

Exploring attentional bias towards threatening faces in chimpanzees



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ABSTRACT

Primates have evolved to rapidly detect and respond to danger in their environment. Two of the most evolutionary relevant threatening stimuli are snakes and threatening faces. Attentional priority is given to threatening stimuli over neutral stimuli which is known as an attentional bias. However, the mechanisms involved in attending to threat are not fully understood. In humans, it has been proposed that two behavioural systems have evolved to respond to fear-relevant stimuli, the predatory defence system and the social submissiveness system. The predatory defence system evolved earlier in response to threat from snakes, and the social submissiveness system later in response to social threat expressed by threatening faces.

The main aim of this thesis was to explore if an attentional bias towards threatening faces can be measured in one of our closest living relatives, the chimpanzee, using two paradigms from human psychological research, and to understand the attentional mechanisms underlying such a bias and how it has developed as an evolutionary adaptation. For this purpose, touchscreen versions of the visual dot probe task and visual search task were used.

Prior to conducting the attentional tasks, I conducted a series of touchscreen matching-to-sample (MTS) experiments to first establish that the chimpanzees could discriminate threatening faces (conspecific neutral, bared teeth and scream faces) and non-threatening faces used as control stimuli (chimpanzee, orangutan and baboon faces). The chimpanzees discriminated all faces above chance but had greater difficulty in discriminating perceptually similar faces than perceptually different faces. In addition, discrimination performance was better when the sample faces were threatening than non-threatening. The attentional component of these discrimination asymmetries was later investigated in a MTS visual search task.

Next, I conducted the first visual dot probe study to examine attentional bias towards threatening faces in chimpanzees. The stimuli were presented for 150 ms, a duration thought optimal for threat detection. Faster response times to touch dots appearing after threatening faces than non-threatening faces were predicted. Response times were faster towards threatening faces versus scrambled faces but not neutral faces. In addition, response times were faster towards chimpanzee versus baboon faces, but not chimpanzee versus orangutan faces. This was likely explained by closer perceptual similarity between chimpanzee and orangutan faces. Overall, no evidence was found that threatening faces specifically facilitated a bias.

This study was followed by a MTS visual search experiment. Based on asymmetries found towards threatening faces in the MTS experiments, I predicted more efficient search (faster response times and higher accuracy) for threatening face targets amongst neutral face distractors than vice versa. In line with prediction, the chimpanzees showed more efficient search for the threatening face than neutral face targets. A serial search pattern indicated the chimpanzees had difficulty in disengaging from the threatening face distractors.

Taken together, these studies revealed that attentional priority was reflected in difficulty to disengage from threatening faces, rather than facilitated attention towards them, consistent with evidence in humans. Partial support was provided for the later evolution of a social submissiveness system in response to social threat from others and the involvement of strategic rather than automatic processing. This thesis provides a foundation on which to further investigate the factors important for attentional bias towards threatening faces in chimpanzees and to understand more about how this bias has developed as an evolutionary adaptation.

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CHAPTER 1

GENERAL INTRODUCTION

1.1. Introduction

1.1.1. Primate visual attention and attentional bias towards threat

The primate visual system is highly developed but has a limited capacity for processing visual information. Therefore, attentional mechanisms have evolved to select the most relevant information for further perceptual processing, whilst filtering out irrelevant information (Pouget et al. 2012). Human and non-human animals are equipped with a preparedness to attend to and associate fear with events and situations that threaten survival (Seligman 1971). Threat has been defined as the “anticipation of a spatially and temporally proximate source of potential harm for the individual” (Dhum et al. 2017, p. 2). It is more evolutionary costly to fail to respond to a potentially dangerous stimulus than to respond to a stimulus that is not dangerous (Öhman 2008). Therefore, threatening stimuli are given attentional priority over other information (Koster et al. 2005). This attentional priority, or more specifically, “differential attentional allocation towards threatening stimuli relative to neutral stimuli” (Cisler and Koster 2010, p. 204) is known as an attentional bias. Threatening stimuli are thought to be attended to rapidly and automatically (Öhman and Mineka 2001).

1.1.2. The predatory defence and social submissiveness systems

For primates, two of the most evolutionary relevant threatening stimuli are snakes and threatening faces. Öhman et al. (1985) proposed that two behavioural systems have evolved to respond to threatening stimuli, the *predatory defence system*, to respond to threat from other species (especially snakes) and the *social submissiveness system* to respond to threat from within one’s own species (conveyed in threatening facial expressions). The primate brain and visual system was first shaped by the efficient detection of snakes and later by other predators including raptors and felines (Isbell 2006; Öhman 2009). More recently in primate evolution, increasing group size is thought to have driven the enlargement of the amygdala and prefrontal cortex in order to process increasingly complex social information such as that conveyed in

threatening faces (Barton and Aggleton 2000; Brothers 1990; Sawaguchi and Kudo 1990). Whilst the amygdala plays a central role in the automatic processing of threat from predators, the prefrontal cortex is thought to be involved in more strategic processing of threat during social conflict (Adolphs 2002; Öhman 2012). The prefrontal cortex can also inhibit the amygdala, allowing greater cognitive control over responses to social threat and the expression of submissive behaviour in response to aggression (Öhman 2009). For larger primates, such as humans and great apes, aggressive encounters during social conflict pose more of a threat to survival than predatory encounters (Öhman 2009). Therefore, efficient detection of facial expressions which signal threat (especially fearful and angry faces) has important adaptive value, enabling social conflict to be avoided and reducing the risk of injury or even death (Horstmann 2007). Understanding the mechanisms underlying attentional biases towards threatening faces in chimpanzees may help us to understand more about how they have evolved as adaptations. Before considering methods for measuring such biases, I will examine how chimpanzees use facial expressions to signal threat, if they can discriminate facial expressions and if they attend differentially to threatening versus non-threatening faces.

1.2. Facial expression and perception in chimpanzees

1.2.1. Facial expression in chimpanzees

Faces are one of most important and salient social stimuli for primates. They convey information about identity, age, sex, attention and emotion (Adachi and Tomonaga 2017). One of the most important signals of social communication in primates are facial expressions. Darwin (1872) was one of the first to speculate that facial expressions convey similar emotions in humans and animals. Facial expressions also convey important information about the motivations and intentions of the sender so that the receiver may modify their behaviour in response (Seyfarth et al. 2010). Parr and colleagues developed the Chimpanzee Facial Action Coding System (ChimpFACS) to objectively categorise the facial expressions of chimpanzees

based on their underlying musculature (Parr et al. 2007). They validated six categories of facial expression (bared teeth, relaxed open mouth or play face, pant-hoot, scream, alert face and whimper). Based on similarity in facial musculature, Parr et al. (2007) proposed that the chimpanzee bared teeth, scream, bulging lip (not validated) and relaxed open mouth expressions are equivalent to human smile, scream, angry and laughter expressions respectively. Three main facial expressions are displayed in threatening contexts in chimpanzees; bared teeth, scream and bulging lip faces. Whilst bared teeth expressions are thought of as homologous to the human smile (Preuschoft and van Hooff 1995) they are also described as fear grimaces (Parr and Waller 2006) and are observed in both positive and negative social contexts “such as approaches, embraces, invitations, play, and in response to aggression” (Parr et al. 2007, p. 175). Scream faces are also observed in positive and negative social contexts “characterized by nervousness, fear and distress, a prolonged response to aggression, during sex, fleeing an attacker, in some play contexts, and in contexts of general agonism” (Parr et al. 2007, p. 176). The bulging lip expression is predominantly used for “glare, prior to attack or copulation, staring” (Parr et al. 2005, p. 81; Goodall 1968). All three expressions are used either to convey threat to others and/or in response to threat from others, depending on the social context.

1.2.2. Visual discrimination of facial expressions in chimpanzees

Chimpanzees not only express emotions such as fear and anger using facial expressions, they can also discriminate the facial expressions of others. Parr et al. (1998) examined the ability of five chimpanzees to discriminate facial expressions (photographs of bared teeth, scream, pant-hoot, play faces, relaxed lip and neutral faces) using a joystick-controlled matching-to-sample (MTS) task. In the task, the face of an individual with one type of facial expression (the sample) was presented on a screen. This was followed by the presentation of different individuals with the same expression type (matching stimulus) or a different expression type (non-matching

stimulus). The chimpanzees were successful in categorical discrimination of all expressions from neutral faces except relaxed lip faces. Overall, discrimination performance was better for expressions with a larger number of different features, suggesting that relative perceptual similarity is important for discrimination. Parr (2001) also investigated the ability of chimpanzees to understand the emotional meaning of facial expressions. Three chimpanzees spontaneously matched videos of positive social situations (e.g. favourite food items) with play faces and negative social situations (e.g. anaesthesia procedures) with scream or bared teeth faces in a matching-to-meaning (MTM) experiment. The chimpanzees' ability to MTM may be explained by their real-life experience of the situations in the videos. However, the extent to which emotional information is consciously processed is difficult to determine (Parr 2001).

Chimpanzees also show an ability to discriminate facial expressions cross-modally and multi-modally. In a cross-modal MTS task, Kojima et al. (2003) found that a chimpanzee was able to select the facial expression of the group member which matched their sample vocalisation (i.e. pant hoots, pant grunts and screams). Also in a MTS task, Izumi and Kojima (2004) found that the same chimpanzee was able to discriminate between pant hoot and food grunt or scream videos based on vocalisations. Parr (2003, 2004) tested the ability of three chimpanzees to discriminate four facial expressions (pant-hoot, scream, play, and bared teeth faces) in a multi-modal MTS task. First, a short video clip was played featuring e.g. a chimpanzee pant-hooting accompanied by a scream vocalisation (an incongruent audio-visual pairing). Then two comparison still images of a pant hoot face and a scream face appeared. If the pant-hoot face was selected, this indicated they preferred to discriminate the expression using the visual modality, whereas if the scream face was selected, they preferred using the auditory modality. The strongest preferences were shown for discriminating scream faces with the visual modality, and pant-hoot faces with the auditory modality. No preference was shown for discriminating bared teeth faces. The author speculated that the auditory modality may have

been preferred for pant hoots, as long-distance vocalisations contain less intra-individual variability, whereas the visual modality was preferred for screams, as short-distance vocalisations contain more variability (Parr 2003). Together, these studies provide strong evidence that chimpanzees can discriminate conspecific facial expressions using visual and auditory modalities and to some extent may understand their emotional meaning.

1.2.3. Attention towards facial and whole-body expressions in chimpanzees

Next, I will consider evidence that chimpanzees attend differentially to facial and bodily stimuli presented in threatening and non-threatening contexts. Recently, innovative experimental methods such as touchscreen tasks (e.g. Kano et al. 2008) and non-invasive eye-tracking measures (e.g. Kano and Tomonaga 2010a) have been used to investigate attentional behaviour towards threatening stimuli (especially facial expressions and scenes) presented as both still images and videos. Kano et al. (2008) presented two chimpanzees with conspecific agonistic scenes amongst a 'list' of neutral scenes in a touchscreen serial probe recognition task. One chimpanzee showed enhanced recognition of agonistic scenes relative to neutral scenes. This was accompanied by behavioural responses such as piloerection, body shaking and even hitting the pictures, suggesting the stimuli were emotionally salient. In an eye-tracking study, Kano and Tomonaga (2009) examined the face scanning patterns of six chimpanzees and 18 humans for chimpanzee facial expressions (neutral, pant hoot, scream and bulging lip) and equivalent human expressions (described as neutral, happy, fear and anger). Interestingly, the chimpanzees scanned different face regions more rapidly than humans, who fixated more on the eyes regardless of expression type. For conspecific pant hoot and scream expressions, chimpanzees focused more on the mouth, whereas for neutral faces they focused on the eyes. The mouth may be a more efficient way to receive emotional information in chimpanzees (Kano and Tomonaga 2009). Another study by Kano and Tomonaga (2010b) found that six chimpanzees viewed videos of conspecific agonistic scenes featuring the whole-body

significantly longer than neutral, excitement or play scenes. However, when they removed the face in the videos looking time decreased equally for all types of facial expression. This suggests that whilst faces are important for conveying general information, facial expressions may be less important for more specific information (Kano and Tomonaga 2010b).

Overall, these attentional studies demonstrate that chimpanzees attend differentially towards facial expressions and whole-body scenes which occur in a threatening context. Having established that chimpanzees use facial expressions to signal threat and attend differentially to threatening versus neutral information in faces and whole bodies, I will now examine experimental methods from human psychological research which have potential for investigating the mechanisms underlying these attentional biases in chimpanzees.

1.3. Measuring attentional biases towards threatening stimuli

A number of theoretical models have been put forward to explain the attentional components, mediating mechanisms and stages of processing involved in attentional bias towards threat in anxious humans (Bar-Haim et al. 2007; Beck and Clark 1997; Eysenck et al. 2007; Matthews and MacIntosh 1998; Mogg and Bradley 1998; Öhman 1996; Wells and Matthews 1994; Williams et al. 1988). Cisler and Koster (2010) propose a useful framework for integrating these elements between models and for investigating attentional bias towards threat more generally (**see Figure 1**). They divide the attentional components into *facilitated attention*, which refers to the “relative ease or speed with which attention is drawn to a threat stimulus.” (Cisler and Koster 2010, p. 208), *difficulty in disengaging*, which refers to “the degree to which a threat stimulus captures attention and impairs switching attention from the threat to another stimulus” (Cisler and Koster 2010, p. 208) and *attentional avoidance*, which refers to “attention...preferentially allocated towards locations opposite the location of the threat cue.” (Cisler and Koster 2010, p. 208). Facilitated attention is thought to involve a threat detection mechanism and is processed primarily by the amygdala, whereas difficulty in disengaging and

attentional avoidance involve greater attentional control and emotional regulation respectively and are processed primarily by the prefrontal cortex and related areas. Facilitated attention involves *automatic processing*, which is “effortless, capacity free, unintentional and outside of conscious control” (Cisler and Koster 2010, p. 211), whilst difficulty in disengagement and attentional avoidance involve greater *strategic processing*, which is “effortful, capacity-limited, intentional and dependent on conscious control.” (Cisler and Koster 2010, p. 211). However, the boundaries between these processing stages and attentional components is not clear. In addition, exactly how the amygdala and prefrontal cortex interact with each other when processing threat is not fully understood. However, automatic processing is consistently thought to underlie facilitated attention to threat across all models (Cisler and Koster 2010).

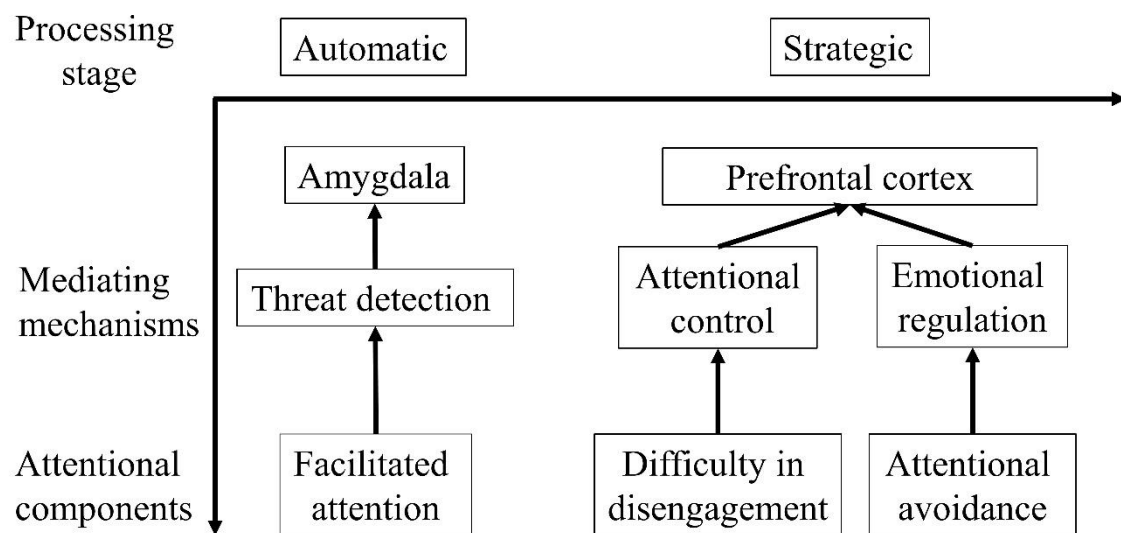


Figure 1. Possible attentional components, mediating mechanisms and processing stages involved in attentional bias towards threat (Adapted from Cisler and Koster 2010).

To investigate the possible mechanisms of attention towards threat in humans, several experimental paradigms have been developed. These include the emotional Stroop, rapid serial visual presentation, visual search and dot probe tasks (Yiend 2010). Modified versions of the emotional Stroop (Allritz et al. 2016) and serial probe recognition task (Kano et al. 2008) have been used to investigate attention towards threatening stimuli in chimpanzees. In addition,

visual search (e.g. Tomonaga and Imura 2015) and visual dot probe tasks (e.g. Tomonaga and Imura 2009) have been used to investigate attentional biases towards faces in chimpanzees. However, to date, no visual dot probe or visual search studies have investigated attentional biases for threatening faces in chimpanzees. In the next section I will briefly introduce these tasks and relevant studies in human and non-human primates.

1.4. The visual dot probe paradigm

The dot probe task was originally developed in humans by MacLeod et al. (1986) with threatening words, and later by Bradley et al. (1997) with threatening faces. In the task, two stimuli (faces) are simultaneously presented on a screen for a short duration (traditionally 500 ms). Typically, one of the stimuli is threatening (angry face) and the other is neutral (non-expressive face). The stimuli disappear and a dot (probe) appears randomly in the spatial location of either the threatening face (congruent trial) or the neutral face (incongruent trial). Response times to detect the dot are recorded using computer keys. It is assumed that if attention is already fixated in the spatial location of one stimulus, detecting the dot in the same location will result in faster response times (Yiend 2010). Faster reaction times on congruent trials indicate attentional bias towards threatening faces (vigilance) and on incongruent trials attentional bias away from threatening faces (avoidance) (Staugaard 2010).

1.4.1. Human dot probe studies with threatening faces

The dot probe task has been used extensively to investigate the relationship between emotion and attention in humans. Attentional biases towards threatening faces are more consistently found in anxious than non-anxious people (Bar-Haim et al. 2007). However, whilst in some studies anxious participants show stronger attentional biases towards threatening faces compared with non-anxious participants (Klumpp and Amir 2009; Mogg and Bradley 2002; Mogg et al. 2004; Pishyar et al. 2004; Sposari and Rapee 2007; Stevens et al. 2009), in other

studies they show avoidance (Chen et al. 2002; Mansell et al. 1999) or no attentional bias (Bradley et al. 1997; Gotlib et al. 2004; Pineles and Mineka 2005). Several methodological differences likely account for these inconsistencies. Two of the most important moderating variables for measuring biases towards threatening faces are the duration between the start of the stimulus and the start of the dot presentation (stimulus onset asynchrony; SOA) and stimulus threat intensity (Cisler and Koster 2010; Yiend 2010; van Rooijen et al. 2017).

Several human studies have found attentional biases towards threatening faces at short SOAs. Stevens et al. (2009) found a bias towards threatening faces at 175 ms but not 600 ms, Cooper and Langton (2006) at 100 ms but not 500 ms, and Holmes et al. (2005) at 30 ms or 100 ms but not 500 ms or 1,000 ms. Biases towards threatening faces have also been found at the longer SOA of 500 ms but not 1,250 ms (Mogg et al. 2004; Bradley et al. 1998). Shorter SOAs are thought to facilitate threat detection by the amygdala and involve more automatic processing, whereas longer SOAs facilitate strategic processing by the prefrontal cortex and involve greater attentional control (Cisler and Koster 2010; Weierich et al. 2008). Overall, SOAs of less than 500 ms appear more suitable for measuring biases towards threatening faces.

Regarding stimuli threat intensity, faces expressing anger are often used as stimuli, as they are more salient, threatening and ecologically valid than words (Schmukle 2005; Staugaard 2009). An interesting study by Wilson and MacLeod (2003) investigated attentional bias to faces of different threat intensity in the dot probe task. Low anxiety participants showed biases towards morphed faces expressing very high anger, but not moderate anger. High anxiety participants showed a bias towards both very high and moderate anger faces. Overall, biases towards threatening faces increased with threat intensity. In a simplified dot probe task in humans, de Valk et al. (2015) found faster response times to touch angry faces than fearful or neutral faces. As angry faces signal a more direct threat to the observer, they likely have a higher threat intensity than fearful faces (Grillon and Charney 2011).

