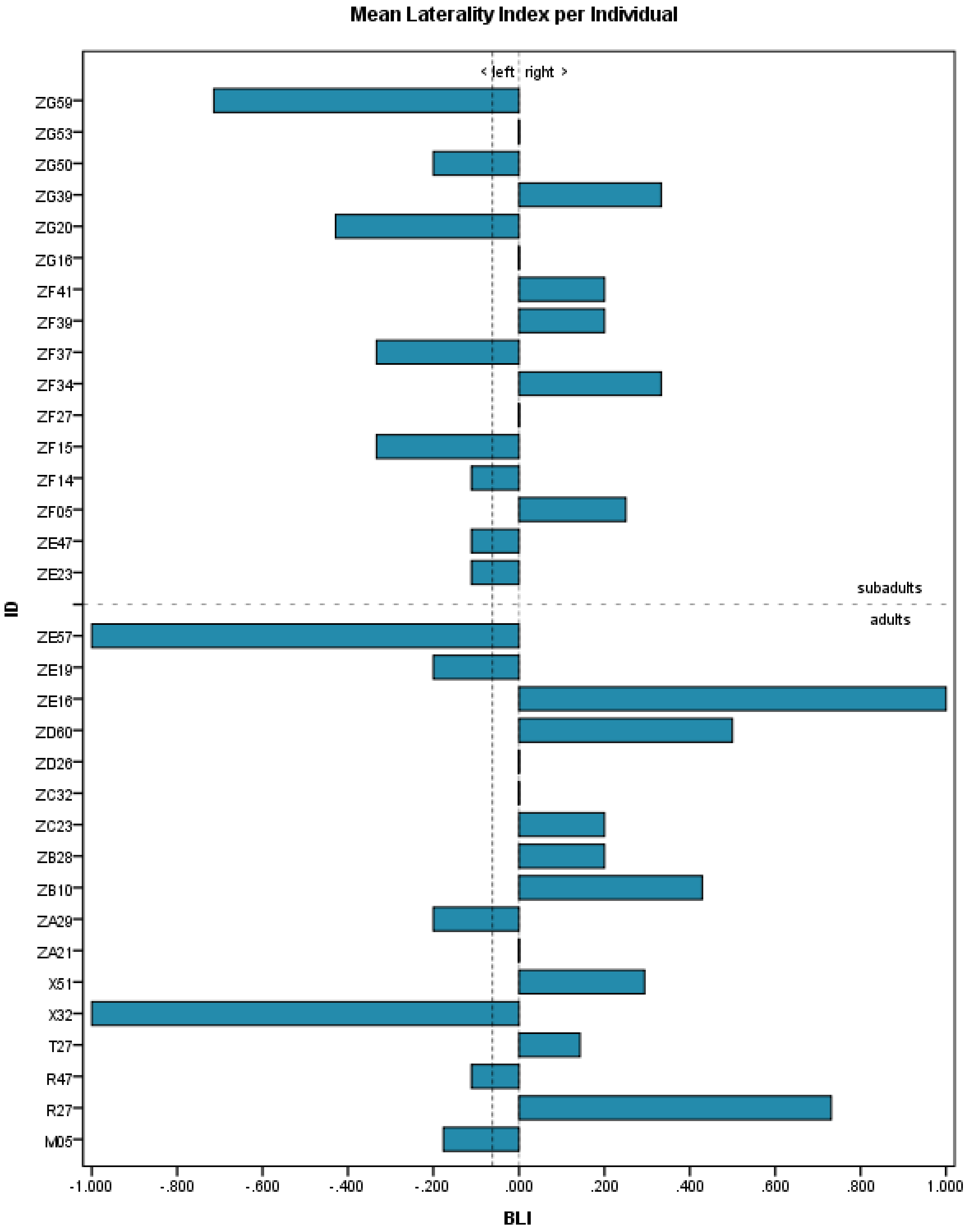

Figure 4.5 | Showing the BLI values for each individual included in analyses. The dashed horizontal line separates the subadults and adults and the dashed vertical line allows comparison with the population mean (-0.062).

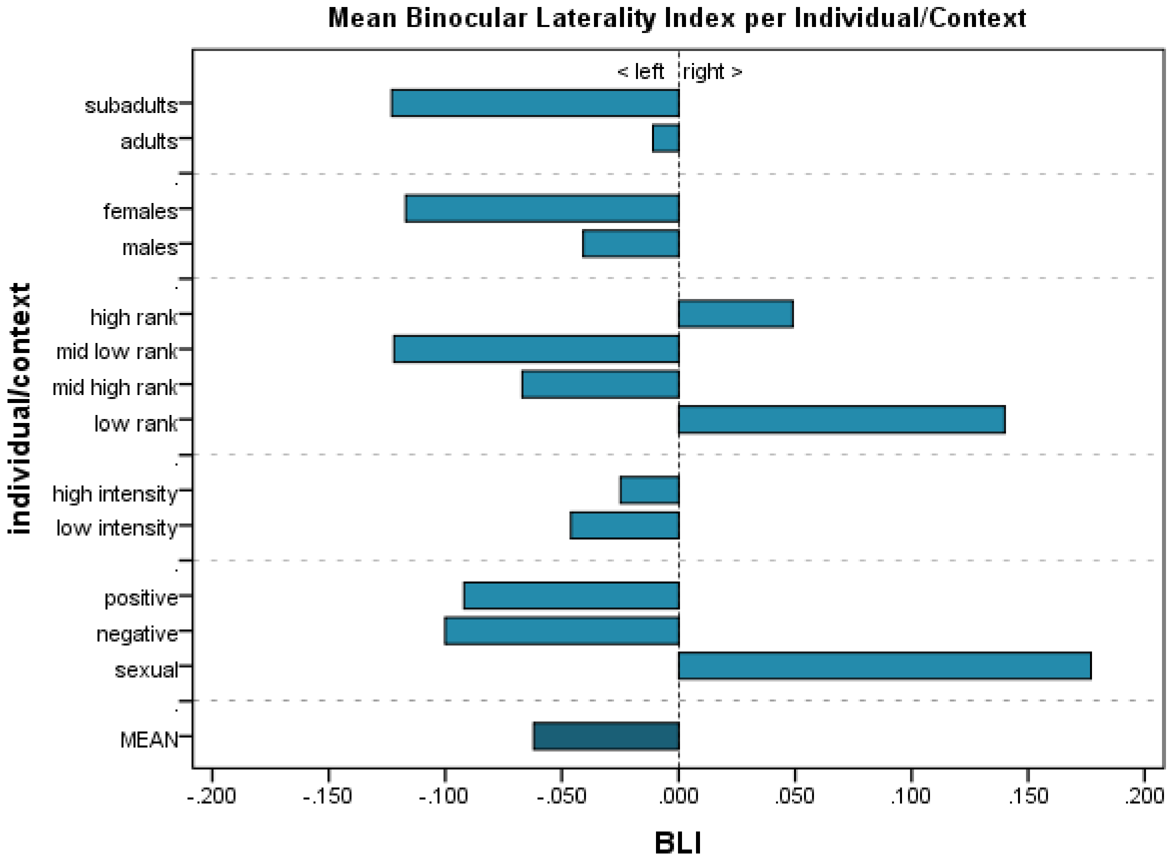

Figure 4.6 | Showing the mean BLI values for each individual/context measured in analyses. The overall population mean has been shown at the bottom.

context		mean	SE	*p*	*r*
age	subadults	-0.123	0.066	0.085	0.057
	adults	-0.011	0.258	0.862	0.057
sex	females	-0.041	0.058	0.489	-0.156
	males	-0.117	0.077	0.174	0.471
rank	high	0.049	0.123	0.700	0.150
	mid high	-0.067	0.050	0.213	-0.431
	mid low	-0.122	0.091	0.240	-0.512
	low	0.140	0.105	0.240	0.512
intensity	high	-0.025	0.106	0.821	0.070
	low	-0.046	0.068	0.510	-0.156
valence	neutral	insufficient data			
	negative	-0.100	0.082	0.254	-0.376
	positive	-0.092	0.076	0.269	-0.045
	sexual	0.177	0.196	0.417	0.412
overall		-0.062	0.047	0.197	-0.238

Table 4.7 | Showing the mean, standard error (SE), statistical significance (p; significant values in bold font) and effect size (Pearson's r) for each context subcategory. Error bars could not be included in Figure 4.6 as this graph was constructed from separately calculated figures and not directly from the main data set but the inclusion of the SE values provide the corresponding information in more detail.

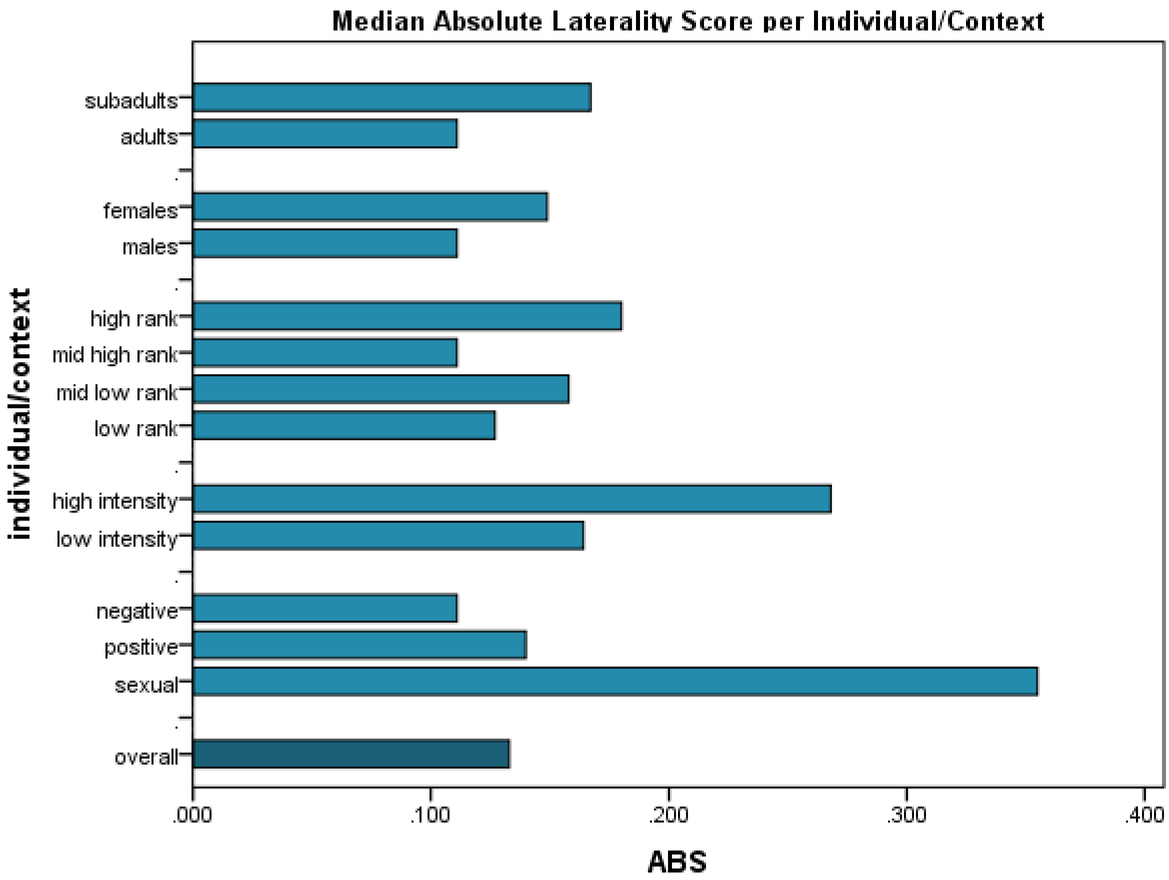

Figure 4.8 | Showing the median ABS values for each individual/context measured in analyses. The overall population median has been shown at the bottom.

		MEDIAN	IQR		p	r
age	subadults	0.167	0.106	0.279	0.152	0.107
	adults	0.111	0.057	0.207	0.918	0.190
sex	females	0.111	0.067	0.223	0.554	0.129
	males	0.149	0.094	0.195	0.575	0.198
rank	high	0.180	0.063	0.485	0.263	0.396
	mid high	0.111	0.080	0.175	0.767	0.099
	mid low	0.158	0.099	0.275	0.249	0.471
	low	0.127	0.067	0.317	0.917	0.043
intensity	**high**	**0.268**	**0.119**	**0.482**	**<0.001**	**0.694**
	low	0.164	0.071	0.375	0.083	0.397
valence	neutral	Insufficient data				
	negative	0.111	0.056	0.304	0.759	0.097
	positive	0.140	0.052	0.293	0.575	0.198
	sexual	0.355	0.000	0.620	0.223	0.545
overall		0.133	0.133	0.077	-	

Table 4.9 | Showing the median, interquartile range (IQR), statistical significance (p; significant values in bold font) and effect size (Pearson's r) for each context subcategory. Similar to Figure 4.6 error bars could not be included in Figure 3.8 but SE values have been provided here accordingly.

4.5.1.1 BLI and ABS data by Age

When the BLI data were split by age they was normally distributed for adults: D(16)=0.163, p=0.200 and subadults: D(13)=0.131, p=0.200. No significant lateral biases were observed for subadults: M=-0.123, SE=0.066, t(12)=-1.878, p=0.085 (Pearson's r=0.057) or adults: M=-0.011, SE=0.258, t(15)=-0.177, p=0.862 (Pearson's r=0.396), and no significant difference was found between these age groups: t(27)=1.203, p=0.240 (Pearson's r=0.226).

The ABS data were not normally distributed for subadults: D(13)=0.239, p=0.041 or adults: D(16)=0.276, p=0.002. There was no significant strength bias observed for subadults: MDN=0.167, IQR=0.106-0.279, W(13)=66.00, Z=1.433, p=0.152 (Pearson's r=0.107), or adults: MDN=0.111, IQR=0.057-0.207, W(16)=66.00, Z=-0.103, p=0.918 (Pearson's r=0.190), and no significant difference was observed between the median subadult and adult ABS values: U(29)=73.50, p=0.181 (Pearson's r=-0.249).

4.5.1.2 BLI and ABS data by Sex

When the BLI data were split by sex the distribution was normal for males: D(8)=0.270, p=0.200, and females: D(21)=0.151, p=0.200. Comparison of LI values for males and females revealed no significant biases for females (M=-0.041, SE=0.058; t(20)=-0.704, p= 0.489, Pearson's r=-0.156) or males (M=-0.117, SE=0.077; t(8)=-1.512, p= 0.174, Pearson's r=0.471) and no significant difference between sex categories (t(31)= -1.207, p= 0.237).

Tests of normality on each of the sex categories revealed that ABS values were normally distributed for males: D(8)=0.270, p=0.088 but not for females: D(21)=0.237, p=0.003. No significant strength biases were observed for females: MDN= 0.111, IQR= 0.067 – 0.223; W(21)= 132.50, p=0.554 (Pearson's r= 0.129); or males: MDN= 0.149, IQR= 0.094 – 0.195; W(8)= 22.00, p= 0.575 (Pearson's r= 0.198); and there was no significant difference observed between sexes: U(29)= 75.00, p= 0.684 (Pearson's r= -0.082).

4.5.1.3 BLI and ABS data by Rank

Splitting the data between the four rank categories revealed that the BLI values for all four ranks were normally distributed; high: D(8)=0.173, p=0.200; mid high: D(9)=0.163, p=0.200; mid low: D(6)=0.185, p=0.200; low: D(6)=0.209, p=0.200. Analysis of the influence of rank upon BLI values revealed no significant directional biases for any rank categories; high: M=0.049, SE=0.123, t(7)=0.401, p=0.700 (Pearson’s r=0.150); mid high: M=-0.067, SE=0.050, t(8)=-1.352, p=0.213 (Pearson’s r=-0.431); mid low: M=-0.122, SE= 0.091, t(5)=-1.334, p=0.240 (Pearson’s r=-0.512); low: M=-0.140, SE=0.105, t(5)=-1.334, p=0.240 (Pearson’s r=-0.512) and no significant effect of rank was observed (F(3,25)=0.817, p= 0.496 (η^2=0.089).

The ABS data were also normally distributed for all four ranks; high: D(8)=0.210, p=0.200; mid high: D(9)=0.244, p=0.130; mid low: D(6)=0.304, p=0.089; low: D(6)=0.302, p=0.093; but as the overall ABS data were not normally distributed the median values of each rank were calculated and compared with the population median. Consideration of the ABS values revealed no significant strength biases in any of the four rank categories; high: MDN=0.180, IQR=0.063–0.485, W(8)=26.00, p=0.263 (Pearson’s r=0.396); mid high: MDN=0.111, IQR=0.080–0.175, W(9)= 20.00, p= 0.767 (Pearson’s r=-0.099); mid low: MDN=0.158, IQR= 0.099–0.275, W(6)= 16.00, p= 0.249 (Pearson’s r=0.471); low: MDN=0.127, IQR= 0.067–0.317, W(6)=11.00, p= 0.917 (Pearson’s r=0.043) and no significant effect of rank was observed (H(3)= 1.243, p= 0.743 (η^2=0.044). As the data for the four valence categories were normally distributed it was possible to compare them using parametric means (one-way ANOVA) which also reported no significant effect of valence: F(3,25)=0.658, p=0.586 (η^2= 0.079).

4.5.1.4 BLI and ABS data by Emotional Intensity

When the data were split by emotional intensity the BLI values were found to be normally distributed for each intensity category; low: D(19)=0.112, p=0.200; high:

D(12)=0.165, p=0.200. No significant lateral biases were observed for either intensity category; low: M=-0.046, SE=0.068, t(18)=-0.672, p=0.510 (Pearson's r=-0.156); high: M=-0.025, SE=0.106, t(11)=-0.232, p=0.821 (Pearson's r=-0.070). BLI values for low and high intensity were then compared and no significant difference was observed between these intensity categories; F(1,29)=0.344, p=0.562 (high vs low fixed coefficient=-0.021 (SE=0.120), t=-0.177, p=0.861), and ID had no effect: ICC=0.00.

The ABS data were also normally distributed when split by emotional intensity (low: D(19)=0.162, p=0.200; high: D(19)=0.194, p=0.201) but as the overall population ABS data were non-normal nonparametric methods were used to compare the expected (population median) ABS value to each emotional intensity median ABS value. The median low intensity ABS value did not differ significantly from the population median; MDN=0.164 IQR=0.071-0.375, W(19)=138.00, Z=1.731, p=0.083 (Pearson's r=0.397); however, high intensity interactions were significantly more strongly lateralised than the population median: MDN=0.268, IQR=0.119-0.482, IQR= W(12)=60.00, Z=2.403, p<0.001 (Pearson's r=0.694) but no significant differences were observed between the emotional intensity categories: F(1,29)=1.125, p=0.298 (high vs low intensity FC=-0.074, t=-1.061, p=0.298), and the random effect had no influence: ICC=0.00.

4.5.1.5 BLI and ABS data by Emotional Valence

When the data were split by emotional valence and the minimum criterion applied within each valence (n≥7 interactions per individual) there were no data from the neutral valence category but BLI data were normally distributed for the remaining three valence categories; negative: D(10)=0.250, p=0.076; positive: D(8)=0.164, p=0.200; sexual: D(5)=0.257, p=0.200. No significant lateral biases were observed for any of these three valence categories; negative: M=-0.100, SE=0.082, t(9)=-1.219, p=0.254 (Pearson's r=-0.376); positive: M=-0.092, SE=0.076, t(7)=-1.200, p=0.269 (Pearson's r=-0.045); or sexual: M=0.177, SE= 0.196, t(4)=0.904, p=0.417 (Pearson's r=0.412) and no significant overall effect of valence was observed: F(2,20)=1.724, p=0.204 (negative vs sexual FC=0.277 p=0.098; negative vs positive FC=0.008, p=0.956; sexual vs positive FC=-0.269, p=0.121) and ID had no effect: ICC=0.0.

The ABS data were also normally distributed for the three valence categories (again excluding neutral valence behaviours); negative: D(10)=0.224, p=0.168; positive: D(8)=0.176, p=0.200; sexual: D(5)=0.239, p=0.200; but comparisons were made with the non-normally distributed population ABS data using nonparametric methods. No significant differences were observed between the population median and the ABS values for each valence category; negative: MDN=0.111, IQR=0.056-0.304, W(10)=30.50, Z=0.306, p=0.759 (Pearson's r=0.097); positive: MDN=0.140, IQR=0.052-0.293, W(8)=22.00, Z=0.560, p=0.575 (Pearson's r=0.198); sexual: MDN=0.355, IQR=0.000-0.620, W(5)=12.00, Z=1.219, p=0.223 (Pearson's r=0.545) and no significant overall effect of valence was observed; F(2,20)=0.858, p=0.439 (negative vs sexual FC=0.113, p=0.261; negative vs positive FC=-0.017, p=0.851; sexual vs positive FC=-0.130, p=0.245) with ID found to have a strong effect upon the overall model: ICC=0.489.

4.5.2—Visual Field Proportions

Median VFP values were calculated for each visual field and then used as the predicted values in subsequent comparisons for each category; extreme left: MDN=4.0%, IQR=0.0-11.1%; mid left: MDN=23.5%, IQR=11.1-33.3%; centre: MDN=32.0%, IQR=22.2-52.8%, mid right: MDN=20.0%, IQR=10.0-24.7%; extreme right: MDN=11.1%, IQR=0.0-19.2% (population median VFP values shown in Figure 4.10). A significant overall difference was found for the five VFP values at the group level; $X^2(4)=40.803$, p<0.001 (Kendall's W= 0.352). Pairwise post-hoc comparisons were then performed between each VFP value, with the level of significance adjusted according to the Holm-Bonferroni method, and found that the central visual field returned a significantly higher VFP value than the extreme left (Z=4.397, p<0.001, Pearson's r=0.817), extreme right (Z=3.257, p=0.001, Pearson's r=0.605), and mid right

(Z=2.959, p=0.003, Pearson's r=0.549) visual fields whilst the VFP value for the extreme left visual field was significantly lower than that of the mid left (Z=-3.710, p<0.001, Pearson's r=-0.689) and mid right (Z=-3.297, p=0.001, Pearson's r=0.612) visual fields.

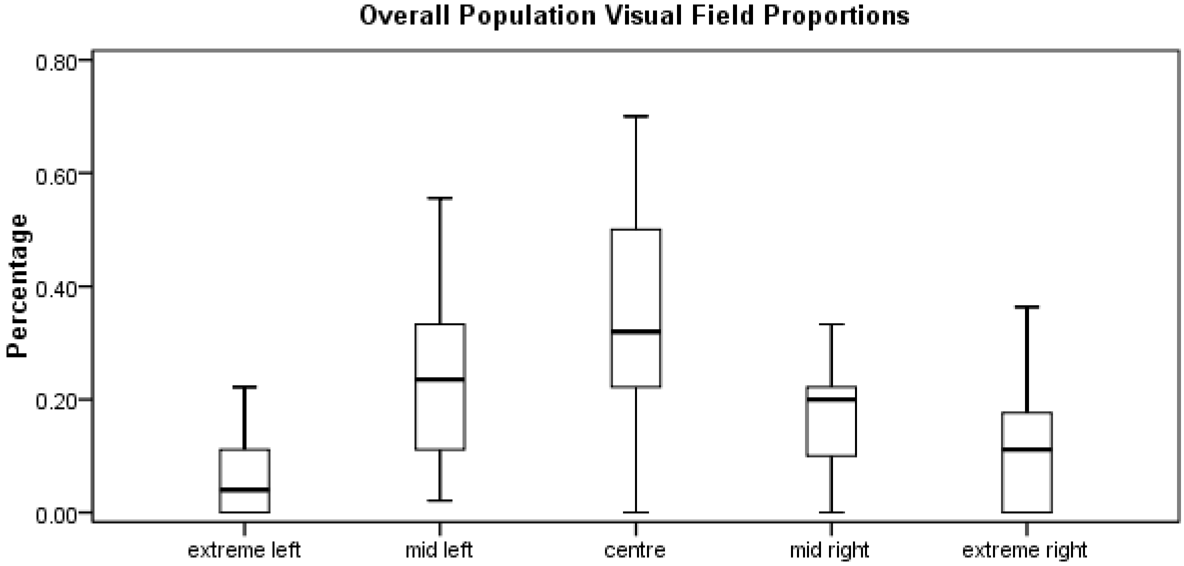

Figure 4.10 | Showing the population median VFP values for the five visual fields for all 29 individuals.

4.5.2.1 Visual Field Proportions and Age

When the data were divided into each age category they were found to be non-normally distributed for subadults and adults. For subadults the data were normally distributed for the mid left (D(13)=0.160, p=0.200) and mid right (D(13)=0.176, p=0.200) VFP values but not for the central visual field (D(13)=0.223, p=0.077) or either extreme visual fields; extreme left: D(13)=0.374, p<0.001; extreme right: D(13)=0.298, p=0.003. For adults only the VFP data for the extreme right visual field were not normally distributed (D(16)=0.243, p=0.012) but the data were normally distributed for each of the other four visual fields; extreme left: D(16)=0.157, p=0.200; mid left: D(16)=0.157, p=0.200; centre: D(16)=0.086, p=0.200; mid right: D(16)=0.154, p=0.200.

For subadults a significant overall difference was observed between the five VFP values ($X^2(4)=29.476$, $p<0.001$, Kendall's W=0.567) but none of these VFP values differed significantly from the predicted VFP values. The highest VFP value was observed for the central visual field: MDN=33.3%, IQR=23.6-65.2%, W(13)=58.00, Z=0.874, p=0.382 (Pearson's r=0.242) whilst both extreme visual fields returned the lowest median VFP values; extreme left: MDN=0.0%, IQR=0.0-11.1%, W(13)=55.00, Z=-0.682, p=0.495 (Pearson's r=-0.189), and extreme right: MDN=0.0%, IQR=0.0-17.2%, W(13)=25.00, Z=-1.458, p=0.145 (Pearson's r=0.404). The data for both mid visual fields were also non-significant: mid left: MDN=25.0%, IQR=13.9-38.1%, W(13)=55.00, Z=0.665, p=0.506 (Pearson's r=0.184); mid right: MDN=20.8% IQR=9.2-25.8%, W(13)=40.00, Z=-0.385, p=0.700 (Pearson's r=0.107).