1.4.2. Non-human primate dot probe studies with threatening faces

Despite extensive use of the dot probe task to investigate attentional biases towards faces in humans, few studies have been conducted with non-human primates (see **Table 1.1**). Of these studies, only four have investigated biases towards threatening faces or whole-bodies. In six rhesus monkeys King et al. (2012) found a bias towards threatening conspecific faces presented for 1,000 ms. Also in six rhesus monkeys, Parr et al. (2013) found a bias towards conspecific threatening faces (bared teeth and open mouth threat expressions) presented for 500 ms. In great apes, Kret et al. (2016) presented four bonobos with conspecific scenes featuring the whole body and scenes of other animals (as control stimuli) in colour for 300 ms. Bonobo images consisted of emotional (i.e. distress, groom, sex, yawn, play, food, pant hoot) and neutral scenes. Attention was biased towards emotional scenes, with the strongest biases towards affiliative and protective behaviours such as sex, yawning and grooming. Kret et al. (2018) presented eight chimpanzees at the Primate Research Institute, Kyoto University, and 711 human participants, with chimpanzee and human threatening body expressions in the dot probe task. The chimpanzee stimuli featured fearful (bared teeth face), angry (bulging lip face) and neutral expressions. Human stimuli featured equivalent body and facial expressions. All stimuli combinations were presented subliminally (33 ms) and supraliminally (300 ms) with backwardly masked neutral body stimuli. It was predicted that subliminal presentation would result in stronger biases towards threatening expressions (Bar-Haim et al. 2007; Cisler and Koster 2010). However, chimpanzees failed to show biases towards either species at either presentation time. Interestingly, humans showed a bias towards both threatening chimpanzee and human expressions, although no difference in bias strength was found between presentation times. The authors suggest that failure to find biases in chimpanzees may be explained by the lower ecological validity of the stimuli compared to Kret et al. (2016) (i.e. greyscale and less naturalistic scenes). Moreover, humans may derive more emotional meaning from images.

Table 1.1. Summary of non-human primate dot probe studies featuring faces, or whole bodies with faces as stimuli (arranged by species and then chronological order).

Species	N	Reference	Stimuli	SOA (ms)	Bias
Rhesus monkeys	6	** King et al. 2012	Threat vs. neutral conspecific faces	1,000	Threat faces
Rhesus monkeys	6	** Parr et al. 2013	Threat vs. scrambled conspecific faces	500	Threat faces
Japanese macaques	2	* Koda et al. 2013	Infant vs. adult conspecific faces	100	No infant bias
Bonobos	4	** Kret et al. 2016	Emotional vs. neutral conspecific scenes	300	Emotional scenes (affiliative)
Chimpanzees	3	* Tomonaga & Imura 2009	Human and conspecific faces or bananas vs. objects	200	Face-specific
Chimpanzees	8	** Kret et al. 2018	Threat vs. neutral conspecific bodies	33 & 300	No threat bias

* Relevant studies ** Especially relevant studies

Overall, evidence from non-human primate studies suggests that the dot probe task can measure attentional biases towards threatening stimuli in monkeys and great apes. However, many methodological inconsistencies in both the human and non-human primate literature exist, including but not limited to: SOA duration, stimuli threat intensity, stimuli pair combination and response methods. Nevertheless, the task offers a promising method to investigate attentional bias in non-human primates. Furthermore, the task is implicit and requires little training, making it ideal for use with non-human primates (van Rooijen et al. 2017).

1.5. The visual search paradigm

In the visual search task a target stimulus is presented amongst a number of ‘distractor’ stimuli, with the aim being to detect the target as quickly as possible (Treisman and Gelade 1980). In a typical visual search experiment using facial expressions, a target face with one type of

expression is presented on a screen amongst a set of distractor faces with another type of expression. Response times and accuracy to detect the target are recorded and indicate the efficiency with which the target is detected. If the facial expression influences attentional allocation search efficiency should differ between expressions (Frischen et al. 2008). For targets that are easy to detect, response times typically do not vary with set size (the number of items in a search array) resulting in a flat search slope. Such rapid target detection is thought to involve parallel search of all items and unconscious and automatic processing (Hansen and Hansen 1988). For targets that are more difficult to detect, response times typically increase with set size. This involves serial search of each item and more conscious and strategic processing. Detection of threatening stimuli is thought to involve unconscious and automatic processing in the visual search task (e.g. Öhman and Mineka 2001).

1.5.1. Human visual search studies with threatening faces

Many human visual search studies examining attentional biases towards facial expressions have used schematic drawings of faces (for a review see Horstmann 2007). Whilst schematic faces allow for greater experimental control, they are less ecologically valid than photographs of real faces and not frequently used in non-human primate studies (although see Tomonaga 2007a). For human visual search studies using real faces, the majority use angry and happy expressions (Calvo and Nummenmaa 2008). Whilst some real face studies have found angry face targets are detected faster amongst neutral face distractors than vice versa (e.g. Fox and Damjanovic 2006; Hansen and Hansen 1988; Horstmann and Bauland 2006) other studies have not (e.g. Byrne and Eysenck 1995; Calvo and Nummenmaa 2008; Fox and Damjanovic 2006; Gilboa-Schechtman et al. 1999; Juth et al. 2005; Purcell et al. 1996; Williams et al. 2005). In addition, several studies have found more efficient search for happy faces compared with angry faces (e.g. Byrne and Eysenck 1995; Juth et al. 2005). This happy superiority advantage is likely explained by the visual saliency of the mouth and teeth. In addition, it has been suggested

that angry faces are less uniform in appearance making them more difficult to detect than happy faces (Calvo and Nummenmaa 2008; Calvo and Marrero 2009). Therefore, differences in search efficiency for angry and happy faces could be explained by perceptual differences in specific facial features, rather than emotional expression itself (Savage et al. 2013).

1.5.2. Non-human primate visual search studies with threatening faces

In non-human primates, most of the work on visual search for faces has been conducted in monkeys and chimpanzees (**see Table 1.2**). To my knowledge, only one study has specifically examined visual search for threatening faces in non-human primates. Kawai et al. (2016) found that three Japanese macaques were faster to detect conspecific threatening face targets amongst neutral face distractors than vice versa. No difference in response times to detect non-face targets (computer pictures) amongst neutral or threatening face distractors was found, suggesting that the threatening face *target* facilitated faster detection. This study provides the first evidence for an attentional bias towards threatening faces in non-human primates.

Table 1.2. Summary of non-human primate visual search studies featuring faces, or whole bodies with faces as stimuli (arranged by species and then chronological order).

Species	N	Reference	Targets	Distractors	Bias
Japanese macaques	3	** Kawai et al. 2016	Threat faces Neutral faces	Neutral faces Threat faces	Threat faces
Chimpanzees	1	* Tomonaga 1999	Human faces/ chimpanzee faces Houses	Houses Human faces/ chimpanzee faces	Faces
Chimpanzees	1	* Tomonaga 2007a	Human faces/ dog faces Hands/chairs	Hands/chairs Human faces/ dog faces	Faces
Chimpanzees	1	* Tomonaga & Imura 2010	Human direct gaze Human averted gaze	Human averted gaze Human direct gaze	Direct gaze
Chimpanzees	3	* Tomonaga & Imura 2015	Human faces/ chimpanzee faces House/car/banana	House/car/banana Human faces/ Chimpanzee faces	Faces

* Relevant studies ** Especially relevant studies

1.5.3. Summary

In summary, human and non-human primate visual dot probe and visual search studies provide mixed evidence for attentional biases towards threatening faces. Stimuli threat intensity and presentation time are important moderating factors in the dot probe task. In humans, the optimum SOA for facilitated attention towards threatening faces is around 100 ms. In non-human primates, biases have been found at 500-1,000 ms (King et al. 2012; Parr et al. 2013) suggesting more strategic processing. However, SOAs optimal for facilitated attention in humans have yet to be tested in non-human primates. In visual search studies, there is evidence that humans and monkeys show attentional biases towards threatening faces. However, these biases may reflect attention towards perceptual properties rather than emotional expression. In addition, unlike in some human studies with snakes (e.g. Öhman et al. 2001) there is no evidence of automatic processing of threatening real faces in the visual search task.

1.6. Thesis outline and experimental approach

1.6.1. Main aim

The main aim of this thesis is to explore if attentional biases towards threatening faces can be measured in chimpanzees using two well-established experimental methods from human psychological research, the visual dot probe task and the visual search task. It is hoped that these tasks will provide insight into the attentional mechanisms underlying bias towards threatening faces in chimpanzees and how they have developed as evolutionary adaptations.

1.6.2. Facial stimuli selection and preparation

The main threatening face stimuli set used in the dot probe and visual search tasks consisted of conspecific neutral, bared teeth and scream expressions. As mentioned above, threat intensity is an important moderating factor for measuring biases in the dot probe task (e.g. Wilson and MacLeod 2003). Bared teeth expressions occur in response to aggression and likely reflect fear,

whereas scream expressions occur in contexts of general agonism and likely reflect anger (Parr et al. 2005; Parr et al. 2007). Although fearful and angry faces both occur in threatening contexts, fearful faces signal an external threat in the environment, whereas angry faces signal a direct threat to the observer (Grillon and Charney 2011). On this basis, I categorised bared teeth faces as ‘lower threat intensity’ and scream faces as ‘higher threat intensity’ expressions. The bared teeth and scream expressions were categorised with the assistance of a certified ChimpFACS coder. In addition, the threatening faces were also categorised on the basis of their perceptual similarity to each other. A previous study with chimpanzees found more shared facial features with bared teeth and scream faces than neutral faces (Parr et al. 1998). Therefore, threatening (bared teeth and scream) and neutral expressions were categorised as ‘perceptually more different’ and bared teeth and scream expressions as ‘perceptually more similar’.

The main non-threatening face stimuli set used in the attentional tasks consisted of primate faces; chimpanzee, orangutan and baboon faces (with neutral expressions). The faces served as additional control stimuli to determine that any biases observed towards the threatening faces are threat-specific and not also found towards non-threatening faces. Primate faces were chosen as they are social but not overtly threatening. The primate faces were initially categorised on the basis of my subjective judgement of their relative perceptual similarity to each other. I categorised baboon and great ape faces (chimpanzee and orangutan) as ‘perceptually more different’ and chimpanzee and orangutan faces as ‘perceptually more similar’. All stimuli featured faces of individuals unfamiliar to the chimpanzees and were presented in greyscale. In addition, luminance was equalised across faces to control for colour hue, luminance and low-level features which may inadvertently bias attention.

1.6.3. Experimental approach

Chapter 2: Visual discrimination of faces in chimpanzees. This chapter consists of two studies on visual discrimination of primate faces in a series of touchscreen MTS experiments.

The primary aim of these experiments was to confirm that the chimpanzees could discriminate the main stimuli sets before using them in the dot probe task. This step was important because failure to find an attentional bias effect could be explained by the chimpanzees' inability to visually discriminate the faces rather than the absence of a bias. A secondary aim was to understand in greater depth the visual (perceptual similarity) and non-visual (familiarity) elements of faces important for discrimination. In the first study on primate face discrimination (**Chapter 2-1: Visual discrimination of primate species based on faces in chimpanzees**) I predicted better discrimination performance (higher accuracy and faster response times) for highly familiar and perceptually different species than unfamiliar and perceptually similar species. In the second study using conspecific threatening faces (**Chapter 2-2: Visual discrimination of threatening faces in chimpanzees**) I predicted better discrimination performance for perceptually different than similar expressions.

Chapter 3: Exploring attentional bias towards threatening faces in chimpanzees using the dot probe task. This chapter examined attentional bias towards conspecific threatening faces in a series of touchscreen dot probe experiments. The primary aim of the experiments was to investigate if the task can measure attentional biases towards threatening faces. I predicted faster response times to touch the dot replacing threatening faces than neutral and scrambled faces. I also predicted faster response times towards faces of higher than lower threat intensity.

Chapter 4: Search asymmetry for threatening faces in chimpanzees. This chapter examined attentional bias towards threatening faces in a series of MTS visual search experiments. The primary aim of the experiments was to investigate if the task can measure attentional biases towards threatening faces. I predicted more efficient search for threatening face targets amongst neutral face distractors than vice versa. I also predicted more efficient search for higher threat intensity face targets amongst lower threat intensity distractors than vice versa.

CHAPTER 2

VISUAL DISCRIMINATION OF FACES IN CHIMPANZEES

CHAPTER 2-1

VISUAL DISCRIMINATION OF PRIMATE SPECIES BASED ON FACES IN CHIMPANZEES

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2-1.1. Abstract

Many primate studies have investigated discrimination of individual faces within the same species. However, few studies have looked at discrimination between primate species faces at the categorical level. This study systematically examined the factors important for visual discrimination between primate species faces in chimpanzees, including colour, orientation, familiarity and perceptual similarity. Five adult female chimpanzees were tested on their ability to discriminate identical and categorical (non-identical) images of different primate species faces in a series of touchscreen matching-to-sample experiments. Discrimination performance for chimpanzee, gorilla and orangutan faces was better in colour than in greyscale. An inversion effect was also found, with higher accuracy for upright than inverted faces. Discrimination performance for unfamiliar (baboon and capuchin monkey) and highly familiar (chimpanzee and human) but perceptually different species was equally high. After excluding effects of colour and familiarity, difficulty in discriminating between different species faces can be best explained by their perceptual similarity to each other. Categorical discrimination performance for unfamiliar, perceptually similar faces (gorilla and orangutan) was significantly worse than unfamiliar, perceptually different faces (baboon and capuchin monkey). Moreover, multidimensional scaling analysis of the image similarity data based on local feature matching revealed greater similarity between chimpanzee, gorilla and orangutan faces than between human, baboon and capuchin monkey faces. I conclude our chimpanzees appear to perceive similarity in primate faces in a similar way to humans. Information about perceptual similarity is likely prioritised over the potential influence of previous experience or a conceptual representation of species for categorical discrimination between species faces.

2-1.2. Introduction

For primates the most important visual cue for gathering social information about another individual is the face (Fujita 1993a; Spencer et al. 1997; Burton et al. 1999). Information about identity, age, gender and emotion can be extracted from the face and facial information leads to the fastest and most accurate identification of an individual (Dahl et al. 2013a; Kano and Tomonaga 2009; Parr 2011; Pascalis and Wirth 2011). The face is also used to discriminate between individuals within the same species and other prey or predator species (Pascalis and Wirth 2011).

Exactly how facial features are processed in human and non-human animals has been a topic of intense study for decades (Bruce and Young 1986; Ge et al. 2009; Valentine 1991). Diamond and Carey (1986) propose that faces are processed according to first and second-order relational features. First-order relational features refer to the eyes, nose and mouth and their fixed position relative to each other, used to discriminate between face and non-face stimuli. Second-order relational features refer to the relative spatial distances between facial features, used to discriminate between the faces of different individuals. Interestingly, when faces are inverted judging distances between their second-order relational features becomes more difficult compared to non-face stimuli. This is known as the ‘inversion effect’ (Yin 1969). The inversion effect is consistently found in humans (Goldstein 1965; Scapinello and Yarmey 1970; Yin 1969) and chimpanzees (Dahl et al. 2013c; Parr et al. 1998; Tomonaga 1999, 2007). Faces are thought to be processed configurally. Configural processing refers to “the emergent features of a face that only become apparent when two or more of its basic features (e.g., the eyes, nose, or mouth) are processed at the same time.” (Piepers and Robbins 2012, p. 2). The integration of this information into a perceptual whole allows individual recognition and discrimination within and between other species (Parr 2011).

A number of primate studies have investigated visual discrimination of species based

on whole body images, including the face. Humphrey (1974) conducted one of the earliest experiments on species discrimination in rhesus monkeys using a habituation task. The monkeys could distinguish individuals within their own species but not between species. Fujita (1987, 1990, 1993b) and Fujita and Watanabe (1995) found longer looking durations for own-species images in Japanese macaques and rhesus monkeys using a sensory reinforcement procedure. In addition, Demaria and Thierry (1988) observed stumptailed macaques looked for longer at own-species images compared to other macaque species images. These experiments show a consistent advantage for processing own species faces in monkeys.

In contrast, in chimpanzees Tanaka (2003, 2007) found a visual preference for human stimuli over other primate species in free-choice tasks. Tanaka (2003) presented five adult chimpanzees with images of humans, chimpanzees, gorillas, orangutans and other monkey species. Human images were touched more than any other species and preference strength did not differ with phylogenetic distance from chimpanzees. Later, Tanaka (2007) tested eight adult and three infant chimpanzees using the same paradigm and species categories. Consistent with the previous study, adult chimpanzees showed a preference for humans, whilst infants showed a preference for either chimpanzees or no species preference. These differences may be explained by social experience during infancy; the adult chimpanzees were mainly raised by humans, whereas the infants were raised by their mothers. Conspecific social experience during infancy may also account for the own-species preferences found in earlier monkeys studies (Fujita 1990, 1993b).

Several studies have also investigated visual discrimination of species based on stimuli featuring only faces. Pascalis and Bachevalier (1998) used a visual paired-comparison (VPC) task to investigate species preference in humans and macaques. In the VPC task a preference for looking at new stimuli is measured after a period of familiarisation with another stimulus. Looking longer at the new stimulus indicates recognition of the familiarised stimulus. An own-

species effect across species was found; humans showed a novelty preference for human faces but not monkey faces, whereas monkeys showed the opposite preference. Dufour et al. (2006) examined recognition of different species faces using the VPC task in humans, Tonkean macaques and brown capuchin monkeys and found recognition was limited to own-species faces. Dahl et al. (2007) used an adaptation paradigm with rhesus monkeys and found they were better at identifying individuals within their own species compared to other species and processed the faces configurally. Gothard et al. (2009) found macaques can recognise individual faces of both macaques and humans. However, recognising own-species faces involved configural and feature-based processing, whilst recognising human faces mainly involved feature-based processing. Consistent with discrimination studies involving the whole body and face, own-species effects are also observed with stimuli featuring only the face.

Related to the own-species effect, other studies have focused on the influence of experience and familiarity. An interesting study in chimpanzees by Martin-Malivel and Okada (2007) used a matching-to-sample task (MTS) to investigate the influence of familiarity on categorical perception (CP) of morphed human and chimpanzee faces. CP “occurs when members of a class of stimuli which vary in their sensory characteristics are nevertheless processed as if they are equivalent.” (Campbell et al. 1997, p. 1429). They found one group of chimpanzees more exposed to human faces than chimpanzee faces showed better discrimination of human than chimpanzee faces, and a CP effect for human faces. In another group of chimpanzees, familiar with both chimpanzees and humans, no discrimination advantage or CP effects for human or chimpanzee faces were found. Also in chimpanzees, Dahl et al. (2013b) investigated the effects of lifetime experience on discriminating individual chimpanzee and human faces using a delayed MTS task. Infant chimpanzees were better at discriminating chimpanzee faces and older chimpanzees were better at discriminating human faces. These results support Tanaka (2003, 2007) in demonstrating the importance of

developmental experience in species discrimination in the same group of chimpanzees.

In addition to experience and familiarity, perceptual features are also important for individual and species discrimination. For example, Quinn and Eimas (1996) found three to four month old human infants used the internal features and outer edges of the face to discriminate between cat and dog images. Roberts and Mazmanian (1988) showed humans had greater difficulty in discriminating between pictures of kingfishers and other birds in greyscale compared to colour. Parr et al. (2000) demonstrated chimpanzees were worse at discriminating conspecific faces with masked eyes compared to control stimuli, but rhesus monkeys were worse when both the eyes and mouth were masked. Marsh and MacDonald (2008) studied the classification of great ape, gibbon and monkey, and prosimian faces by orangutans using a two-choice touch screen procedure. Discrimination performance was best for stimuli in colour and featuring the face only, and worst for stimuli in greyscale and with modified eyes, i.e. removed eyes or inserted infant eyes. Together, such visual cues help primates to discriminate faces.

Although many studies have investigated discrimination of individual faces within the same species, few studies have investigated discrimination between primate species faces at the categorical level, especially in chimpanzees. The aim of the current study was to systematically examine the factors important for visual discrimination between different species faces in chimpanzees using a MTS task. Examining how chimpanzees, our closest living relatives, visually discriminate between primate species faces may give us greater insight into how the human visual system has evolved to perceive similarities and differences in categories of faces. I predicted discrimination accuracy would be higher for faces in colour than greyscale, upright than inverted orientation, highly familiar than unfamiliar species faces, and perceptually different than perceptually similar species faces. In addition, higher discrimination accuracy was predicted for identical compared to categorical (non-identical) faces within the same species.

2-1.3. Methods

2-1.3.1. Participants and housing

Five adult female chimpanzees (*Pan troglodytes*) participated in the study at the Primate Research Institute, Kyoto University (KUPRI), Japan (**Table 2-1**) (Watanuki et al. 2014). The chimpanzees were members of a social group of 12 individuals living in an environmentally enriched facility consisting of two outdoor enclosures (250 m² and 280 m²), an open-air outdoor enclosure (700 m²) and indoor living rooms linked to testing rooms. The open air outdoor enclosure was equipped with 15 m high climbing frames and included streams and trees (Matsuzawa et al. 2006; Yamanashi and Hayashi 2011). No food or water deprivation was used in the study. The experimental protocol was approved by the Animal Welfare and Care Committee of the KUPRI and the Animal Research Committee of Kyoto University and followed the *Guidelines for the Care and Use of Laboratory Primates* of the KUPRI (Version 3, 2010). The chimpanzees had extensive experience participating in perceptual and cognitive tasks using a touchscreen, including MTS tasks (e.g. Dahl et al. 2013b; Tomonaga 1999).

Table 2-1. Basic information about the five chimpanzees

Name	GAIN ID Number ^a	Sex	Age (at study start)
Ai	0434	Female	40
Chloe	0441	Female	36
Cleo	0609	Female	16
Pal	0611	Female	16
Pendensa	0095	Female	38

^aIdentification number (ID) for each chimpanzee listed in the database of the Great Ape Information Network (GAIN): <https://shigen.nig.ac.jp/gain/>

2-1.3.2. Apparatus

Experiments were conducted in an experimental booth ($1.80 \times 2.15 \times 1.75$ m) inside a testing room. Each chimpanzee voluntarily walked to the booth through an overhead walkway connected to the living rooms. Two 17-inch touch-sensitive LCD monitors (1280×1024 pixels) encased inside Plexiglas were used to present visual stimuli at approximately 40 cm distance. Food rewards (eight-millimetre apple cubes) were delivered via a universal feeder device. All experimental events were controlled by a PC and the computer task was programmed using Microsoft Visual Basic 2010 (Express Edition).

2-1.3.3. Stimuli

Photographs (200×225 pixels) of six species of primate faces including; chimpanzee (*Pan troglodytes*), western lowland gorilla (*Gorilla gorilla*), orangutan (*Pongo pygmaeus* and *Pongo abelii*) (20 images each), Japanese human (*Homo sapiens*), olive baboon (*Papio anubis*) and white-headed capuchin monkey (*Cebus capucinus*) faces (10 images each) were obtained from the internet and colleagues. All images were cropped and featured unfamiliar faces with a neutral closed-mouth expression against a variety of naturalistic backgrounds. The images were prepared in colour, greyscale, upright and inverted format and controlled for luminance and contrast using Adobe Photoshop CS2 (Version 9.0). In addition, for conditions presenting faces of two primate species, 10 ‘random dot’ control images (five images for each species) were composed by randomly assigning each pixel of the original primate face images to a new position. This procedure ensured content-related information was removed while average brightness levels were maintained.

2-1.3.4. Procedure

The chimpanzees participated in a series of zero-delay MTS tasks (**Figure 2-1.1**). To begin each trial the chimpanzees touched a blue start key at the bottom-center of the screen, followed by a sample stimulus directly above the start key position. When the sample was touched it

disappeared and three comparison stimuli appeared in the middle of the screen. When a correct choice was made (the comparison touched matched the sample) a chime sound was played and a food reward given, when an incorrect choice was made (the comparison did not match the sample) a buzzer sound was played and no food reward given. The inter-trial interval was two seconds. The number of correct choices and response times (ms) were recorded by a PC.



Figure 2-1.1 Chimpanzee 'Pal' choosing an orangutan face in the colour condition

2-1.3.5. Conditions

The study consisted of five conditions to investigate the influence of colour, orientation, familiarity, and perceptual similarity on the ability to discriminate primate faces under identical and categorical matching formats. On identical matching trials, the sample and correct comparison stimuli were identical to each other, whilst on categorical matching trials, the images were different from each other but within the same species category. Identical and categorical matching was alternated on each trial in each of the conditions. For the orientation condition only identical matching was presented. The chimpanzees completed a total of 864

trials (72 trials $\times$ 12 sessions) for each condition. Trial order was randomised within and across sessions.

In Condition 1 the chimpanzees matched chimpanzee, gorilla and orangutan faces in colour and greyscale. In Condition 2 they matched the same species in upright and inverted orientation in greyscale. Both the sample and comparison images were presented in the same orientation (Tomonaga 1999; Dahl et al. 2013c). In Conditions 3, 4 and 5 they matched greyscale baboon and capuchin monkey faces (unfamiliar and perceptually different), chimpanzee and human faces (highly familiar and perceptually different), and orangutan and gorilla faces (unfamiliar and perceptually similar) respectively. Perceptual similarity was defined as the relative similarity between faces of two different species as perceived by the experimenters. In Conditions 3, 4 and 5 a third ‘random dot’ control image was added to the two comparison face images to ensure an equal number of choices across all conditions. Ten novel chimpanzee, gorilla and orangutan faces were used in Conditions 4 and 5 to reduce the possible influence of learning effects.

2-1.3.6. Image similarity analysis

Similarity between chimpanzee, orangutan, and gorilla faces (20 images each) and baboon, capuchin monkey and human faces (10 images each) in greyscale was calculated. First, the faces were aligned vertically and eyes positioned centrally. Using a customised programme written in Python and OpenCV commands AKAZE (Accelerated KAZE) local features were then extracted (cf. Alcantarilla, Nuevo and Bartoli 2011). These features were analysed using the Brute-Force Matcher method and “cv2.bfmatcher” function. The programme generated similarity values for each face pair, where lower values indicate higher similarity based on local feature matching (OpenCV Development Team, 2014). This similarity-matrix data was used for metric multidimensional scaling using the “cmdscale” function in the library “stats” of R version. 3.2.2 (R Core Team, 2015). This produced spatial representations of similarities

between stimuli. I adopted a two-dimensional solution for the present analysis. To evaluate goodness of fit, the “cmdscale” function generated a GOF (Goodness of Fit) value. The higher the GOF value the better the spatial solution.

2-1.3.7. Statistical analysis

The data were analysed using SPSS (version 23). Paired-comparison *t*-tests and repeated measures analysis of variance (ANOVAs) were used to analyse accuracy (the mean number of correct choices) and response times (on correct trials). One-sample *t*-tests were used to analyse difference in accuracy from chance level. Trials with response times of five seconds or longer after the sample image presentation disappeared may not have been retained and so were excluded from the analysis. In Conditions 3, 4 and 5 the third random dot control image was never touched and so chance level was 50%.

2-1.4. Results

2-1.4.1. Condition 1: Colour effects

Figure 2-1.2. shows the mean percentage of correct choices for identical and categorical matching in colour and greyscale. One-sample *t*-tests found accuracy was above chance level (33.33%) in all conditions; identical colour ($M = 95\%$ correct, $t_{(4)} = 42.59$, $p < .001$), categorical colour ($M = 59\%$ correct, $t_{(4)} = 16.92$, $p < .001$), identical greyscale ($M = 87\%$ correct, $t_{(4)} = 20.49$, $p < .001$) and categorical greyscale ($M = 44\%$ correct, $t_{(4)} = 3.30$, $p = .030$). A two-way ANOVA, with colour type (colour and greyscale) and matching type (identical and categorical) as independent variables was conducted. A main effect of colour type on accuracy was found, with higher accuracy for colour ($M = 77\%$ correct) than greyscale ($M = 65\%$ correct) matching ($F_{(1,4)} = 172.19$, $p < .001$). A main effect of matching type was also found, with higher accuracy for identical ($M = 91\%$ correct) than categorical ($M = 52\%$ correct) matching ($F_{(1,4)} = 166.38$, $p < .001$). No interactions were found. For response times on correct trials, a two-way ANOVA

found a main effect of colour type, with faster response times for colour ($M = 768$ ms) than greyscale ($M = 938$ ms) matching ($F_{(1,4)} = 25.46, p = .007$). A main effect of matching type was found, with faster response times for identical ($M = 696$ ms) than categorical ($M = 1010$ ms) matching ($F_{(1,4)} = 27.29, p = .006$). No interactions were found. For Individual chimpanzee data see **Appendix I**.

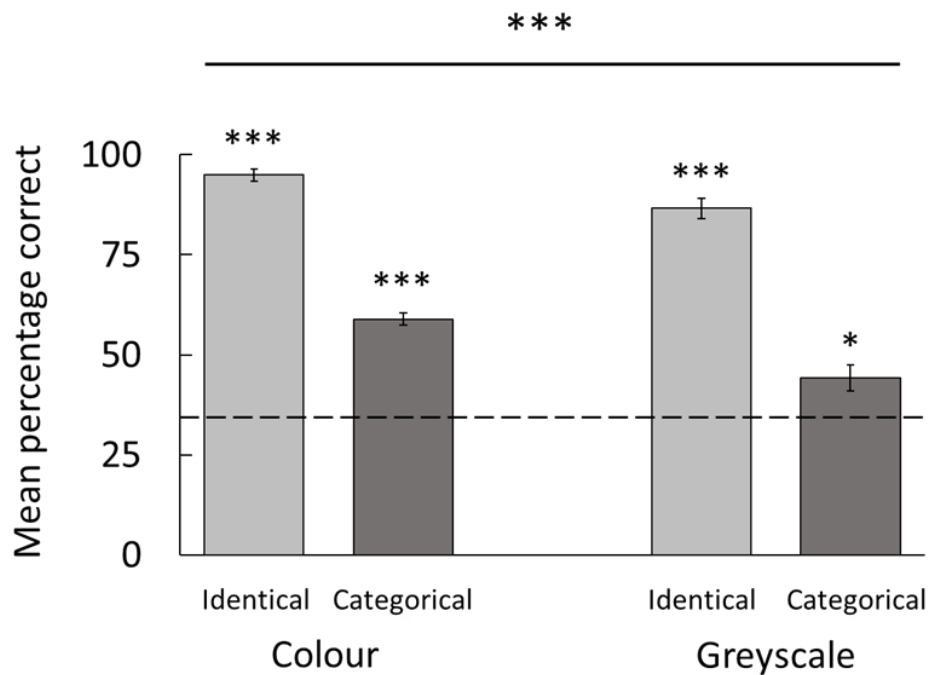


Figure 2-1.2 Mean percentage of correct choices for identical and categorical matching of chimpanzee, gorilla and orangutan faces in colour and greyscale. The solid horizontal line indicates a main effect of colour on accuracy. The dashed line represents 33.33% chance level. Error bars represent the standard error of the mean

2-1.4.2. Condition 2: Orientation effects

Figure 2-1.3. shows the mean percentage of correct choices for identical matching in upright and inverted orientation in greyscale. One sample t -tests found accuracy was above chance level (33.33%) in both orientations; upright ($t_{(4)} = 8.91, p = .001$) and inverted ($t_{(4)} = 8.84, p = .001$). A paired comparison t -test found accuracy was higher for upright ($M = 75\%$ correct) than inverted ($M = 66\%$ correct) matching ($t_{(4)} = 3.06, p = .038$). A paired comparison t -test

found no difference in response times on correct trials between upright ($M = 889$ ms) and inverted ($M = 882$ ms) orientation. For individual chimpanzee data see **Appendix II**.

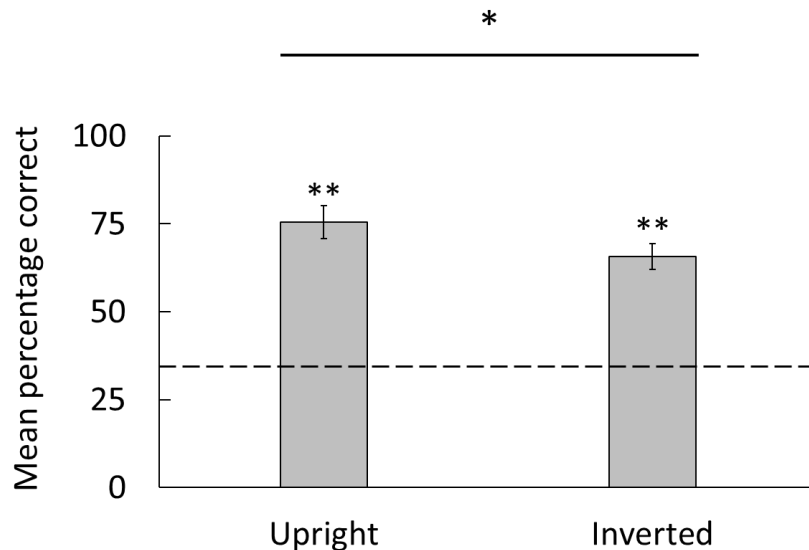


Figure 2-1.3 Mean percentage of correct choices for identical matching of chimpanzee, gorilla and orangutan faces in upright and inverted orientation in greyscale. The solid horizontal line indicates a significant difference in accuracy between orientation presentations. The dashed line represents 33.33% chance level. Error bars represent the standard error of the mean

2-1.4.3. Conditions 3, 4 and 5: Familiarity and perceptual similarity effects

Figure 2-1.4. shows the mean percentage of correct choices for identical and categorical matching of baboon and capuchin monkey (Condition 3), chimpanzee and human (Condition 4), and gorilla and orangutan (Condition 5) faces in greyscale. One-sample t -tests found accuracy was above chance level (50%) in all conditions; baboon and capuchin monkey (identical: $M = 91\%$ correct, $t_{(4)} = 20.67$, $p < .001$), (categorical: $M = 82\%$ correct, $t_{(4)} = 15.43$, $p < .001$), chimpanzee and human (identical: $M = 95\%$ correct, $t_{(4)} = 23.79$, $p < .001$), (categorical: $M = 87\%$ correct, $t_{(4)} = 10.72$, $p < .001$) and gorilla and orangutan (identical: $M = 83\%$ correct, $t_{(4)} = 14.03$, $p < .001$), (categorical: $M = 58\%$, $t_{(4)} = 8.77$, $p = .001$). A 3 x 2 ANOVA with stimulus type (baboon and capuchin monkey, chimpanzee and human, and gorilla and orangutan) and matching type (identical and categorical) as independent variables was conducted. A main effect of stimulus type was found with higher accuracy for matching

baboon and capuchin monkey ($M = 87\%$) and chimpanzee and human ($M = 91\%$) than gorilla and orangutan ($M = 70\%$) faces ($F_{(2,8)} = 26.48, p < .001$). A main effect of matching type was found, with higher accuracy for identical ($M = 90\%$) than categorical ($M = 76\%$) matching ($F_{(1,4)} = 78.30, p < .001$). An interaction between stimulus type and matching type was found, with a sharp decline in accuracy for categorical gorilla and orangutan face matching ($F_{(1,4)} = 51.80, p < .001$). For response times on correct trials a 3 x 2 ANOVA was conducted. A main effect of stimulus type was found ($F_{(1,4)} = 4.60, p = .047$) with longer response times for matching gorilla and orangutan (772 ms) than baboon and capuchin monkey (698 ms) or chimpanzee and human (668 ms) faces. A main effect of matching type was found with faster response times for identical (669 ms) than categorical (756 ms) matching ($F_{(1,4)} = 48.93, p = .002$). No interactions were found. For individual chimpanzee data see **Appendix III**.

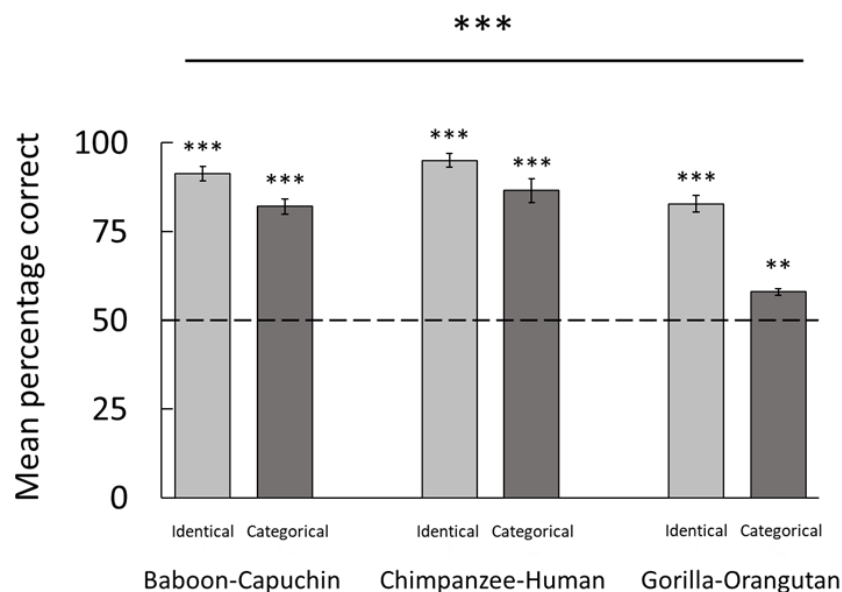


Figure 2-1.4 Mean percentage of correct choices for identical and categorical matching of baboon and capuchin monkey, chimpanzee and human, and gorilla and orangutan faces in greyscale. The solid horizontal line indicates a main effect of stimulus type on accuracy. The dashed line represents 50% chance level. Error bars represent the standard error of the mean

2-1.4.4. Image similarity analysis

Figure 2-1.5. shows the two-dimensional representation of the Multidimensional Scaling analysis of the image similarity data based on local feature matching. The GOF value was 0.207.

The chimpanzee, gorilla and orangutan features were grouped more closely together indicating greater image similarity, and the human, baboon and capuchin monkey features were grouped further away indicating less similarity.

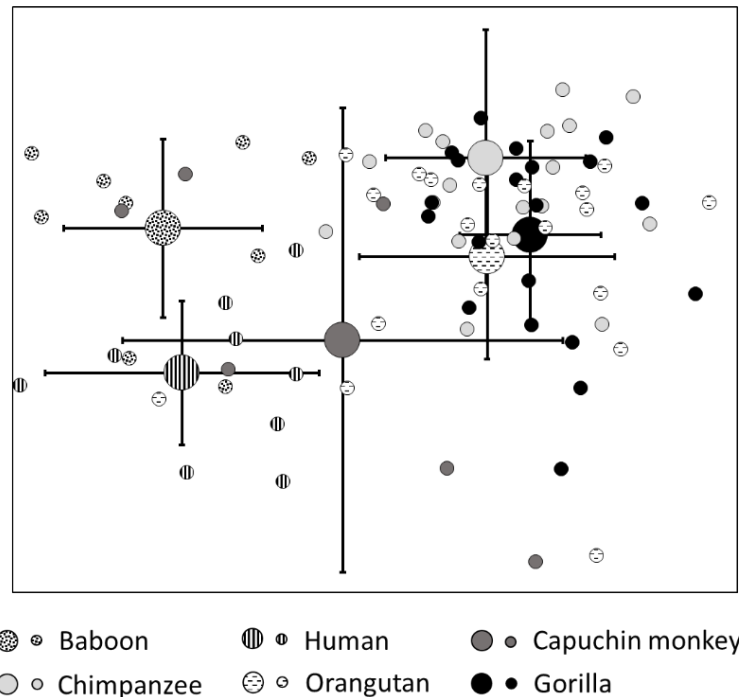


Figure 2-1.5 Two-dimensional representation of the Multidimensional Scaling analysis of the image similarity data based on local feature matching. Large circles represent average values and small circles represent individual values. Chimpanzee, gorilla and orangutan faces consisted of 20 images each, and human, baboon and capuchin monkey faces consisted of 10 images each

2-1.5. Discussion

This study focused on the visual elements important for categorical discrimination between primate species faces. As predicted, discrimination performance for great ape faces was better in colour than in greyscale. This is consistent with the findings of Roberts and Mazmanian (1988) in humans and Marsh and MacDonald (2008) in orangutans, that pictures of animals and faces are easier to discriminate in colour than greyscale. An inversion effect for discriminating great ape faces was found, with lower accuracy for discriminating inverted faces, suggesting the stimuli were perceived as faces and processed configurally. Previous MTS and visual search studies with our chimpanzees (Tomonaga 1999, 2007) have found

inversion effects for images of faces but not houses, chairs or hands as control stimuli, suggesting my results are also face-specific.

Interestingly, although discrimination performance was high for both unfamiliar (baboon and capuchin monkey) and highly familiar (chimpanzee and human) perceptually different species faces, it was not significantly better for highly familiar species faces as predicted. Two studies in chimpanzees have examined the influence of familiarity on discrimination of individual human and chimpanzee faces using the MTS task (Dahl et al. 2013b; Martin-Malivel and Okada 2007). Both studies found discrimination accuracy was highest for species to which the chimpanzees had the most real-life previous exposure. Given that previous experience enhances discrimination of individual faces within species, why did previous experience appear to have no influence on discrimination between species at the categorical level in the current study?

One explanation may be from an evolutionary perspective, discrimination of individuals within one's own species is especially important for the social lives of primates. In chimpanzees, higher-order features (a combination of first and second-order features) influence individual face discrimination within species (Dahl et al. 2013b; Martin-Malivel and Okada 2007). However, discrimination between individuals of other species, or between species at the categorical level, is less socially relevant and likely to involve fewer processing resources allocated to recognition (Pascalis and Wirth 2011). Studies examining the other-race effect have found humans are better at recognising faces of individuals within their own race and better at categorising faces of other races (Ge et al. 2009; Levin 1996, 2000). This may be due to greater processing resources allocated to individuating information of own-race faces we are experienced with, and to categorical information of other-race faces we are less experienced with (Ge et al. 2009). Similarly, when discriminating between categories of primate species

faces, rather than within own-species faces, our chimpanzees may have paid more attention to information important for categorisation than recognition.