A significant overall difference between the five visual fields was also observed for adults ($X^2(4)=15.747$, p=0.003, Kendall's W=0.246) but none of the VFP values differed significantly from the predicted values. The highest median VFP value was found for the central visual field: MDN=30.6%, IQR=20.5-43.6%, W(16)=57.00, Z=-0.170, p=0.865 (Pearson's r=-0.043) whilst the lowest median VFP value was found for the extreme left visual field: MDN=6.1%, IQR=0.0-11.8%, W(16)=89.00, Z=1.654, p=0.098 (Pearson's r=0.414). For the other three visual fields the median VFP values were calculated as follows: mid left: MDN=21.7%, IQR=11.1-30.6%, W(16)=54.00, Z=-0.724, p=0.469 (Pearson's r=-0.181); mid right: MDN=19.4% IQR=10.6-26.0%, W(16)=53.00, Z=-0.398, p=0.691 (Pearson's r=-0.100); and extreme right: MDN=15.1%, IQR=7.0-28.1%, W(16)=98.00, Z=1.553, p=0.121 (Pearson's r=0.388).

Comparison of the median VFP values for subadults and adults found no significant differences in any of the visual fields; extreme left: U=82.50, p=0.322 (Pearson's r=0.184); mid left: U=84.50, p=0.391 (Pearson's r= 0.159); centre: U=81.00, p=0.313 (Pearson's r= 0.188); mid right: U=101.00, p=0.895 (Pearson's r= 0.025); extreme right: U=63.50, p=0.070 (Pearson's r= 0.337). The median VFP values for each age category have been shown in Figure 4.11.

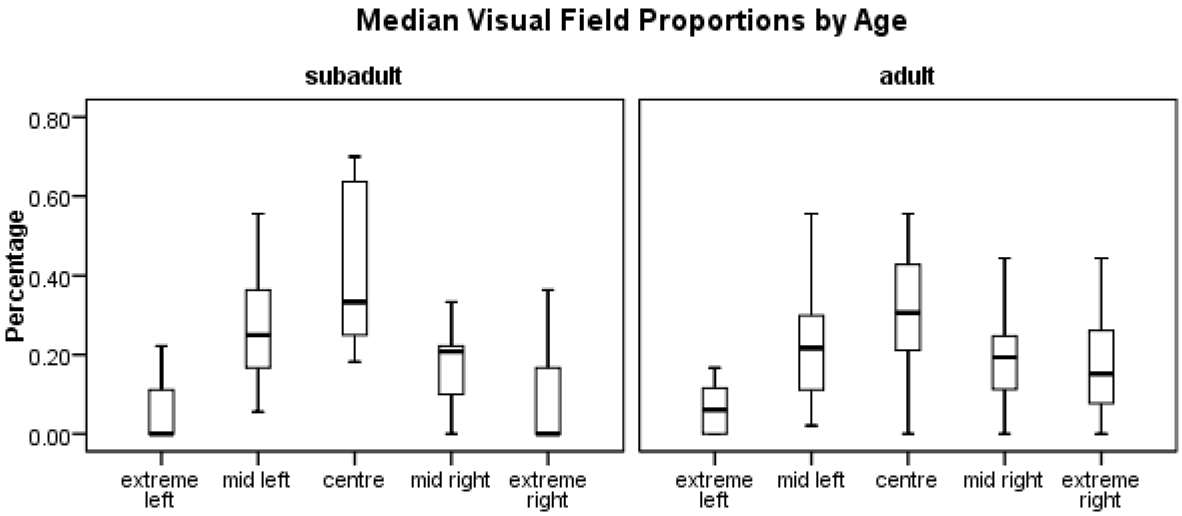

Figure 4.11 | Showing the median VFP values for subadult (n=13) and adult (n=16) subjects.

4.5.2.2 Visual Field Proportions and Sex

When the data were separated into the male and female categories they were found to be non-normally distributed for both. For females, the data were not normally distributed for the extreme left (D(21)=0.216, p=0.012) or extreme right (D(21)=0.238, p=0.003) visual fields but were normal for the remaining three visual fields; mid left: D(21)=0.168, p=0.125; centre: D(21)=0.124, p=0.200; mid right: D(21)=0.238, p=0.200. The data for males were non-normally distributed for the extreme left visual field (D(8)=0.387, p=0.001) but were normally distributed for the other four visual fields: mid left: D(8)=0.168, p=0.200; centre: D(8)=0.168, p=0.200; mid right D(8)=0.188, p=0.200; extreme right: D(8)=0.180, p=0.200.

A significant overall difference between the five VFP values was observed for females ($X^2(4)=28.205$, p<0.001, Kendall's W=0.336) but comparison of the five VFP values for each sex category with the predicted VFP values from the population median VFP values reported no significant differences for any visual field. The highest VFP value was observed for the central visual field: MDN=33.3%, IQR=23.6-65.2%, W(21)=114.00, Z=0.336, p=0.737 (Pearson's r=0.073) whilst both extreme visual fields returned the lowest median VFP values; extreme left: MDN=0.0%, IQR=0.0-11.1%, W(21)=149.00, Z=1.656, p=0.098 (Pearson's r=0.361), and extreme right: MDN=0.0%, IQR=0.0-17.2%, W(21)=115.00, Z=-0.017, p=0.986 (Pearson's r=-0.004). The data for both mid visual fields were also non-significant: mid left: MDN=25.0%, IQR=13.9-38.1%, W(21)=103.00, Z=-0.435, p=0.664 (Pearson's r=-0.095); mid right: MDN=20.8% IQR=9.2-25.8%, W(21)=116.00, Z=0.411, p=0.681 (Pearson's r=0.090).

For males a significant overall difference between the five VFP values was also observed ($X^2(4)=17.790$, p=0.003, Kendall's W=0.556) although none of the VFP values differed significantly from the predicted values. The highest median VFP value was found for the central visual field: MDN=33.3%, IQR=23.6-65.2%, W(8)=22.00, Z=0.561, p=0.575 (Pearson's r=-0.595) whilst the joint lowest median VFP values were observed for the extreme visual fields; extreme left: MDN=0.0%, IQR=0.0-11.1%, W(8)=21.00, Z=0.431, p=0.666 (Pearson's r=0.152); extreme right: MDN=0.0%, IQR=0.0-17.2%, W(8)=22.00, Z=0.561, p=0.575 (Pearson's r=0.198). The mid visual field VFP values were also non-significant for males: mid left: MDN=25.0%, IQR=13.9-38.1%, W(8)=24.00, Z=0.841, p=0.400 (Pearson's r=0.297); mid right: MDN=20.8% IQR=9.2-25.8%, W(8)=6.00, Z=-1.684, p=0.092 (Pearson's r=-0.595).

Comparison of the median VFP values for males and females found no significant differences between any of the visual fields; extreme left: U=79.00, p=0.798 (Pearson's r=0.048); mid left: U=70.00, p=0.494 (Pearson's r= 0.127); centre: U=80.50, p=0.864 (Pearson's r= 0.032); mid right: U=47.00, p=0.070 (Pearson's r= 0.337); extreme right: U=74.0, p=0.618 (Pearson's r= 0.092). Figure 4.12 shows the median VFP values for males and females.

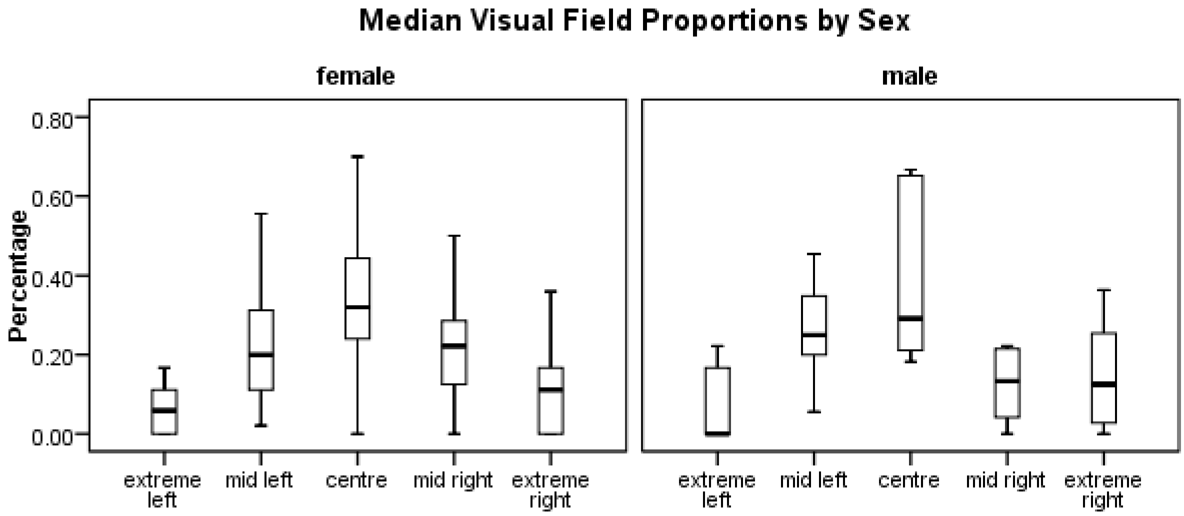

Figure 4.12 | Showing the median VFP values males (n=8) and females (n=21).

4.5.2.3 Visual Field Proportions and Rank

When the data were split into the four rank categories and tested for normality high and mid high rank categories contained normally distributed data in all five visual fields whilst the mid low and low ranked categories did not. For the highest rank category data were normally distributed; extreme left: D(8)=0.213, p=0.200; mid left: D(8)=0.251, p=0.148; centre: D(8)=0.180, p=0.200; mid right: D(8)=0.257, p=0.130; extreme right: D(8)=0.264, p=0.107. Data were also normally distributed for the mid high rank category; extreme left: D(9)=0.252, p=0.103; mid left: D(9)=0.159, p=0.200; centre: D(9)=0.196, p=0.200; mid right: D(9)=0.253, p=0.102; extreme right: D(9)=0.216, p=0.200. In the remaining two rank categories data were normally distributed in four of the five visual fields. For the mid low rank data were non-normal for the extreme right visual field (D(6)=0.355, p=0.017) but were normally distributed for the remaining visual fields; extreme left: D(6)=0.196, p=0.200; mid left: D(6)=0.186, p=0.937; centre: D(6)=0.203, p=0.200; mid right: D(6)=0.242, p=0.200. In the lowest rank category data were not normally distributed for the extreme left visual field (D(6)=0.398, p=0.003) but were normal for the remaining four visual fields; mid left: D(6)=0.209, p=0.200; centre: D(6)=0.174, p=0.200; mid right: D(6)=0.150, p=0.200; extreme right: D(6)=0.244, p=0.200.

There was no significant overall difference between the VFP values for the high rank category, X^2(8)=5.219, p=0.266, Kendall’s W=0.163; and none of the VFP values were significantly different from expected, extreme left: MDN=7.5%, IQR=0.0-16.7%, W(8)=26.00, Z=1.127, p=0.260 (Pearson’s r=0.398); mid left: MDN=13.9%, IQR=6.6-21.9%, W(8)=8.00, Z=-1.400, p=0.161 (Pearson’s r=-0.495); centre: MDN=25.7%, IQR=20.6-42.2%, W(8)=29.00, Z=0.771, p=0.441 (Pearson’s r=0.273); mid right: MDN=11.8% IQR=9.7-20.8%, W(8)=6.00, Z=-1.680, p=0.093 (Pearson’s r=-0.594); extreme right: MDN=17.1%, IQR=10.4-40.8%, W(8)=30.00, Z=1.682, p=0.092 (Pearson’s r=0.595).

A significant overall difference between the VFP values was found for the mid high rank category, X^2(4)=20.682, p<0.001, Kendall’s W=0.575, but none of the VFP values were significantly different from the predicted values; extreme left: MDN=5.9%, IQR=0.0-11.6%, W(9)=31.00, Z=1.016, p=0.310 (Pearson’s r=0.339); mid left: MDN=23.5%, IQR=11.1-36.7%, W(9)=23.00, Z=0.059, p=0.953 (Pearson’s r=0.197); centre: MDN=36.3%, IQR=23.1-55.6%, W(9)=29.00, Z=0.771, p=0.441 (Pearson’s r=0.257); mid right: MDN=22.2% IQR=18.8-24.7%, W(9)=8.00, Z=-0.524, p=0.600 (Pearson’s r=-0.175); extreme right: MDN=9.1%, IQR=0.0-13.8%, W(9)=16.00, Z=-0.773, p=0.440 (Pearson’s r=0.258).

For the mid low rank category there was also a significant difference between the five VFP values, X2(4)=12.852, p=0.012 Kendall’s W=0.535; but there were no significant contrasts between the expected and the observed VFP values for each visual field; extreme left: MDN=5.1%, IQR=0.0-10.3%, W(6)=10.00, Z=0.677, p=0.498 (Pearson’s r=0.276); mid left: MDN=22.5%, IQR=10.8-32.5%, W(6)=9.00, Z=-0.314, p=0.753 (Pearson’s r=-0.128); centre: MDN=46.5%, IQR=30.3-65.2%, W(6)=13.00, Z=1.483, p=0.138 (Pearson’s r=0.605); mid right: MDN=14.4% IQR=6.0-29.2%, W(6)=8.00, Z=-0.524, p=0.600 (Pearson’s r=0.214); extreme right: MDN=0.0%, IQR=0.0-13.7%, W(6)=6.00, Z=-0.970, p=0.332 (Pearson’s r=-0.396).

A significant overall difference between the VFP values for the lowest rank category was also observed, X^2(4)=13.346, p=0.010, Kendall’s W=0.556; and the mid left VFP value was significantly higher for this rank than the expected VFP value, MDN=31.0%, IQR=25.0-43.9%, W(6)=21.00, Z=2.207, p=0.027 (Pearson's r=0.901), but no other significant differences were observed: extreme left: MDN=0.0%, IQR=0.0-11.7%, W(6)=11.00, Z=0.108, p=0.914 (Pearson's r=0.044); centre: MDN=26.8%, IQR=8.3-37.5%, W(6)=5.00, Z=-1.153, p=0.249 (Pearson's r=0.102); mid right: MDN=24.7% IQR=12.5-36.1%, W(6)=14.00, Z=0.734, p=0.463 (Pearson's r=0.300); extreme right: MDN=15.5%, IQR=0.0-21.2%, W(6)=12.00, Z=0.315, p=0.752 (Pearson's r=0.129). The median VFP values for all four rank categories have been shown in Figure 4.13.

The four rank categories were then compared within each visual field but no significant effect of rank was observed; extreme left: $X^2(3)=1.322$, p=0.724, $\eta^2=0.047$; mid left: $X^2(3)=6.803$, p=0.078, $\eta^2=0.243$, centre: $X^2(3)=4.776$, p=0.189, $\eta^2=0.171$; mid right: $X^2(3)=3.215$, p=0.360, $\eta^2=0.115$; extreme right: $X^2(3)=5.958$, p=0.114, $\eta^2=0.213$.

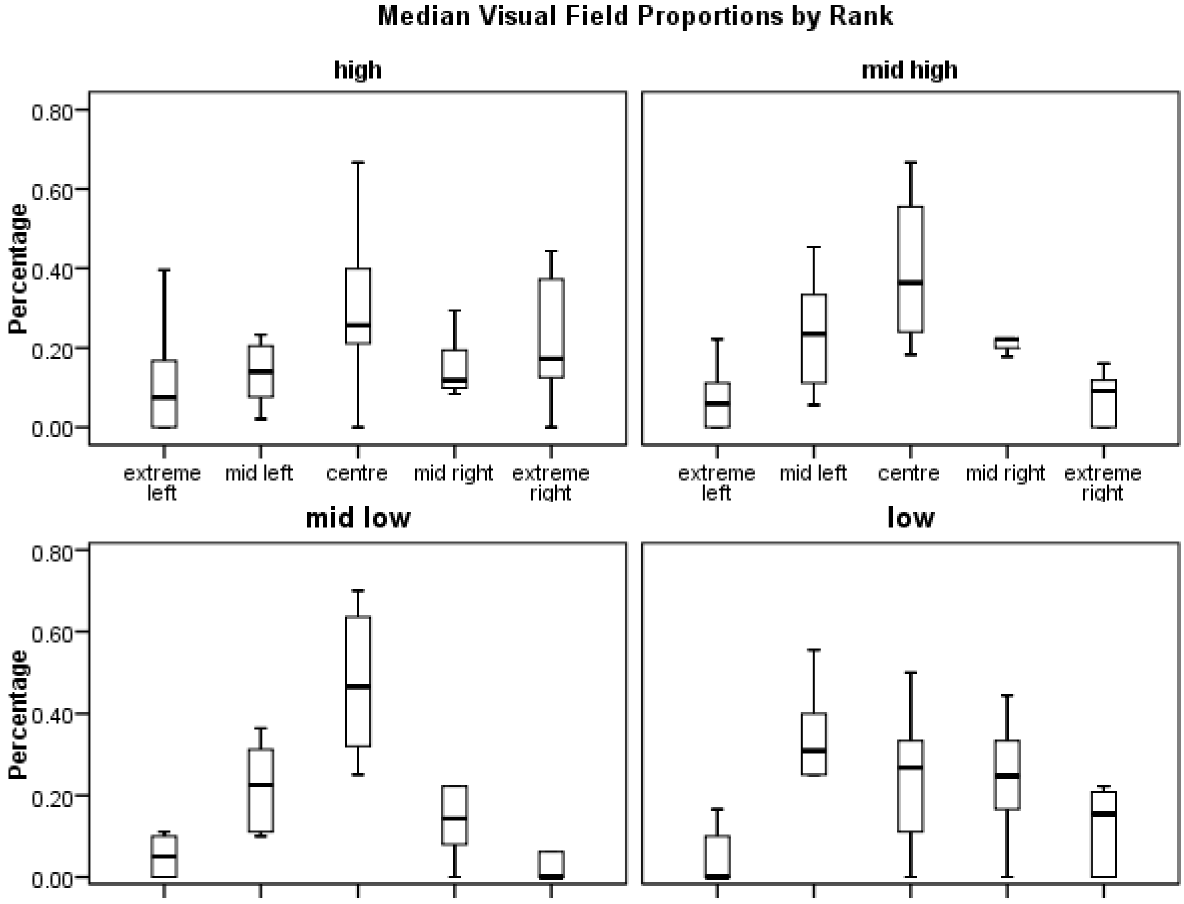

Figure 4.13 | Showing the median VFP values for the four rank categories (high n=8, mid high n=9, mid low n=6, low n=6)

4.5.2.4 Visual Field Proportions and Emotional Intensity

Non-normally distributed data were found for both subcategories of emotional intensity. In low emotional intensity contexts the data were not normally distributed in the extreme left visual field: D(19)=0.247, p=0.004, but were normally distributed for the remaining four VFP values: mid left: D(19)=0.114, p=0.200; centre: D(19)=0.147, p=0.200; mid right: D(19)=0.144, p=0.200; extreme right: D(19)=0.182, p=0.097. For the high intensity emotion subcategory data were not normally distributed for the extreme left visual field, D(12)=0.313, p=0.002, but were normally distributed for the mid left: D(12)=0.201, p=0.194; centre: D(12)=0.178, p=0.200; mid right: D(12)=0.158, p=0.200; and extreme right: D(12)=0.236, p=0.063 visual fields.

A significant overall difference between the five VFP values was reported for the low intensity emotion category: X^2(4)=11.474, p=0.022 (Kendall's W=0.151) whilst the extreme left VFP value was higher than expected: MDN=11.1%, IQR=0.0-15.4%, W(19)=155.00, Z=2.431, p=0.015 (Pearson's r=0.558), but no other significant differences from the expected values were found: mid left: MDN=20.0%, IQR=7.7-33.3%, W(19)=86.00, Z=-0.363, p=0.717 (Pearson's r=-0.083); centre: MDN=26.7%, IQR=14.3-42.9%, W(19)=75.00, Z=-0.805, p=0.421 (Pearson's r=0.185); mid right: MDN=20.0% IQR=14.3-28.6%, W(19)=83.00, Z=0.308, p=0.758 (Pearson's r=-0.071); extreme right: MDN=15.4%, IQR=0.0-28.6%, W(19)=136.00, Z=1.657, p=0.098 (Pearson's r=0.380).

A significant overall difference was also observed between the VFP values for high intensity emotion behaviours: X^2(4)=11.036, p=0.026 (Kendall's W=0.230) but only the mid right VFP was significantly different (lower) than the expected value: MDN=14.3% IQR=4.5-21.7%, W(12)=10.00, Z=-2.046, p=0.041 (Pearson's r=-0.591) whilst the remaining visual fields did not differ significantly from expected; extreme left: MDN=0.0%, IQR=0.0-12.6%, W(12)=35.00, Z=-0.321, p=0.738 (Pearson's r=0.093); mid left: MDN=14.8%, IQR=1.8-35.4%, W(12)=27.00, Z=-0.943, p=0.346 (Pearson's r=0.272); centre: MDN=35.7%, IQR=24.4-59.3%, W(12)=50.00, Z=0.863, p=0.388 (Pearson's r=0.249); extreme right: MDN=9.7%, IQR=0.0-28.6%, W(12)=46.00, Z=0.553, p=0.580 (Pearson's r=0.160). The median VFP values for high and low intensity emotions have been plotted in Figure 4.14.

A generalised linear mixed model was then used to compare each VFP value for both categories of emotional intensity but no significant effect was found in any of the visual fields; extreme left: F(1,29)=0.065, p=0.801, ICC=0.133 (FC=0.010, p=0.801); mid left: F(1,29)=0.203, p=0.656, ICC=0.00 (FC=0.030, p=0.656); centre: F(1,29)=4.103, p=0.052, ICC=0.432 (high vs low FC=-0.128, p=0.052); mid right: F(1,29)= 3.116, p=0.088, ICC=0.00 (FC=0.074, p=0.088); extreme right: F(1,29)=0.000, p=0.996, ICC=0.353 (FC=0.000, p=0.996).

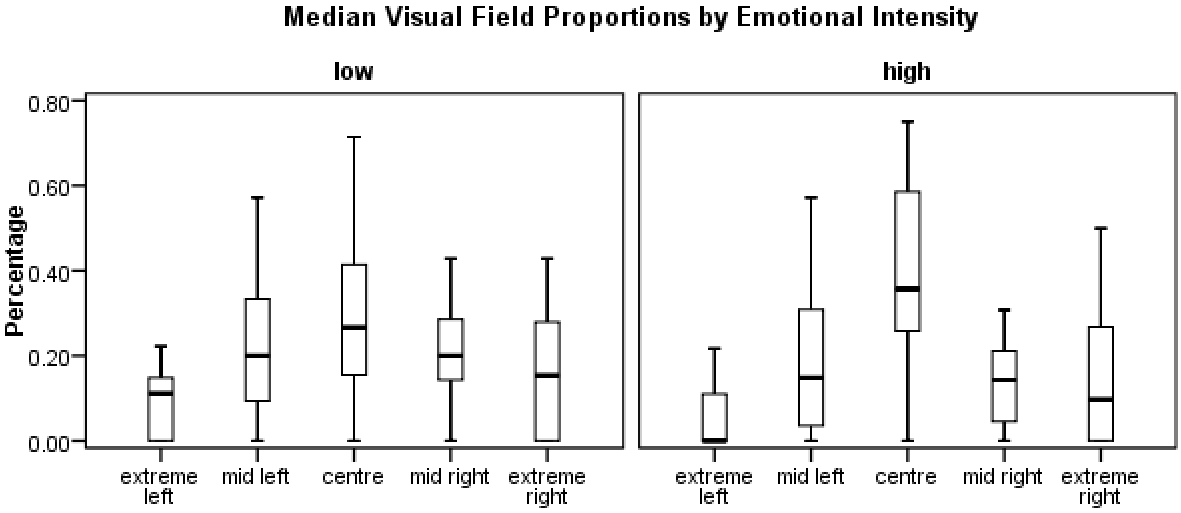

Figure 4.14 | Showing the median VFP values for the categories of high (n=12) and low (n=19) emotional intensity.

4.5.2.5 Visual Field Proportions and Emotional Valence

When the data were split into the four valence categories and the minimum criterion of seven interactions per individual was applied no subjects met this criterion for the neutral valence category and calculations were thus made upon the three remaining emotional categories. Of these categories only the data from the sexual category were normally distributed in all five visual fields; extreme left: D(5)=0.203, p=0.200; mid left: D(5)=0.226, p=0.200; centre: D(5)=0.240, p=0.200; mid right: D(5)=0.341, p=0.059; extreme right:

D(5)=0.222; p=0.200. For negative valence behaviours the extreme left VFP values were not normally distributed, D(10)=0.368, p<0.001, whilst the remaining visual fields were normally distributed; mid left: D(10)=0.368, p<0.001; centre: D(10)=0.212, p=0.200; D(10)=0.185, p=0.200; mid right: D(10)=0.255, p=0.065; extreme right: D(10)=0.161, p=0.200. Positive valence VFP data were also not normally distributed for the extreme left visual field: D(8)=0.451, p<0.001; mid left: t(8)=0.175, p=0.200; centre: D(8)=0.185, p=0.200; mid right: D(10)=0.158, p=0.200; extreme right: D(8)=0.271, p=0.087.

A significant overall difference was found between the five VFP values for negative valence behaviours: X2(4)=12.593, p=0.013, Kendall's W=0.315; but none of the observed VFP values differed significantly from expected: extreme left: MDN=0.0%, IQR=0.0-14.3%, W(10)=34.00, Z=0.679, p=0.497 (Pearson's r=0.215); mid left: MDN=25.4%, IQR=13.5-40.7%, W(10)=35.00, Z=0.765, p=0.444 (Pearson's r=0.242); centre: MDN=27.9%, IQR=21.7-42.9%, W(10)=28.00, Z=0.051, p=0.959 (Pearson's r=0.016); mid right: MDN=25.4% IQR=7.5-28.9%, W(10)=28.50, Z=0.102, p=0.918 (Pearson's r=0.032); extreme right: MDN=14.3%, IQR=0.0-30.0%, W(10)=39.00, Z=1.177, p=0.239 (Pearson's r=0.372).

The overall difference between each of the VFP values for positive valence behaviours was also significant, X^2(4)=13.203, p=0.010, Kendall's W=0.413, although none of the individual VFP values were significantly different from expected; extreme left: MDN=0.0%, IQR=0.0-9.4%, W(8)=15.00, Z=-0.439, p=0.660 (Pearson's r=-0.155); mid left: MDN=15.3%, IQR=2.3-37.7%, W(8)=11.00, Z=-0.981, p=0.326 (Pearson's r=-0.296); centre: MDN=52.3%, IQR=24.1-82.9%, W(8)=30.00, Z=1.680, p=0.093 (Pearson's r=0.507); mid right: MDN=16.8% IQR=3.6-29.3%, W(8)=14.00, Z=-0.561, p=0.575 (Pearson's r=-0.169); extreme right: MDN=4.5%, IQR=0.0-11.6%, W(8)=9.00, Z=-1.278, p=0.201 (Pearson's r=-0.385).

For behaviours of a sexual valence there was no overall difference between the five VFP values, X^2(4)=6.274, p=0.180, Kendall's W=0.314, but a significantly lower than expected VFP value was found for the mid left (MDN=6.3%, IQR=0.0-10.9%, W(5)=0.00, Z=-2.032, p=0.042, Pearson's r=-0.909) and a significantly higher than expected VFP value was found for the extreme right (MDN=37.5%, IQR=22.4-70.0%, W(5)=15.00, Z=2.023, p=0.043, Pearson's r=-0.905) visual fields. No significant difference was found for the remaining three VFP values; extreme left: MDN=14.3%, IQR=0.0-9.4%, W(5)=12.00, Z=1.214, p=0.225 (Pearson's r=0.543); centre: MDN=18.8%, IQR=0.0-36.1%, W(5)=3.00, Z=-1.219, p=0.223 (Pearson's r=-0.545); mid right: MDN=6.3% IQR=0.0-26.4%, W(5)=5.00, Z=-0.677, p=0.498 (Pearson's r=-0.303).

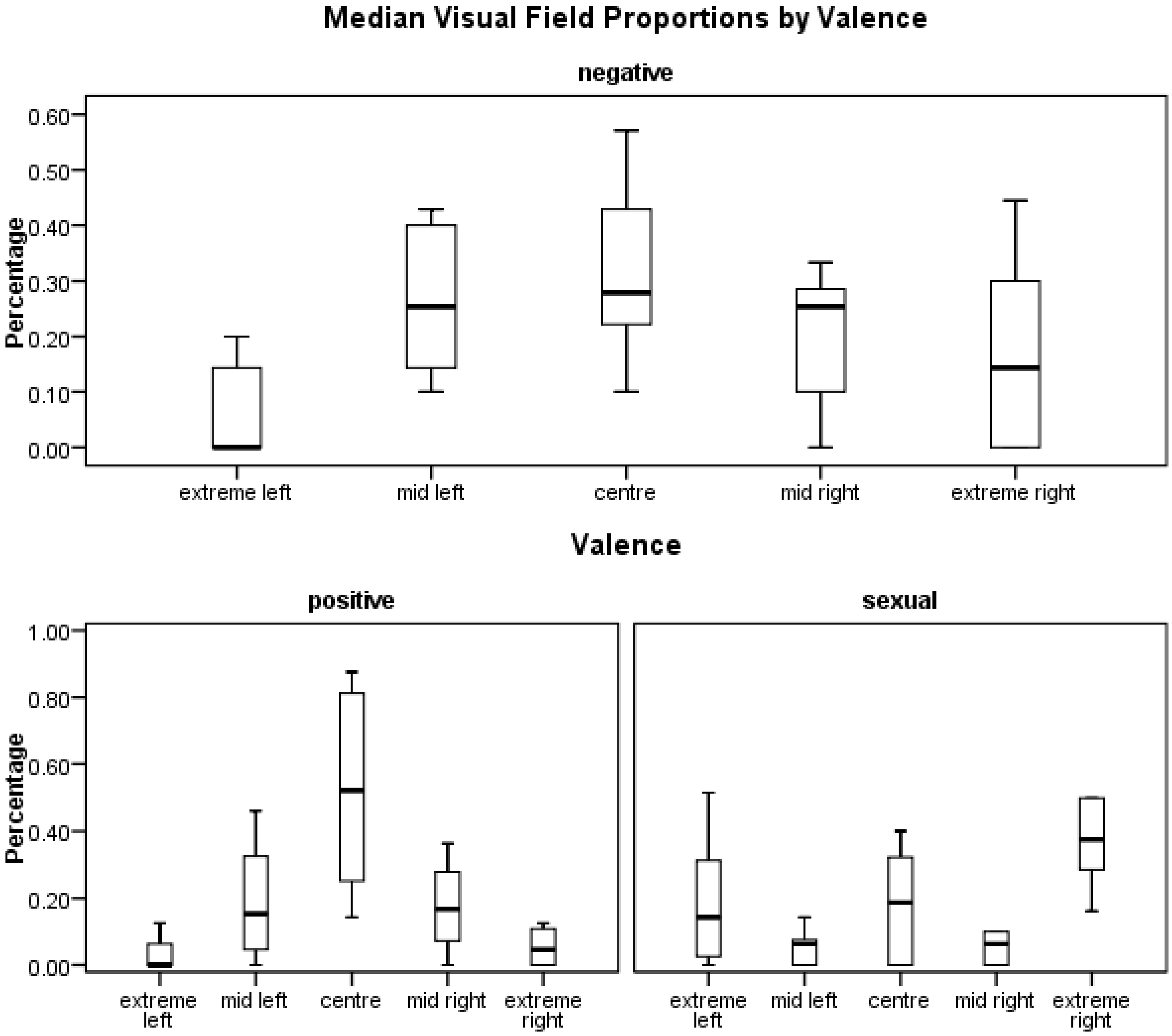

Figure 4.15 | Showing the VFP values for three valence categories (there was insufficient data for the neutral valence category; negative n=10, positive n=8, sexual n=5).

The VFP values for each valence category were then compared within each visual field using a generalised linear mixed model and a significant effect of valence was found for four of the five visual fields; extreme left: F(2,20)=5.559, p=0.012, ICC=0.136; mid left: F(2,20)=5.163, p=0.016, ICC=0.273; centre: F(2,20)=4.341, p=0.027, ICC=0.00; extreme right: F(2,20)=7.331, p=0.004, ICC=0.00; but there was no significant effect found in the mid right visual field: F(2,20)=0.565, p=0.577, ICC=0.00.

Sexual valence behaviours reported a significantly higher VFP than negative valence behaviours in both extreme visual fields; extreme left: FC=2.711, p=0.020; extreme right: FC=2.961, p=0.008; whilst sexual behaviours reported a significantly lower VFP value than negative behaviours in the mid left visual field: FC=-3.210, p=0.009; but no other significant contrasts were observed. Figure 4.15 compares the VFP values for negative, positive and sexual valence behaviours.

4.5.3—Overall Mixed Model Comparison

Using a generalised mixed linear model it was possible to analyse the influence of all factors included in this study (age, sex, rank, emotional intensity, and emotional valence) upon whether behaviours were performed in the left, centre or right visual field with individual ID set as a random effect. A significant overall effect of this model was reported (F(18,409)=2.441, p=0.001, ICC=0.000) with emotional valence (F(6,449)=4.708, p<0.001) and emotional intensity (F(2,449)=8.934, p<0.001) found to have a significant effect within this model. Sexual valence behaviours had a significantly greater effect upon behaviours occurring non-centrally (left FC=1.307, p=0.029; right FC=2.717, p<0.001) than neutral valence behaviours whilst sexual valence behaviours were significantly more likely to occur in the right visual field when compared with negative valence behaviours (FC=1.587, p=0.004). Additionally, low intensity behaviours had a significantly greater influence towards a right side bias than high intensity behaviours (FC=1.422, p<0.001). A second model comparing the influence of all factors upon interactions occurring in the left visual field vs those occurring in the right found no significant overall effect (F(9,312)=1.049, p=0.400, ICC=0.817).

4.6 | Discussion

Overall, this study found no evidence of a population level lateral bias and only five of the 29 subjects included in analyses expressed significant lateral biases at the individual level (three left side biased and two right side biased) therefore this distribution was not significantly different from what might be expected on the basis of chance. In comparison with previous studies of emotional lateralisation in rhesus macaques, the left side group level biases reported by Ifune *et al.* (1984), Hauser (1993) and Hauser & Akre (2001) were not supported by this study with the mixed model analysis also confirming that no significant lateral bias existed for this population and therefore the first hypothesis (H_1) was not supported as no evidence was found that the right hemisphere controls emotion. No significant directional lateral biases were observed for any contexts however a significant strength bias was found for high intensity interactions. There was no significant strength bias observed for low intensity interactions or a significant contrast found between high and low intensity interactions. The fifth hypothesis (H_5) did predict a stronger left side bias for high intensity interactions than low intensity interactions but as the results from the present study only reported a significant strength bias with no specific left side preference then the fifth hypothesis was not supported in full. This observation does however support Casperd & Dunbar (1996) and Wallez & Vauclair (2011), which reported significant strength biases during scenarios of high arousal in gelada and olive baboons respectively, and Campbell (1978), who reported a continuum between lateral bias and emotional arousal in humans. Although no significant strength biases were observed in any of the valence categories the ABS value for sexual behaviours was markedly higher than those of negative or positive valence behaviours and within both of the extreme visual fields sexual behaviours returned significantly higher VFP values than negative valence behaviours, with this also supported by the results from the mixed model analysis. Although no significant lateral biases were observed for any of the emotional contexts it is interesting to note the contrast in bias direction between the sexual valence behaviours, which were right sided, and the positive and negative valence behaviours, which displayed a left side preference. Ventolini *et al.*'s (2005) study on black-winged stilts also reported a contrast between sexual behaviours and those of a different emotional context however they found a left side bias for sexual behaviours and a right side bias for other behaviours – opposite lateral biases to those reported by the present study. Indeed, and similar to Ventolini *et al.*, Bullock & Rogers (1986) and Gülbetekin *et al.* (2007) also found that sexually guided behaviours were lateralised to the left; further suggesting that the results of the present study should be interpreted with caution, especially given that no significant lateral biases were observed for any of the four emotional contexts.

As sexual behaviours are mainly high intensity interactions this may suggest that sexual behaviours are an underlying cause of the significant strength bias reported for high intensity behaviours. Ideally, the interaction between emotional valence and intensity could then have been examined as part of a two-way interaction within the mixed model analysis but the overall data set was too small to permit this calculation. Indeed, the small sample sizes may have been a major confounding factor within this study in terms of the total number of individuals observed and the total number of interactions observed per individual. Furthermore, the method employed by this study appears to have further exacerbated this issue. A stated aim of this thesis (Section 1.8) was to address the perceived caveats of the method of calculating lateralisation used by Casperd & Dunbar (1996) and Baraud *et al.* (2009). In their method, all observed interactions were included in analyses; no minimum criterion of interactions per individual was set and the data were not weighted per individual. The chief criticism of this method was that it may be susceptible to bias from individuals with a disproportionately small or large number of interactions, particularly if the lateralisation of such individuals did not reflect the population average. However, this method appears to be advantageous when dealing with a small data set as no data are eliminated from analyses. For example, the total number of interactions observed during data collection for this study was

529 and when a minimum criterion of seven interactions per individual was applied, this number was reduced to a total of 489 interactions. However, when the data were split by valence and this criterion was again applied, the total number of interactions used to analyse the influence of valence was 268 (almost halved from the original total of 529 interactions) and only three valence categories were included as there were insufficient data remaining to include neutral behaviours. This is clearly a significant caveat of the weighted method employed by this study and therefore its application to future studies must be carefully considered. However, it is again worth highlighting the contrast in results that can be obtained between the weighted and pooled methods. As reported, there was no significant overall bias at the population level for this species although a nominal left side preference was found (mean BLI=-0.062, p=0.197) but had the pooled method of Casperd & Dunbar and Baraud *et al.* instead been employed a significant right side bias (mean BLI=+0.090, p=0.026) would have been observed. The contrast in these results reinforces the importance of weighting the data at the individual level before calculating averages for categories or at the population level. For example, the macaque 'R27' contributed one fifth (52 out of 268) of the total number of interactions included in analyses for this study and was also found to express a very strong and highly significant right side bias (BLI=0.635, p<0.001). It is therefore probable that this individual's data would have heavily influenced the data for the group as a whole had the weighted method not been applied. Indeed, removing R27's data and then using the pooled method to calculate the group mean instead results in a non-significant and nominal right side preference (BLI= +0.005, p=0.903). By contrast, the method employed by the present study ensured that the data from individuals with a large number of data points, such as R27, were weighted equally with data from other individuals observed for much fewer interactions to ensure that no individual lateral biases skewed the data from the overall population and this again highlights that the weighted method provides a much more accurate assessment of lateralisation.

The lack of significant effect upon the direction or strength of bias from the categories of age, sex or rank therefore implies that no support was found for hypotheses two (H_2), three (H_3) or four (H_4) respectively. In comparison with the results of the olive baboon study in Chapter 3, which reported significant left side biases for adults and for negative valence behaviours, these results were not only not replicated but in the case of age differences in particular the contrasts between subadults and adults were markedly different. Again, no significant BLI or ABS values were reported for either age category but a more profound left-side bias was found for subadults rather than adults with subadults also expressing a stronger bias, as denoted by the higher ABS value. The contrast of this result in light of the olive baboon data from chapter 3 and previous observations of stronger hand preferences in adults in a number of other studies (Lehman, 1970; 1978; Vauclair & Fagot, 1987; Westergaard & Suomi, 1993; Hopkins, 1994; Vauclair *et al.*, 2005) makes the interpretation of these observations difficult. A possible explanation may relate to the comparative ages of the subadults included in this macaque study as opposed to the previous baboon chapter. As has been outlined in the methods, all individuals were categorised as adult or subadult for the purposes of this thesis, however, subadults were defined as any individuals that had not yet reached sexual maturity. Several of these subadults from the macaque data were infants that were not fully weaned therefore it is possible that the stronger lateral biases expressed by these individuals may have been influenced by strong nipple preferences. Furthermore, as nipple preferences have been found to decrease as infants age (Tomaszycki *et al.*, 1998) this may also explain why the lateral bias diminished substantially from subadults to adults.

The higher BLI and ABS values reported for sexual behaviours rather than either of the positive or negative valence categories is particularly interesting when considering the season during which the study was performed. Rhesus macaques are seasonal breeders with their normal period of sexual activity being from October to December (Lindburg, 1971; Wenyuan *et al.*, 1993). As data collection for the present study was conducted almost entirely during these months it therefore coincided with the mating season whereby all observations of adult females would have taken place during various stages of oestrus. Aside from the associated change in behaviour, rhesus macaques also undergo physiological changes during this time whereby significant increases in oestrogens and progestogens occur (Bielert *et al.*, 1976). The influence of masculinising hormones, namely testosterone, upon lateralisation has been previously documented in primates whereby its inhibition of the development of the left hemisphere has led to the dominance of the right hemisphere and thus a stronger left handedness in males rather than females (Milliken *et al.,* 1989; Ward *et al.*, 1990) although the influence of female sex hormones has not previously been considered in lateralisation studies. An increase in testosterone in human females during ovulation has previously been found (Persky *et al.*, 1976; Persky *et al.*, 1978; Morris *et al.*, 1987) although if testosterone was to affect lateralisation, the studies by Milliken *et al.* and Ward *et al.* would predict that such a bias would likely result in a left rather than right side bias. It is therefore likely that should these results evidence an effect of hormones that it is due to female sex hormones rather than male sex hormones, although such a suggestion remains speculative at this stage.

A spotted hyaena at FSBR, University of California, Berkeley, CA, USA

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Chapter 5 | *Crocuta crocuta*

Chapter 5

The Lateralisation of Emotion in Spotted Hyaena *Crocuta crocuta*

5.1 | Abstract

Primates have been the main focus of much of the laterality literature but our greater understanding of the evolution of hemispheric specialisation has been considerably shaped by research involving non-primate species. This chapter describes a study investigating the lateralisation of social behaviour in the spotted hyaena, *Crocuta crocuta* (*n*=15), whereby the two competing theories that explain the hemispheric specialisation of emotion, Campbell's Right Hemisphere Hypothesis (1982) and Silberman & Weingartner's Valence Hypothesis (1986), shall be objectively compared. This study shall consider population and individual laterality in terms of direction and strength of side biases and the use of visual fields during approaches to initiate social interactions. Laterality was examined in terms of overall direction and strength of biases and visual field preferences and in relation to age, sex and rank. In addition, several solo behaviours (leg cross, shoulder roll, stick scratch) that involve a strong emotional component were observed during this study that have also been included and tested for lateral bias.

The hyaenas showed a significant population level left side bias during social interactions and five of the individuals were significantly biased towards using their left visual field. Adults and females were lateralised to the left at the group level while subadults and males were not and a left side bias was also found for dominant individuals whilst subordinate individuals were weakly biased. The social interactions were also categorised in terms of their emotional valence and intensity and a significant left side bias was found for sexual behaviours and high intensity behaviours but no lateral biases were found for other behavioural contexts

although sexual, negative and positive valence behaviours were significantly less centralised than neutral valence behaviours. Analysis of the additional solo behaviours also revealed a significant left side bias for the group.

Overall, this study provides some of the first evidence of lateral bias in an African carnivore and thus supports Campbell's (1982) Right Hemisphere hypothesis. The results of this study suggest that masculinising hormones may play a significant role in the ontogenic development of left side bias and that continued exposure to these hormones may reinforce left side biases as evidenced by the results for dominant individuals and females.

5.2 | Introduction

There are two theories that purport to explain the lateralisation of emotion. The Right Hemisphere Hypothesis (Campbell, 1982) suggests that emotion is entirely processed by the right hemisphere whilst the Valence Hypothesis (Silberman & Weingartner, 1986) alternatively proposes that only emotions of a negative valence are controlled by the right hemisphere with the left hemisphere responsible for the control of positive emotion. Research based upon the observation of positive valence behaviours is therefore crucial for determining how emotion is lateralised but to date this has only been addressed in studies of primates. Comparative research in non-human primates has played a significant role in developing our understanding of the evolution of laterality in humans however the ubiquity of behavioural laterality throughout the Animal Kingdom demonstrates that investigating the evolutionary significance of this phenomenon should not be limited to a single Order.

The identification of limb preferences has been a common topic of research in a number of non-primate species and studies. A left leg preference for prey manipulation has been found in spitting spiders, *Scytodes globula* (Ades & Ramires, 2002), and a left flipper preference has been observed in wild bottlenose dolphins, *Tursiops truncates*, during social contact behaviour (Sakai *et al.*, 2006), whilst walruses, *Odobenus rosmarus*, expressed a right flipper preference during underwater feeding (Levermann *et al.*, *2003*), Channel catfish, *Ictalurus punctatus*, are right fin biased for sound production by pectoral stridulation (Fine *et al.*, 1996) and wild black bears, *Ursus americanus*, have a right paw foraging bias (Reimchen & Spoljaric, 2011). Consistent with MacNeilage *et al.*'s (1987) assertion that higher complexity tasks are most likely to offer a better indication of manual laterality in primates, Rutledge & Hunt (2004) observed highly lateralised beak use at the individual level in New Caledonian crows, *Corvus moneduloides*, as they manufactured tools from leaves. Furthermore, a study by Magat & Brown (2009) comparing individuals from eight Australian parrot species (cockatiel, *Nymphicus hollandicus*; budgerigar, *Melopsittacus undulates*; galah, *Eolophus rosiecapilla*;

gang-gang cockatoo, *Callocephalon fimbriatum*; red-tailed black cockatoo, *Calyptorhynchus banksii*; sulphur-crested cockatoo, *Cacatua galerita*; Australian king parrot, *Alisterus scapularis*; superb parrot, *Polytelis swainsonii*) found that individuals which expressed lateralised behaviour (eye or foot preferences) demonstrated superior cognitive abilities to their non-lateralised conspecifics.

Andrew & Brennan's (1983) study on the domestic chick was the first non-human study of laterality and also the first to demonstrate the lateralisation of emotional processes outside of the human species. Using temporary eye patches to blind chicks in one eye, Andrew & Brennan then presented these chicks with illuminated coloured beads and compared the results from left and right-eye occluded chicks. They observed that fear responses were significantly lateralised and that a much stronger reaction was expressed when chicks viewed the stimulus with their left than right eye and Andrew & Brennan posited that the more intense fear response elicited by chicks viewing a novel stimulus with the left, rather than right, eye may be indicative of right hemispheric control for the interpretation and expression of emotion. A year prior to Andrew & Brennan's study, Campbell (1982) had reviewed the literature on the lateralisation of emotion in humans and had postulated that the right hemisphere was especially involved in the analysis and display of emotion, particularly negative emotion, and Andrew & Brennan's findings were therefore supportive of this Right Hemisphere hypothesis. However, a further review of the human literature by Silberman & Weingartner (1986) posited the alternative Valence Hypothesis: agreeing with Campbell's suggestion that the perception and expression of negative emotion were lateralised to the right hemisphere, but contending that positive emotion was lateralised to the left hemisphere.

As only a negative emotional context had been considered by Andrew & Brennan's (1983) study, their observations were therefore congruent with both Campbell (1982) and Silberman & Weingartner (1986) and unable to provide insight into which of the two hypotheses may be valid. Additionally, much of the subsequent literature (*e.g.* Evans *et al.*, 1993; Cantalupo *et al.*, 1995; Casperd & Dunbar, 1996) has also focused upon negative emotional contexts alone and has therefore been unable to differentiate between Campbell's and Silberman & Weingartner's competing theories.

Using a paradigm similar to Andrew & Brennan (1983), whereby the expression of visual laterality was observed as an indicator of a corresponding neural lateralisation of emotional processes, Dharmaretnam & Andrew (1994) presented newly hatched domestic chicks with a novel light source over a period of days and found that although a right eye bias was found at eight-day olds, a left eye bias emerged after 11 days. Furthermore, when Dharmaretnam & Andrew replaced the light stimulus with an adult hen they found a right eye bias after 11 days. Dharmaretnam & Andrew suggested that the change in bias during the light stimulus test with the chicks provided evidence of the influence of age upon the development of lateralisation. However, the right bias observed in response to the hen suggested that the emotional context of the stimulus may be related to the direction of lateral bias.

Following from Andrew & Brennan (1983) and Dharmaretnam & Andrew (1994) Cantalupo *et al.* (1995) also elicited negative emotional contexts in goldbelly topminnow, *Girardinus falcatus*, but instead by presenting them with a simulated predator with the intention of eliciting an unambiguous fear response. Initially, Cantalupo *et al.* reported a right turn bias, thereby ensuring left eye visual attention towards the fear-inducing stimulus, but with continuing trials the right turn bias became a left turn bias. Cantalupo *et al* proposed that this was due to subjects becoming habituated to the stimulus with the effect of changing the emotional context of the scenario. However, whilst the initial fearful emotional context could be easily identified it is unclear if the change in emotional context due to habituation resulted in an affectively positive context or whether the fish were instead expressing a right eye bias for monitoring behaviour once they had determined there was no imminent threat. As a right eye bias for monitoring behaviour had also previously been observed in guppies (Dugatkin, 1991) it may therefore be difficult to interpret Cantalupo *et al.*'s results as providing support for Silberman & Weingartner's (1986) Valence Hypothesis. Furthermore, Bisazza *et al.* (1997) performed a similar turn bias study with two species of poeciliid fish and reported that goldbelly topminnow and eastern mosquitofish, *Gambusia holbrooki ,*expressed left turn (and thus right eye monitoring) behaviour towards a dummy predator, which seems to further support Dugatkin's study whilst also being incompatible with both Campbell's (1982) and Silberman & Weingartner's (1986) theories.

Perhaps related to the right eye bias for monitoring behaviour reported by Dugatkin (1991), Cantalupo *et al.* (1995) and Bisazza *et al.* (1997), predatory behaviour was found to elicit a right side bias in male cane toads (Vallortigara *et al.*, 1998), green tree frogs (Robins & Rogers, 2006) and black-winged stilts (Ventolini *et al.*, 2005) although determining the emotional context of predatory behaviour (as positive, negative or neutral) and how it can be reconciled with either of Campbell's (1982) or Silberman & Weingartner's (1986) theories for the lateralisation of emotion is unclear. Within the same studies, however, Vallortigara *et al.* and Robins & Rogers also found a left side bias for aggressive behaviour in male cane toads and green tree frogs. As aggression is a negative valence behaviour the results from Vallortigara *et al.* and Robins & Rogers are demonstrative of a right hemisphere bias for this behaviour and are therefore supportive of both Campbell's and Silberman & Weingartner's theories. However, as it is behaviours of a positive emotional valence that differentiate these theories further research is clearly necessitated to compare the validity of each.