Another explanation is the perceived similarity between species faces. I chose primate faces representing a range of phylogenetic groups including humans, great apes, old world monkeys and new world monkeys, to examine the potential relationship between phylogenetic distance and discrimination ability. Performance for categorical discrimination of unfamiliar, perceptually similar and phylogenetically closer faces (gorilla and orangutan) was significantly worse than for unfamiliar, perceptually different and phylogenetically more distant faces (baboon and capuchin monkey). In support of this finding, Campbell et al. (1997) found humans were better able to discriminate between physically morphed faces of monkeys and cows, and humans and cows, compared to humans and monkeys. Categorical perception was sharpest for monkey and cow and human and cow faces, suggesting the phylogenetically and morphologically closer human and monkey faces were perceived as more similar to each other. In our chimpanzees, Tanaka (2003, 2007) did not find a relationship between visual preference of primate species and phylogenetic distance from chimpanzees, although they were not required to directly discriminate between species. After excluding effects of colour and familiarity, I propose difficulty in discriminating between primate species faces can be best explained by their perceived similarity to each other. This conclusion is supported by both the behavioural data; categorical discrimination performance for perceptually similar primate faces was significantly worse than for perceptually different faces, and the Multidimensional Scaling analysis of the stimuli; greater local feature similarity between chimpanzee, gorilla and orangutan faces than between human, baboon and capuchin monkey faces. Greater perceptual similarity between great ape faces likely explains the relatively poor discrimination performance in the absence of colour cues, and greater perceptual difference explains the high discrimination performance for baboon and capuchin monkey, and chimpanzee and human

faces. Although I do not exclude the possibility previous experience has some influence on categorical discrimination between species faces, information about perceptual similarity appears to be prioritised. This could have masked the potential influence of previous experience or a conceptual representation of species (cf. Martin-Malivel et al. 2006).

In this study I made subjective judgements about the relative perceptual similarity of primate species faces. This was subsequently supported by the objective Multidimensional Scaling analysis of the stimuli. However, a useful future extension to this study would be to test whether my findings generalise across primate species, by testing them under the same experimental conditions as our chimpanzees. If the same pattern of responses are found, I could more concretely conclude non-human primates perceive similarity in different species faces like humans. In addition, although the Multidimensional Scaling analysis revealed the relative similarities between faces by local feature matching, it does not tell us which specific features, e.g. external face contours or internal features such as the eyes, nose, and mouth may be responsible for discrimination between species. Although the inversion effect I observed provides evidence of configural processing, further analysis of part-based processing by extracting curvature information about the eyes, nose and mouth image surfaces (e.g. Dahl et al. 2014a, b) or systematic removal of different facial features (e.g. Parr et al. 2000; Quinn and Eimas 1996; Tomonaga and Imura 2015) may help to reveal features most important for between species discrimination. Finally, I acknowledge some of the general limitations of my study including the small sample size, the limited stimuli number and species used for each phylogenetic group, and the fact sex differences could not be examined as all the chimpanzees were female. I conclude our chimpanzees appear to perceive similarity in primate faces in a similar way to humans. Information about perceptual similarity is likely prioritised over the potential influence of previous experience or a conceptual representation of species for categorical discrimination between species faces.

Appendix I: Individual data

Condition 1: Colour effects (mean percentage correct)

Chimpanzee	Colour		Greyscale	
	Identical	Categorical	Identical	Categorical
Ai	95	63	82	57
Chloe	98	61	93	38
Cleo	92	55	80	44
Pal	98	61	92	41
Pendensa	91	56	87	41

Condition 1: Colour effects (mean response times in ms)

Chimpanzee	Colour		Greyscale	
	Identical	Categorical	Identical	Categorical
Ai	577	690	740	1006
Chloe	603	1047	750	1263
Cleo	598	802	700	822
Pal	633	978	760	1117
Pendensa	718	1038	886	1341

Appendix II: Individual data

Condition 2: Orientation effects (mean percentage correct)

Chimpanzee	Upright	Inverted
Ai	76	69
Chloe	91	77
Cleo	62	62
Pal	75	65
Pendensa	73	55

Condition 2: Orientation effects (mean response times in ms)

Chimpanzee	Upright	Inverted
Ai	924	976
Chloe	794	877
Cleo	890	860
Pal	782	803
Pendensa	1056	897

Appendix III: Individual data

Conditions 3, 4 and 5: Familiarity and perceptual similarity effects (mean percentage correct)

Chimpanzee	Baboon-Capuchin		Chimpanzee-human		Gorilla-orangutan	
	Identical	Categorical	Identical	Categorical	Identical	Categorical
Ai	93	86	94	92	78	59
Chloe	94	84	99	89	91	60
Cleo	94	85	88	75	81	57
Pal	92	82	96	83	83	55
Pendensa	84	74	98	94	81	59

Conditions 3, 4 and 5: Familiarity and perceptual similarity effects (mean response times in ms)

Chimpanzee	Baboon-Capuchin		Chimpanzee-human		Gorilla-orangutan	
	Identical	Categorical	Identical	Categorical	Identical	Categorical
Ai	618	645	600	657	691	769
Chloe	652	734	588	691	671	867
Cleo	595	688	649	750	657	743
Pal	592	645	611	698	654	717
Pendensa	870	921	684	756	901	1051

CHAPTER 2-2

VISUAL DISCRIMINATION OF THREATENING FACES IN CHIMPANZEES

2-2.1. Abstract

One of the most important signals of social communication in primates are facial expressions. However, exactly how such expressions are discriminated is not fully understood. This study examined if chimpanzees can discriminate conspecific threatening facial expressions (bared teeth and scream) from each other, and from neutral expressions in a touchscreen matching-to-sample (MTS) task. Consistent with previous MTS studies in chimpanzees, all expressions were discriminated from each other significantly from chance. Discrimination between bared teeth or scream and neutral expressions (categorised as perceptually more different) was more accurate and faster than discrimination between bared teeth and scream expressions (categorised as perceptually more similar). In addition, threatening expressions appeared to capture attention to a greater extent than neutral expressions and, to some extent, scream expressions appeared to capture attention to a more than bared teeth faces. However, it remains to be investigated what specific features of threatening faces capture attention.

2-2.2. Introduction

One of the most important signals of social communication in primates are facial expressions. Facial expressions provide the receiver with information about the emotional state, motivations and intentions of the sender, so that they may appropriately modify their behaviour in response (Seyfarth et al. 2010). Similarities in human and animal facial expressions are thought to reflect similarity in emotions (Chevalier-Skolnikoff 1973; Darwin 1872). Facial expressions conveying fear and anger (e.g. bared teeth and scream in chimpanzees) signal threat in the environment or directly towards the observer and thus are given attentional priority over neutral expressions (Parr et al. 2007). However, exactly how such expressions are discriminated is not fully understood.

Several experimental studies have investigated the ability of non-human primates to discriminate conspecific facial expressions. Kanazawa (1996) demonstrated that a Japanese macaque could discriminate conspecific facial expressions (described as bared teeth, threat, tense-mouth and neutral) with above 80% accuracy in a matching-to-sample (MTS) task. In addition, Parr and Heintz (2009) found that seven rhesus monkeys were better able to discriminate facial expressions (scream, bared teeth, open-mouth threat and play) in a MTS task when the distractor was a neutral face compared to other expressions. More recently, Calcutt et al. (2017) observed that nine capuchin monkeys could discriminate between images of emotional and neutral facial expressions in an oddity paradigm. Specifically, they were better able to discriminate open-mouth than scalp-lift expressions from neutral expressions. Thus, several species of monkey can discriminate facial expressions from neutral expressions, as well as from other expressions.

In chimpanzees, discrimination of facial expressions has been studied extensively by Parr and colleagues. Parr et al. (1998) were the first to examine discrimination of facial expressions (bared teeth, scream, pant hoot, play faces, relaxed lip and neutral faces) in five

chimpanzees using a joystick-controlled MTS task. The chimpanzees were successful in categorical discrimination of all expressions from neutral faces except relaxed lip faces. Overall, discrimination performance was better for expressions with more different than similar features. However, some expressions were discriminated on the first testing session regardless of similarity (e.g. scream) suggesting they were especially salient. In a more recent study, Parr et al. (2008) tested the ability of six chimpanzees to discriminate computer-generated standardised facial expressions (bared teeth, scream, whimper, pant-hoot, two types of play faces and pout) in a joystick operated MTS task and found they could categorically discriminate all expressions from each other. Interestingly, Parr (2001) found that three chimpanzees were able to spontaneously match videos of positive social situations with play faces and negative social situations with scream or bared teeth faces in a matching-to-meaning (MTM) experiment. The author suggests that the ability to MTM may be explained by the chimpanzees' real-life experience of the situations in the videos (e.g. anaesthetic administration), although emotional information in the expressions may not be consciously processed. Overall, empirical evidence indicates that monkeys and chimpanzees are better able to discriminate between perceptually different than similar expressions.

The aim of this study was to examine if our chimpanzees can discriminate conspecific threatening facial expressions (bared teeth and scream) from each other, and from neutral expressions in a touchscreen MTS task. I predicted higher accuracy for discriminating between threatening (bared teeth and scream) and neutral expressions (perceptually more different from each other) and lower accuracy for discriminating between bared teeth and scream expressions (perceptually more similar to each other) (cf. Parr et al. 1998; Wilson and Tomonaga 2018a).

2-2.3. Methods

2-2.3.1. Participants and housing

Five adult female chimpanzees (*Pan troglodytes*) participated in the study at the Primate Research Institute, Kyoto University (KUPRI), Japan (**Table 2-2**) (Watanuki et al. 2014). The chimpanzees were members of a social group of 11 individuals living in an environmentally enriched facility consisting of two outdoor enclosures (250 m² and 280 m²), an open-air outdoor enclosure (700 m²) and indoor living rooms linked to testing rooms. The open air outdoor enclosure was equipped with 15 m high climbing frames and included streams and trees (Matsuzawa et al. 2006; Yamanashi and Hayashi 2011). No food or water deprivation was used in the study. The experimental protocol was approved by the Animal Welfare and Care Committee of the KUPRI and the Animal Research Committee of Kyoto University and followed the *Guidelines for the Care and Use of Laboratory Primates* of the KUPRI (Version 3, 2010). The chimpanzees had extensive experience participating in perceptual and cognitive tasks using a touchscreen, including MTS tasks (e.g. Dahl et al. 2013; Tomonaga 1999).

Table 2-2. Basic information about the five chimpanzees

Name	GAIN ID Number ^a	Sex	Age (at study start)
Ai	0434	Female	42
Chloe	0441	Female	37
Cleo	0609	Female	18
Pal	0611	Female	18
Pendensa	0095	Female	41

^aIdentification number (ID) for each chimpanzee listed in the database of the Great Ape Information Network (GAIN): <https://shigen.nig.ac.jp/gain/>

2-2.3.2. Apparatus

Experiments were conducted in an experimental booth ($1.80 \times 2.15 \times 1.75$ m) inside a testing room. Each chimpanzee voluntarily walked to the booth through an overhead walkway connected to the living rooms. A 17-inch touch-sensitive LCD monitors (1280×1024 pixels) encased inside Plexiglas were used to present visual stimuli at approximately 40 cm distance. Food rewards (eight-millimetre apple cubes) were delivered via a universal feeder device. All experimental events were controlled by a PC and the computer task was programmed using Microsoft Visual Basic 2010 (Express Edition).

2-2.3.3. Stimuli

Facial stimuli consisted of cropped photographs (200×225 pixels) of unfamiliar conspecific neutral (expressionless), bared teeth and scream expressions (10 images each). Stimuli were obtained from photographs taken of chimpanzees at Kumamoto Sanctuary, Kyoto University, or from personal collections. All faces were presented in greyscale and the average luminance of each face was scaled to the average luminance of all faces. This was to control for differences in colour hue, luminance and low-level features. Chimpanzee threatening faces were categorised into ‘scream’ and ‘bared teeth’ expressions. A chimpanzee scream expression was defined as: “a raised upperlip with lip corners pulled back exposing the upper teeth, lower lip depressed also exposing the lower teeth, and mouth stretched wide open with lips parted” which is thought to reflect “general agonism” (Parr et al. 2007, p. 176). A chimpanzee bared teeth expression was defined as: “an open mouth with lips parted, a raised upper lip, and retracted lip corners functioning to expose the teeth” which occurs “in response to aggression” (Parr et al. 2007, p. 175) and likely reflects fear. The scream and bared teeth facial expression stimulus set was reviewed by a certified Chimp Facial Action Coding System (Chimp FACS) coder (<http://www.chimpfacs.com/>) who found the expressions consistent with my categorisation.

2-2.3.4. Procedure

The chimpanzees participated in a zero-delay MTS touchscreen task (**Figure 2-2.1**). To begin each trial the chimpanzees touched a blue start key at the bottom-center of the screen, followed by a sample stimulus directly above the start key position. When the sample was touched it disappeared and two comparison stimuli appeared in the middle of the screen. When a correct choice was made (the comparison touched matched the sample) a chime sound was played and a food reward given, when an incorrect choice was made (the comparison did not match the sample, i.e. the ‘distractor’ was touched) a buzzer sound was played and no food reward given. The inter-trial interval was two seconds. The number of errors and response times (ms) were recorded by a PC.



Figure 2-2.1 Chimpanzee ‘Pal’ choosing a bared teeth face (left) with scream face distractor (right)

2-2.3.5. Experimental design

The chimpanzees discriminated facial expressions under both identical and categorical matching formats. On identical matching trials the sample and target were identical to each other, whilst on categorical matching trials the sample and target consisted of different

individuals with the same facial expression. Identical and categorical matching was alternated on each trial. Each facial expression was paired with every other expression as both sample and distractor. The chimpanzees completed 576 trials (48 trials $\times$ 12 sessions) and trial order was randomised within and across sessions.

2-2.3.6. Statistical analysis

The data were analysed using SPSS (version 24). Repeated measures analysis of variance (ANOVAs) were used to analyse accuracy (mean number of errors) and overall mean response times. Chimpanzees showed faster responses on correct trials than incorrect trials (a speed–accuracy trade-off) suggestive of guessing behaviour. Therefore, analyses were conducted on overall response times (averaged across correct and incorrect trials) (cf. Tomonaga 2007a). One-sample *t*-tests were used to analyse the difference in accuracy from chance level. Trials with response times of five seconds or longer after the sample image presentation disappeared may not have been retained and so were excluded from the analysis. In R (version 3.5.2) the ‘lmerTest’ package was used to perform a Generalized Linear Mixed Model (GLMM) analysis using the ‘glmer’ function on the relationship between accuracy (mean number of errors) and matching type (identical or categorical) for each stimulus type (neutral-bared teeth, neutral-scream and bared teeth-scream) and ‘lmer’ function on the relationship between overall mean response times and matching type for each stimulus pair type. As fixed effects, matching type and stimulus type (with interaction term) were entered into the model. Chimpanzee and session were included as random intercepts. Visual inspection of residual plots revealed the data were normally distributed, so for error analysis a binomial distribution with a logit link function was chosen and for response time analysis a log (RT) function was chosen. The model with the smallest AIC values was chosen.

2-2.4. Results

2-2.4.1. Accuracy: Errors

Figure 2-2.2. shows the mean percentage of errors for identical and categorical matching of neutral-bared teeth, neutral-scream and bared teeth-scream pairs. One sample t tests found that errors were significantly different from chance level (50%) for all stimulus pairs; neutral-bared teeth (identical: $M = 11\%$ incorrect, $t_{(4)} = 10.25$, $p = 0.001$), (categorical: $M = 21\%$ incorrect, $t_{(4)} = 5.29$, $p = 0.006$), neutral-scream (identical: $M = 6\%$ incorrect, $t_{(4)} = 20.80$, $p < 0.001$), (categorical: $M = 18\%$ incorrect, $t_{(4)} = 7.84$, $p = 0.001$) and bared teeth-scream (identical: $M = 21\%$ incorrect, $t_{(4)} = 13.43$, $p < 0.001$), (categorical: $M = 40\%$ incorrect, $t_{(4)} = 4.14$, $p = 0.014$). A 3×2 repeated measures ANOVA, with stimulus type and matching type as independent variables was conducted. A main effect of stimulus type was found ($F_{(2,8)} = 11.51$, $p = 0.004$) with more errors for matching bared teeth and scream ($M = 31\%$) than neutral and bared teeth ($M = 16\%$) and neutral and scream ($M = 12\%$) expressions. A main effect of matching type was found ($F_{(1,4)} = 17.95$, $p = 0.013$) with less errors for identical ($M = 13\%$) than categorical ($M = 26\%$) matching. In addition, an interaction between stimulus type and matching type was found, with a sharp increase in errors for categorical matching of bared teeth and scream expressions ($F_{(2,8)} = 6.31$, $p = 0.023$). For individual chimpanzee data see **Appendix IV**.

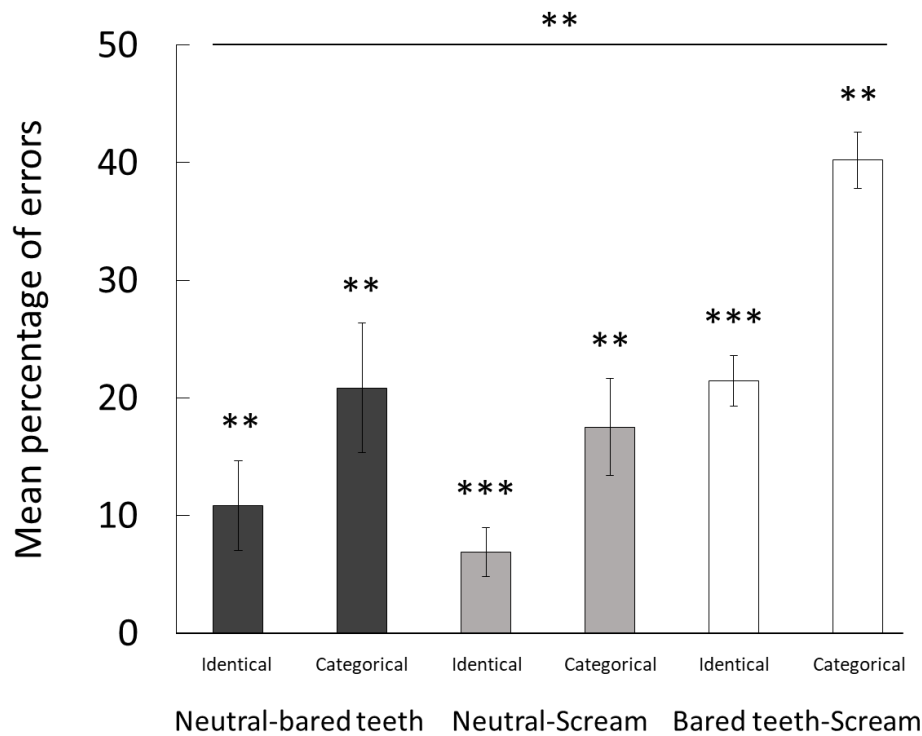


Figure 2-2.2 Mean percentage of errors for identical and categorical matching of neutral-bared teeth, neutral-scream and bared teeth-scream pairs. The solid horizontal line indicates a main effect of stimulus type on accuracy. Error bars represent the standard error of the mean

2-2.4.2. Response times

Figure 2-2.3. shows the overall mean response times for identical and categorical matching of neutral-bared teeth, neutral-scream and bared teeth-scream pairs. A 3×2 repeated measures ANOVA, with stimulus type and matching type as independent variables was conducted. A main effect of stimulus type was found ($F_{(2,8)} = 8.28, p = 0.011$) with slower response times for matching bared teeth and scream ($M = 783$ ms) than neutral and bared teeth ($M = 737$ ms) and neutral and scream ($M = 723$ ms) expressions. A main effect of matching type was found with faster response times for identical (713 ms) than categorical (783 ms) matching ($F_{(1,4)} = 8.00, p = 0.047$). No interactions were found. For individual chimpanzee data see **Appendix IV**.