Baraud *et al.* (2009) remains the only study thus far to observe the lateralisation of positive, as well as negative, emotional behaviours during naturally occurring interactions and was therefore able to compare the Right Hemisphere Hypothesis and the Valence Hypothesis. Baraud *et al.*'s study was performed in two species of mangabeys and found no differences between the lateralisation of positive and negative emotions within either species but a contrast was instead found between both species as grey-cheeked mangabeys expressed a left side bias whilst red-capped mangabeys instead demonstrated a right side bias. As a consequence, Baraud *et al.*'s observations from one species, the red-capped mangabeys, supported Campbell's (1982) hypothesis however the results from the grey-cheeked mangabeys instead provided no support for either of the established theories for the lateralisation of emotion. It is therefore clear that further systematic examination of the different emotional behaviour categories remains necessary to fully compare the validity of the Right Hemisphere and Valence hypotheses. In addition, though non-human primates have featured prominently in research on the lateralisation of emotion and laterality in general due to the comparative perspective they offer, a less anthropocentric focus may permit a fascinating additional insight into the convergent evolution of hemispheric specialisation and the spotted hyaena provides an ideal out-group for such a study.

Similar to olive baboons, rhesus macaques and many species of cercopithecine primates spotted hyaenas inhabit large multi-male/multi-female groups that demonstrate a complex social hierarchy (Kruuk, 1972). Spotted hyaenas also possess large and highly developed brains, as might be predicted by the social brain hypothesis (Barton & Dunbar, 1997; Dunbar, 1998; Kudo & Dunbar, 2001), and recent studies on spotted hyaenas have demonstrated an aptitude for co-operation and problem-solving on par with the great apes (Drea & Carter, 2009; Benson-Amram & Holekamp, 2012); therein further identifying their similarities with the two primate species included in the previous chapters. In contrast with olive baboons and rhesus macaques, spotted hyaenas are carnivores and maintain their diet primarily through cooperative hunting behaviour that requires a high level of cooperation between group members (Kruuk, 1972; Drea & Carter, 2009; Benson-Amram & Holekamp, 2012). No evidence has been found of cooperative hunting in macaques (Young *et al.*, 2012) and although collective predatory behaviour has been observed in baboons it does not appear to be coordinated to the same degree as that of social carnivores, such as the spotted hyaena, and is instead representative of independent individuals acting simultaneously rather than a group acting cooperatively (Butynski, 1982; Cheney, 1992). As the review by Vallortigara &

Rogers (2005) suggests, lateralised behaviour at the group level may confer a benefit to that group when attempting to coordinate group behaviour therefore it may be interesting to examine whether strong lateral biases are evident in this species rather than in rhesus macaques or olive baboons. Furthermore, Zucca *et al.*'s (2011) research into leading-limb preferences in captive lions, *Panthera leo*, which reported a significant population-level right forelimb bias, remains the only study thus far to investigate lateralisation in a large predator; highlighting how comparatively under-researched large predators are.

Additional to investigating whether emotion is lateralised this study shall also consider whether lateralisation is influenced by a number of factors, namely: age, sex, rank and the emotional intensity of each interaction.

The influence of age upon laterality appears well established in the handedness literature with a number of studies reporting stronger manual preferences in adults than non-adults (*e.g.* Lehman, 1970; 1978; Hopkins, 1994; Westergaard & Suomi, 1993; Vauclair & Fagot, 1987; Vauclair *et al.*, 2005) although the direction of hand preference was not consistent across species. In the non-handedness literature, however, there appears to be little evidence of an age effect upon lateralisation with only Dharmaretnam & Andrew's (1994) study, which found that lateral biases for hatchling chicks viewing a visual stimulus were not established until after two weeks, reporting an ontogenic effect. This contrast in the influence of age between studies of handedness and the rest of the laterality literature is curious and certainly suggests that further study is welcomed. This contrast may also be explained by taxonomical differences between the primates in the handedness studies and the chicks in the turn bias studies, therefore a study on spotted hyaenas may also address this concern.

Although some studies of visual field preferences have examined differences between males and females, these have generally reported no sex differences (Güntürkün & Kischkel, 1992; Gülbetekin *et al.*, 2007; 2009). However, the evidence for sex differences in handedness studies instead suggests that a male/female contrast may exist as Ward *et al.* (1990) found left hand biases in six species of lemur for males but not females whilst Stafford *et al.* (1990) observed right hand biases in female gibbons but not males. Furthermore, several studies have found similar results within a single species as Milliken *et al.* (1989; ring-tailed lemur), Wells (2003; dogs) and Corp & Byrne (2004; chimpanzees) reported left forelimb bias in males but right forelimb bias in females. Milliken *et al.* (1989) and Ward *et al.* (1990) suggested that these observed sex differences may have been caused by testosterone impairing the early development of the left hemisphere and thereby leading to right hemisphere dominance in males. The suggestion that testosterone influences the early development of lateralisation may also prove particularly intriguing for the present study as the level of testosterone produced by female spotted hyaena is equal to that of the males for the first two years after birth (Licht *et al.*, 1992; Glickman *et al.*, 1992, 2006).

Social rank has also been suggested to influence lateralisation as Baraud *et al.* (2009) reported that higher ranked red-capped mangabeys displayed a more pronounced right side bias but only for negative valence behaviour whilst grey-cheeked mangabeys displayed a more pronounced left side bias but only for affiliative behaviour. As Baraud *et al.* remains the only study thus far to consider rank as a factor the interpretation of these results is unclear. Additionally, as Baraud *et al.* based their observations upon two small populations each containing only five individuals it may be interesting to investigate whether a similar pattern emerges from a larger population.

The method employed by this study is similar to that of Baraud *et al.* (2009) by allowing for the comparison of positive, negative and neutral behaviours. Furthermore, a separate category for sexual behaviours is included to allow for the assessment of such interactions (Ventolini *et al.* 2005). An additional consideration will be of the influence of rank upon behavioural laterality as Baraud *et al.* had observed that higher ranked individuals were more actively approached on their left side. Finally, the influence of emotional intensity upon lateral bias shall be considered for the first time in a non-primate study, based upon Sackeim

& Gur’s (1980) observation that emotions were expressed more intensely on the left side of the face it may be predicted that a stronger left side bias exists for higher intensity interactions.

In addition to investigating the lateralisation of emotion, and whether it is influenced by age, sex, rank, valence, and intensity, this study also included three further study measures. Some of the oldest hyaenas kept at the University of California, Berkeley’s Field Station for Behavioral Research were hand-reared (M.L. Weldele, personal communication) and, as such, are accustomed to interacting with humans in an affiliative manner. Consequently, many of the hyaenas directly approach familiar humans (keepers and researchers) by walking towards the fence and presenting their head or neck to be tickled or scratched by the keepers using a long stick that existed for that purpose as a form of enrichment. In the process of doing so the hyaenas often aligned themselves parallel to the fence and so it may be interesting to perform an additional analysis upon whether a lateral preference is expressed during this behaviour. Furthermore, spotted hyaenas perform a number of socially significant solo behaviours that involve a considerable emotional component and an expression of lateral preference. Spotted hyaenas have occasionally been observed to perform scent rubbing behaviour whereby they roll in an odoriferous substance to transfer this substance to their body so as to increase the level of attention received from conspecifics (Drea *et al.*, 2002) but in initiating this roll, the hyaena often starts on one shoulder or the other. Additionally, male spotted hyaenas perform a ‘leg-cross’ behaviour as part of their courtship ritual whereby one forelimb is lifted and positioned across the other, standing forelimb, although the function of this behaviour is not clear (M.L. Weldele, personal communication). As such, the shoulder-roll, leg-cross and stick scratch behaviours may provide an additional insight into the lateralisation of behavioural function in spotted hyaenas.

5.3 | Hypotheses

H_1 All emotion is controlled by the right hemisphere therefore behaviours in all emotional contexts should be lateralised to the left visual hemifield at the group level; thus supporting Campbell's (1982) Right Hemisphere Hypothesis

H_2 Adults should express a stronger left side bias than subadults.

H_3 Males should express a more pronounced left side bias than females.

H_4 Stronger left side lateral biases should be found in higher ranked individuals than low ranked individuals.

H_5 Interactions with high emotional arousal should elicit stronger left side lateral biases than low arousal interactions.

H_6 A significant left side bias should be evident during the solo behaviours.

5.4 | Methods

5.4.1—Observation

All observations were performed from outside the enclosure where the observer had access to three sides of each (four-sided) enclosure as well as additional access to a central elevated platform, thus permitting visible contact with subjects at all times. Observations took place between 8am – 4pm, Monday – Friday over a period of 12 weeks from May to August (excluding specific dates designated by the university, school closures, national holidays etc.).

5.4.1.1—Live Observation

No change was made to the general methodology given in section 2.4 as subjects were selected pseudorandomly and care was taken to ensure no individual was observed more than twice per day or four times within a week. Subjects were then video-recorded for 15 minute focals and all behavioural interactions subsequently observed and noted during coding. With the exception of three individuals housed in a triad, all hyaenas were housed in dyads, thus facilitating easy identification of both the study subject and the conspecific with which they interacted. These dyads were also regularly rotated thus permitting the observation of different pairs of interacting individuals.

5.4.1.2—Archive Observation

The author was also given access to video footage of hyaena behaviours and interactions taken several years previously from the same location. In such instances, the author selected a video at random from the archive and, upon viewing, then selected and identified a subject. A 15 minute focal on this subject was then performed by coding all observations following the same guidelines as detailed in section 2.4.4.

5.4.1.3—Coding Rank

As explained in the introduction, all females are ranked higher than all males in spotted hyaena (Kruuk, 1972) social groupings. Therefore, whilst it may be possible to code all observed spotted hyaenas in a similar method to the olive baboons and rhesus macaques by allocating them one of four social rank categories these ranks would consequently correlate strongly with sex. Furthermore, as the hyaenas were housed in dyads rather than large social groups the identification of each individual interacting with the focal subject was made very simple. As such, for this study species it was decided to assess the rank of the focal subject as relative to the individual with which it interacted, rather than relative to its position within the population as a whole (as per the olive baboons and rhesus macaques). Therefore, in each interaction the focal subject has been coded as dominant or subordinate and the resulting data set has been analysed with rank as a between and within-subjects factor using mixed model analysis.

5.4.2—Preparation of Data Set for Analyses

Upon completion of coding 684 separate interactions had been observed from a total of 24 individuals but when the minimum criterion of seven interactions per individual was applied this data set was reduced to 667 interactions from 15 individuals (interactions per individual: mean=44.5, min=7, max=117; see Appendix A7 for table on number of focals/interactions per individual). As detailed in section 2.6.2 this minimum criterion was also applied when the data from each individual were split for the analyses of interactions rank, emotional intensity and emotional valence, thereby a minimum of seven interactions per subject per subcategory were required, but as a mixed model was used for these analyses if a subject met this criterion for only one subcategory it was still included in analyses. Once these minimum criteria had been applied it was determined that the small number of data points for some individuals may impact the power of the overall analyses and thus the data for each individual were randomly sampled with replacement using 5,000 bootstrap replications (Adams & Anthony, 1996) as per the method explained in Section 2.6.2.before the analyses were performed.

Between-Subjects Comparison			Mixed-Model Comparison		
Age	Subadult	5	Rank	Dominant	9
	Adult	10		Subordinate	9
Sex	Male	6	Intensity	High	15
	Female	9		Low	8
			Valence	Neutral	4
				Negative	7
				Positive	6
				Sexual	12

Table 5.1 | Reporting the number of individual subjects that met the minimum criterion (n≥7 interactions) for each context subcategory.

The number of individual subjects included in analyses for each context has been noted in Table 5.1 with the biological data for all individuals included in analyses reported in Table 5.2 and in Table 5.3 the ethogram of behaviours performed by the spotted hyaena subjects included in analyses has been provided, including the coding of these behaviours in terms of emotional intensity and valence, which was done in collaboration with researchers on-site: M. Weldele, S. Glickman, L. Frank, M. Gardner.

Id	Sex	Rank Group	Dob	Id	Sex	Rank Group	Dob
Cody*	Female	High	24-Mar-92	**2 Notch***	Male	Mid Low	01-Nov-84
Domino	Female	High	04-Aug-95	**Bear***	Male	Mid Low	15-Oct-85
Eyeore*	Female	High	15-Nov-85	**Bramble**	Male	Mid Low	04-Jun-92
Nairobi	Female	High	05-Feb-92	**Gremlin**	Male	Mid Low	15-May-94
Nakuru	Female	High	05-Feb-94	**Gulliver**	Male	Mid Low	15-May-94
Sal*	Female	High	14-Nov-88	**Rocco**	Male	Mid Low	14-Nov-88
BJ	Female	Mid High	22-Dec-96	**Winnie**	Male	Mid Low	27-Jun-94
Zonker	Female	Mid High	07-Jan-92				

Table 5.2 | Detailing the sex, rank and age of each individual included in analyses (*denotes this hyaena was included from archive footage).

Action	Description	Intensity	Valence
Appease	individual moves away from another individual with head down and mouth open: a submissive behaviour	Low	Negative
Avoid	an individual walks/runs away from an approaching individual: a submissive behaviour		
Threaten	individual adapts aggressive posture towards another with head down and tail and mane raised		
Bite	an individual uses their teeth to make/attempt to make physical contact with another: an aggressive behaviour	High	
Chase	an individual may run or trot after an avoiding individual: an aggressive behaviour		
Lick	individual licks the head or body of another individual: an affiliative behaviour	Low	Positive
Nuzzle	individual rubs its muzzle against that of another individual: highly affiliative behaviour	High	
Play	individual, usually infant or subadult, interacts with another and may be observed as jumping, trotting, rolling around, or mock fighting		
Approach	individual walks casually toward another stationary individual displaying no signs of aggression	Low	Neutral
Follow	individual casually walks towards and after another non-stationary individual		
Greet	simultaneous 'present' behaviour by two individuals standing parallel to each other in a head-to-tail fashion	High	Sexual
Inspect	individual closely looks at and/or smells the anogenital region of another		
Mount	individual approaches the back of another and elevates on hindlegs to enact or simulate copulatory behaviour		
Present	individual presents anogenital region to another individual by standing stationary and lifting a hind leg		

Table 5.3 | Ethogram of behaviours included in analyses: detailing the description of each behaviour and its coding as emotional intensity and valence.

5.4.3—Statistical Analyses

5.4.3.1 Testing for Normality

Prior to each analysis, a Kolmogorov-Smironov test was performed on the data to test for normality in the distribution. BLI, ABS and VFP data were all found to be normally distributed for the overall data; BLI: D(15)=0.121, p=0.200; ABS: D(15)=0.175, p-0.200; VFP: extreme left: D(15)=0.210, p=0.074; mid left: D(15)=0.140, p=0.200; centre: D(15)=0.138, p=0.200; mid right: D(15)=0.113, p=0.200; extreme right: D=(15)=0.155, p=0.200). However, when the data were split for valence the data for BLI, ABS and VFP values were not normal therefore nonparametric methods were used for analyses in these instances.

5.4.3.2 Analysis of Binocular Laterality Indexes

BLI values were calculated for each individual and then compared to a predicted value of zero (no lateral bias) using a one-sample t-test to determine whether these individuals were significantly lateralised. A chi-square test was then used to determine whether the number of significantly lateralised individuals was significantly different from chance and therefore if population-level lateralisation was evident.

Mean BLI values for overall population and for each category could then be calculated and these values were also compared to the predicted value of zero (no lateral bias) using a one-sample t-test, except for the valence categories which were compared to the predicted value of zero using a Wilcoxon signed-rank test.

Between-subjects comparisons (*e.g.* age and sex categories) were performed using independent t-tests whilst rank and emotional intensity were analysed using a linear mixed model and emotional valence was analysed using a generalised linear mixed model.

5.4.3.3 Analysis of Absolute Laterality Scores

Once ABS values had been calculated for each individual a median ABS value for the population could then be calculated and this was used as the expected value for all subsequent tests. Median ABS values were then calculated for each category and compared to the expected ABS value using a Wilcoxon signed-rank test. Whilst the overall ABS value were normally distributed, when the data were split for some of the categories (*e.g.* valence) the ABS values were non-normally distributed therefore a median population ABS value was calculated in place of a mean and nonparametric methods were used.

Comparisons within age and sex categories were performed using Mann-Whitney U-tests whilst the influences of rank, emotional intensity and emotional valence were each analysed using generalised linear mixed models.

5.4.3.3 Analysis of Visual Field Proportions

For each of the five visual fields median VFP values were calculated for the overall population and these were then used as the predicted values for subsequent comparisons with each context using a Wilcoxon-signed rank test. A Friedman's test was used for each context to compare each set of five VFP values to determine whether the overall difference between these five values was significant.

Independent samples Mann-Whitney tests were used for between-subjects VFP comparisons (age and sex). Rank, emotional intensity and emotional valence were each compared using a generalised linear mixed model.

5.4.3.3 Overall Mixed Models Analysis

The influence of all factors was then analysed using a single generalised linear mixed model with individual ID set as the random effect and age, sex, rank, emotional intensity and emotional valence set as fixed effects.

5.4.3.5 Additional Data

Whilst the key focus of this study was upon behavioural interactions between conspecifics a number of additional behaviours were observed during coding and these have also been examined for lateral bias. These solo behaviours were: leg crosses, shoulder rolls and stick scratches. Leg crosses form part of the male's courtship ritual whereby, prior to approaching a female to greet and attempt to copulate, the male lifts one foreleg and crosses it over the other foreleg and holds this position for brief a period. The exact function of this behaviour is unclear as it is not always performed in full view of the female and to date no further consideration of this behaviour has been given (M.L. Weldele, personal communication) but as this behaviour created an additional opportunity for observing lateralisation it was included in this section. Shoulder rolls are comparatively better understood and are performed by spotted hyaenas upon discovering a odiferous substance whereby an individual rolls in this substance with the intention of transferring it to its body as this has been found to increase the attractiveness of this individual to other clan members and often brings social benefits (Drea *et al.*, 2002). The final behaviour, stick scratch, was based upon the observer's direct interactions with individuals from the spotted hyaena population using a long wooden stick. A number of the older hyaenas from the colony at the University of California's FSBR were hand reared by the keepers and as such often approach the fence when a familiar person appears in the hope of being scratched or groomed with this behaviour also replicated by the younger hyaenas. Due to the obvious potential danger of directly interacting with spotted hyaenas this was therefore done with complete caution using a 1m long wooden stick, thereby ensuring the keeper/observer did not get too close to the fence. Lateral biases were observed during this behaviour as, upon walking towards the fence, the spotted hyaenas often turned their head or complete body parallel to the fence to be scratched and thus the side presented to the observer was recorded. Following the standard set elsewhere in this thesis a minimum of seven interactions per individual ($n \geq 7$) were required for inclusion in analyses and the occurrence of left *vs.* right side preferences was analysed by calculating a Laterality Index to determine sidedness, using the same formula as the Binocular Laterality Index (no centrally occurring behaviours were observed), and a chi-square analysis to determine whether this was significant, with the expected value for each case being the mean number of interactions observed on the left and right.

5.5 | Results

5.5.1—Binocular Laterality Indexes and Absolute Laterality Scores

The mean LI for this population was -0.185 (SE=0.065) and a one-sample t-test determined that this overall bias was significantly different from a test value of 0 (no bias): t(14)=-2.845, p=0.013 (Pearson's r=0.605). Although the overall ABS data were normally distributed, when they were split for the different categories the data were not normally distributed for all of the valence categories. As a population average ABS value was to be used as the predicted value of ABS for all comparisons it has therefore been calculated as a mean (M=0.303, SE=0.063) for all parametric tests and as a median (MDN=0.205, IQR=0.06-0.395) for the nonparametric tests involving emotional valence.

At the individual level, five of the 15 subjects were significantly lateralised with all five expressing a left side bias: Bear: BLI=-0.400, t(119)=-5.949, p<0.001 (Pearson's r=-0.479); BJ: BLI=-0.214, t(95)=-2.123, p=0.036 (Pearson's r=-0.213); Cody: BLI=-0.786, t(6)=-5.998, p=0.001 (Pearson's r=-0.926); Nakuru: BLI=-0.268, t(27)=-2.727, p=0.011 (Pearson's r=-0.465); and Sal: BLI=-0.395, t(18)=-2.727, p=0.014 (Pearson's r=- 0.541), whilst the remaining subjects were not significantly lateralised (see Table 5.4 for the BLI values of all individuals; these values have also been plotted in Figure 5.5). A chi-square analysis reveals this population was significantly not lateralised $X^2(2)=10.00$, p=0.007 (Pearson's r=0.877).

ID	Original	BLI	*p*	*r*	Lateralised
2 Notch	-0.182	-0.205	0.186	-0.286	-
Bear	-0.392	-0.400	0.000	-0.479	Left
BJ	-0.208	-0.214	0.036	-0.213	Left
Bramble	-0.026	-0.066	0.872	-0.027	-
Cody	-0.857	-0.786	0.001	-0.926	Left
Domino	0.089	0.099	0.831	0.021	-
Eyeore	0.111	0.056	0.057	0.444	-
Gremlin	-0.043	-0.065	0.525	-0.137	-
Gulliver	-0.100	-0.150	0.343	-0.316	-
Nairobi	-0.429	-0.429	0.263	-0.309	-
Nakuru	-0.250	-0.268	0.011	-0.463	Left
Rocco	-0.009	-0.018	0.841	0.019	-
Sal	-0.421	-0.395	0.014	-0.541	Left
Winnie	0.300	0.233	0.071	0.329	-
Zonker	-0.171	-0.171	0.160	-0.239	-

Table 5.4 | Reporting the non-bootstrapped BLI values (original), bootstrapped BLI values (BLI), and the significance (p) and effect size (r) for each individual BLI value. The final column notes which individuals were significantly lateralised.

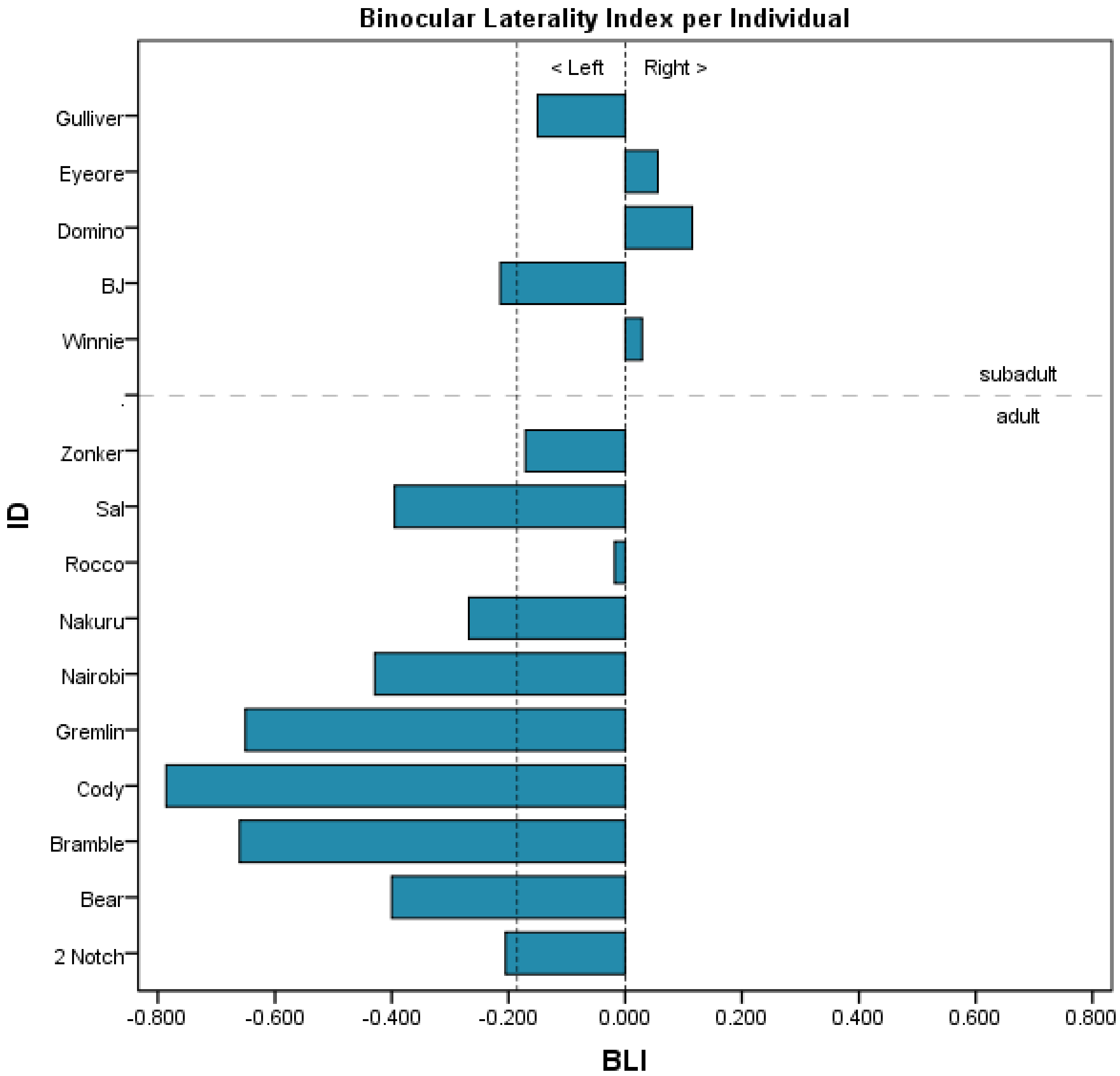

Figure 5.5 | Showing the BLI value for each individual included in analyses. The dashed horizontal line denotes the division between subadults and adults whilst the dashed vertical line illustrates the population mean BLI (-0.185).

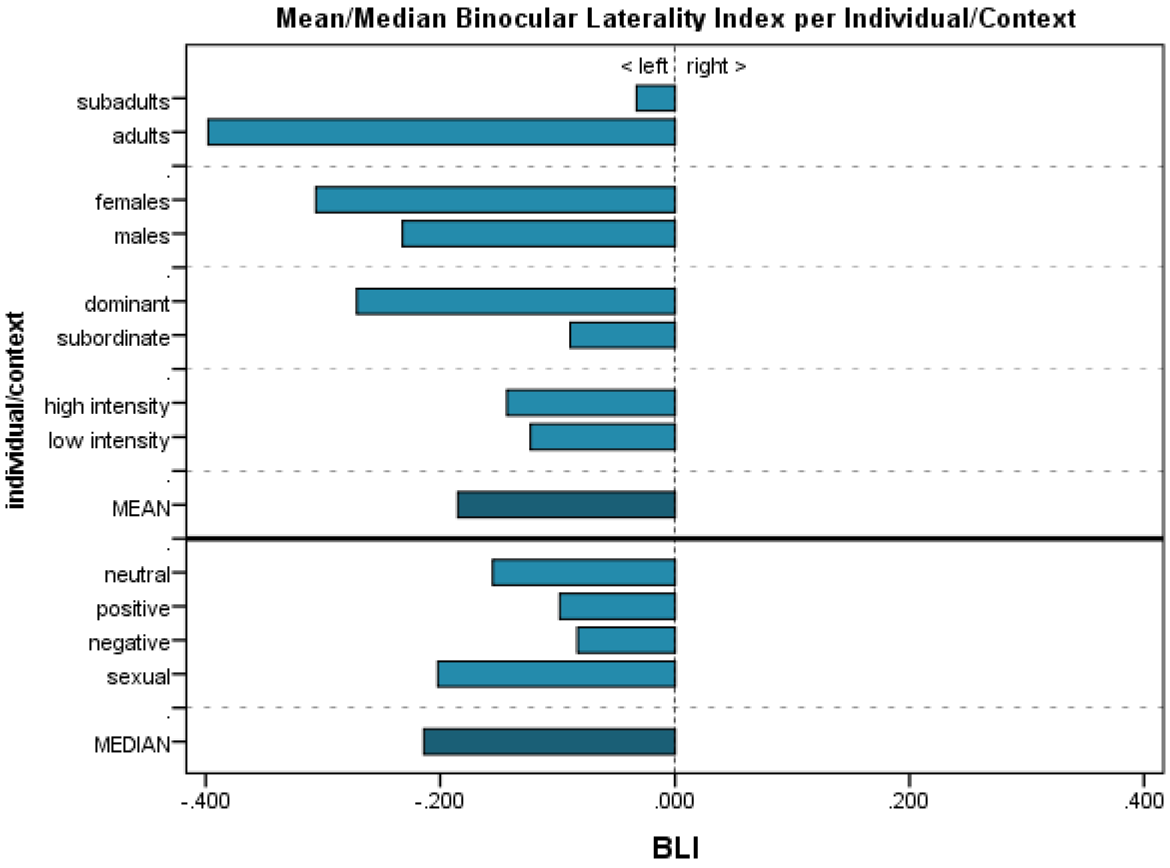

Figure 5.6 | Showing the mean BLI values for the age, sex, rank and emotional intensity contexts with the mean population BLI value shown for comparison. As the valence categories were analysed using nonparametric methods the median BLI values for each have been provided below the solid horizontal line with the median population BLI value shown at the bottom.

context		M	SE		p	r
age	subadults	-0.033	0.063		0.632	-0.251
	adults	**-0.398**	**0.077**		**0.001**	**-0.865**
sex	males	-0.232	0.104		0.076	-0.707
	females	**-0.306**	**0.1**		**0.015**	**-0.715**
rank	**dominant**	**-0.271**	**0.089**		**0.016**	**-0.76**
	subordinate	-0.089	0.075		0.268	-0.388
intensity	**high**	**-0.143**	**0.061**		**0.034**	**-0.518**
	low	-0.123	0.105		0.278	-0.406
overall		**-0.185**	**0.065**		**0.013**	**0.605**
context		**MDN**	**IQR**		**p**	**r**
valence	neutral	-0.155	-0.383	-0.067	0.068	-0.913
	negative	-0.083	-0.294	0.043	0.116	-0.594
	positive	-0.098	-0.228	0.093	0.249	-0.471
	sexual	**-0.202**	**-0.399**	**0.042**	**0.033**	**-0.616**
overall		-0.214	-0.429	-0.018	-	

Table 5.7 | Showing the mean, standard error (SE), statistical significance (p; significant values in bold font) and effect size (Pearson's r) for each context subcategory. Error bars could not be included in Figure 5.6 as this graph was constructed from separately calculated figures and not directly from the main data set but the inclusion of the SE values provide the corresponding information in more detail.

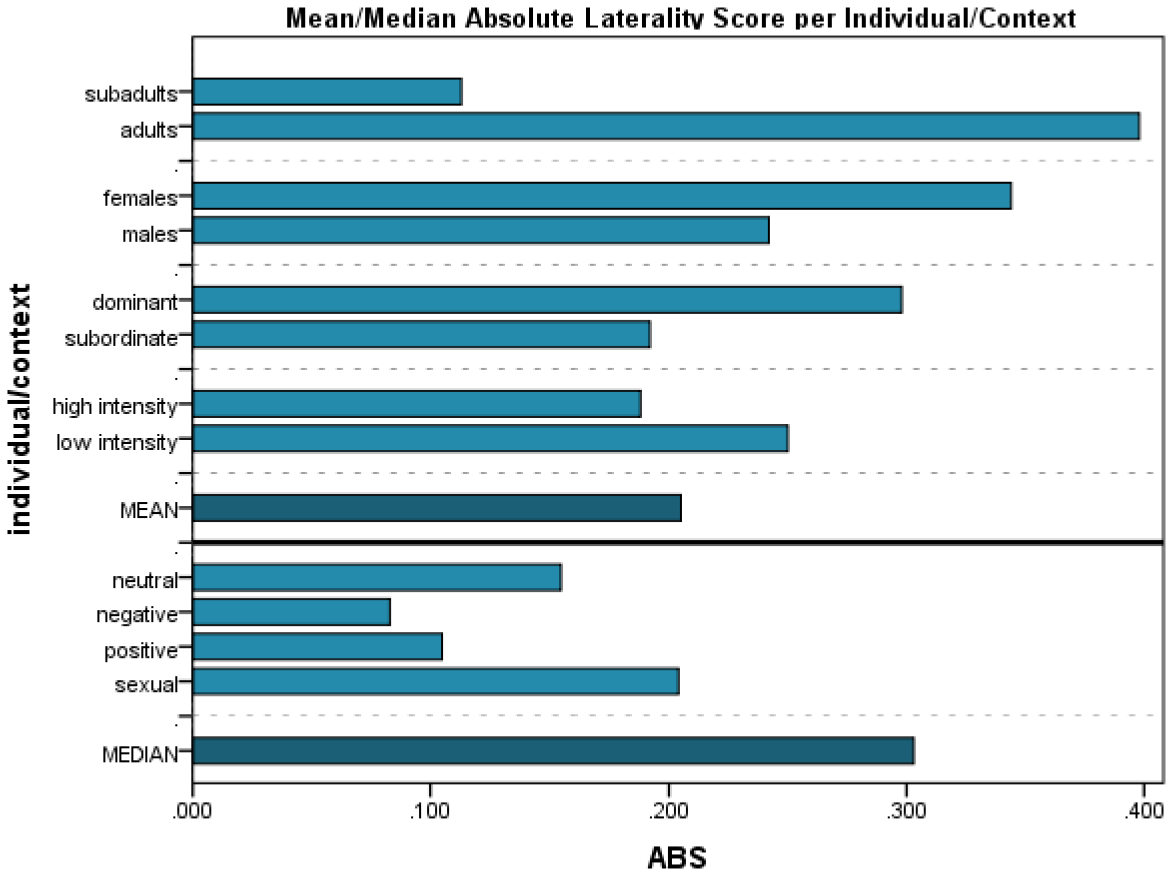

Figure 5.8 | Showing the mean ABS values for the age, sex, rank and emotional intensity contexts with the mean population ABS value shown for comparison. As the valence categories were analysed using nonparametric methods the median ABS values for each have been provided below the solid horizontal line with the median population ABS value shown at the bottom.

context		MEAN	SE		p	r
age	adults	0.398	0.077		0.248	0.381
	subadults	**0.113**	**0.033**		**0.005**	**0.932**
sex	males	0.242	0.099		0.567	0.212
	females	0.344	0.083		0.635	0.162
rank	dominant	0.298	0.077		0.061	0.022
	subordinate	**0.192**	**0.044**		**0.036**	**0.664**
intensity	**high**	**0.188**	**0.051**		**0.042**	**0.664**
	low	0.25	0.065		0.44	0.022
overall		0.303	0.063		-	
context		**MEDIAN**	**IQR**		**p**	**r**
valence	neutral	0.155	0.067	0.383	0.273	0.548
	negative	0.083	0.043	0.294	0.063	0.703
	positive	**0.105**	**0.089**	**0.228**	**0.028**	**-0.899**
	sexual	0.204	0.084	0.399	0.239	-0.34
overall		0.205	0.06	0.395	-	

Table 5.9 | Showing the mean/median, interquartile range (IQR), statistical significance (p; significant values in bold font) and effect size (Pearson's r) for each context subcategory. Similar to Figure 5.6 error bars could not be included in Figure 3.8 but SE values have been provided here accordingly.

5.5.1.1 BLI and ABS data by Age

When split by age the data were normally distributed for subadults (D(5)=0.269, p=0.200) and adults (D(10)=0.150, p=0.200). No significant directional bias was observed for subadults (M=-0.033, SE=0.063, *t*(4)=-0.518, *p*=0.632, Pearson's r=-0.251), but a significant left side bias was found for adults (M=-0.398, SE= 0.077, *t*(9)=-5.171, *p*= 0.001, Pearson's r=0.865) and a significant difference was found between these age groups (*t*(13)= -3.070, *p*= 0.009, Pearson's r=0.865).

When the ABS data were split into each age categories they were also found to be normally distributed; subadult: D(5)=0.179, p=0.200; adult: D(10)=0.150, p=0.200. No significant difference from the expected value was found for adults (M= 0.398, SE= 0.077, t(9)=1.236, p=0.248, Pearson's r=0.381) but a significantly weaker strength bias was found for subadults (M= 0.113, SE= 0.033, t(5)=-5.751, p= 0.005 (Pearson's r= 0.932) and a significant difference in ABS values was observed between these age categories: t(13)=2.520, p= 0.026 (Pearson's r=0.573).

5.5.1.2 BLI and ABS data by Sex

When split by sex the data were normally distributed for males (D(6)=0.209, p=0.200) and females (D(9)=0.118, p=0.200). No significant directional bias was observed for males (M=-0.232, SE=0.104, *t*(5)=-2.235, *p*=0.076, Pearson's r=-0.707), but a significant left side bias was found for females (M=-0.306, SE= 0.100, *t*(9)=-3.068, *p*= 0.015, Pearson's r=0.715). No significant difference was found between these sex categories (*t*(13)=0.493, *p*= 0.630, Pearson's r=0.135).

When the ABS data were split by sex they were also found to be normally distributed; males: D(5)=0.227, p=0.200; females: D(10)=0.175, p=0.200. No significant difference from the expected value was found for males (M= 0.242, SE= 0.099, t(6)=-0.613, p=0.567, Pearson's r=0.212) or for females (M= 0.344, SE= 0.083, t(9)=0.493, p=0.635, Pearson's r= 0.162) and no significant difference in ABS values was observed between these sex categories: t(13)=-0.783, p=0.447 (Pearson's r=0.212).

5.5.1.3 BLI and ABS data by Rank

When the BLI data were split for both of the rank categories normal distribution was observed for dominant (D(9)=0.171, p=0.200) and subordinate categories (D(9)=0.154, p=0.200). The mean BLI value for dominant individuals was found to be significantly lateralised to the left: M=-0.271, SE=0.089, t(8)=-3.306, p=0.016, Pearson's r=0.760; but no significant lateralisation was found for the subordinate rank category: M=-0.089, SE=0.075, t(8)=-1.190, p=0.268, Pearson's r=0.388). When these ranks were compared using a linear mixed model, no significant difference was observed: F(1,11.92)=1.481, p=0.247, ICC=0.396)

The ABS data were also normally distributed when split by rank; subordinate: D(9)=0.164, p=0.200; dominant: D(9)=0.219, p=0.200. The subordinate category reported a significantly weaker lateral bias than expected (M=0.192, SE=0.044, t(8)=-2.512, p=0.036, Pearson's r=0.664) whilst there was no significant difference observed for the dominant rank category (M=0.298, SE=0.077, t(8)=-0.061, p=0.953, Pearson's r=0.022) and no significant difference was observed between these rank categories: F(1,4.61)=0.736, p=0.433, ICC=0.583.

5.5.1.4 BLI and ABS data by Emotional Intensity

Dividing the data into the two categories of emotional intensity revealed normal distribution for low (D(8)=0.245, p=0.171) and high intensities (D(15)=0.177, p=0.200). The mean BLI value for high intensity interactions was found to be significantly lateralised to the left: M=-0.143, SE=0.061, t(15)=-2.344, p=0.034, Pearson's r=-0.518; but no significant lateralisation was found for the low intensity category: M=-0.123, SE=0.105, t(7)=-1.175, p=0.278, Pearson's r=-0.406). When both emotional intensity categories were compared using a linear mixed model, no significant difference was observed: F(1,8.25)=0.004, p=0.951, ICC=0.554)

The ABS data were also normally distributed when divided by emotional intensity; low: D(8)=0.173, p=0.200; high: D(15)=0.210, p=0.074. The high intensity interactions category returned a significantly weaker lateral bias than expected (M=0.188, SE=0.051, t(14)=-2.242, p=0.042, Pearson's r=0.664) whilst there was no significant difference observed for the low intensity category (M=0.250, SE=0.065, t(7)=-0.818, p=0.440, Pearson's r=0.022) and no significant difference was observed between these categories of emotional intensity: F(1,6.68)=2.048, p=0.197, ICC=0.670.

5.5.1.5 BLI and ABS data by Emotional Valence

When the BLI values were split into each of the four valence categories they were found to be normally distributed for three of the four valences; negative: D(7)=0.218, p=0.200; positive: D(6)=0.203, p=0.200; and sexual: D(12)=0.105, p=0.200; whilst there were insufficient data points (only four) to conduct a Kolmogorov-Smirnov test on the neutral valence category but as the kurtosis (2.614, SE=2.619) and skewness (-1.426, SE=1.014) values for negative valence behaviours were suggestive of non-normal distribution for the neutral valence data, nonparametric methods were used for comparisons. A significant left side bias was observed for the sexual valence category: MDN=-0.202, IQR=-0.399- +0.042 ,W(12)=9.00, Z=-2.134, p=0.033, Pearson's r=-0.616; but no other significant lateral biases were observed; negative: MDN=-0.083, IQR=-0.294- +0.043 , W(7)=3.00, Z=-1.572, p=0.116, Pearson's r=-0.594; positive: MDN=-0.098, IQR=-0.228-+0.093, W(6)=5.00, Z=-1.153, p=0.249, Pearson's r=-0.471; neutral: MDN=-0.155, IQR=-0.383- -0.067, W(4)=0.00, Z=-1.826, p=0.068, Pearson's r=0.913. A generalised linear mixed model found no significant overall effect of valence upon lateral bias: F(3,25)=0.632, p=0.601, ICC=0.40.

Splitting the ABS data set by valence revealed that the data for the sexual (D(12)=0.177, p=0.200) and negative valence (D(7)=0.275, p=0.119) were normally distributed whilst the data for the positive valence category were not normally distributed (D(6)=0.334, p=0.035. There were insufficient data points from the neutral valence category but calculation of kurtosis (2.614, SE=2.619) and skewness (1.282, SE=1.741) suggest that these data were not normally distributed and therefore nonparametric methods have been used. A significantly weaker bias than expected ABS value was found for positive valence behaviours (MDN=0.105, IQR=0.089-0.228, W(6)=0.00, Z=-2.201, p=0.028, Pearson's r=-0.899) but no other significant differences were observed; sexual: MDN=0.204, IQR=0.084-0.399, W(12)=24.00, Z=-1.177, p=0.239, Pearson's r=-0.340; negative: MDN=0.083, IQR=0.043-0.294, W(7)=3.00, Z=-1.859, p=0.063, Pearson's r=0.703; neutral: MDN=0.155, IQR=0.067-0.383, W(4)=2.00, Z=-1.095, p=0.273, Pearson's r=0.548. No significant overall effect of valence was found: F(3,25)=0.696, p=0.563, ICC=0.286.

5.5.2—Visual Field Proportions Overall

Once VFP values had been calculated for each individual subject it was possible to calculate the overall population average. As reported in section 5.4.3.1 the overall population VFP data were normally distributed, however when the data were split into categores all VFP values were not normally distributed therefore median population values have been calculated for each visual field to be used as the predicted variables for subsequent comparisons; extreme left: MDN=20.00%, IQR=12.50-28.57%; mid left: MDN=30.00%, IQR=23.53-39.13%; centre: MDN=10.00%, IQR=8.57-12.50%; mid right: MDN=22.73%, IQR=15.79-35.38%; extreme right: MDN=10.00%, IQR=0.00-18.46% and these values have been plotted in Figure 5.10. A significant overall difference was found between these VFP values: X^2(4)=25.572, p<0.001, Kendall's W=0.426.

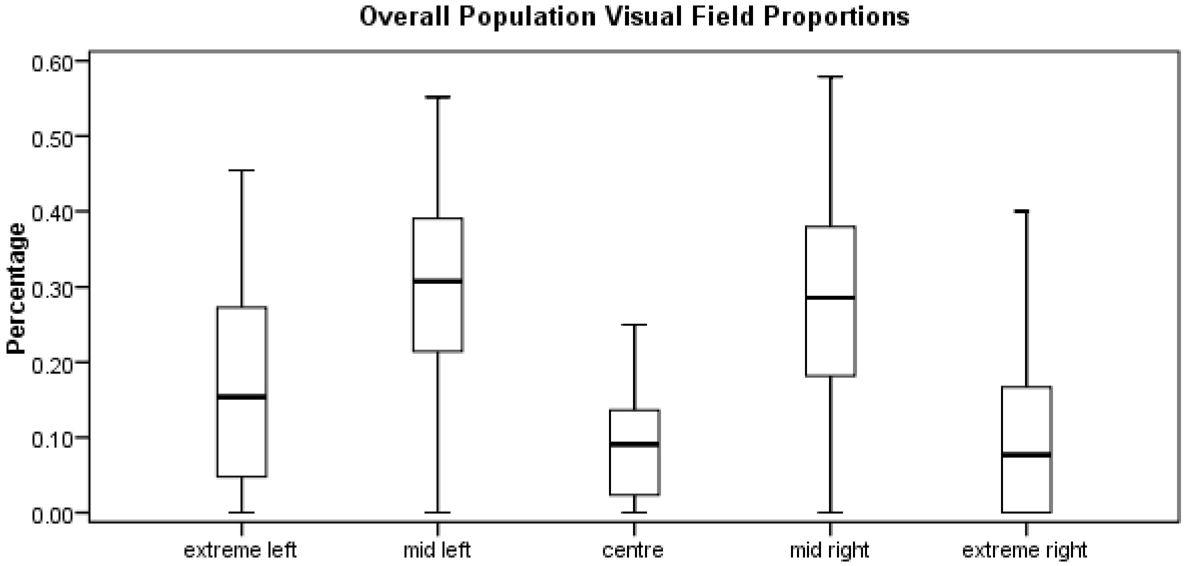

Figure 5.10 | Showing the population median VFP values for the five visual fields for the population (n=15)

5.5.2.1 Visual Field Proportions and Age

Dividing the data into each age category revealed that the data were normally distributed for subadults (extreme left: D(5)=0.274, p=0.200; mid left: D(5)=0.217, p=0.200; centre: D(5)=0.224, p=0.200; mid right: D(5)=0.184, p=0.200; extreme right: D(5)=0.229, p=0.200) but for adults the VFP data were not normally distributed for the extreme left (D(10)=0.296, p=0.013) although they were normal for the remaining visual fields (mid left: D(10)=0.121, p=0.200; centre: D(10)=0.222, p=0.178; mid right: D(10)=0.194, p=0.200; extreme right: D(10)=0.177, p=0.200).

No significant overall difference was observed between the five VFP values for subadults ($X^2(4)=6.779$, p=0.148, Kendall's W=0.339) and no significant differences between the observed and predicted VFP values were found; extreme left: MDN=12.50%, IQR=9.73-26.67%, W(5)=4.00, Z=-0.365, p=0.715, Pearson's r=-0.163; mid left: MDN=30.00%, IQR=14.54-36.21%, W(5)=4.00, Z=-0.365, p=0.715, Pearson's r=-0.163; centre: MDN=11.11%, IQR=8.85-15.08%, W(5)=8.00, Z=1.095, p=0.490, Pearson's r=-0.059; mid right: MDN=30.00%, IQR=18.58-41.22%, W(5)=12.00, Z=1.214, p=0.225, Pearson's r=0.543; extreme right: MDN=10.00%, IQR=3.65-28.68%, W(5)=6.00, Z=0.365, p=0.715, Pearson's r=0.163.

For adults the overall difference between the five VFP values was significant ($X^2(4)=22.968$, p<0.001, Kendall's W=0.574) but none of the VFP values differed from expected; extreme left: MDN=24.28%, IQR=15.16-34.59%, W(10)=38.00, Z=1.071, p=0.284, Pearson's r=0.479; mid left: MDN=30.91%, IQR=23.23-39.14%, W(10)=25.00, Z=0.296, p=0.767, Pearson's r=0.132; centre: MDN=9.13%, IQR=7.74-11.61%, W(10)=14.00, Z=-1.008, p=0.314, Pearson's r=-0.451; mid right: MDN=20.30%, IQR=14.52-33.37%, W(10)=24.00, Z=-0.357, p=0.074, Pearson's r=-0.160; extreme right: MDN=8.60%, IQR=0.00-15.92%, W(10)=25.00, Z=-0.205, p=0.837, Pearson's r=-0.092.

Comparison of the VFP values for subadults and adults within each visual field also revealed no significant effect of age was observed; extreme left: U=14.00, Z=-1.348, p=0.178, Pearson's r=-0.348; mid left: U=20.50, Z=-0.552, p=0.594, Pearson's r=-0.143; centre: U=15.50, Z=-1.166, p=0.254, Pearson's r=-0.301; mid right: U=15.50, Z=-1.165, p=-0.301, Pearson's r=-0.301; extreme right: U=20.500, Z=-0.556, p=0.578, Pearson's r=-0.144). The median VFP values for both age categories have been shown in Figure 5.12.

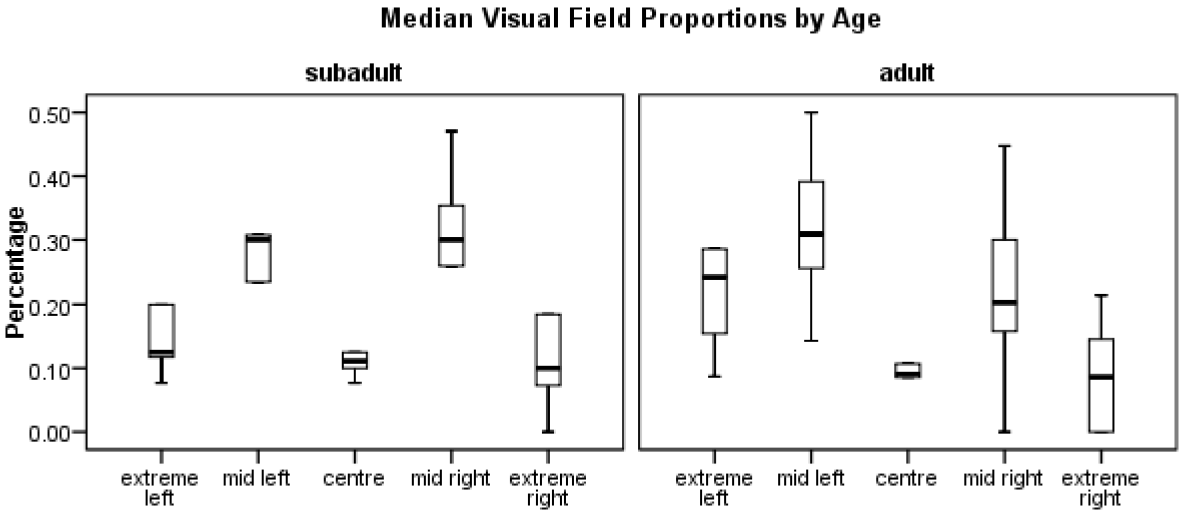

Figure 5.11 | Showing the median VFP values for subadult (n=5) and adult (n=9) subjects.

5.5.2.2 Visual Field Proportions and Sex

When split by sex, the VFP data for females were found to be normally distributed (extreme left: D(9)=0.204, p=0.200; mid left: D(9)=0.130, p=0.200; centre: D(9)=0.158, p=0.200; mid right: D(9)=0.146, p=0.200; extreme right: D(9)=0.150, p=0.200) but for males the VFP data were not all normally distributed (extreme left: D(6)=0.153, p=0.200; mid left: D(6)=0.206, p=0.200; centre: D(6)=0.422, p=0.001; mid right: D(6)=0.241, p=0.200; extreme right: D(6)=0.211, p=0.200).