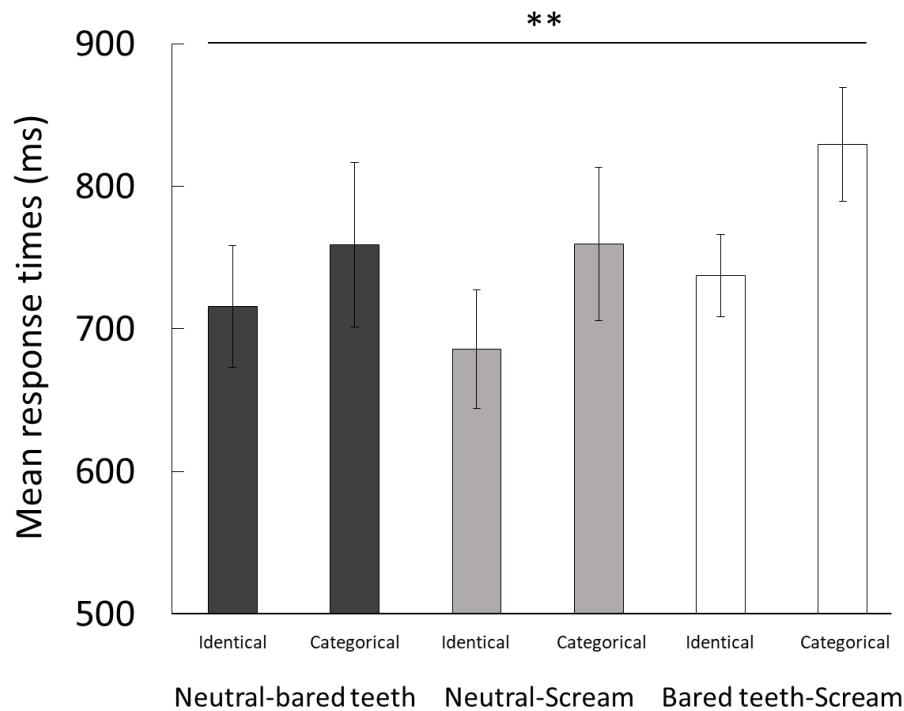


Figure 2-2.3 Mean response times (ms) for identical and categorical matching of neutral-bared teeth, neutral-scream and bared teeth-scream pairs. The solid horizontal line indicates a main effect of stimulus type on response times. Error bars represent the standard error of the mean

2-2.4.3. Asymmetries: Errors

Figure 2-2.4. shows the mean percentage of errors for identical and categorical matching of neutral-bared teeth, neutral-scream and bared teeth-scream pairs presented as either the sample or distractor. For identical matching, the percentage of errors was significantly lower when bared teeth was the sample and neutral was the distractor ($M = 5\%$ incorrect) than vice versa ($M = 17\%$ incorrect), ($\beta = 1.47$, $SE = 0.35$, $p < 0.001$, 95% CI [0.77, 2.16]), when scream was the sample and neutral was the distractor ($M = 3\%$ incorrect) than vice versa ($M = 10\%$ incorrect), ($\beta = 1.22$, $SE = 0.42$, $p = 0.003$, 95% CI [0.40, 2.04]), and when scream was the sample and bared teeth was the distractor ($M = 17\%$ incorrect) than vice versa ($M = 26\%$ incorrect), ($\beta = 0.58$, $SE = 0.23$, $p = 0.010$, 95% CI [0.14, 1.03]). For categorical matching, the percentage of errors was significantly lower when bared teeth was the sample and neutral was the distractor ($M = 12\%$ incorrect) than vice versa ($M = 30\%$ incorrect), ($\beta = 1.13$, $SE = 0.24$, $p < 0.001$, 95% CI [0.65, 1.61]) and when scream was the sample and neutral was the distractor

($M = 12\%$ incorrect) than vice versa ($M = 23\%$ incorrect), ($\beta = 0.78$, $SE = 0.25$, $p = 0.002$, 95% CI [0.28, 1.27]). The percentage of errors did not differ when scream was the sample and bared teeth was the distractor ($M = 40\%$ incorrect) and vice versa ($M = 40\%$ incorrect), ($\beta = 0.02$, $SE = 0.19$, $p = 0.925$, 95% CI [-0.35, 0.39]).

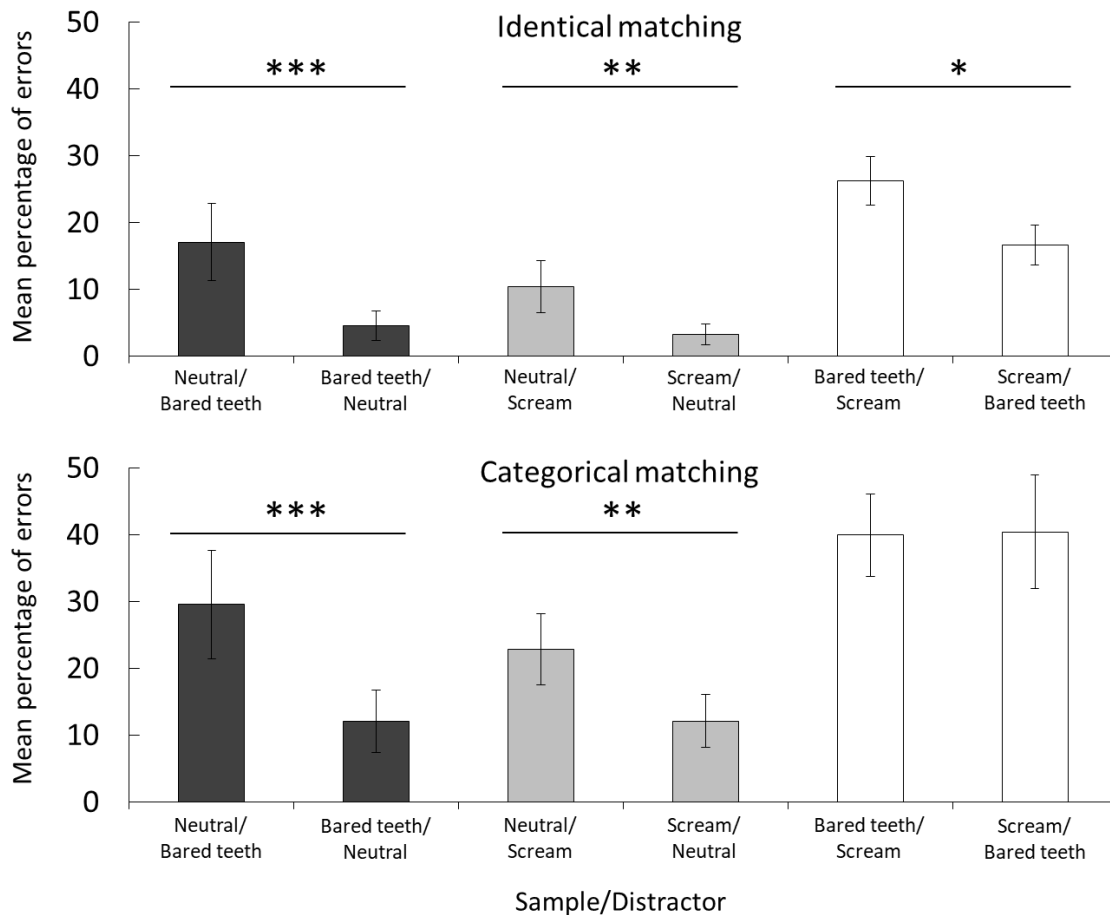


Figure 2-2.4 Mean percentage of errors for identical and categorical matching of neutral-bared teeth, neutral-scream and bared teeth-scream pairs presented as either the sample or distractor. Error bars represent the standard error of the mean

2-2.4.4. Response times

Figure 2-2.5. shows the overall mean response times for identical and categorical matching of neutral-bared teeth, neutral-scream and bared teeth-scream pairs presented as either the sample or distractor. For identical matching, response times were significantly faster when bared teeth was the sample and neutral was the distractor ($M = 682$ ms) than vice versa ($M = 750$ ms), ($\beta = -0.08$, $SE = 0.03$, $p = 0.002$, 95% CI [-0.13, -0.03]) and when scream was the sample and

bared teeth was the distractor ($M = 717$ ms) than vice versa ($M = 757$ ms), ($\beta = -0.06$, $SE = 0.03$, $p = 0.042$, 95% CI $[-0.11, -0.00]$). However, response times did not differ when scream was the sample and neutral was the distractor ($M = 664$ ms) and vice versa ($M = 707$ ms), ($\beta = -0.04$, $SE = 0.03$, $p = 0.136$, 95% CI $[-0.09, 0.01]$). For categorical matching, response times were significantly faster when bared teeth was the sample and neutral was the distractor ($M = 746$ ms) than vice versa ($M = 772$ ms), ($\beta = -0.08$, $SE = 0.03$, $p = 0.007$, 95% CI $[-0.13, -0.02]$). Response times did not differ when scream was the sample and neutral was the distractor ($M = 738$ ms) and vice versa ($M = 781$ ms), ($\beta = -0.04$, $SE = 0.03$, $p = 0.159$, 95% CI $[-0.09, 0.01]$), and when scream was the sample and bared teeth was the distractor ($M = 836$ ms) and vice versa ($M = 823$ ms), ($\beta = 0.01$, $SE = 0.03$, $p = 0.671$, 95% CI $[-0.08, 0.05]$).

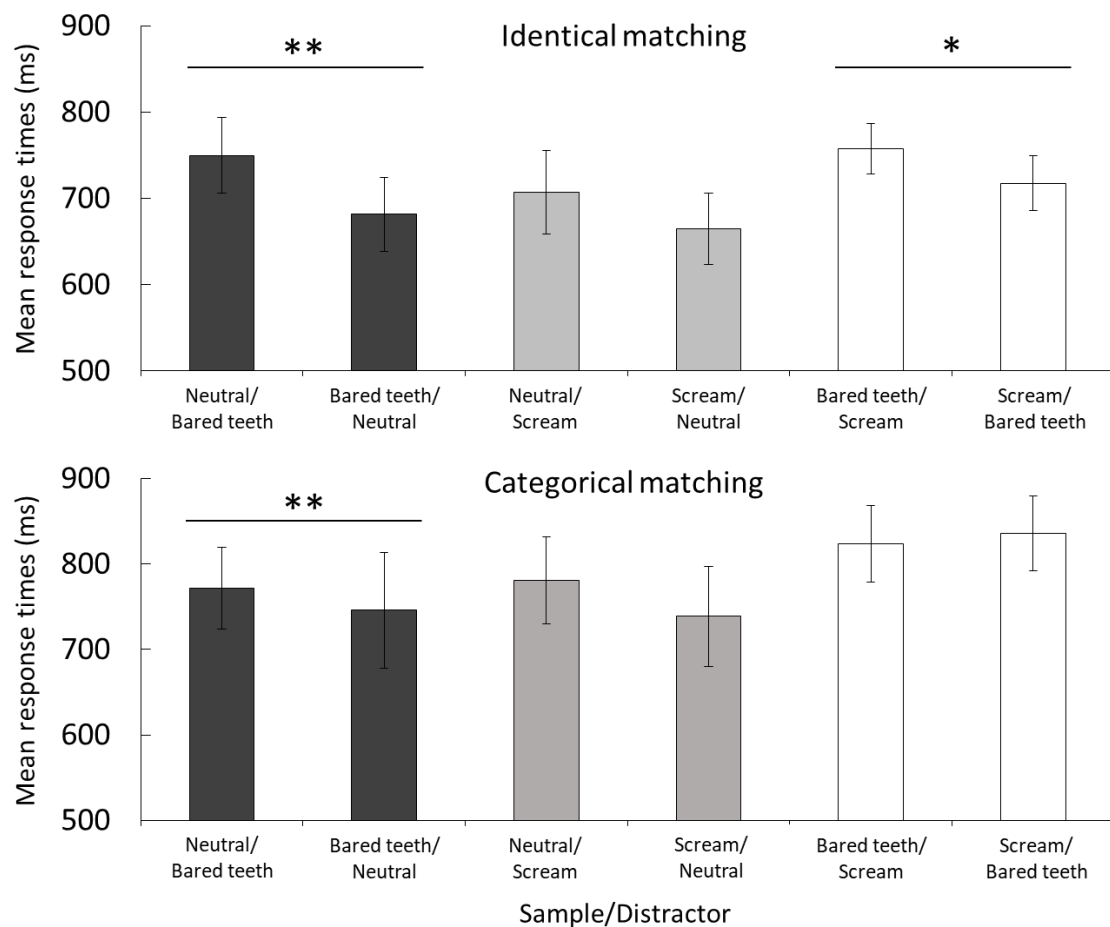


Figure 2-2.5 Mean response times (ms) for identical and categorical matching of neutral-bared teeth, neutral-scream and bared teeth-scream pairs presented as either the sample or distractor. Error bars represent the standard error of the mean

2-2.5. Discussion

This study investigated if our chimpanzees can discriminate conspecific threatening facial expressions from each other. All three expression types were discriminated significantly from chance in both identical and categorical matching. This is consistent with other MTS facial expression studies which found chimpanzees can successfully discriminate between several different expressions, including bared teeth and scream (Parr et al. 1998, 2008). In line with prediction, discriminating between bared teeth or scream and neutral expressions (perceptually more different) was more accurate and faster than discriminating between bared teeth and scream expressions (perceptually more similar). This is consistent with Wilson and Tomonaga (2018a) who found the same chimpanzees showed better performance at discriminating between baboon and capuchin monkey faces and chimpanzee and human faces (perceptually more different) than gorilla and orangutan faces (perceptually more similar). Parr et al. (1998) also found chimpanzees could discriminate bared teeth and scream faces above chance, despite both expressions sharing a relatively large number of features. The authors speculate that cues from the social context or emotional meaning of the expressions were used for discrimination. Parr et al. (2008) conducted a multidimensional scaling analysis (MDS) and identified that scream and bared teeth expressions only differed in the dimension of mouth opening, suggesting the mouth was the most important feature used for discrimination. Similarly, the mouth area may have been important for discrimination in the present study.

Interestingly, asymmetries in errors were observed depending on whether the expressions were presented as the sample or distractor. For both identical and categorical matching, significantly fewer errors were observed when the sample was a threatening face (bared teeth and scream) and the distractor was a neutral face than vice versa. In addition, for identical matching, significantly fewer errors were observed when the sample was scream and the distractor was bared teeth (17% incorrect) than vice versa (26% incorrect). However, for

categorical matching, no difference in errors was observed when the sample was scream and the distractor was bared teeth or vice versa. In comparison, Parr et al. (1998) found that categorical discrimination accuracy was significantly above chance (set at 67%) when the sample was scream and the distractor was bared teeth (83% correct) but not for vice versa (58% correct). However, Parr et al. (2008) did not find any asymmetries in categorical discrimination of bared teeth and scream expressions as the sample or distractor using standardised faces. It is not immediately clear why asymmetries were observed in some studies and not others, but differences in stimuli set size, content and presentation format (i.e. photos and computer-generated faces) are likely important factors. Overall, my results suggest that threatening faces are more salient and capture attention more than neutral faces. To some extent, this may also be true for scream versus bared teeth faces.

So far, evidence from non-human primate studies suggest that both featural and holistic processing are used to discriminate facial expressions (e.g. Parr et al. 2008; Parr and Heintz 2009; Calcutt et al. 2017). In the present study, it remains unclear which facial features may be responsible for biasing attention towards threatening faces. In an eye-tracking experiment, Kano and Tomonaga (2009) found that chimpanzees fixated more on the mouth for scream expressions and more on the eyes for neutral faces. In future experiments, it would be useful to systematically remove the eyes or mouth, or artificially darken the mouth area of threatening faces (cf. Parr et al. 2000). If discrimination asymmetries disappear after such manipulations, this would suggest that these features are important for attentional capture. It would also be useful to test for the inversion effect (described in Chapter 2-1, p. 21) to examine if threatening faces are processed holistically. In addition, to understand if these asymmetries are threat-specific, non-threatening faces and non-face stimuli should be tested. Another extension to my study is to examine the attentional component of these discrimination asymmetries. This could be done using the MTS-visual search task which is particularly sensitive to measuring

attentional asymmetries (e.g. Tomonaga 1993). Finally, I acknowledge the general limitations of my study, including the small sample size and limited number of stimuli, although it is very difficult to obtain high quality images of chimpanzee facial expressions during natural social interactions.

In conclusion, our chimpanzees were able to discriminate between conspecific neutral, bared teeth and scream expressions, although perceptually similar expressions (bared teeth and scream) were discriminated with less accuracy than perceptually different expressions. In addition, asymmetries in discrimination performance between the sample and distractor suggested that threatening expressions may capture attention to a greater extent than neutral expressions. The attentional component of these asymmetries should be investigated in future experiments.

Appendix IV: Individual data

Mean percentage of errors

Chimpanzee	Neutral-bared teeth		Neutral-scream		Bared teeth-scream	
	Identical	Categorical	Identical	Categorical	Identical	Categorical
Ai	2	2	0	2	26	44
Chloe	10	35	10	26	19	47
Cleo	7	21	4	23	17	38
Pal	9	19	10	19	27	40
Pendensa	25	27	9	18	19	33

Mean response times (ms)

Chimpanzee	Neutral-bared teeth		Neutral-scream		Bared teeth-scream	
	Identical	Categorical	Identical	Categorical	Identical	Categorical
Ai	583	577	558	571	688	701
Chloe	802	903	776	887	786	943
Cleo	649	709	626	756	654	821
Pal	761	860	761	835	804	876
Pendensa	784	746	708	748	756	806

CHAPTER 3

EXPLORING ATTENTIONAL BIAS TOWARDS THREATENING FACES IN CHIMPANZEES USING THE DOT PROBE TASK

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3.1. Abstract

Primates have evolved to rapidly detect and respond to danger in their environment. However, the mechanisms involved in attending to threatening stimuli are not fully understood. The dot probe task is one of the most widely used experimental paradigms to investigate these mechanisms in humans. However, to date, few studies have been conducted in non-human primates. The aim of this study was to investigate whether the dot probe task can measure attentional biases towards threatening faces in chimpanzees. Eight adult chimpanzees participated in a series of touch screen dot probe tasks. I predicted faster response times towards chimpanzee threatening faces relative to neutral faces and faster response times towards faces of high threat intensity (scream) than low threat intensity (bared teeth). Contrary to prediction, response times for chimpanzee threatening faces relative to neutral faces did not differ. In addition, I found no difference in response times for faces of high and low threat intensity. In conclusion, I found no evidence that the touch screen dot probe task can measure attentional biases specifically towards threatening faces in our chimpanzees. Methodological limitations of using the task to measure emotional attention in human and non-human primates, including stimulus threat intensity, emotional state, stimulus presentation duration and manual responding are discussed.

3.2. Introduction

Faces are one of the most important and salient social stimuli for primates. They convey information about identity, age, sex, attention and emotion (Adachi and Tomonaga 2017). Humans display a wide range of facial expressions to communicate their emotions, including anger, fear, disgust, sadness, surprise and happiness (Ekman 1973; Ekman and Friesen 1971). Similarity in human and animal facial expressions have long been thought to reflect similarity in basic emotions (Chevalier-Skolnikoff 1973; Darwin 1872). The animal fear system has evolved to rapidly detect and respond to danger in the environment and is particularly sensitive to threatening stimuli such as snakes and angry faces (LeDoux 1996; Morris et al. 1998). Thus, information from threatening stimuli is given attentional priority over other information (Koster et al. 2005). This attentional bias refers to “differential attentional allocation towards threatening stimuli relative to neutral stimuli” (Cisler and Koster 2010, p. 204).

To investigate the mechanisms involved in attending to threatening stimuli in humans, several experimental paradigms have been developed. These include emotional Stroop, visual search, attentional probe, spatial cueing and rapid serial visual presentation tasks (Cisler and Koster 2010; Yiend 2010). One of the most widely used spatial cueing tasks is the visual dot probe task, originally developed by MacLeod et al. (1986). Two stimuli (words or images) are simultaneously presented on a screen for a short duration (traditionally 500 ms). Typically, one of the stimuli is threatening (angry face) and the other is neutral (non-expressive face). The stimuli disappear and a dot (probe) appears randomly in the spatial location of either the threatening stimulus (congruent trial) or the neutral stimulus (incongruent trial). Response times to detect the dot are recorded using computer keys. It is assumed if attention is already fixated in the spatial location of one stimulus, detecting the dot in the same location will result in faster response times (Yiend 2010). Faster reaction times on congruent trials indicate

attentional bias towards threatening faces (vigilance) and on incongruent trials attentional bias away from threatening faces (avoidance) (Staugaard 2010).

The dot probe task has been used extensively to investigate the relationship between emotion and attention in humans. Attentional biases towards threatening faces are more consistently found in anxious than non-anxious people. However, whilst in some studies anxious participants show stronger bias towards threatening faces compared with non-anxious participants (Klumpp and Amir 2009; Mogg and Bradley 2002; Mogg et al. 2004; Pishyar et al. 2004; Sposari and Rapee 2007; Stevens et al. 2009), in other studies they show avoidance (Chen et al. 2002; Mansell et al. 1999) or no attentional bias (Bradley et al. 1997; Gotlib et al. 2004; Pineles and Mineka 2005). Several methodological differences likely account for these inconsistencies. Two of the most important moderating variables for measuring biases towards threatening faces are the duration between the start of the stimulus and the start of the dot presentation (stimulus onset asynchrony; SOA) and stimulus threat intensity (Cisler and Koster 2010; Yiend 2010; van Rooijen et al. 2017).

Several human studies have found biases towards threatening faces at short SOAs. Shorter SOAs are thought to facilitate threat detection by the amygdala and involve more automatic processing, whereas longer SOAs facilitate strategic processing by the prefrontal cortex and involve greater attentional control (Cisler and Koster 2010; Weierich et al. 2008). Stevens et al. (2009) found biases towards threatening faces at 175 ms but not 600 ms, Cooper and Langton (2006) at 100 ms but not 500 ms, and Holmes et al. (2005) at 30 ms or 100 ms but not 500 ms or 1,000 ms. Biases towards threatening faces have also been found at the longer SOA of 500 ms but not 1,250 ms (Mogg et al. 2004; Bradley et al. 1998). Overall, SOAs of less than 500 ms appear more suitable for measuring biases towards threatening faces. In addition, shorter SOAs prevent attention from switching between the two stimuli in the dot probe task (Weierich et al. 2008). Eye saccades are “rapid, ballistic eye movements that move

the fovea (the region of highest visual acuity) towards the target stimulus” (Bourne 2006, p. 381) and can occur within 200 ms. Therefore, SOA duration should ideally be limited to 150 ms, to prevent attention from switching during stimuli presentation (Bourne 2006).

Regarding stimuli threat intensity, faces expressing anger are often used as stimuli, as they are more salient, threatening and ecologically valid than words (Schmukle 2005; Staugaard 2009). An interesting study by Wilson and MacLeod (2003) investigated attentional bias to faces of different threat intensity in the dot probe task. Low anxiety participants showed biases towards morphed faces expressing very high anger, but not moderate anger. High anxiety participants showed biases towards both very high and moderate anger faces. Overall, biases towards threatening faces increased with threat intensity. In a simplified dot probe task in humans, de Valk et al. (2015) found faster response times to touch angry faces than fearful or neutral faces. Although both angry and fearful faces signal danger in the environment, angry faces signal a more direct threat to the observer (Grillon and Charney 2011). Therefore, angry faces likely have a higher threat intensity than fearful faces.