There was a significant overall difference between the five VFP values for females ($X^2(4)=10.471$, p=0.033, Kendall's W=0.291) although no significant differences between the observed and predicted VFP values were found; extreme left: MDN=28.87%, IQR=13.40-42.98%, W(9)=33.00, Z=1.245, p=0.213, Pearson's r=0.415; mid left: MDN=28.57%, IQR=15.04-37.94%, W(9)=17.00, Z=-0.652, p=0.515, Pearson's r=-0.217; centre: MDN=10.71%, IQR=6.48-13.40%, W(9)=21.00, Z=-0.178, p=0.859, Pearson's r=-0.059; mid right: MDN=17.14%, IQR=10.91-30.71%, W(9)=17.00, Z=-0.652, p=0.515, Pearson's r=-0.217; extreme right: MDN=10.53%, IQR=1.32-20.71%, W(9)=28.00, Z=0.654, p=0.513, Pearson's r=0.218.

For males the overall difference between the five VFP values was also significant ($X^2(4)=19.235$, p=0.001, Kendall's W=0.801) but none of the VFP values differed from expected; extreme left: MDN=17.72%, IQR=11.00-23.51%, W(6)=4.00, Z=-0.944, p=0.345, Pearson's r=-0.385; mid left: MDN=30.91%, IQR=28.38-39.14%, W(6)=8.00, Z=1.095, p=0.273, Pearson's r=0.447; centre: MDN=9.59%, IQR=8.99-11.91%, W(6)=4.00, Z=-0.365, p=0.715, Pearson's r=0.149; mid right: MDN=30.00%, IQR=21.84-44.37%, W(6)=19.00, Z=1.787, p=0.074, Pearson's r=0.730; extreme right: MDN=8.35%, IQR=0.00-13.87%, W(6)=5.00, Z=-0.677, p=0.498, Pearson's r=-0.276.

Comparison of the VFP values for males and females within each visual field also revealed no significant effect of sex was observed; extreme left: U=17.00, Z=-1.180, p=0.238, Pearson's r=-0.305; mid left: U=21.00, Z=-0.708, p=0.479, Pearson's r=-0.183; centre: U=25.00, Z=-0.236, p=0.813, Pearson's r=0.061; mid right: U=12.00, Z=-1.769, p=0.077, Pearson's r=-0.457; extreme right: U=19.00, Z=-0.951, p=0.341, Pearson's r=-0.246). The median VFP values for each sex category have been plotted in Figure 5.11.

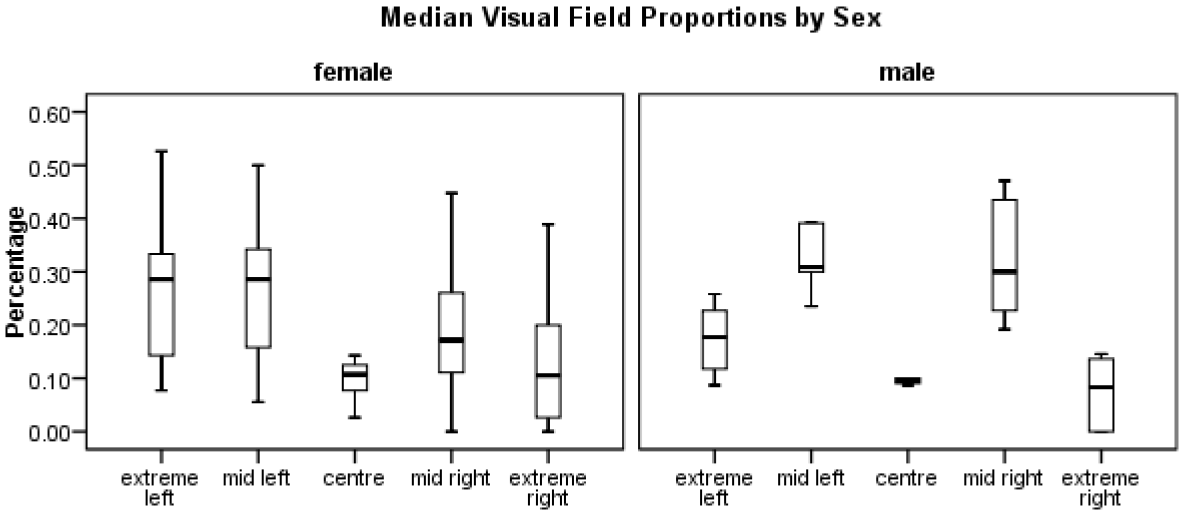

Figure 5.12 | Showing the median VFP values for males (n=6) and females (n=9).

5.5.2.3 Visual Field Proportions and Rank

When the VFP data were split by rank category they were not normally distributed for subordinate individuals in the central visual field (D(9)=0.290, p=0.028) but were normally distributed for the remaining four visual fields; extreme left: D(9)=0.229, p=0.200; mid left: D(9)=0.229, p=0.193; mid right: D(9)=0.200, p=0.200; extreme right: D(9)=0.161, p=0.200). For dominant individuals the VFP data were not normally distributed for the extreme left (D(9)=0.325, p=0.007) but they were normal for the remaining visual fields (mid left: D(9)=0.155, p=0.200; centre: D(9)=0.173, p=0.200; mid right: D(9)=0.161, p=0.200; extreme right: D(9)=0.269, p=0.059).

A significant overall difference was observed between the five VFP values for subordinate individuals ($X^2(4)=17.195$, p=0.002, Kendall's W=0.478) but no significant differences between the observed and predicted VFP values were found; extreme left: MDN=15.79%, IQR=7.69-37.22%, W(9)=21.00, Z=-0.178, p=0.859, Pearson's r=-0.163; mid left: MDN=30.00%, IQR=16.23-36.00%, W(9)=13.00, Z=-0.700, p=0.484, Pearson's r=-0.163; centre: MDN=10.00%, IQR=6.98-11.37%, W(9)=13.00, Z=-0.169, p=0.866, Pearson's r=-0.059; mid right: MDN=30.00%, IQR=19.45-44.11%, W(9)=36.00, Z=1.599, p=0.110, Pearson's r=0.543; extreme right: MDN=10.53%, IQR=2.98-16.58%, W(9)=23.50, Z=0.119, p=0.906, Pearson's r=0.163.

For the dominant category the overall difference between the five VFP values was significant ($X^2(4)=14.337$, p=0.006, Kendall’s W=0.574) but none of the VFP values differed from expected; extreme left: MDN=28.57%, IQR=13.40-30.26%, W(9)=30.00, Z=1.684, p=0.092, Pearson’s r=0.479; mid left: MDN=28.57%, IQR=17.32-42.50%, W(9)=17.00, Z=-0.140, p=0.767, Pearson’s r=0.132; centre: MDN=10.71%, IQR=5.98-13.40%, W(9)=19.00, Z=0.140, p=0.888, Pearson’s r=-0.451; mid right: MDN=20.00%, IQR=5.36-28.02%, W(9)=14.00, Z=-1.008, p=0.314, Pearson’s r=-0.160; extreme right: MDN=10.00%, IQR=1.67-20.72%, W(10)=22.00, Z=0.563, p=0.574, Pearson’s r=-0.092. The median VFP values have been plotted for each rank category in Figure 5.13.

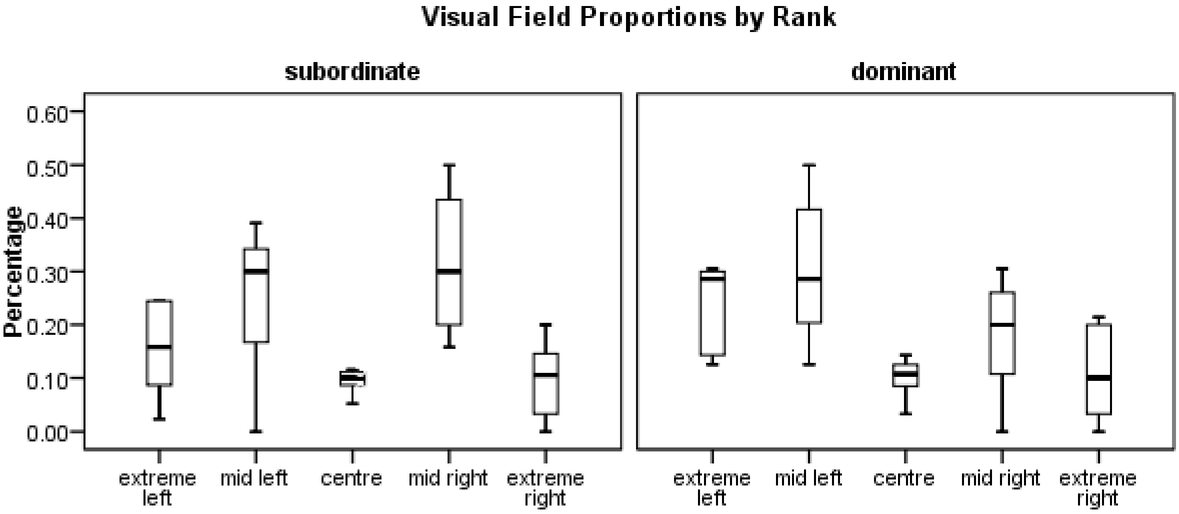

Figure 5.13 | Comparing the median VFP values for dominant (n=9) and subordinate (n=9) individuals.

5.5.2.4 Visual Field Proportions and Emotional Intensity

Separating the VFP data into each category of emotional intensity revealed they were not normally distributed in the right mid visual field (D(8)=0.317, p=0.018) but were normally distributed for the remaining four visual fields; extreme left: D(8)=0.258, p=0.127; mid left: D(8)=0.194, p=0.200; centre: D(8)=0.231, p=0.200; extreme right: D(8)=0.276, p=0.072). For dominant individuals the VFP data were normally distributed for all five visual fields; extreme left (D(15)=0.208, p=0.080; mid left: D(15)=0.127, p=0.200; centre: D(15)=0.147, p=0.200; mid right: D(15)=0.136, p=0.200; extreme right: D(15)=0.174, p=0.200).

A significant overall difference was observed between the five VFP values for low intensity interactions ($X^2(4)=9.854$, p=0.043, Kendall's W=0.308) but no significant differences between the observed and predicted VFP values were found; extreme left: MDN=17.51%, IQR=8.31-22.87%, W(8)=13.00, Z=-0.700, p=0.484, Pearson's r=-0.247; mid left: MDN=34.85%, IQR=15.71-46.24%, W(8)=19.00, Z=0.140, p=0.889, Pearson's r=0.049; centre: MDN=9.30%, IQR=0.00-11.35%, W(8)=14.00, Z=-0.563, p=0.574, Pearson's r=-0.199; mid right: MDN=31.52%, IQR=23.80-34.25%, W(8)=29.00, Z=1.542, p=0.123, Pearson's r=0.545; extreme right: MDN=4.06%, IQR=0.00-27.73%, W(8)=16.00, Z=-0.281, p=0.778, Pearson's r=0.099.

For the high intensity interactions the overall difference between the five VFP values was also significant ($X^2(4)=22.958$, p<0.001, Kendall's W=0.383) but none of the VFP values significantly differed from expected; extreme left: MDN=22.22%, IQR=13.11-31.25%, W(15)=65.00, Z=0.785, p=0.433, Pearson's r=0.203; mid left: MDN=24.72%, IQR=21.05-36.17%, W(15)=39.00, Z=-1.193, p=0.233, Pearson's r=-0.308; centre: MDN=10.00%, IQR=7.87-13.11%, W(15)=62.00, Z=0.597, p=0.551, Pearson's r=0.142; mid right: MDN=22.95%, IQR=15.38-35.96%, W(15)=69.00, Z=0.511, p=0.609, Pearson's r=0.132; extreme right: MDN=11.11%, IQR=0.00-18.18%, W(15)=63.00, Z=0.171, p=0.864, Pearson's r=0.044.

Comparison of each of the VFP values for low and high intensity categories found no effect of emotional intensity; extreme left: F(1,21)=0.841, p=0.370, ICC<0.001; mid left: F(1,21)=0.357, p=0.556, ICC=0.429; centre: F(1,21)=1.774, p=0.197, ICC=0.154; mid right: F(1,21)=0.469, p=0.501, ICC=0.500; extreme right: F(1,21)=0.003, p=0.954, ICC=0.500. The median VFP values for both emotional intensities have been shown in Figure 5.14.

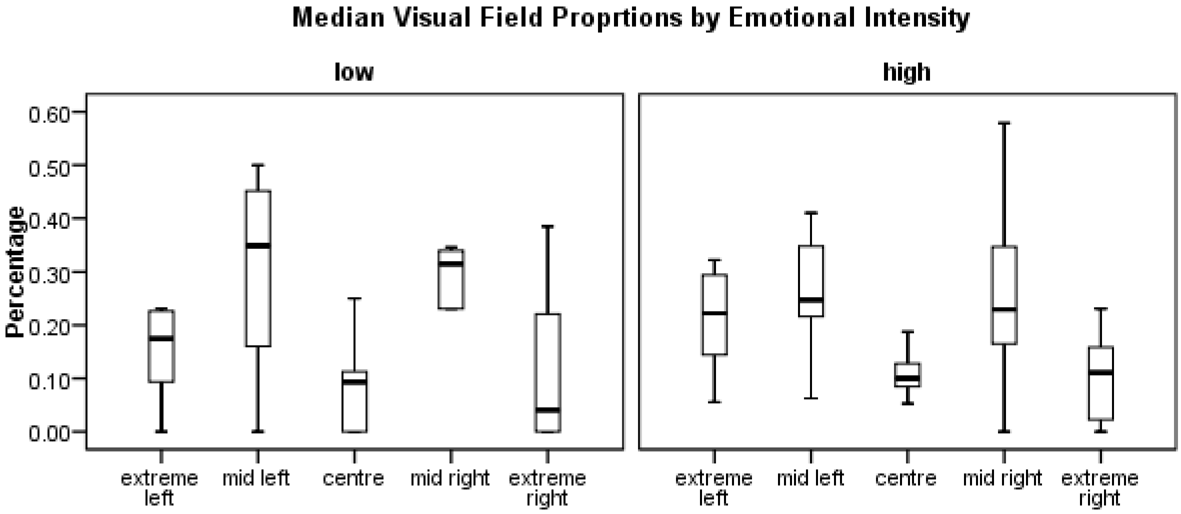

Figure 5.14 | Showing the median VFP values for high (n=15) and low (n=8) intensity interactions.

5.5.2.5 Visual Field Proportions and Emotional Valence

When the VFP data were split into the four valence categories only the negative valence data were normally distributed in all five visual fields; extreme left: D(7)=0.298, p=0.060; mid left: D(7)=0.202, p=0.200; centre: D(7)=0.262, p=0.159, mid right: D(7)=0.264, p=0.149, extreme right: D(7)=0.220, p=0.200. Sexual valence VFP data were not normally distributed for the mid right visual field (D(12)=0.285, p=0.008) but were normally distributed for the remaining four visual fields; extreme left: D(12)=0.238, p=0.058; mid left: D(12)=0.139, p=0.200; centre: D(12)=0.164, p=0.200; extreme right: D(12)=0.145, p=0.200; whilst positive valence VFP data were not normally distributed for the extreme right visual field (D(6)=0.358, p=0.016) but were normal for the other four visual fields; extreme left: D(6)=0.275, p=0.174; mid left: D(6)=0.157, p=0.200; centre: D(6)=0.313, p=0.067; mid right: D(6)=0.173, p=0.200. As only four data points were recorded for neutral valence behaviours Kolmogorov-Smirnov statistics could not be calculated but the kurtosis (k) and skewness (s) data for suggest that at least three of the five VFP values were not normally distributed; extreme left: k=3.352 (SE=2.619), s=1.831 (SE=1.014); mid left: k=1.594 (SE=2.619), s=1.083 (SE=1.014); centre: k=-0.037 (SE=2.619), s=0.514 (SE=1.014); mid right: k=0.591 (SE=2.619), s=-0.851 (SE=1.014); extreme right: k=4.000 (SE=2.619), s=2.000 (SE=1.014).

A significant overall difference was observed between the five VFP values for sexual valence behaviours (X^2(4)=14.521, p=0.006, Kendall's W=0.303) and a significantly higher VFP value was found for the extreme left visual field (MDN=26.30%, IQR=17.40-34.61%, W(12)=64.00, Z=1.962, p=0.050, Pearson's r=0.566) whilst a significantly lower than predicted VFP value was found for the central visual field (centre: MDN=9.72%, IQR=5.73-13.22%, W(12)=0.00, Z=-3.062, p=0.002, Pearson's r=-0.884) but no other significant differences were observed in the remaining visual fields; mid left: MDN=25.43%, IQR=11.69-33.21%, W(12)=22.00, Z=-1.334, p=0.182, Pearson's r=-0.385; mid right: MDN=19.05%, IQR=9.40-23.22%, W(12)=27.00, Z=-0.941, p=0.347, Pearson's r=-0.272; extreme right: MDN=12.79%, IQR=1.92-22.62%, W(12)=46.00, Z=1.158, p=0.247 Pearson's r=0.334.

For negative valence behaviours the overall difference between the five VFP values was non-significant (X^2(4)=6.760, p=0.149, Kendall's W=0.241) and with the exception of the central visual field which returned a significantly lower VFP value than expected (MDN=11.54%, IQR=0.00-16.67%, W(7)=0.00, Z=-2.384, p=0.017, Pearson's r=0.901) there were no other significant differences from expected in the remaining visual fields; extreme left: MDN=11.54%, IQR=5.88-25.00%, W(7)=8.00, Z=-1.014, p=0.310, Pearson's r=-0.383; mid left: MDN=27.03%, IQR=16.67-46.15%, W(7)=10.00, Z=-0.105, p=0.917, Pearson's r=-0.040; mid right: MDN=30.00%, IQR=25.00-35.29%, W(7)=22.00, Z=1.352, p=0.176, Pearson's r=0.511; extreme right: MDN=16.22%, IQR=3.85-35.71%, W(7)=20.00, Z=1.014, p=0.310, Pearson's r=0.383.

The positive valence category demonstrated a significant overall difference between the five VFP values (X^2(4)=18.789, p=0.001, Kendall's W=0.783) and significant differences were observed for all five visual fields as lower than predicted VFP values were found for both extreme visual fields (extreme left: MDN=2.95%, IQR=0.00-10.87%, W(6)=0.00, Z=-2.207, p=0.027, Pearson's r=-0.901; extreme right: MDN=0.00%, IQR=0.00-5.40%, W(6)=1.00, Z=-2.049, p=0.040, Pearson's r=0.837) and the central visual field (MDN=4.17%, IQR=0.00-15.15%, W(6)=1.00, Z=-1.997, p=0.046, Pearson's r=-0.815) but significantly higher than predicted VFP values were found for both mid visual fields; mid left: MDN=40.94%, IQR=31.82-52.31%, W(6)=20.00, Z=1.992, p=0.046, Pearson's r=0.813; mid right: MDN=40.40%, IQR=33.11-52.05%, W(6)=21.00, Z=2.201, p=0.028, Pearson's r=0.899.

No significant overall difference was observed between the five VFP values for neutral valence behaviours ($X^2(4)$=6.278, p=0.179, Kendall's W=0.392) and none of the VFP values significantly differed from expected; extreme left: MDN=2.38%, IQR=0.00-21.64%, W(4)=1.00, Z=-1.473, p=0.141, Pearson's r=-0.737; mid left: MDN=34.85%, IQR=29.76-36.17%, W(4)=9.00, Z=1.461, p=0.144, Pearson's r=0.731; centre: MDN=13.85%, IQR=2.38-29.54%, W(4)=1.00, Z=-1.461, p=0.144, Pearson's r=0.731; mid right: MDN=30.95%, IQR=20.78-36.91%, W(4)=9.00, Z=1.461, p=0.144, Pearson's r=0.132; extreme right: MDN=0.00%, IQR=0.00-32.15%, W(4)=4.00, Z=-0.378, p=0.705, Pearson's r=0.189.

A generalized linear mixed model was then used to compare the VFP values of all four valence categories within each visual field, using the neutral valence category as a reference. A significant effect of valence was found in the extreme left visual field (F(3,25)=3.985, p=0.019, ICC=0.00), where the sexual valence category returned a significantly higher VFP value than the reference (FC=0.226, p=0.027). A significant effect of valence was also found in the mid left visual field (F(3,25)=5.456, p=0.005, ICC=0.857) but within this field sexual behaviours exhibited a significantly lower VFP value than the reference: FC=-0.134, p=0.040. Additionally, a significant overall effect of valence was found for the mid right visual field (F(3,25)=4.135, p=0.016, ICC=0.909 but no significant contrasts were found within this visual field and no significant effects of valence were found for the central visual field (F(3,25)=0.444, p=0.724, ICC=0.00) or extreme right visual field (F(3,25)=1.281, p=0.303, ICC=0.003. The median VFP values for all four valence categories have been shown in Figure 5.15.

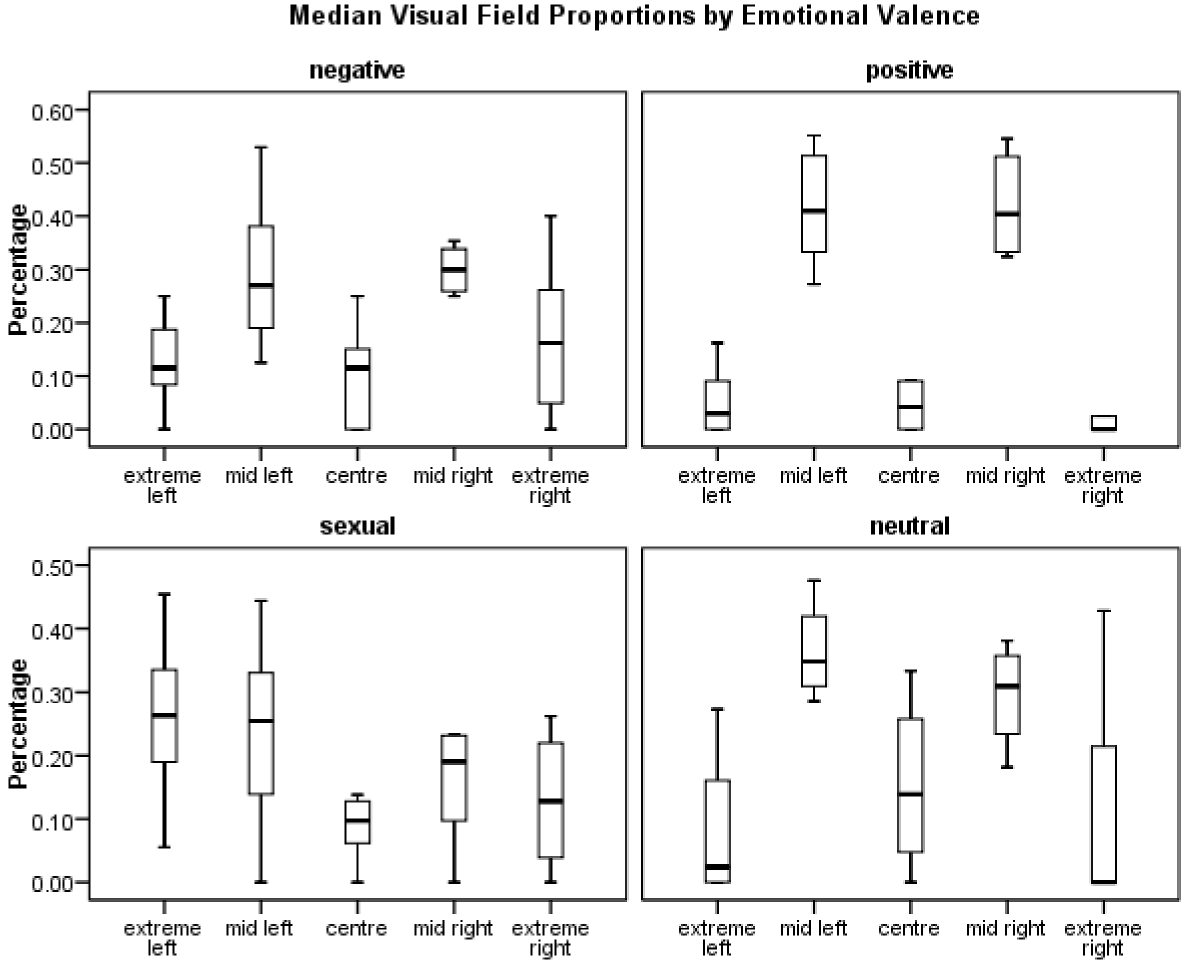

Figure 5.15 | Comparing the median VFP values for each emotional valence category (neutral n=4, negative n=7, positive n=6, sexual n=12).

5.5.3—Overall Mixed Model

Including age, sex, rank, emotional intensity and emotional valence as fixed effects and ID as the random effect a significant overall effect was found using a generalised linear mixed model (F(14,651)=2.647, p=0.001, ICC=0.000) with significant effects also found for emotional intensity (F(2,651)=6.753, p=0.001) and emotional valence (F(6,651)=5.206, p=0.001). Within this model low intensity interactions had a significantly greater effect upon left (FC=1.933, p<0.001) and right (FC=1.563, p=0.003) visual fields than high intensity interactions. Within the valence categories, and using neutral as the reference, significant contrasts with neutral valence behaviours were found in both lateral directions for positive (left FC=3.209, p<0.001; right FC= 2.652, p<0.001), negative (left FC=2.609, p<0.001; right

FC=2.041, p<0.001) and sexual valence behaviours (left FC=3.668, p<0.001; right FC=2.739, p<0.001) but by comparing left side bias against right side bias in a second model no significant overall effect was reported (F(7,595)=1.009, p=0.424).