Despite extensive use of the dot probe task to investigate emotional attention in humans, few studies have been conducted with animals (Coleman and Pierre 2014). Recently, a handful of dot probe studies in non-human primates have been conducted using touchscreens. In monkeys, Koda et al. (2013) presented two Japanese macaques with conspecific infant and adult faces for 100 ms. Attention was captured by visual cues, but no bias was found towards infant faces. In six rhesus monkeys King et al. (2012) found biases towards threatening conspecific faces presented for 1,000 ms. Also in six rhesus monkeys Parr et al. (2013) found biases towards conspecific threatening faces (bared teeth and open mouth threat expressions) presented for 500 ms. In great apes, Tomonaga and Imura (2009) conducted the first visuo-spatial cueing (dot probe) experiment with three chimpanzees. Neutral chimpanzee and human faces and random objects were presented for 200 ms. Attentional biases were observed towards

chimpanzee and human faces versus objects, but not bananas versus objects, indicating a face-specific bias. More recently, Kret et al. (2016) presented four bonobos with images of conspecifics and other animals as control stimuli for 300 ms. Bonobo images consisted of either emotional scenes (i.e. distress, groom, sex, yawn, play, food, pant hoot) or neutral scenes, including the whole body. Attention was biased towards emotional scenes, with the strongest biases towards affiliative and protective behaviours such as sex, yawning and grooming. However, when Kret et al. (2018) presented eight chimpanzees with conspecific whole-body threatening stimuli (fearful and display expressions) paired with neutral stimuli for 33 ms and 300 ms no bias towards threatening stimuli was found.

Overall, evidence from non-human primate studies suggests the dot probe task can successfully measure attentional biases to emotional stimuli in monkeys and great apes. However, many methodological inconsistencies in both the human and non-human primate literature exist, including but not limited to: SOA duration, stimuli threat intensity, stimuli pair combination and response methods. Nevertheless, the task offers a promising method to investigate attentional processes in emotional perception in non-human primates. Furthermore, the task is implicit and requires little training, making it ideal for use with non-human primates and other animal species (van Rooijen et al. 2017).

The aim of the present study was to investigate whether the dot probe task can measure attentional biases towards threatening faces in chimpanzees. I predicted faster response times to touch the dot replacing threatening faces than neutral faces or scrambled faces. In addition, I predicted faster response times towards faces of higher than lower threat intensity (de Valk et al. 2015; Grillon and Charney 2011).

3.3. Materials and Methods

3.3.1. Participants and housing

Eight adult chimpanzees (*Pan troglodytes*), six females and two males, participated in the study at the Primate Research Institute, Kyoto University, Japan (**Table 3.1**) (Watanuki et al. 2014). The chimpanzees were members of a social group of 11 individuals living in an environmentally enriched facility consisting of two outdoor enclosures (250 m² and 280 m²), an open-air outdoor enclosure (700 m²) and indoor living rooms linked to testing rooms. The open-air outdoor enclosure was equipped with 15 m high climbing frames and included trees (Matsuzawa et al. 2006; Yamanashi and Hayashi 2011). The chimpanzees had extensive experience participating in touchscreen cognitive tasks.

Table 3.1 Basic information about the eight chimpanzees

Name	GAIN ID Number ^a	Sex	Age (at study start)
Ai	0434	Female	41
Ayumu	0608	Male	16
Chloe	0441	Female	37
Cleo	0609	Female	17
Gon	0437	Male	51
Pal	0611	Female	16
Pendensa	0095	Female	39
Popo	0438	Female	34

^aIdentification number (ID) for each chimpanzee listed in the database of the Great Ape Information Network (GAIN): <https://shigen.nig.ac.jp/gain/>

3.3.2. Apparatus

Experiments were conducted in an experimental booth ($1.80 \times 2.15 \times 1.75$ m) inside a testing room. Each chimpanzee voluntarily walked to the booth through an overhead walkway connected to the living rooms. Two 17-inch touch-sensitive LCD monitors (1280×1024 pixels) encased in Plexiglas were used to present visual stimuli at approximately 40 cm distance. Food rewards (8 mm apple cubes) were delivered via a universal feeder device. All experimental events were controlled by a PC and the computer task was programmed using Microsoft Visual Basic 2010 (Express Edition).

3.3.3. Stimuli

Facial stimuli consisted of cropped photographs (200×250 pixels, 53 mm $\times$ 66 mm) of unfamiliar chimpanzee (*Pan troglodytes*), orangutan (*Pongo pygmaeus* and *Pongo abelii*) and olive baboon (*Papio anubis*) faces. Stimuli were obtained from photographs taken of chimpanzees at Kumamoto Sanctuary, Kyoto University, or from personal collections. All faces were presented in greyscale and the average luminance of each face was scaled to the average luminance of all faces in each experiment. This was to control for differences in colour hue, luminance and low-level features which may inadvertently bias attention. Chimpanzee threatening faces were categorised into ‘scream’ (higher threat intensity) and ‘bared teeth’ (lower threat intensity) expressions. A chimpanzee scream expression was defined as: “a raised upperlip with lip corners pulled back exposing the upper teeth, lower lip depressed also exposing the lower teeth, and mouth stretched wide open with lips parted” which is thought to reflect “general agonism” (Parr et al. 2007, p. 176). A chimpanzee bared teeth expression was defined as: “an open mouth with lips parted, a raised upper lip, and retracted lip corners functioning to expose the teeth” which occurs “in response to aggression” (Parr et al. 2007, p. 175) and likely reflects fear. The scream and bared teeth facial expression stimulus set was reviewed by a certified Chimp Facial Action Coding System (ChimpFACS) coder

(<http://www.chimpfacs.com/>) who found the expressions consistent with my categorisation. Colour stimuli consisted of two shades of red; ‘light red’ and ‘dark red’. Object stimuli consisted of two chairs against a nondescript background in colour. Control stimuli consisted of scrambled images. Scrambled chair images were composed by randomly shuffling each pixel of the original images to a new position (box scrambling). This ensured content-related information was removed while average brightness levels were maintained. Scrambled face images were composed by calculating the average power spectrum of the original images to generate phase randomised images (phase scrambling). This preserved the same spatial frequency spectrum as the original images (Ales et al. 2012). Stimuli pairs were presented at a distance of 114 mm (432 pixels) between their center points. The inside edge of each stimulus was presented at 4° from central fixation so that each stimulus was presented unilaterally to the left and right visual fields (Bourne and Hole 2006; Young 1982).

3.3.4. Procedure

The chimpanzees participated in a series of touchscreen dot probe tasks (**Figure 3.1**). All chimpanzees participated in all experiments which took place every weekday (one session per day). Experiments ran consecutively. To begin each trial the chimpanzees touched a fixation cue (blue square) just below the center of the screen. This was followed by simultaneous presentation of two stimuli directly above the fixation cue. The stimuli and fixation cue then disappeared together and a black dot (probe) appeared immediately in the spatial location of one of the stimuli. The Stimulus Onset Asynchrony (SOA) was 150 ms (Bourne 2006). When the dot was touched a chime was played and a food reward given. If the dot was not touched it remained on the screen. Response times (ms) to touch the dot were recorded by a PC. The inter-trial interval was 2 s. For each stimuli pair, the dot replaced the stimulus predicted to facilitate faster response times (congruent trials) or the stimulus predicted to lead to slower response times (incongruent trials). In each session half the trials were congruent and half were

incongruent. Stimuli presentation (left or right) and congruency (congruent or incongruent dot presentation) was randomised across trials.

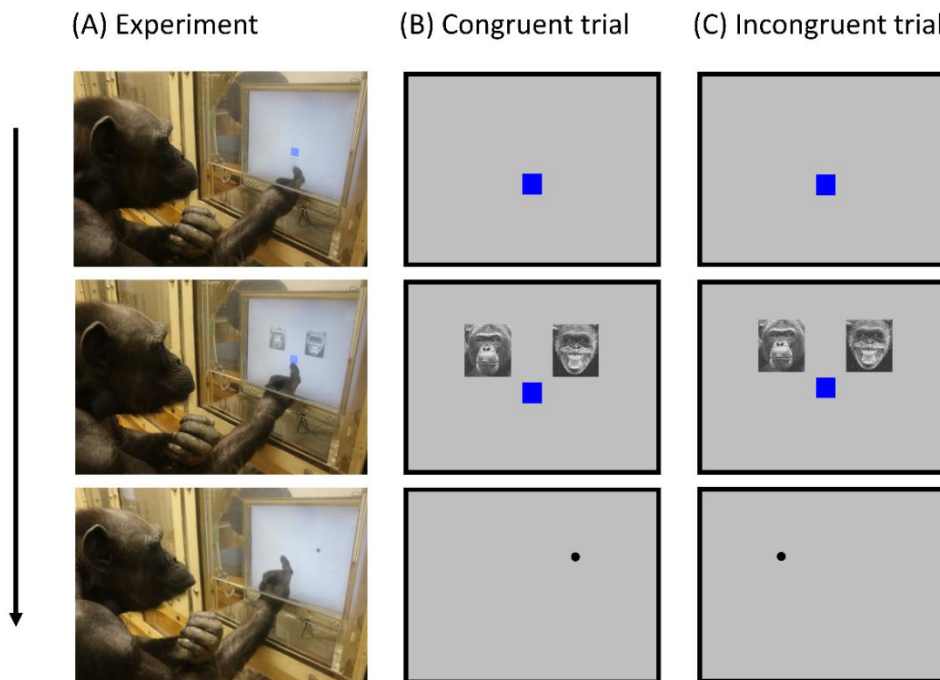


Figure 3.1 Schematic diagram of the dot probe task. (A) Experiment: Chimpanzee ‘Ai’ participating in the threatening face experiment. (B) Congruent trial: dot replaces threatening face. (C) Incongruent trial: dot replaces neutral face. Response times (ms) to touch the dot were recorded

3.3.5. Preliminary experiments

Prior to conducting the main experiment to examine biases towards threatening faces, I conducted three preliminary experiments. The aim of these experiments was (a) to examine the sensitivity of the dot probe task to measure attentional biases towards stimuli of increasing visual, social and emotional complexity and (b) to serve as control experiments to determine that attentional biases measured towards threatening faces are threat-specific and not also found towards non-social or non-threatening stimuli. In Experiment 1 (Colour) I presented two shades of red (two images; dark red and light red) paired with each other or unpaired with any stimuli. Red was chosen because evidence in humans demonstrates that red captures attention and facilitates faster motor responses than non-red cues in the dot probe task; an effect which is

enhanced further for images with an emotional context (Kuniecki et al. 2015). I predicted faster response times towards dark red than light red, as there was greater contrast between dark red against the grey background screen than light red. In Experiment 2 (Object) I presented two chairs (two images) paired with scrambled chairs or unpaired with any stimuli. Chairs were chosen as they are not social, threatening or novel for our chimpanzees. I predicted faster response times towards chairs than scrambled chairs, as scrambled chairs lack content-related information. In Experiment 3 (Primate faces) I presented chimpanzee faces (36 images) paired with orangutan (12 images), baboon (12 images) or scrambled chimpanzee (36 images) faces. Primate faces were chosen as they are social but not overtly threatening. In addition, I wanted to build on Tomonaga and Imura's (2009) dot probe study in chimpanzees which found face-specific attentional biases, by examining whether the task is sensitive to detecting differences in perceptual similarity and familiarity between faces. Chimpanzees are faster at discriminating perceptually different than perceptually similar primate faces (Wilson and Tomonaga 2018a) and show better performance for discriminating familiar than unfamiliar primate species faces (e.g. Dahl et al. 2013b; Tanaka 2007). Therefore, I predicted a significant difference in response times for perceptually different faces (chimpanzee paired with baboon) but not for perceptually similar faces (chimpanzee paired with orangutan), with faster response times towards highly familiar faces (chimpanzee) than unfamiliar faces (orangutan or baboon). For Experiment 1, 36 trials $\times$ 6 sessions were completed, for Experiment 2, 36 trials $\times$ 6 sessions were completed and for Experiment 3, 36 trials $\times$ 12 sessions were completed. Trial order was randomised within and across sessions.

3.3.6. Main experiment

In Experiment 4 (Threatening faces), chimpanzee bared teeth faces (12 images) and scream faces (12 images) were paired with neutral faces (12 novel chimpanzee face images) or

scrambled faces (12 images each). For Experiment 4, 48 trials $\times$ 12 sessions were completed. Trial order was randomised within and across sessions.

3.3.7. Statistical analysis

Responses times less than 150 ms and longer than 5,000 ms were excluded from the analysis, as fast response times may have reflected anticipatory responding and slow response times distraction (Koster et al. 2006; Lacreuse et al. 2013). In addition, for each chimpanzee, condition and session, data two standard deviations above the mean were excluded, resulting in elimination of a total of 513 trials (4.3% of trials). I used R version 3.4.3 (R Core Team 2015) and the ‘lme4’ package to perform a Generalized Linear Mixed Model (GLMM) analysis on the relationship between response times and congruency for each stimuli pair comparison. The ‘glmer’ function was used to extract Z values. As fixed effects, I entered congruency and stimuli pair comparison (with interaction term) into the model. The value of the intercept may differ over chimpanzees and sessions, so random intercepts were included. Visual inspection of residual plots revealed the data were skewed, so a gamma probability distribution with a log link function was selected. I chose the model with the smallest AIC values. SPSS (version 24) was also used to analyse response times with repeated measures analysis of variance (ANOVA). Effect sizes were reported with partial etas squared (η_p^2).

3.4. Results

3.4.1. Preliminary experiments

Figure 3.2(A). shows the mean response times in Experiment 1 (Colour). Response times to touch the dot were significantly faster for dark red (congruent, $M = 386$ ms) than no stimulus (incongruent, $M = 437$ ms), ($\beta = 0.13$, $SE = 0.02$, $Z = 5.65$, $p < 0.001$), and light red (congruent, $M = 392$ ms) than no stimulus (incongruent, $M = 438$ ms), ($\beta = 0.12$, $SE = 0.02$, $Z = 5.19$, $p < 0.001$). No significant difference in response times was found for dark red (congruent, $M = 409$

ms) versus light red (incongruent, $M = 421$ ms), ($\beta = 0.02$, $SE = 0.02$, $Z = 0.98$, $p = 0.329$). No other pair comparisons were significant. For individual chimpanzee data see **Appendix V**.

Figure 3.2(B). shows the mean response times in Experiment 2 (Object). Response times were significantly faster for chairs (congruent, $M = 403$ ms) than scrambled chairs (incongruent, $M = 443$ ms), ($\beta = 0.09$, $SE = 0.02$, $Z = 5.54$, $p < 0.001$), chairs (congruent, $M = 392$ ms) than no stimulus (incongruent, $M = 446$ ms), ($\beta = 0.12$, $SE = 0.02$, $Z = 7.06$, $p < 0.001$) and scrambled chairs (congruent, $M = 398$ ms) than no stimulus (incongruent, $M = 435$ ms), ($\beta = 0.09$, $SE = 0.02$, $Z = 5.24$, $p < 0.001$). No other pair comparisons were significant. For individual chimpanzee data see **Appendix VI**.

Figure 3.2(C). shows the mean response times in Experiment 3 (Primate faces). Response times were significantly faster for chimpanzee faces (congruent, $M = 423$ ms) than baboon faces (incongruent, $M = 438$ ms), ($\beta = 0.04$, $SE = 0.01$, $Z = 2.49$, $p = 0.013$) and chimpanzee faces (congruent, $M = 417$ ms) than scrambled chimpanzee faces (incongruent, $M = 440$ ms), ($\beta = 0.05$, $SE = 0.01$, $Z = 3.79$, $p < 0.001$). No significant difference in response times was found for chimpanzee faces (congruent, $M = 429$ ms) versus orangutan faces (incongruent, $M = 433$ ms), ($\beta = 0.01$, $SE = 0.01$, $Z = 1.03$, $p = 0.304$). No other pair comparisons were significant. For individual chimpanzee data see **Appendix VII**.

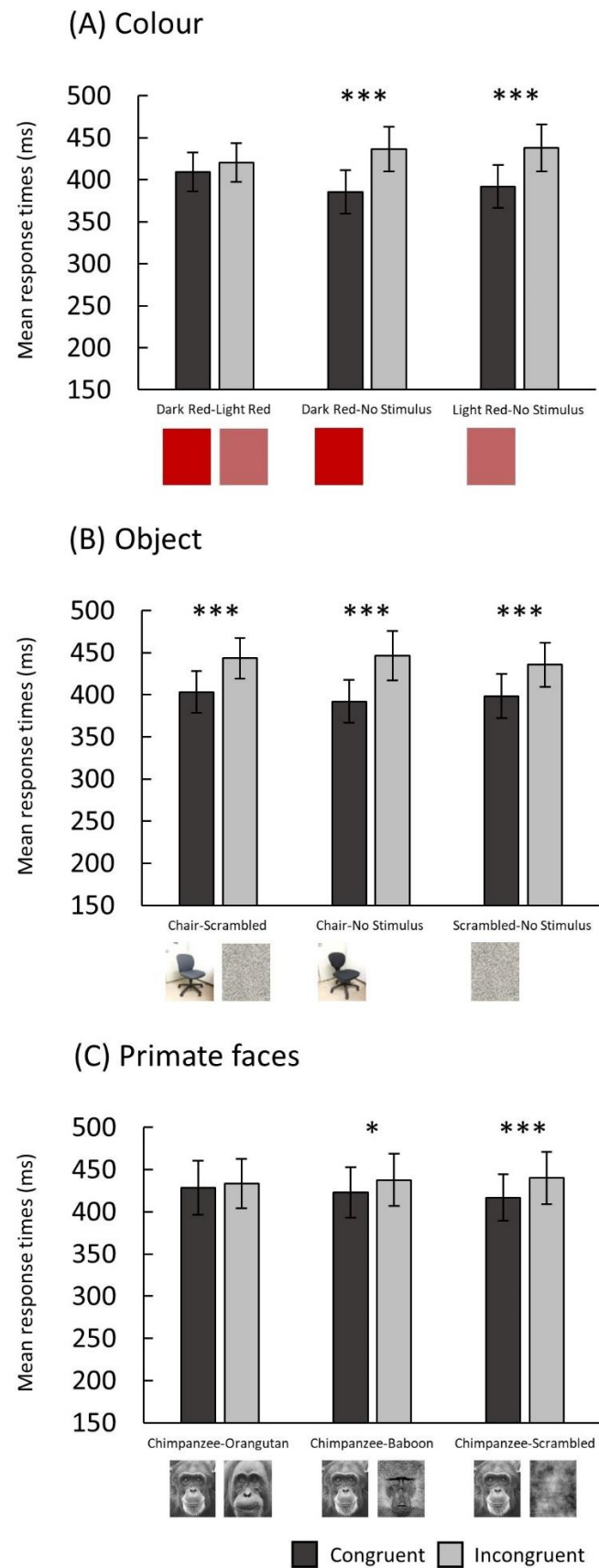


Figure 3.2 Mean response times (ms) for congruent and incongruent trials in (A) colour, (B) object, and (C) primate face experiments. Error bars indicate the standard error of the mean

3.4.2. Main experiment

Figure 3.3. shows the mean response times in the threatening faces experiment. Response times were significantly faster for bared teeth faces (congruent, $M = 418$ ms) than scrambled bared teeth faces (incongruent, $M = 430$ ms), ($\beta = 0.03$, $SE = 0.01$, $Z = 2.34$, $p = 0.019$) and scream faces (congruent, $M = 420$ ms) than scrambled scream faces (incongruent, $M = 440$ ms), ($\beta = 0.05$, $SE = 0.01$, $Z = 3.28$, $p = 0.001$). No significant difference in response times was found for bared teeth faces (congruent, $M = 428$ ms) versus neutral faces (incongruent, $M = 433$ ms), ($\beta = 0.01$, $SE = 0.01$, $Z = 0.61$, $p = 0.544$), or scream faces (congruent, $M = 421$ ms) versus neutral faces (incongruent, $M = 432$ ms), ($\beta = 0.03$, $SE = 0.01$, $Z = 1.83$, $p = 0.067$). No other pair comparisons were significant. No significant difference in response times between bared teeth faces (congruent, $M = 418$ ms) and scream faces (congruent, $M = 420$ ms), ($\beta = 0.01$, $SE = 0.01$, $Z = 0.42$, $p = 0.677$) paired with scrambled faces was found. For individual chimpanzee data see **Appendix VIII**. To investigate the possibility that bias towards threatening faces may decrease across sessions, I analysed overall response times for each session using Pearson's Correlation Coefficient. There was no significant relationship between sessions and response times ($M = 427$ ms, $SE = 23$ ms), ($r = 0.27$, $n = 12$, $p = 0.403$), indicating no decreasing trend in biases across sessions.