5.5.4—Additional Data

Supplementary to the primary data collected for this study a number of additional behavioural observations were made of the spotted hyaena population including three further behaviours: leg cross, shoulder roll and stick scratch. As only a small number of observations of these behaviours were made only limited analysis was possible (all observations of these behaviours have been included in Appendix A8). Laterality Indexes were calculated for each individual following the BLI formula given in the methods chapter. Chi-squared numbers were calculated with the expected value set as the mean number of interactions for each individual and these data have been shown in Table 5.16.

behaviour	ID	left	right	total	LI	X^2	*p*
leg cross	Gremlin	7	3	10	-0.400	0.900	0.343
shoulder roll	Bear	6	4	10	-0.200	0.100	0.752
	Domino	7	1	8	-0.750	3.120	0.077
stick scratch	**Domino**	**24**	**6**	**30**	**-0.600**	**9.640**	**0.002**
	Rocco	19	16	35	-0.086	0.120	0.729
	Haji	4	3	7	-0.143	0.000	1.000
	Dusty	7	1	8	-0.750	3.120	0.077
	Scooter	**8**	**0**	**8**	**-1.000**	**6.120**	**0.013**
	Zawadi	7	2	9	-0.556	1.780	0.182

Table 5.16 | Showing the data from individuals that met the minimum criterion (n≥7 interactions) for the three additional behaviours observed. The number of interactions on the left and right have been provided, along with the totals, Laterality Index (LI), chi-square calculation and its significance.

5.6 | Discussion

The results of this study found significant left side biases for adults, females, dominant individuals, high intensity interactions and sexual behaviours and a significant overall left side bias for the group, thereby providing the first evidence of lateral bias in the spotted hyaena and these observations were confirmed using the mixed model analysis which reported a significant effect when all five factors (age, sex, rank, emotional intensity and valence) were considered. In addition, five subjects were significantly lateralised at the individual level whilst subadults, subordinate individuals, high intensity interactions and positive valence behaviours returned a significantly weaker strength bias (ABS) than predicted by the population average.

The observation of a significant overall left side bias suggests that the right hemisphere controls the interpretation and expression of emotional behaviour and thus supports Campbell's (1982) hypothesis. The general prevalence of a left side bias is illustrated by the overall pattern of left side preferences across all contexts including the significant left side biases found for several subcategories within these contexts and further evidences the dominance of the right hemisphere in emotional behaviour processing for this species. The results of this study therefore support hypothesis one (H_1) and the findings of Casperd & Dunbar (1996) and Baraud *et al.* (2009), which also found left side preferences at the population level.

Sex differences in lateralisation have also been reported in the manual laterality literature as Milliken *et al.* (1989) and Ward *et al.* (1990) both found left handedness in male but not female lemurs and postulated that this was due to masculinising hormones inhibiting left hemisphere development in the womb, thereby causing right hemisphere dominance. In the spotted hyaena, however, female cubs are also exposed to androgens during their foetal development and for the first two years after birth levels of testosterone in the females are equal to those of the males (Licht *et al.*, 1992; Glickman *et al.*, 1992; 2006). It is therefore possible that elevated testosterone levels during early development in female spotted hyaenas may have had a more pronounced effect than in males and may explain the stronger left side bias found in the females of this population; results which do not therefore support hypothesis three (H_3) which predicted stronger lateral biases for males. An alternative explanation for females, but not males, demonstrating a significant lateral bias may relate to the dominance hierarchy that exists within spotted hyaena clans. Female hyaenas exert complete dominance over their male counterparts and even the highest ranking male is subordinate to the lowest ranking female, with the females also larger than the males at full sexual maturity (Frank, 1986). With the intention of attempting to separate the effect of rank from the effect of sex this study investigated rank on a per interaction basis rather than considering the rank position of each subject within the overall group social hierarchy. However, as all females are dominant over all males chance dictates that females will have a greater likelihood of being the dominant individual in any given interaction thus it is probable that rank may still be responsible for the sex differences observed. The observation of a significant left side bias for dominant individuals and not subordinate individuals may further support this suggestion whilst additionally supporting the observation of Baraud *et al.* (2009), which also observed stronger lateral preferences in higher ranked individuals, and hypothesis four (H_4). It is possible that the strong left side bias observed for dominant individuals during the present study was related to social monitoring behaviour whereby lower ranked individuals, which are more likely to be subject to agonistic interactions from other, higher ranked, conspecifics, are vigilant across a wider visual spectrum and do not thereby express the same left side concentrated visual attention as their higher ranking counterparts. Although, as elevated testosterone levels are also associated with elevated rank in spotted hyaenas including females (Licht *et al.*, 1992; Glickman *et al.*, 1992, 2006) it is possible that sex hormones may also underpin this example of lateralisation.

A number of previous studies have identified age effects on lateralisation with Lehman (1970) and Vauclair & Fagot (1987), and Vauclair *et al.*(2005) reporting significant limb preferences and Hauser & Andersson (1994) observing significant group-level orientation biases for adults but not subadults in several primate species. The results from the present study, which found a significant left side bias for adult spotted hyaenas, therefore support these findings as well as the results from the olive baboon chapter. Additionally, calculation of

ABS values for both age categories revealed that subadults expressed a significantly weaker lateralisation than adults when compared with the population mean. This further evidences that behavioural function becomes more profoundly biased with maturation and thus supports Dharmaretnam & Andrew's (1994) proposal, that lateralisation is subject to ontogenic ritualisation, and supports hypothesis two (H_2). Furthermore, whilst the limited number of additional solo behaviours observed offers only slight additional input into the interpretation of results the significant left side bias found for Domino during the 'stick scratch' provides further evidence of the effect of age upon lateralisation. The data from Domino included in the main analyses was limited to archived footage from Domino as a subadult and as their BLI value demonstrates a non-significant right side bias was observed. However, as the LI value calculated from the stick scratch behaviour shows, a significant left side bias was found and this was based upon the observations of Domino as an adult, thereby provided an individual case-study on the influence of age upon lateralisation.

A further observation from the three solo behaviours was the left side bias evident from every individual during these behaviours. In total, eight individuals were observed performing solo behaviours with Domino recorded during the stick scratch and shoulder roll behaviours. Of these, only Domino and Scooter were found to express significant lateral (left side) biases and for both of these individuals this bias was observed during the stick scratch behaviour, however, calculating the mean of all of these LI values combined (stick scratch, shoulder roll, leg cross) revealed a significant left side bias (LI=-0.511, p=0.003) for solo behaviours overall. This could therefore provide further support to the findings from the main study on the lateralisation of behavioural interactions and thus demonstrates the strength of the left side bias that exists in this population

Although no significant overall effect of emotional valence or intensity upon the direction or strength of bias was found, sexual behaviours were found to be significantly biased to the left for the population whilst positive valence behaviours were significantly less strongly lateralised than the group mean. The lack of significant contrasts between emotional valence categories is similar to the observation of Baraud *et al.* (2009) but the existence of a significant left side bias for sexual behaviours, and no other valence categories, requires further consideration. Ventolini *et al.* (2005) and Gülbetekin *et al.* (2007) observed left side biases for sexually guided behaviour in black winged stilts and Japanese quail respectively so a precedent exists for this example of lateralisation although its cause remains unclear. Levels of sex hormones may also be related to this observation as testosterone levels often increase during sexual behaviour (Batty, 1978) although, whilst Milliken *et al.* (1989) and Ward *et al.* (1990) postulated that testosterone may have impaired foetal hemispheric development the suggestion that sex hormones can also temporarily impair hemispheric function in maturation is novel. A significant left side bias was also found for high intensity behaviours, which therefore supports hypothesis five (H_5) and as all sexual behaviours included in analyses for this species were considered high intensity there is likely a relationship between these factors. The significantly weaker bias strength observed for positive valence behaviours is difficult to interpret as although it may be reasonable to suggest that sexual and negative valence behaviours may elicit stronger lateral biases than positive valence behaviours due to their comparatively higher emotional intensity, that the opposite was not true of neutral valence behaviours appears to confound this suggestion. The more pronounced left side bias during high intensity interactions suggests that these behaviours may involve a reduced scope of social monitoring immediately preceding their elicitation and possibly suggesting that higher intensity interactions may be initiated more impulsively than lower intensity interactions whereby an individual performs a greater scan of their conspecifics before engaging one in an interaction.

The additional solo behaviours also provided an interesting additional measure of lateral preference that may be worth exploring in further detail in future studies. In the case of the shoulder roll, which is a behaviour that serves to transfer an odiferous substance onto the individual performing this behaviour, it is probable that this could be simply replicated in a specifically designed study by providing the hyaenas with such substances and observing their responses. Indeed, this behaviour is known to exist in a number of social carnivores (Fox, 1975) which would create the opportunity for cross-species comparison. The stick scratch behaviour, however, may prove more difficult to replicate as it was somewhat dependent upon prior conditioning due to the hyaenas having previously learnt that approaching the fence near to a keeper often resulted in being groomed and therefore this behaviour may not be observable in other populations. The third of these solo behaviours, the leg cross, has been identified as a component of the male spotted hyaena's mating ritual but is not well understood (M.L. Weldele, personal communication) and indeed only features once in any previous literature on this species (Szykman *et al.*, 2003) and as no other species perform an obviously analogous behaviour any replicate studies would be limited to spotted hyaena. Nonetheless, as a pre-mating ritual and as a behaviour that is therefore likely to be of high arousal this does provide a rare opportunity to observe lateralised solo emotional behaviour being expressed and would be an intriguing topic for further study in this species at least.

A potential methodological issue with the hyaena study, in comparison with previous research, was the housing of the subjects in dyads as this meant that at any given occasion subjects were only required to monitor the position of one other conspecific, however, rather than perceiving this as a caveat of the hyaena study this may in fact have proven to be a benefit. The reason for this being that as the individual hyaenas did not regularly need to scan the entire enclosure to locate the other conspecific it is reasonable to assume that, subsequent to the initial observation of this conspecific's position, each focal individual could therefore position themselves in such a way as to best monitor the one other conspecific. As such, the strong lateral biases expressed by subjects in this hyaena study may suggest that the biases observed in previous studies may have been diluted by the need of the subjects in these previous studies to monitor a wider field of vision.

A spotted hyaena at FSBR, University of California, Berkeley, CA, USA

6

Chapter 6 | *General Discussion*

6.1 | Discussion

The most significant observation from this thesis was the group-level left side bias observed for the population of spotted hyaenas, therein providing the first evidence of lateralisation in that species although no significant lateral biases were observed for the populations of olive baboons or rhesus macaques and as Table 6.1 shows, there were no consistent effects of any of the factors (age, sex, rank, emotional intensity or emotional valence) across all three species except that hypothesis three (males should express a significantly stronger left side bias than females) was rejected by all three studies.

Species	Mean BLI	Individual Lateralisation	Significant Results
Papio anubis	-0.078	1 left : 3 Right : 30 none	adults: left side biased
			males: higher proportion of mid and centrally occurring behaviours than females
			low intensity: higher proportion of mid and centrally occurring behaviours than high intensity
			neutral valence: low proportion of behaviours in extreme visual fields
			positive valence: low proportion of behaviours in mid visual fields
			negative valence: left side biased; high strength of bias
			non-oestrus: low proportion of behaviours in central visual field; high strength of bias; stronger bias than in-oestrus subjects
Macaca mulatta	-0.062	3 left : 2 right : 24 none	high intensity: high strength of bias
			sexual valence: higher proportion of behaviours in both extreme visual fields than neutral valence
Crocuta crocuta	-0.185	5 left : 0 right : 10 none	population-level left side bias
			adults: left side biased
			subadults: low strength of bias
			females: left side biased
			dominant individuals: left side biased
			subordinate individuals: low strength of bias
			high intensity: left side biased; low strength of bias
			sexual valence: left side biased; low proportion of behaviours in central visual field
			positive valence: low strength of bias; low proportion of behaviours in central and both extreme visual fields but high proportion of behaviours found in both mid visual fields
			negative valence: low proportion of behaviours in central visual field

Table 6.1 | Summarising the significant observations found in each species.

hypothesis	olive baboons	rhesus macaques	spotted hyaena
emotion is controlled by the right hemisphere, therefore behaviours in all emotional contexts should be lateralised to the left visual field at the population level	✘	✘	✔
adults should express a stronger left side bias than subadults	✔	✘	✔
a stronger left side bias should be evident in males than in females	✘	✘	✘
stronger left side biases should be found in higher ranked individuals	✘	✘	✔
high intensity interactions should elicit stronger left side biases than low intensity interactions	✘	✘	✔

Table 6.2 | Showing whether the primary hypotheses of each chapter were met.

As Table 6.2 demonstrates a number of hypotheses were met by this thesis, particularly by the hyaena study. Aside from the prediction of population-level left side bias which was only supported by the spotted hyaena study, the significant left side bias found for adults in spotted hyaenas and olive baboons appears to suggest that this factor may have the greatest influence upon lateralisation, therefore supporting a number of similar observations (Lehman, 1970; 1978; Dharmaretnam & Andrew, 1994; Hopkins, 1994; Westergaard & Suomi, 1993; Vauclair & Fagot, 1987; Vauclair *et al.*, 2005).

No effect of rank was reported by either monkey studies but for spotted hyaena dominant individuals returned a significant left side bias, thus supporting Baraud *et al.* (2009) but this result is made more intriguing by the difference between how rank was determined for the monkeys and the hyaenas. In the monkey studies each subject was allocated to a rank group based upon its position within the overall social rank of the group and the data for both monkey species were analysed accordingly. For the hyaena study, however, rank was determined on a per interaction basis with the subject coded as being dominant or subordinate for each individual interaction. As such, whilst a subject's rank was constant for each individual within the monkey studies, for the hyaena study most subjects were observed during interactions as the dominant and also as the subordinate individual. This would therefore suggest that the direction or strength of lateralisation of a subject was subject to change during an interaction. This seems improbable and the results from the hyaena study are likely best explained by higher ranking individuals accounting for a larger number of interactions as the dominant individuals. Nonetheless, a within-subjects study comparing the lateralisation of behaviours for each subject during dominant and subordinate behaviours may prove interesting in future studies.

At first consideration, the lack of consistent population-level lateralisation for all three species impairs the ability of this thesis to conclusively elucidate the comparative validity of Campbell's (1982) Right Hemisphere hypothesis or Silbmerman & Weingartner's (1986) Valence hypothesis. However, the significant results from the hyaena study (Chapter 5), which demonstrated right hemisphere control of affective processes and therefore support for Campbell's model, highlight the benefit that cross-species studies provide.

From an evolutionary perspective, hemispheric specialisation has been found to confer clear benefits (for review, see: Vallortigara & Rogers, 2005) as it halves the expenditure of bodily resources that would be needed to support the function and development of two hemispheres and permits the other hemisphere to specialise in alternative or additional functions (Levy, 1977). Both monkey species have been found to express significantly lateralised behaviour for other functions, such as handedness (olive baboons: Vauclair *et al.*, 2005; Meguerditchian & Vauclair, 2006; 2009; Meguerditchian *et al.*, 2011; rhesus macaques: Lehman, 1970; 1978; Westergaard & Suomi, 1996; Westergaard *et al.,* 1997; 2001) so it is curious that lateralisation was not also apparent during perceptual functions given that they likely underlie the lateralisation of motor functions (Rogers & Andrew, 2008; Rogers *et al.*, 2013). This is also important as by designating control of a particular behavioural function to one hemisphere it eliminates the possibility for inter-hemisphere conflict which may be particularly disadvantageous in agonistic interactions (Andrew, 1991; Vallortigara, 2000). By considering the fitness benefit that may be derived from expressing lateralised behaviour during agonistic interactions it may therefore be possible to interpret the significant left side bias found during negative valence behaviours in olive baboons as being due to this reason. Indeed, the results of Casperd & Dunbar (1996), which were based solely upon agonistic encounters, also reported a significant left side bias and significantly lateralised behaviour during aggressive bouts and displays has been reported in a number of other studies (gelada baboons: Drews, 1996; deer: Jennings, 2012; lizards: Deckel, 1995; Hews & Worthington, 2002; and fish: Cantalupo, *et al.* 1996).

It may therefore be suggested that significant lateral biases may only serve an important function for particular valence categories which further implies that lateralisation during sexual valence behaviours is comparatively most important for spotted hyaenas. Considering the nature of sexual valence behaviours in spotted hyaenas this may well be the case. Whilst negative valence agonistic behaviours include highly aggressive physical interactions this valence also includes comparatively low arousal non-physical threats (Kruuk, 1972). By contrast, sexual valence behaviours all take place at close-quarters and during the greeting ceremony in particular, individuals expose their genitals to the other greeting hyaena in a vulnerable three-legged stance with one hind-leg raised. The need for an individual to be wary of the movements of a nearby hyaena during this behaviour is therefore of critical importance and thus it might be expected, following Andrew (1991) and Vallortigara's (2000) suggestion, that the presenting hyaena orientates its more perceptually attuned side towards the other individual. The lack of lateral bias for negative, sexual or any valence of behaviours for rhesus macaques, however, does not provide any further support for this suggestion.

A possible explanation for the lack of consensus in results and the existence of a (left side) population bias in the spotted hyaena but neither of the monkey species may relate to a difference in group behaviour between these species. There was no distinct difference in feeding strategy between the captive populations covered in this study as each population, irrespective of species, was fed by the keepers of their respective facility. However, there is a considerable difference in feeding habits between these species in the wild. Both monkey species are omnivorous but generally solitary feeders (Dunbar & Dunbar, 1974; Nowak, 1999; Richard *et al.*, 1989) whilst the spotted hyaena is an efficient cooperative hunter (Kruuk, 1972; Glickman *et al.*, 1997; Holekamp *et al.*, 2007) and evidence of highly efficient cooperative problem-solving has also been documented in this species in a captive population (Drea & Carter, 2009). There are some examples of alliances or coalitions being formed in baboons and macaques for the purposes of mobbing a predator and in baboons during the pursuit of potential prey (Silk & Boyd, 1983; Bercovitch, 1988; Cheney & Seyfarth, 1992; 2008) but it has been argued that rather than groups acting as a cooperative and cohesive unit that these behaviours are instead examples of individuals acting simultaneously but independently with chimpanzees the only primate observed to perform cooperative hunts on a level similar to social carnivores such as lions, wolves and indeed spotted hyaenas (Altmann & Altmann, 1970; Strum, 1981; Cheney & Seyfarth, 1992). It can therefore be argued that both monkey species are much more individualistic whilst a tendency for stronger social cohesion and behavioural synchrony exists in spotted hyaenas. It therefore follows that population-level lateralisation may confer benefit to this species when performing cooperative tasks that require a high level of coordination. The study by Drea & Carter (which was performed upon the same captive population of hyaenas observed for the present study) also demonstrated that although these hunting strategies were no longer required, the aptitude for cooperation remains even in captivity, thereby suggesting that the population-level bias observed for this species is related to its inherent coordinative ability that appears lacking in olive baboons or rhesus macaques. Conversely, whilst uniform lateralisation within a group may benefit a predator, such as the spotted hyaena, a lack of group-level lateral biases in potential prey animals, which may include baboons and macaques, may be advantageous to the individual as predictability in terms of possessing a ‘weaker’ side could be exploited.

It may also be worth considering the comparative differences in facial morphology between the three species as being a root cause of the observed differences in behavioural lateralisation. Whilst all three species have a large central binocular visual field overlap the extent of this overlap and the extent of each subject's peripheral vision is likely different between the three species. Van Essen *et al.* (1984) have estimated the overall visual field of rhesus macaques to be approximately 210° with a central binocular field of approximately 140° and whilst there is no available data for the range of binocular vision in spotted hyaenas it may be reasonable to use domestic dogs as an approximate model, based on their similar facial morphology, and which have an overall visual field of approximately 240° and a central binocular visual field of approximately 60° (Miller & Murphy, 1995). Again based upon a comparison of facial morphology between these three species it is reasonable to suggest that olive baboons may be found between these two species in terms of their overall and binocular visual fields. As spotted hyaenas would therefore have the least binocular overlap they would also therefore have a correspondingly greater total decussation of their optic fibres (resulting in images being projected to only one hemisphere rather than both) and larger monocular visual fields which might therefore lead to more distinct lateralised behaviour being expressed. For the same reason, rhesus macaques would then have the least complete decussation of their optic fibres and the smallest monocular visual fields which may therefore explain the lack of lateralised behaviour for this species, with olive baboons falling between these species as their results suggest. It may therefore be proposed that a more accurate approach for future studies should involve estimating the boundaries of binocular and monocular vision for each species and using these as references for determining the position of behaviours in the overall visual spectrum of the subjects being studied.

A further suggestion for the difference between spotted hyaena and the monkey species may relate to the effect of masculinising hormones on hemispheric development. Previous studies in lemurs (Milliken *et al.*, 1989; Ward *et al.*, 1990) reported left arm preferences in male but not females and suggested that these results may have been due to the effect of testosterone which had been previously found to impair the prenatal development of the left hemisphere, thus leading to right hemisphere dominance (Geschwind & Behan, 1982). As female juvenile spotted hyaenas are uniquely known to produce as much testosterone as their male counterparts for their first two years after birth (Licht *et al.,* 1992; Glickman *et al.,* 1992; 2006), it is probable that the development of the left hemisphere would be equally inhibited in males and females, therefore explaining the group-level right hemisphere dominance and left side behavioural bias in both sexes of hyaena that is absent from the monkey species.

Furthermore, whilst Milliken *et al.* (1989) and Ward *et al.* (1990) referenced only testosterone is it possible that other sex hormones may also play a role in lateralisation, as suggested by the difference in strength of lateralisation for in-oestrus and non-oestrus olive baboons whereby a stronger lateral bias was found by the latter category. Aside from obvious morphological changes during the different stages of the oestrus cycle in olive baboons there is also a fluctuation in the level of female sex hormones with the oestrogen peak occurring during the most receptive stages of the oestrus cycle (Hodges *et al.*, 1986; Higham *et al.,* 2008) and as the results from the baboon study demonstrate, females in oestrus express a significantly weaker lateral bias than females at other stages of the cycle; thus suggesting that females sex hormones may also play a significant role in behavioural lateralisation.

On the basis of a superficial comparison of the three study populations and a further suggestion for the existence of a lateral bias in hyaenas but neither of the monkey species may be due how the subjects were housed and the potential effect this had upon vigilance behaviour. Denenberg (1981) and Vallortigara & Rogers (2005) have suggested that lateralisation at the species or group level may be disadvantageous and particularly for prey species as obvious lateralisation could be exploited by predators attacking from the prey's perceived weaker side. Whilst none of the population groups observed during this study were subject to any form of predation, vigilance behaviour is still an important activity for individual animals within a large group with a dynamic hierarchical structure as, irrespective of rank, they must monitor other group members. This is particularly the case when competing for a mate, food or other resources as a decision to engage in attritional physical aggression is dictated by this monitoring behaviour (Maynard Smith, 1974) and may have serious short or long term effects upon that individual's fitness. In comparison with both of the monkey species which were housed together as a single group, the population of spotted hyaenas were housed in 11 dyads and one triad to reduce aggression within the population (M.L. Weldele, personal communication). As such, vigilance behaviour for this population is likely to have been considerably lower than for either of the monkey species as each hyaena need only monitor the location of one other individual[8]. It is therefore possible that both hyaenas within a dyad could orient themselves so that the other individual is regularly monitored in the left visual field, whilst both of the monkey species which were housed in much larger groups (baboon *n*=41; macaque *n*=42) and therefore the possibility for maintaining other individuals within a single visual hemifield is much lower.

In comparison with the handedness literature for both of the monkey species, it is possible that the lack of pronounced lateral biases for visual field preferences may be a consequence of the lack of self-reinforcement that may exist in manual biases. In an extensive review paper on social learning in primates, Caldwell & Whiten (2002) outline a number of factors that contribute to successful social learning through imitation. One of these, 'Perceptual Opacity' (Heyes & Ray, 2000), suggests that the ability of an individual to see themselves repeatedly perform an action they are attempting to imitate greatly increases the success of this imitation and the learning of the action. Therefore, as an individual watches themselves perform a manual function with one hand they are also reinforcing that manual preference. This suggestion is supported by the examples of handedness strength increasing with age, thereby implying that continued used of a particular hand over time leads to a more

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[8] None of the hyaenas housed in a triad were included in analyses.

pronounced manual preference (*e.g.* Vauclair & Fagot, 1987; Vauclair *et al.,* 2005). Visual field preferences, however, are entirely perceptually opaque therefore no such reinforcement exists which may explain the lack of lateral biases found. A further relationship between the results of the present study for baboons and the handedness literature is the correlation that appears to exist between visual field preferences and manual preferences during neutral emotional contexts. As Chapter 3 demonstrates, a pronounced (though, non-significant) lateral bias was found during neutral behaviours in olive baboons that was in the same direction as the examples of handedness for that species (Vauclair *et al.,* 2005; Meguerditchian & Vauclair, 2006; Meguerditchian & Vauclair, 2009; Meguerditchian *et al.,* 2011). Whilst the data set for the rhesus macaque study was too small to assess whether this was also true of this species and there is no existing data on limb preferences in spotted hyaena it remains to be seen whether, in lieu of any overt emotional context that may influence lateral bias, that behavioural lateralisation is instead influenced by the lateralisation of other functions such as handedness.

6.2 | Methodological Limitations & Considerations

Given a lack of overall consistency in findings it is reasonable to consider whether the method employed by the present study influenced the (lack of) results. Observation of a significant population level bias in one species appears to suggest that this is not the case, although questions remain why neither of the other species expressed similar results. On a basic level, the difference between results may simply reflect a lack of bias in these populations but the extensive literature on examples of lateralisation in both olive baboons and rhesus macaques suggests that this may be unlikely. That said, whilst it is felt that observing naturally occurring behaviours (replicating the method of Casperd & Dunbar, 1996 and Baraud *et al.,* 2009) is preferable to observing artificially elicited behaviours (such as the method employed by Hauser, 1993; Hauser & Andersson, 1994; Dharmaretnam & Andrew, 1994; Cantalupo *et al.,* 1995) as their interpretation is comparatively less ambiguous, the considerable benefit of basing a study upon artificially elicited behaviours is the relative control that can be exercised regarding the number of trials and thus the sample size. In studies where the observed behaviours are triggered by the experimenter it may be possible to not only accelerate the collection of data but also control the type of behaviour that is being expressed whereas in studies based upon naturally occurring behaviours this is not possible. This was most apparent when the data were split for comparison within categories and particularly when comparing the four valence categories as the ability to have increased the number of interactions from one or a number of individuals for one or more valence categories would certainly have been beneficial. In addition, this thesis may have been a victim of its own ambition in terms of cross-species comparison as had only a single species been the subject of the research project it is probable that three times as many data could then have been collected for that species, thus avoiding the issue of small sample sizes for some individuals and/or categories and allowing a more in-depth analysis. Power-analyses may have provided the opportunity for this issue to have been highlighted prior to commencing research but as these were not performed this opportunity was missed. Furthermore, as the data coding from all three studies was not completed until after the third study, any potential issues regarding sample size from the first or second studies could not subsequently be addressed. This was not a design of the method but as the first two periods of observation were back-to-back and the process of video coding effectively involved repeating 12 weeks of observation for each study (without permitting for teaching and other commitments) the problems of the first two studies were not realised until after the third study had also been completed.