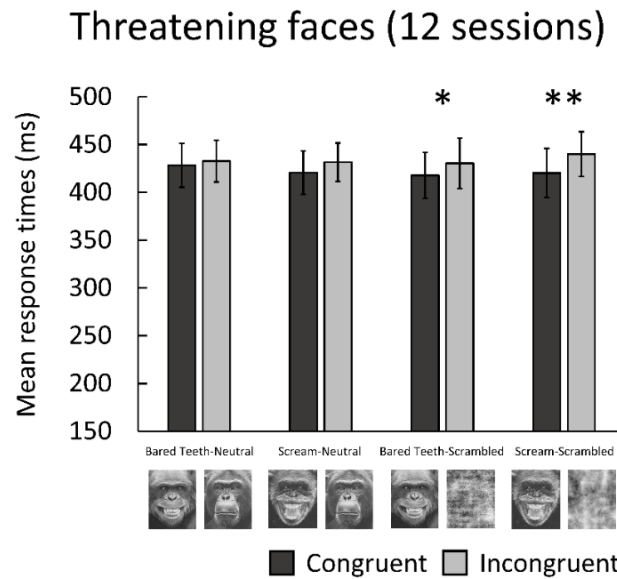


Figure 3.3 Mean response times (ms) for congruent and incongruent trials in the threatening face experiment. Error bars indicate the standard error of the mean

I also explored whether attentional bias effects were more evident at an early stage of the experiment by analysing the mean response times in the first session using GLMM. Fixed effects were congruency and stimuli pair comparisons and the random effect was chimpanzees.

Figure 3.4. shows the mean response times in the first session of the threatening faces experiment. Response times were significantly faster for bared teeth faces (congruent, $M = 420$ ms) than neutral faces (incongruent, $M = 457$ ms), ($\beta = 0.09$, $SE = 0.04$, $Z = 2.52$, $p = 0.012$), and scream faces (congruent, $M = 401$ ms) than scrambled scream faces (incongruent, $M = 445$ ms), ($\beta = 0.10$, $SE = 0.04$, $Z = 2.72$, $p = 0.006$). No significant differences in response times were found for scream faces (congruent, $M = 413$ ms) versus neutral faces (incongruent, $M = 420$ ms), ($\beta = 0.02$, $SE = 0.04$, $Z = 0.55$, $p = 0.584$), or bared teeth faces (congruent, $M = 421$ ms) versus scrambled bared teeth faces (incongruent, $M = 440$ ms), ($\beta = 0.04$, $SE = 0.04$, $Z = 1.21$, $p = 0.228$). No other pair comparisons were significant. No significant difference in response times between bared teeth faces (congruent, $M = 420$ ms) paired with neutral faces, and scream faces (congruent, $M = 401$ ms) paired with scrambled scream faces ($\beta = -0.03$, $SE = 0.04$, $Z = -0.91$, $p = 0.365$) was found.

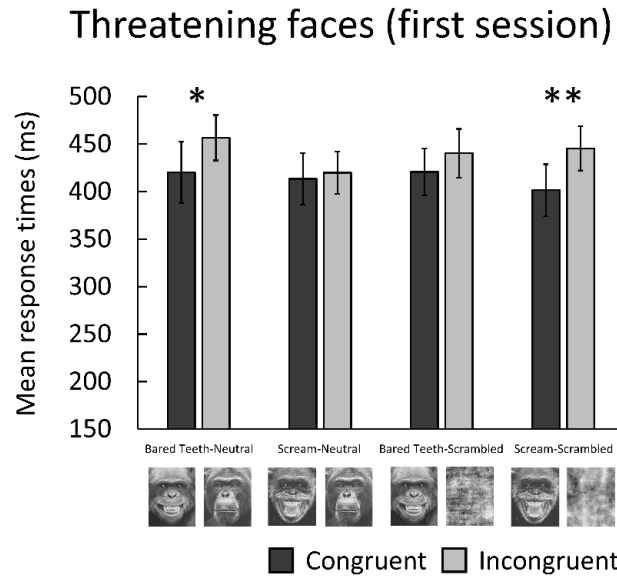


Figure 3.4 Mean response times (ms) for congruent and incongruent trials in the first session of the threatening face experiment. Error bars indicate the standard error of the mean

To examine emotional laterality effects, specifically a right brain hemisphere advantage for processing emotional stimuli, reflected in faster response times for threatening faces presented to the left visual field (Mogg and Bradley 2002; Fox 2002; Mogg and Bradley 1999; Wilson et al. 2016), I used a 2×2 repeated measures ANOVA to compare response times for threatening face (combined bared teeth faces and scream faces) position (left or right visual field) and dot probe position (left or right) as independent variables. No difference in response times was found between threatening faces presented in the left visual field ($M = 427$ ms, $SE = 28$ ms) and right visual field ($M = 428$ ms, $SE = 27$ ms), ($F_{(1,7)} = 0.21$, $p = 0.664$, $\eta_p^2 = 0.028$). In addition, no significant difference was found between touching the dot in the left position ($M = 457$ ms, $SE = 30$ ms) and the right position ($M = 397$ ms, $SE = 25$ ms), ($F_{(1,7)} = 4.45$, $p = 0.073$, $\eta_p^2 = 0.389$), and no interactions were found. Overall, no laterality effects were found.

3.4.3. Comparison of reaction times across experiments

I further analysed the possibility of increasing or decreasing trends in response times across preliminary and main experiments. A 2×3 repeated measures ANOVA was conducted to

compare reaction times between experiments with congruency (congruent and incongruent trials) and experiments (1, 2 and 3) as independent variables. To make equivalent comparisons across experiments, only those stimuli paired with scrambled control images were analysed; Experiment 2 (chair–scrambled chair); Experiment 3, (chimpanzee face–scrambled chimpanzee face) and Experiment 4 (combined bared teeth face–scrambled bared teeth face and scream face–scrambled scream face). In addition, only the first six sessions in each experiment were analysed. A significant main effect of congruency was found, with faster response times for congruent trials ($M = 410$ ms, $SE = 26$ ms) than incongruent trials ($M = 439$ ms, $SE = 27$ ms) across experiments, ($F_{(1,7)} = 13.72$, $p = 0.008$, $\eta_p^2 = 0.662$). However, no significant difference was found in response times between experiments, ($F_{(2, 14)} = 0.29$, $p = 0.756$, $\eta_p^2 = 0.039$), and no interactions were found. Our chimpanzees showed no systematic trends in response times across experiments.

3.5. Discussion

This study was the first to investigate attentional bias specifically towards threatening faces in chimpanzees using the dot probe task. In the preliminary experiments, significant biases towards chairs and neutral chimpanzee faces paired with scrambled faces were found. In addition, a significant bias towards highly familiar chimpanzee faces paired with unfamiliar baboon faces was found, but not when chimpanzee faces were paired with unfamiliar orangutan faces. This result is likely explained by the closer perceptual similarity between chimpanzee and orangutan faces than chimpanzee and baboon faces. Wilson and Tomonaga (2018a) found faster responses for discriminating perceptually different chimpanzee and human faces, or baboon and capuchin monkey faces, than perceptually similar gorilla and orangutan faces. The present study suggests detection of perceptually different faces is possible, even at very short presentation times. In the same chimpanzee group, Tomonaga and Imura (2009) found

attentional biases towards chimpanzee or human faces paired with random objects, but not towards bananas paired with objects, indicating a face-specific bias. Furthermore, Tomonaga and Imura (2015) found chimpanzees rapidly detected faces amongst non-face distractors in a visual search task. Together, these results suggest the dot probe task is sensitive to detecting a general bias towards faces, as well as larger perceptual differences between faces.

In the main experiment, significant biases towards chimpanzee threatening faces paired with scrambled faces were found. However, there were no significant biases for threatening faces paired with neutral faces, and response times towards threatening faces with higher threat intensity (scream) and lower threat intensity (bared teeth) did not differ. In rhesus monkeys, Parr et al. (2013) found a significant bias towards threatening faces versus scrambled images at an SOA of 500 ms. However, these biases may not have been observed if the threatening faces were paired with neutral faces, and so it is unclear whether they are threat-specific. Interestingly, when I analysed the data for the first session, chimpanzees showed an attentional bias towards bared teeth faces (but not scream faces) versus neutral faces. However, this bias disappeared when response times for all sessions were analysed. Similarly, King et al. (2012) found a significant bias towards threatening faces versus neutral faces at an SOA of 1000 ms in rhesus monkeys which disappeared over time. It is possible that a threat-specific attentional bias occurred early in my experiment and that repeated exposure to the stimuli weakened this bias, although my shorter SOA of 150 ms may have limited exposure to some extent. Alternatively, this bias could also be explained by individual variation in response times between chimpanzees in the first session. Indeed, biases appear to become more reliable when the dot probe task is repeated daily over a number of weeks (van Rooijen et al. 2017). Overall, in combination with the biases found towards chairs and neutral chimpanzee faces paired with scrambled faces in the preliminary experiments, these results suggest faster response times

towards threatening faces reflect a general bias towards faces, rather than threatening faces specifically.

Although I found no convincing evidence for threat-specific attentional biases, it is premature to conclude they do not exist. Several methodological issues may account for my results. One issue may be that the stimuli threat intensity was too weak to facilitate biases. In humans, Wilson and MacLeod (2003) found morphing angry facial expressions to increase their threat intensity enhanced biases. This would be an interesting manipulation to explore in future chimpanzee studies. Another possibility is the stimuli lacked threat intensity as they were presented in greyscale rather than colour. Whilst some evidence suggests chimpanzees can recognise conspecific emotions from greyscale images (e.g. Parr 2003), other evidence suggests effects are only obtained in colour (e.g. Kret et al. 2014). Therefore, in future dot probe studies it would be useful to test threatening stimuli in colour. In addition, although I were unable to verify the sex of my stimuli, presenting male chimpanzee faces may be more threatening than female faces, as male chimpanzees are more aggressive (Wilson and Wrangham 2003; Muller and Mitani 2005). Finally, testing chimpanzees with limited exposure to facial stimuli may help to maintain their emotional salience. Our chimpanzees have extensive experience participating in cognitive tasks using facial stimuli, so may be habituated to faces in general.

Another issue is the influence of emotional state on the task. Emotional state has been shown to influence attention in non-human primates (Bethell et al. 2012; Bethell et al. 2016; Marzouki et al. 2014). Rhesus macaques in a stressful state showed greater avoidance and slower responses to threatening conspecific faces than when in a neutral state (Bethell et al. 2012; Bethell et al. 2016). However, these studies presented stimuli for 10-60 seconds and were not restricted to measuring initial threat detection at very short presentation times, as in the present study. In human dot probe studies, failure to observe bias towards threatening faces is

often attributed to low trait anxiety or failure to induce a high state of anxiety experimentally (Bradley et al. 1997; Gotlib et al. 2004; Pineles and Mineka 2005). Behaviourally, our chimpanzees appeared to be in a relaxed state during the tasks, so anxiety levels may have been too low to facilitate threat-specific biases.

Conversely, attentional training has been shown to influence emotional state in humans (for a review see Bar-Haim 2010). In a modified version of the dot probe task, the dot location is systematically manipulated to increase the proportion of dots appearing in the location of the threatening stimuli or the neutral stimuli. Repeated training leads to an implicitly learned bias towards or away from threat and subsequently an increase or decrease in anxiety respectively (e.g. Eldar et al. 2008; MacLeod et al. 2002). In chimpanzees, increasing the predictability of visual social precues (gaze) and non-social cues leads to stronger cueing effects (Tomonaga 1997; Tomonaga 2007b). Therefore, it may be possible to induce a learned bias towards threatening faces and subsequently an anxious state in chimpanzees using a modified dot probe task.

A third issue is the stimuli presentation duration may not have been optimal for facilitating bias towards threatening faces. Although I presented stimuli at an SOA of 150 ms based on a review of the human literature (e.g. Stevens 2009; Cooper and Langton 2006; Holmes et al. 2005; Bourne 2006) this duration may not have been optimal for chimpanzees. Biases towards threatening faces has been found at SOAs as short as 17 ms (i.e. subliminal presentation) in humans (Monk et al. 2008). However, in chimpanzees Kret et al. (2018) failed to find biases towards threatening whole-body images presented at 33 ms (also subliminal presentation) and 300 ms. Together, these results suggest the optimal SOA for facilitating biases may be very precise and so it would be useful to test additional SOAs in the future.

Finally, manual response dot probe tasks may not be sensitive enough to detect biases towards threatening faces in chimpanzees. In non-human primates, touchscreen response times

are used as an indirect measure of attention. This method assumes gaze location directly corresponds to motor responses. However, more direct measures such as eye tracking and event-related potentials may reveal biases otherwise masked by hand movement and are generally considered more reliable (Fashler and Katz 2016; Hirata et al. 2013; Torrence and Troup 2017). In an example of eye tracking use in non-human primates Pine et al. (2009) found monkeys looked significantly longer at threatening than neutral human faces. Bethell et al. (2012) observed rhesus macaques were faster to direct initial gaze towards threatening than neutral conspecific faces from video recordings. For further study in chimpanzees, it would be useful to examine to what extent initial gaze location corresponds to manual responses in the dot probe task using eye tracking.

In conclusion, this study found the touchscreen dot probe task can measure attentional biases not only towards faces, but perceptually different faces in chimpanzees. However, no evidence for attentional biases specific to threatening faces was found. More research investigating stimuli threat intensity, emotional state, stimuli presentation duration and direct measures of attention is needed to fully explore the potential of the dot probe task to assess emotional attention in non-human primates.

Appendix V: Individual data

Colour experiment: Congruent dot presentation (mean response times in ms)

Chimpanzee	Dark Red- Light Red	Dark Red- No Stimulus	Light Red- No Stimulus
Ai	352	296	317
Ayumu	381	383	409
Chloe	373	337	360
Cleo	378	370	337
Gon	461	476	464
Pal	351	306	332
Pendensa	443	447	428
Popo	537	464	490

Colour experiment: Incongruent dot presentation (mean response times in ms)

Chimpanzee	Dark Red- Light Red	Dark Red- No Stimulus	Light Red- No Stimulus
Ai	377	425	409
Ayumu	365	358	403
Chloe	386	432	391
Cleo	367	381	417
Gon	530	528	544
Pal	343	345	362
Pendensa	443	462	449
Popo	555	562	538

Appendix VI: Individual data

Object experiment: Congruent dot presentation (mean response times in ms)

Chimpanzee	Chair- Scrambled	Chair- No Stimulus	Scrambled- No Stimulus
Ai	351	332	314
Ayumu	357	429	349
Chloe	377	346	366
Cleo	343	316	368
Gon	508	478	474
Pal	344	316	340
Pendensa	436	437	456
Popo	502	484	518

Object experiment: Incongruent dot presentation (mean response times in ms)

Chimpanzee	Chair- Scrambled	Chair- No Stimulus	Scrambled- No Stimulus
Ai	384	406	402
Ayumu	390	367	389
Chloe	407	409	401
Cleo	422	402	387
Gon	524	578	560
Pal	391	380	365
Pendensa	453	455	442
Popo	564	567	538

Appendix VII: Individual data

Primate faces experiment: Congruent dot presentation (mean response times in ms)

Chimpanzee	Chimpanzee- Orangutan	Chimpanzee- Baboon	Chimpanzee- Scrambled
Ai	364	364	348
Ayumu	381	359	377
Chloe	367	381	366
Cleo	366	364	371
Gon	597	559	555
Pal	376	381	369
Pendensa	431	422	430
Popo	539	551	515

Primate faces experiment: Incongruent dot presentation (mean response times in ms)

Chimpanzee	Chimpanzee- Orangutan	Chimpanzee- Baboon	Chimpanzee- Scrambled
Ai	376	365	411
Ayumu	366	395	377
Chloe	385	385	401
Cleo	405	389	366
Gon	586	593	601
Pal	379	388	378
Pendensa	430	426	435
Popo	540	558	549

Appendix VIII: Individual data

Threatening faces experiment: Congruent dot presentation (mean response times in ms)

Chimpanzee	Bared teeth- Neutral	Scream- Neutral	Bared teeth- scrambled	Scream- Scrambled
Ai	362	358	343	337
Ayumu	372	389	389	395
Chloe	393	391	377	378
Cleo	413	362	377	372
Gon	515	506	512	534
Pal	391	394	375	388
Pendensa	441	435	438	432
Popo	536	528	527	527

Threatening faces experiment: Incongruent dot presentation (mean response times in ms)

Chimpanzee	Bared teeth- Neutral	Scream- Neutral	Bared teeth- scrambled	Scream- Scrambled
Ai	394	398	415	409
Ayumu	396	378	348	369
Chloe	387	388	389	403
Cleo	384	418	373	419
Gon	512	505	507	514
Pal	400	393	402	400
Pendensa	439	440	441	432
Popo	543	530	573	567

CHAPTER 4

SEARCH ASYMMETRY FOR THREATENING FACES IN CHIMPANZEES

4.1. Abstract

For primates, the ability to efficiently detect facial expressions which signal threat is particularly important for survival. However, the mechanisms underlying the detection of threatening faces are not fully understood. This study examined whether chimpanzees show asymmetries in visual search for conspecific threatening faces. Five adult chimpanzees participated in a touchscreen MTS visual search task. More efficient detection (faster response times) of threatening face targets (bared teeth or scream expressions) amongst neutral face distractors and scream face targets (higher threat intensity) amongst bared teeth distractors (lower threat intensity) than vice versa was predicted. In line with prediction, a threat-superiority effect was found, with faster response times for threatening face targets than neutral face targets and scream face targets than bared teeth face targets. A serial search strategy suggested the chimpanzees had difficulty in disengaging from threatening face distractors and that they were processed strategically rather than automatically. This study provides partial support for the later evolution of a social submissiveness system in chimpanzees.

4.2. Introduction

Faces are one of the most important and salient social stimuli for primates. They convey information about identity, age, sex, attention and emotion (Adachi and Tomonaga 2017). Facial expressions provide the receiver with information about the motivations and intentions of the sender so that behaviour can be modified appropriately in response (Seyfarth et al. 2010). The efficient detection of facial expressions displayed during social conflict (e.g. angry or fearful faces) has adaptive value, enabling potential harm to be avoided. Therefore, threatening faces should be given attentional priority over non-threatening faces (Horstmann 2007). One of the most widely used paradigms to study such threat-superiority effects for evolutionary relevant threatening stimuli (esp. snakes and angry faces) is the visual search task.

In the visual search task a target stimulus is presented amongst a number of distractor stimuli, with the aim being to detect the target as quickly as possible (Treisman and Gelade 1980). In a typical visual search task using facial expressions, a target face with one type of expression is presented on a screen amongst a set of ‘distractor’ faces with another type of expression. Response times and accuracy to detect the target are recorded and indicate the efficiency with which the target is detected. If the facial expression influences attentional priority, search efficiency should differ between expressions (Frischen et al. 2008). For targets that are easy to detect, response times typically do not vary with increasing set size (the number of items in a search array). Such rapid target detection is thought to involve parallel search of all items. Some researchers suggest that parallel search for threatening faces provides evidence of automatic processing of threat (e.g. Hansen and Hansen 1988). However, other researchers argue that low-level visual features are responsible for parallel search (e.g. Purcell et al. 1996). For targets that are more difficult to detect, response times typically increase with increasing set size. This involves serial search of each item in turn and greater strategic processing. The more similar the target is to the distractors the less efficiently it is detected. Moreover, it is

easier to detect a target amongst an array of homogeneous (identical) distractors than heterogeneous (non-identical) distractors (Wolfe 2018). It can also be easier to find e.g. target A amongst B distractors than target B amongst A distractors. Such search asymmetries are due to the presence rather than absence of a particular visual feature (Treisman and Souther 1985).

Many human visual search studies examining attentional biases towards facial expressions have used schematic drawings of faces (for a review see Horstmann 2007). Whilst schematic faces allow for greater experimental control, they are less ecologically valid than photographs of real faces and not frequently used in non-human primate studies (although see Tomonaga 2007a). The majority of human visual search studies with real faces use angry and happy expressions (Calvo and Nummenmaa 2008). Whilst some studies have found a threat-superiority effect, with angry face targets detected faster than neutral face targets (e.g. Fox and Damjanovic 2006; Hansen and Hansen 1988; Horstmann and Bauland 2006; Lipp et al. 2009a, 2009b; Pinkham et al. 2010; Savage et al. 2013) other studies have not (e.g. Byrne and Eysenck 1995; Calvo and Nummenmaa 2008; Gilboa-Schechtman et al. 1999; Juth et al. 2005; Purcell et al. 1996; Williams et al. 2005). Interestingly, several studies have found more efficient search for happy compared with angry faces (e.g. Byrne and Eysenck 1995; Juth et al. 2005). This happy-superiority advantage is likely explained by the visual saliency of the mouth and teeth area. Moreover, it has been suggested that angry faces are less uniform in appearance making them more difficult to detect than happy faces (Calvo and Nummenmaa 2008; Calvo and Marrero 2009). Therefore, differences in search efficiency for angry and happy faces could be explained by perceptual differences in specific facial features, rather than emotional expression per se (Savage et al. 2013).