As has been stated, sample size was a considerable issue when performing the analyses for this thesis. By bootstrapping all data it was possible to moderately increase the power of the analyses but it is clear they still suffered from the small sample sizes and this was exacerbated by the method of analyses employed by this thesis. By weighting rather than pooling the data for each individual before including this data in overall calculations it is strongly felt that this method ensures a more accurate interpretation of lateralisation however it resulted in a significant reduction in the size of the data used in analyses. As it is understandable that research on naturally occurring behavioural interactions using the focal study method is unlikely to yield a large volume of data without also performing a correspondingly extensive study in terms of time/length discarding valuable data points from an already small sample size can markedly reduce the strength of the analyses that can be performed. However, by weighting the data it is considerably less susceptible to skew from one or a small number of individuals with a disproportionately large number of data points and it also provides a better control against anomalous data that may be derived from individuals with a small number of data points. In comparison with the method of Casperd & Dunbar (1996) in particular, where in most cases only a single data point but no more than four data points were contributed from each individual, the data from their study may be highly susceptible to anomalies and may not therefore provide an accurate representation of the population. Baraud *et al.* (2009) also pooled their data to compare valence categories and whilst their sample sizes are certainly larger than Casperd & Dunbar the potential problems of pooled data remain. Once again providing a comparison based upon the data from Chapter 4, a non-significant left side bias was found for this population (mean BLI=-0.062, p=0.197) but had the pooled method of Casperd & Dunbar and Baraud *et al.* been employed a significant right side bias would instead have been observed (mean BLI=+0.090, p=0.026) and the difference between the two outcomes from the same data set is striking. Whilst this may explain the lack of significant population-level bias for the olive baboon and rhesus macaque studies when compared with the results of Casperd & Dunbar (1996) and Baraud *et al.* (2009), important considerations are therefore raised by the clear difference between the outcomes of the two methods. Firstly, this appears to once again highlight the greater accuracy that may be derived from the weighted method and reinforces why it should be used as the standard for subsequent studies. However, whilst the lack of significant results from some species or contexts in this study, in comparison with Casperd & Dunbar and Baraud *et al.*, may be explained by the differences in analytical methods it is possible that the observed lack of laterality in the data may also be a product of the small sample sizes. As the weighted method is more conservative than the pooled method it is less likely to result in Type I errors however by using small sample sizes the possibility exists that significant effects are not detected, thus resulting in Type II errors. However, the mixed models allowed for the inclusion of all observed data points from each study and the results of these mixed models supported the outcomes of analyses reported elsewhere within each study. Indeed, due to the effectiveness of the generalised linear mixed models in particular as a confirmatory model it is recommended that these should be used as the primary method of analysis in future studies of behavioural lateralisation for determining overall effects and the influence of specific factors with the smaller fine-grained tests, such as the t-tests etc., instead used post-hoc to tease apart the data where a significant effect was found.

With a view to avoiding some of the methodological problems that have been noted in the present study it is certainly recommended that the collection of a much larger sample size is encouraged for future study. The bootstrapping procedure, whilst most helpful in increasing the power of the calculations on small samples such as those included in this thesis, should only be an alternative solution when a larger data sample is not available and power analyses should be performed in advance to inform any further study. Thus, in order to detect a large effect size (Pearson's $r=0.5$) at the $\alpha=0.05$ (two-tailed) level of significance and using Cohen's (1988) recommendation for statistical power at the level of 80% as the minimum benchmark, a minimum of 28 interactions per individual should be set as the requirement for inclusion in future studies. Furthermore, with the intention of accurately determining the population level outcome for lateralisation using a chi-squared analysis a minimum of 15 subjects should be required for analyses as this allows for the commonly recommended minimum number of five (subjects) to be set as the expected value for the three possible outcomes of lateralisation: left, right and none.

A feature of this project was the implementation of a novel five visual field model by dividing the overall visual spectrum into sections covering the extreme left, mid left, centre, mid right, and extreme right of a subject's visual range. This model may not possess the comparative simplicity of the LI or BLI calculation but it provides a valuable complement to these calculations. As highlighted by several examples in this species (*e.g.* males and high intensity interactions in olive baboons, positive valence interactions in spotted hyaenas) the calculation of VFP values allows for the observation of effects that may otherwise be masked by simple left/right comparisons.

The inclusion of sexual behaviours as a distinct emotional valence category appears to have provided at least some additional insight into the lateralisation of emotion in spotted hyaenas although there were no similar observations made of the two monkey species. Sexual behaviours were included as a separate valence category due to the author's personal observation that interactions preceding or involving mating frequently appeared to be best characterised as agonistic and that the previous, arguably anthropomorphic, inclusion of sexual behaviours in the positive valence category was misleading. Indeed, review of the literature reveals that Hauser & Akre (2001) had also noted the difficulty of categorising a copulation call as affiliative due to the aggressive behaviour that these calls frequently elicited from conspecifics. However, it is now apparent in hindsight that this sexual behaviour category should, itself, have been further divided as the combination of behaviours of a sexual context into a single category ignored some of the nuances that also exist in sexual interactions. These differences were largely related to rank disparity between the engaging parties but it was clear that in some contexts copulation was a mutually acquiescent behaviour of moderate or low arousal whilst in others it was a highly intense act of submission/dominance, and thus attempting to reconcile these vastly contrasting emotional contexts into a single valence may be misleading. Therefore, it is recommended that future research upon emotional contexts and behavioural interactions should maintain the sexual valence category, but divide it so that the difference in affiliative and agonistic sexual interactions can be better investigated.

A final consideration of the method is based upon the results of the hyaena study which raise an interesting question regarding the interpretation of 'population-level' laterality. As has been reported, the mean BLI value for the overall population of spotted hyaenas was significantly left side biased however the number of subjects significantly lateralised at the individual level (five left-side biased) was only a third of the total number of individuals included in the study. This would therefore imply that twice as many subjects did not express a significant lateral bias as those that did and thus suggests that this population may not have been significantly lateralised by more conservative means. The proclamation of population-level laterality by the present study, based upon a mean overall BLI value, replicates the method of several previous studies of emotional laterality (*e.g.* Casperd & Dunbar, 1996; Ventolini *et al.*, 2005; Baraud *et al.*, 2009), however, the handedness literature, from which emotional laterality research has derived much of its method, requires a significant number of individuals to be similarly lateralised within a given population before determining that the population is also lateralised (*e.g.* Hopkins, 1995). The universal left-side bias observed in all contexts for spotted hyaenas, coupled with the significant overall value of lateralisation reported for this species suggests that two tiers of population-level lateralisation should be used in further studies so that results may be accordingly compared. It is therefore recommended that populations where the number of similarly lateralised individuals within that population is significant should be considered Tier 1 lateralisation, whilst populations such as the spotted hyaena group included in this study, where a significant lateral bias was observed but not a significant number of lateralised individuals, should be considered Tier 2 lateralisation.

6.3 | Summary & Future Directions

The observation of emotional lateralisation in the spotted hyaena represents the most significant finding from this thesis and therefore offers some support to the Right Hemisphere Hypothesis (Campbell, 1984) but the strength of support is somewhat tempered by the lack of population-level results from either of the two primate studies. Further owing to the lack of robust cross-species consensus the application of these findings is limited however future application of the method employed by this study certainly has merit. In addition, although population-level lateralisation was absent from both primate species the results from these studies should not be dismissed out of hand, as the possibility that some species simply do not express lateralisation must be considered as important a contribution to knowledge as the potential observation of significant lateralisation. The benefit derived from studying a non-primate outgroup should also be highlighted as although comparative studies are understandably anthropocentric, by focusing upon a more evolutionarily distant species it is possible to generate a better understanding of the origins of lateralisation. The observation of lateralisation in the hyaena study is a great example of convergent evolution and provides an opportunity to look for common selective pressures that resulted in a shared phenomenon in distinct taxa.

It is strongly felt that the methodology developed for the present study, though it may have suffered due to the small sample sizes, provides a robust template for future studies. Weighting the data for each individual is crucial to ensuring that calculations at the group level are representative of the group and not just a small number of individuals and this should be recommended as a basic standard. It is certainly acknowledged by the author that the data within the present study may not have been suitable for the implementation of this method however that does not diminish the benefit that this model brings when employed in more suitable data sets. The formula for calculating BLI values allows for a simple and accurate assessment of lateralisation in binocular species that should certainly be employed by future studies in similar species whilst the calculation of VFP values provides a much more detailed assessment of the occurrence of behaviours within an individual's overall visual spectrum and is a valuable complement to the calculation of lateralisation indexes. By also using set criteria for distinguishing population-level lateralisation (*e.g.* Tier 1 & 2) in future studies it may be possible to eliminate some of the ambiguity when comparing behavioural laterality studies whilst also allowing for a more direct comparison with handedness studies that already employ similar standards.

Whilst an obvious next step might be to perform further research on the same or different species employing the method set out in this study, perhaps a more beneficial follow-up study might be to review the findings of previous research using the method set out in this study to determine whether behavioural lateralisation was still evident. No significant population-level lateral biases (Tier 1 or 2) were found for either primate species in this thesis despite a number of previous studies suggesting this should be the case. However, it is important to consider that, whilst finding no evidence of lateralisation is perceived as unremarkable, this must be considered as equally significant. It is widely accepted that humans are the only species with species-level handedness (MacNeilage *et al.,* 1987; Fagot & Vauclair, 1991; Marchant & McGrew, 1997) and all other species feature at various levels of handedness below humans with many providing no evidence of manual lateralisation whatsoever. From an evolutionary perspective, these varying degrees of handedness in different species contribute to our understanding of the development of handedness. Similar observations may also therefore be made of other examples of behavioural lateralisation whereby some species express it and others do not. Although the results of this thesis are somewhat inconclusive it is suggested that they should not necessarily be dismissed, but rather that they may indicate the need to re-evaluate the findings of previous studies and, importantly, to re-evaluate the unfortunately popular position that only positive results are significant.

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Appendix A1

Inter-Observer Reliability: Test Form

species ______________________   focal number___________

Naive observer		Experimenter			
Behaviour	Visual Field	Behaviour		Visual Field	

Appendix A2: Inter-observer reliability results for olive baboon focals

focal	Naive observer		Experimenter			
	Behaviour	Visual Field	Behaviour		Visual Field	
1	bite	C	bite		LC	x
	chase	LL	chase		LL	
	chase	LC	chase		LL	x
2	follow	LC	follow		LC	
	play	C	play		C	
	play	C	play		C	
3	avoid	RC	avoid		RC	
	avoid	LL	avoid		LL	
	avoid	RC	avoid		RR	x
	chase	RR	chase		RR	
	displace	LC	displace		LC	
	displace	RC	displace		RC	
	inspect	RC	inspect		RC	
	bite	LL	bite		LC	x
	bite	RR	bite		RR	
	bite	LL	bite		LL	
4	avoid	LC	avoid		LL	x
	bite	LL	bite		LL	
5	bite	C	bite		C	
	play	RC	play		RC	
	play	C	play		C	

KEY: ‘x’ denotes mismatch

LL = extreme left, LC = mid left, C = centre, RC = mid right, RR = extreme right

Outcome: All behaviours successfully identified by naive observer. 16 out of 21 visual fields successfully identified by naive observer with five incorrectly identified although the direction of mismatches was not consistent.

Appendix A3: Inter-observer reliability results for rhesus macaque focals

focal	Naive observer		Experimenter			
	Behaviour	Visual Field	Behaviour		Visual Field	
1	groom	RR	groom		RR	
	displace	RR	displace		RR	
	displace	RC	displace		RR	x
	play	C	play		C	
2	groom	LL	groom		LL	
3	groom	C	groom		C	
4	mount	RR	mount		RR	
	mount	RC	mount		RR	x
	mount	LL	mount		LL	
	mount	LL	mount		LL	
	mount	LC	mount		LL	x
	mount	RC	mount		RC	
	mount	RC	mount		RC	
	mount	RC	mount		RC	
	mount	RC	mount		C	x
	mount	RR	mount		RR	
	mount	LC	mount		LL	x
	mount	LC	mount		LC	
	mount	RR	mount		RR	
5	avoid	LC	avoid		LL	x
	avoid	RC	avoid		RC	

KEY: ‘x’ denotes mismatch

LL = extreme left, LC = mid left, C = centre, RC = mid right, RR = extreme right

Outcome: All behaviours successfully identified by naive observer. 15 out of 21 visual fields successfully identified by naive observer with six incorrectly identified although the direction of mismatches was not consistent.

Appendix A4: Inter-observer reliability results for spotted hyaena focals

focal	Naive observer		Experimenter			
	Behaviour	Visual Field	Behaviour		Visual Field	
1	avoid	LC	avoid		LC	
	lick	LC	lick		LC	
	mount	LC	mount		LC	
	lick	LC	lick		LC	
2	inspect	RR	inspect		RR	
	avoid	RC	avoid		RC	
	inspect	C	inspect		C	
	nuzzle	LL	nuzzle		LL	
	nuzzle	LL	nuzzle		LL	
	inspect	LL	inspect		LL	
	nuzzle	LC	nuzzle		LC	
	nuzzle	LC	nuzzle		LC	
	inspect	LC	inspect		LC	
	nuzzle	RC	nuzzle		RC	
	inspect	LC	inspect		LC	
	open mouth appease	LC	open mouth appease		LC	
	nuzzle	RC	nuzzle		RC	
	open mouth appease	LL	open mouth appease		LL	
	inspect	LL	inspect		LL	
	lick	LC	lick		LC	
3	play	LC	play		LC	
	play	RC	play		RC	
	nuzzle	RC	nuzzle		RC	
	play	LC	play		LC	
	play	RC	play		RC	
	play	LC	play		LC	
	play	LC	play		LC	
	play	RC	play		RC	
	play	LC	play		LC	
4	avoid	RR	avoid		RR	
5	groom	C	groom		C	
	avoid	LC	avoid		LC	
	open mouth appease	RC	open mouth appease		RC	
	groom	RC	groom		RC	
	avoid	LC	avoid		LC	
	inspect	LL	inspect		LL	
	groom	RC	groom		RC	

KEY: ‘x’ denotes mismatch

LL = extreme left, LC = mid left, C = centre, RC = mid right, RR = extreme right

Outcome: All 37 behaviours and visual fields successfully identified by naive observer.

Appendix A5: BLI, ABS & VFP values for olive baboon data set

ID	Total Observed		Laterality Indexes		Visual Field Proportions				
	Focals	Behavs	BLI	ABS	Extreme Left	Mid Left	Centre	Mid Right	Extreme Right
1	23	42	0.012	0.012	4.76%	23.81%	40.48%	28.57%	2.38%
2	19	20	-0.175	0.175	5.00%	30.00%	45.00%	17.50%	2.50%
3	23	38	0.184	0.184	2.63%	10.53%	50.00%	34.21%	2.63%
4	24	52	-0.221	0.221	23.08%	32.69%	9.62%	17.31%	17.31%
5	20	15	-0.198	0.198	20.00%	26.67%	20.00%	13.33%	20.00%
6	20	13	-0.154	0.154	15.38%	23.08%	30.77%	15.38%	15.38%
79	23	9	-0.085	0.085	11.11%	22.22%	0.00%	22.22%	44.44%
83	19	27	-0.037	0.037	14.81%	18.52%	33.33%	22.22%	11.11%
96	22	38	-0.039	0.039	28.95%	18.42%	7.89%	18.42%	26.32%
105	20	8	0.057	0.057	0.00%	25.00%	0.00%	50.00%	25.00%
106	25	12	-0.250	0.250	25.00%	16.67%	33.33%	25.00%	0.00%
111	22	34	-0.015	0.015	17.65%	23.53%	14.71%	14.71%	29.41%
119	20	13	0.269	0.269	23.08%	0.00%	7.69%	7.69%	61.54%
349	19	52	-0.010	0.010	11.54%	26.92%	21.15%	26.92%	13.46%
351	24	7	-0.286	0.286	28.57%	28.57%	0.00%	0.00%	42.86%
355	21	12	0.083	0.083	16.67%	16.67%	16.67%	33.33%	16.67%
358	25	18	-0.111	0.111	33.33%	16.67%	5.56%	5.56%	38.89%
437	22	8	-1.000	1.000	37.50%	62.50%	0.00%	0.00%	0.00%
447	24	69	0.109	0.109	26.09%	11.59%	11.59%	14.49%	36.23%
629	23	32	-0.109	0.109	37.50%	9.38%	15.63%	25.00%	12.50%
804	19	28	0.071	0.071	10.71%	14.29%	39.29%	32.14%	3.57%
805	17	12	0.088	0.088	23.53%	11.76%	11.76%	23.53%	29.41%
816	23	28	0.107	0.107	7.14%	21.43%	28.57%	39.29%	3.57%
818	19	15	-0.233	0.233	13.33%	26.67%	40.00%	13.33%	6.67%
821	25	20	-0.175	0.175	5.00%	40.00%	25.00%	10.00%	20.00%
825	21	25	-0.020	0.020	4.00%	36.00%	20.00%	16.00%	24.00%
959	19	14	0.000	0.000	0.00%	28.57%	35.71%	28.57%	7.14%
960	18	7	-0.500	0.500	0.00%	71.43%	14.29%	14.29%	0.00%
968	25	32	0.203	0.203	6.25%	21.88%	21.88%	28.13%	21.88%
985	22	15	-0.033	0.033	6.67%	20.00%	46.67%	26.67%	0.00%
988	24	28	0.214	0.214	7.14%	17.86%	21.43%	28.57%	25.00%
989	19	21	0.190	0.190	33.33%	0.00%	4.76%	28.57%	33.33%
1000	24	41	-0.220	0.220	43.90%	12.20%	7.32%	21.95%	14.63%
1001	18	7	-0.357	0.357	42.86%	14.29%	14.29%	14.29%	14.29%

Detailing the Binocular Laterality Indexes (BLI) , Absolute Laterality Indexes (ABS) and Visual Field Proportions (VFP) calculated for each individual. Additionally, the total number of focals in which each subject was observed (focals), and the total number of behavioural interactions (behavs) recorded for each individual have also been included.

Appendix A6: BLI, ABS & VFP values for rhesus macaque data set

ID	Total Observed		Laterality Indexes		Visual Field Proportions				
	Focals	Behavs	BLI	ABS	Extreme Left	Mid Left	Centre	Mid Right	Extreme Right
M05	19	48	-0.135	0.135	39.58%	2.08%	29.17%	12.50%	16.67%
R27	17	52	0.635	0.635	3.85%	9.62%	0.00%	9.62%	76.92%
R47	17	17	-0.059	0.059	5.88%	23.53%	41.18%	17.65%	11.76%
T27	14	11	0.000	0.000	9.09%	18.18%	36.36%	27.27%	9.09%
X32	17	10	-0.600	0.600	10.00%	40.00%	50.00%	0.00%	0.00%
X51	21	25	0.160	0.160	4.00%	20.00%	32.00%	8.00%	36.00%
ZF41	17	11	-0.182	0.182	0.00%	45.45%	18.18%	0.00%	36.36%
ZA21	19	30	-0.017	0.017	16.67%	23.33%	20.00%	10.00%	30.00%
ZA29	18	16	-0.156	0.156	6.25%	31.25%	37.50%	18.75%	6.25%
ZB10	15	9	0.056	0.056	0.00%	33.33%	11.11%	33.33%	22.22%
ZB28	14	7	-0.071	0.071	0.00%	28.57%	28.57%	28.57%	14.29%
ZC23	19	18	0.056	0.056	16.67%	5.56%	44.44%	16.67%	16.67%
ZD26	20	9	-0.111	0.111	11.11%	11.11%	55.56%	22.22%	0.00%
ZD60	17	9	0.111	0.111	0.00%	11.11%	55.56%	22.22%	11.11%
ZE16	16	9	0.270	0.270	0.00%	11.11%	22.22%	22.22%	44.44%
ZE23	14	25	-0.100	0.100	12.00%	28.00%	24.00%	20.00%	16.00%
ZE47	20	9	-0.222	0.222	0.00%	55.56%	0.00%	44.44%	0.00%
ZE57	15	11	-0.479	0.479	0.00%	36.36%	63.64%	0.00%	0.00%
ZF05	18	24	0.125	0.125	0.00%	25.00%	33.33%	20.83%	20.83%
ZF14	12	12	-0.130	0.130	16.67%	25.00%	25.00%	16.67%	16.67%
ZF27	19	9	-0.111	0.111	11.11%	11.11%	55.56%	22.22%	0.00%
ZF34	21	17	0.224	0.224	0.00%	17.65%	35.29%	29.41%	17.65%
ZF37	14	10	-0.207	0.207	10.00%	10.00%	70.00%	10.00%	0.00%
ZF41	11	18	0.167	0.167	0.00%	5.56%	66.67%	22.22%	5.56%
ZG16	16	12	-0.083	0.083	0.00%	16.67%	66.67%	8.33%	8.33%
ZG20	14	9	-0.333	0.333	22.22%	33.33%	22.22%	22.22%	0.00%
ZG39	19	8	0.063	0.063	0.00%	25.00%	25.00%	50.00%	0.00%
ZG50	15	15	-0.100	0.100	0.00%	40.00%	26.67%	33.33%	0.00%
ZG59	15	9	-0.556	0.556	11.11%	55.56%	22.22%	11.11%	0.00%

Detailing the Binocular Laterality Indexes (BLI) , Absolute Laterality Indexes (ABS) and Visual Field Proportions (VFP) calculated for each individual. Additionally, the total number of focals in which each subject was observed (focals), and the total number of behavioural interactions (behavs) recorded for each individual have also been included.

Appendix A7: BLI, ABS & VFP values for spotted hyaena data set

ID	Total Observed		Laterality Indexes		Visual Field Proportions				
	Focals	Behavs	BLI	ABS	Extreme Left	Mid Left	Centre	Mid Right	Extreme Right
archive observation									
2 Notch	17	27	-0.205	0.205	22.73%	31.82%	9.09%	22.73%	13.64%
Bear	18	117	-0.400	0.400	25.83%	39.17%	9.17%	19.17%	6.67%
Cody	17	7	-0.786	0.786	71.43%	14.29%	14.29%	0.00%	0.00%
Sal	19	18	-0.395	0.395	52.63%	15.79%	5.26%	15.79%	10.53%
Eyeore	19	18	0.056	0.056	33.33%	5.56%	11.11%	11.11%	38.89%
live observation									
BJ	26	93	-0.214	0.214	12.50%	41.67%	12.50%	26.04%	7.29%
Bramble	28	38	-0.066	0.066	15.79%	34.21%	2.63%	44.74%	2.63%
Domino	23	99	0.099	0.099	18.63%	23.53%	6.86%	34.31%	16.67%
Gremlin	30	23	-0.065	0.065	8.70%	39.13%	8.70%	43.48%	0.00%
Gulliver	23	10	-0.150	0.150	20.00%	30.00%	10.00%	30.00%	10.00%
Nairobi	27	14	-0.429	0.429	14.29%	50.00%	14.29%	21.43%	0.00%
Nakuru	25	28	-0.268	0.268	28.57%	28.57%	10.71%	10.71%	21.43%
Rocco	27	110	-0.018	0.018	15.45%	30.00%	10.00%	30.00%	14.55%
Winnie	23	30	0.233	0.233	6.67%	16.67%	23.33%	50.00%	3.33%
Zonker	28	35	-0.171	0.171	28.57%	25.71%	8.57%	17.14%	20.00%

Detailing the Binocular Laterality Indexes (BLI) , Absolute Laterality Indexes (ABS) and Visual Field Proportions (VFP) calculated for each individual. Additionally, the total number of focals in which each subject was observed (focals), and the total number of behavioural interactions (behavs) recorded for each individual have also been included.

Appendix A8: Supplementary data from spotted hyaena

Behaviour	ID	left	right	Total
leg cross	2 Notch	0	2	2
	Bramble	0	1	1
	Gremlin	7	3	10
	Winnie	0	1	1
	Total	**7**	**7**	**14**
shoulder roll	2 Notch	2	2	4
	Bear	6	4	10
	Domino	7	1	8
	Gulliver	0	2	2
	Nairobi	1	2	3
	Rocco	1	0	1
	Sal	1	0	1
	Winnie	1	5	6
	Zonker	1	0	1
	Total	**20**	**16**	**36**
stick scratch	Domino	24	6	30
	Rocco	19	16	35
	Haji	4	3	7
	BJ	4	2	6
	Kidogo	3	0	3
	Winnie	6	0	6
	Zonker	3	1	4
	Robie	4	2	6
	Bramble	0	1	1
	Dusty	7	1	8
	Scooter	8	0	8
	Zawadi	7	2	9
	Denali	0	1	1
	Tusker	3	0	3
	Total	**92**	**35**	**127**

Showing the frequency of behaviours occurring on the left or right side of the hyaena subjects for each behaviour.

Everything is possible for one who believes.

Mark 9:23