In non-human primates, most of the empirical work on visual search has been conducted in monkeys and chimpanzees. Japanese macaques were faster to detect snakes amongst flowers or fear-irrelevant animal distractors than vice versa (Kawai and Koda 2016;

Shibasaki and Kawai 2009). Kawai et al. (2016) found that three Japanese macaques were faster to detect unfamiliar conspecific threatening face targets amongst neutral face distractors than vice versa. In addition, no difference in response times to detect non-face targets (pictures of computers) amongst neutral or threatening face distractors was found, suggesting that the threatening face target facilitated faster detection. Together, these studies demonstrate an attentional bias towards evolutionary-relevant threatening stimuli in monkeys.

In chimpanzees, visual search for faces has been studied extensively by Tomonaga and colleagues. Tomonaga (1999) found an adult female chimpanzee showed worse performance in searching for photographs of human and chimpanzee faces presented in an inverted than upright or horizontal orientation. This inversion effect was not found with photographs of houses. In the same chimpanzee, Tomonaga (2007a) demonstrated an inversion effect for finding pictures of human and dog faces, but not for hands and chairs. In three adult chimpanzees, Tomonaga and Imura (2015) reported that they were able to efficiently find faces of humans and chimpanzees amongst non-face objects. Furthermore, search efficiency was impeded for inverted faces suggesting that the chimpanzees processed the faces holistically (see Chapter 2-1, p. 21). In addition, Tomonaga and Imura (2010) showed that a chimpanzee was more efficient in searching for a human face target with a direct gaze amongst human face distractors with an averted gaze than vice versa, consistent with findings in humans. Together, these findings demonstrate that chimpanzees, like humans, are particularly efficient at searching for faces and use similar search strategies.

To date, no studies have investigated visual search efficiency for facial expressions in chimpanzees. The aim of this study was to examine whether chimpanzees show asymmetries when searching for conspecific threatening faces (bared teeth and scream expressions). I predicted a threat-superiority effect, i.e. more efficient search (faster response times) for threatening face targets (bared teeth or scream expressions) amongst neutral face distractors

than vice versa (e.g. Kawai et al. 2016). As scream faces likely signal a more direct threat to the observer than bared teeth faces, I predicted more efficient search for scream face targets (higher threat intensity) amongst bared teeth distractors (lower threat intensity) than vice versa (Davis and Whalen 2001; Parr et al. 2007). In addition, if threatening faces are detected automatically, I expected to see evidence of parallel search for threatening but not neutral face targets. Finally, I predicted more efficient search amongst homogeneous than heterogeneous distractors.

4.3. Methods

4.3.1. Participants and housing

Five adult female chimpanzees (*Pan troglodytes*) participated in the study at the Primate Research Institute, Kyoto University (KUPRI), Japan (**Table 4.1**) (Watanuki et al. 2014). The chimpanzees were members of a social group of 11 individuals living in an environmentally enriched facility consisting of two outdoor enclosures (250 m² and 280 m²), an open-air outdoor enclosure (700 m²) and indoor living rooms linked to testing rooms. The open air outdoor enclosure was equipped with 15 m high climbing frames and included streams and trees (Matsuzawa et al. 2006; Yamanashi and Hayashi 2011). No food or water deprivation was used in the study. The experimental protocol was approved by the Animal Welfare and Care Committee of the KUPRI and the Animal Research Committee of Kyoto University and followed the *Guidelines for the Care and Use of Laboratory Primates* of the KUPRI (Version 3, 2010). The chimpanzees had extensive experience participating in cognitive touchscreen tasks, including MTS and visual search (e.g. Tomonaga 1999; Tomonaga and Imura 2015).

Table 4.1 Basic information about the five chimpanzees

Name	GAIN ID Number ^a	Sex	Age (at study start)
Ai	0434	Female	42
Chloe	0441	Female	38
Cleo	0609	Female	18
Pal	0611	Female	18
Pendensa	0095	Female	41

^aIdentification number (ID) for each chimpanzee listed in the database of the Great Ape Information Network (GAIN): <https://shigen.nig.ac.jp/gain>

4.3.2. Apparatus

The experiment was conducted in an experimental booth ($1.80 \times 2.15 \times 1.75$ m) inside a testing room. Each chimpanzee voluntarily walked to the booth through an overhead walkway connected to the living rooms. A 17-inch touch-sensitive LCD monitor (1280×1024 pixels) encased inside Plexiglas was used to present visual stimuli at approximately 40 cm distance. Food rewards (eight-millimetre apple cubes) were delivered via a universal feeder device. All experimental events were controlled by a PC and the computer task was programmed using Microsoft Visual Basic 2010 (Express Edition).

4.3.3. Stimuli

Facial stimuli consisted of cropped photographs (200×225 pixels) of unfamiliar chimpanzees. Stimuli were obtained from photographs taken of chimpanzees at Kumamoto Sanctuary, Kyoto University, or from personal collections. All faces were presented in greyscale and the average luminance of each face was scaled to the average luminance of all faces in each experiment. This was to control for differences in colour hue, luminance and low-level features which may inadvertently bias attention. Chimpanzee faces featured neutral or threatening expressions. Threatening faces were categorised into ‘scream’ and ‘bared teeth’ expressions. A chimpanzee

scream expression was defined as: “a raised upperlip with lip corners pulled back exposing the upper teeth, lower lip depressed also exposing the lower teeth, and mouth stretched wide open with lips parted” which is thought to reflect “general agonism” (Parr et al. 2007, p. 176). A chimpanzee bared teeth expression was defined as: “an open mouth with lips parted, a raised upper lip, and retracted lip corners functioning to expose the teeth” which occurs “in response to aggression” (Parr et al. 2007, p. 175) and likely reflects fear. The scream and bared teeth facial expression stimulus set was reviewed by a certified Chimpanzee Facial Action Coding System (ChimpFACS) coder who found the expressions consistent with our categorisation (Wilson and Tomonaga 2018b). 10 images were presented for each expression.

4.3.4. Procedure

The chimpanzees participated in a matching-to-sample (MTS) visual search task (cf. Tomonaga 1993) (**Figure 4.1**). To begin each trial the chimpanzees touched a blue start key at the bottom of the screen, followed by a sample stimulus in the center of the screen. When the sample was touched it disappeared and sets of three, five or eight comparison stimuli appeared in the top half of the screen at random locations. The comparison stimuli consisted of the target face (identical to the sample) presented amongst several distractor faces. The faces remained on the screen until a face was touched or five seconds had elapsed. On homogeneous distractor trials the faces were identical to each other, whilst on heterogeneous distractor trials the faces were of different individuals showing the same expression. Homogeneous distractors were used to measure baseline performance and heterogeneous distractors were used to increase search difficulty. Homogeneous and heterogeneous distractor presentation was alternated on each trial, and set size was randomised across trials. When a correct choice was made (the target was touched) a chime sound was played and a food reward given and when an incorrect choice was made (a distractor was touched) a buzzer sound was played and no food reward was given. An incorrect choice was followed by a correction trial in which the same sample

and target were presented again without distractors. This was to try and prevent idiosyncratic error response patterns developing and to maintain motivation during the task. The inter-trial interval was two seconds. Response times (ms) and the number of errors were recorded by a PC. A total of 576 trials (48 trials $\times$ 12 sessions) were completed. Trial order was randomised within and across sessions.

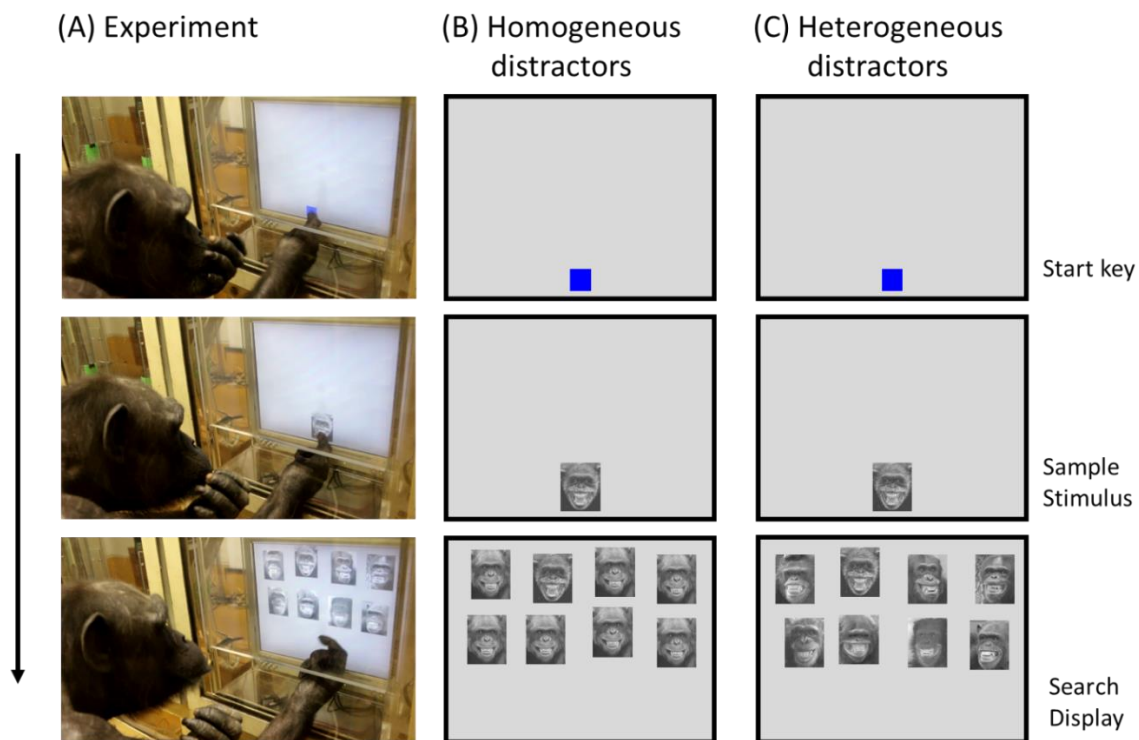


Figure 4.1 (A) Chimpanzee 'Ai' participating in the MTS visual search experiment. To begin each trial a start key (blue square) at the bottom of the screen was touched. A sample image then appeared and was touched. The target (sample) was then presented amongst an array of distractors. (B) Example of homogeneous distractor trial: scream face target amongst identical bared teeth face distractors. (C) Example of heterogeneous distractor trial: scream face target amongst non-identical bared teeth face distractors. Response times (ms) and errors were recorded.

4.3.5. Statistical analysis

The data were analysed using R (version 3.5.2). Trials with response times of five seconds or longer after the sample image presentation disappeared may not have been retained and so were excluded from the analysis. The 'lmerTest' package was used to perform a Generalized Linear Mixed Model (GLMM) analysis using the 'lmer' function on the relationship between overall

response times and target stimuli for each set size and ‘glmer’ function on the relationship between the number of errors and target stimuli for each set size. Chimpanzees showed faster responses on correct trials than incorrect trials (a speed–accuracy trade-off) indicating guessing behaviour. Therefore, analyses were conducted on overall response times (averaged across correct and incorrect trials) (cf. Tomonaga 2007a). As fixed effects, target stimulus and set size (with and without interaction term) were entered into the model. Chimpanzees and sessions were included as random intercepts. Visual inspection of residual plots revealed the data were normally distributed, so for error analysis a binomial distribution with a logit link function was chosen and for response time analysis a log (RT) function was chosen. The models with the smallest AIC values were chosen.

4.4. Results

4.4.1. Response times

Figure 4.2. shows the mean response times (ms) as a function of set size for each threatening face target. For homogeneous distractors, response times were significantly faster for bared teeth than neutral targets ($\beta = 0.08$, $SE = 0.03$, $p = 0.007$, 95% CI [0.02, 0.13]) and slowed with set size ($\beta = 0.06$, $SE = 0.01$, $p < 0.001$, 95% CI [0.05, 0.08]). Response times were significantly faster for scream than neutral targets ($\beta = -0.10$, $SE = 0.03$, $p = 0.001$, 95% CI [-0.15, -0.04]) and slowed with set size ($\beta = 0.08$, $SE = 0.01$, $p < 0.001$, 95% CI [0.06, 0.09]). Response times were significantly faster for scream than bared teeth targets ($\beta = -0.07$, $SE = 0.03$, $p = 0.030$, 95% CI [-0.13, -0.01]) and slowed with set size ($\beta = 0.09$, $SE = 0.01$, $p < 0.001$, 95% CI [0.07, 0.10]). For heterogeneous distractors, no significant difference in response times between neutral and bared teeth targets was found ($\beta = 0.05$, $SE = 0.03$, $p = 0.098$, 95% CI [-0.01, 0.10]). However, response times slowed with set size ($\beta = 0.08$, $SE = 0.01$, $p < 0.001$, 95% CI [0.07, 0.09]). Response times were significantly faster for scream than neutral targets ($\beta = -0.12$, $SE = 0.03$, $p < 0.001$, 95% CI [-0.16, -0.05]) and slowed with set size ($\beta = 0.09$, $SE = 0.01$, $p <$

0.001, 95% CI [0.07, 0.10]). Response times were significantly faster for scream than bared teeth targets ($\beta = -0.07$, $SE = 0.03$, $p = 0.028$, 95% CI [-0.13, -0.01]) and slowed with set size ($\beta = 0.07$, $SE = 0.01$, $p < 0.001$, 96% CI [0.06, 0.09]). For individual chimpanzee data see **Appendix IX**.

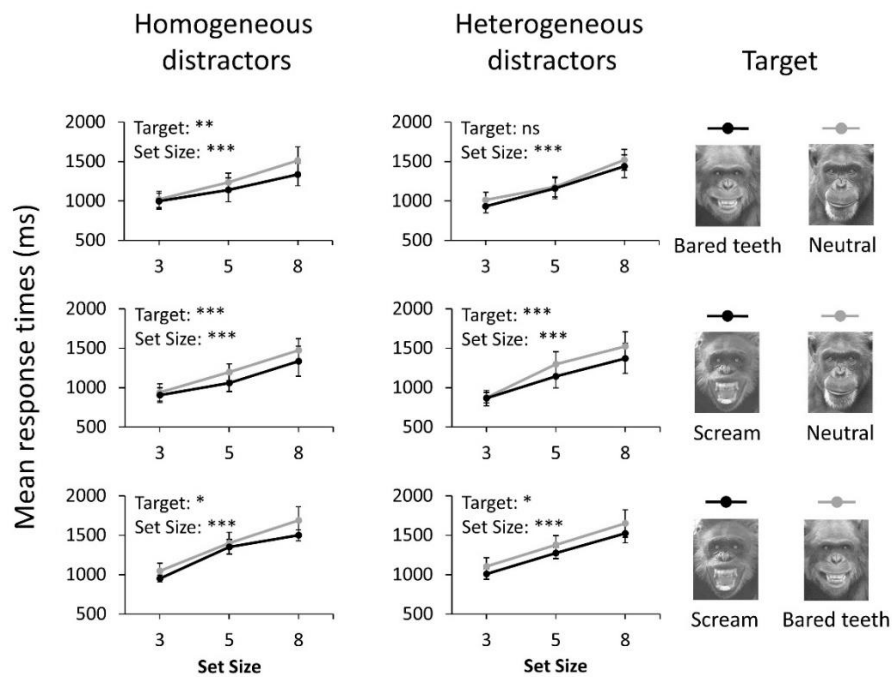


Figure 4.2 Mean response times (ms) as a function of set size for each threatening face target. Error bars indicate the standard error of the mean

4.4.2. Errors

Figure 4.3. shows the mean percentage of errors as a function of set size for each threatening face target. For homogeneous distractors, errors were significantly lower for bared teeth than neutral targets ($\beta = 0.42$, $SE = 0.21$, $p = 0.043$, 95% CI [0.01, 0.83]). However, no difference in errors as a function of set size was found ($\beta = -0.03$, $SE = 0.05$, $p = 0.511$, 95% CI [-0.13, 0.07]). Errors were significantly lower for scream than neutral targets ($\beta = -0.86$, $SE = 0.27$, $p = 0.001$, 95% CI [-1.38, -0.34]). However, no difference in errors as a function of set size was found ($\beta = -0.04$, $SE = 0.06$, $p = 0.562$, 95% CI [-0.16, 0.09]). Errors were significantly lower for scream than bared teeth targets ($\beta = -0.87$, $SE = 0.17$, $p < 0.001$, 95% CI [-1.20, -0.54]) and

increased with set size ($\beta = -0.15$, $SE = 0.04$, $p < 0.001$, 95% CI [0.07, 0.23]). For heterogeneous distractors, errors were significantly lower for bared teeth than neutral targets ($\beta = 0.59$, $SE = 0.19$, $p = 0.002$, 95% CI [0.21, 0.97]) and increased with set size ($\beta = -0.21$, $SE = 0.05$, $p < 0.001$, 95% CI [0.12, 0.30]). No significant difference in errors between neutral and scream targets was found ($\beta = -0.73$, $SE = 0.66$, $p = 0.266$, 95% CI [-0.56, 2.03]). However, errors increased with set size ($\beta = 0.37$, $SE = 0.07$, $p < 0.001$, 95% CI [0.23, 0.51]). An interaction between the target and set size was also found ($\beta = -0.24$, $SE = 0.12$, $p = 0.025$, 95% CI [-0.45, -0.03]). Errors were significantly lower for scream than bared teeth targets ($\beta = -0.55$, $SE = 0.16$, $p < 0.001$, 95% CI [-0.86, -0.24]) and increased with set size ($\beta = -0.22$, $SE = 0.04$, $p < 0.001$, 95% CI [0.15, 0.30]). For individual chimpanzee data see **Appendix IX**.

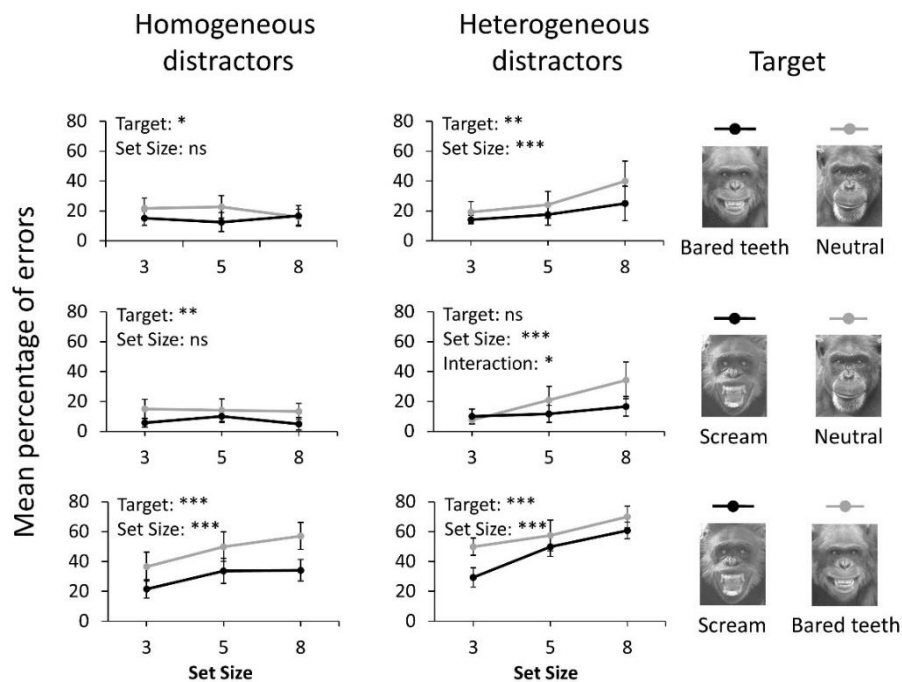


Figure 4.3 Mean percentage of errors as a function of set size for each threatening face target. Error bars indicate the standard error of the mean

4.5. Discussion

This study investigated search asymmetries for threatening facial expressions in chimpanzees.

As predicted, search was more efficient for threatening face targets (bared teeth and scream)

than neutral face targets, although no difference in response times was found for detecting bared teeth and neutral face targets presented amongst heterogeneous distractors. Also in line with prediction, response times were faster for scream face targets (higher threat intensity) than bared teeth targets (lower threat intensity). Overall, response times increased and accuracy decreased with increasing set size, indicating inefficient search and a serial search strategy. Therefore, threatening face distractors were likely more difficult to disengage from than neutral face distractors resulting in slower response times for detecting neutral targets. Similarly, it was more difficult to disengage from scream distractors than bared teeth distractors resulting in slower response times for detecting bared teeth targets.

These attentional asymmetries are broadly consistent with the pattern of discrimination asymmetries described in Chapter 2-2 and provide support for visual search studies in humans and monkeys which have found a search advantage for angry faces (humans: e.g. Lipp et al. 2009a, 2009b; Pinkham et al. 2010; Savage et al. 2013, monkeys: Kawai et al. 2016). However, in contrast to some human visual search studies with snakes, which demonstrate parallel search for snake targets but not mushroom or flower (non-threatening) targets (Lipp 2006; Öhman et al. 2001), no evidence of automatic processing of threatening faces was found in our chimpanzees. These results point towards more strategic processing of threatening faces involving the prefrontal cortex (Cisler and Koster 2010). The implication of greater cognitive control over search for threatening faces provides partial support for the later evolution of a social submissiveness system to respond to threat from one's own species (see Öhman et al. 1985). Although this study found evidence of attentional biases towards threatening faces, it does not tell us which facial features may be responsible for difficulty in disengagement. In humans, Horstmann and Bauland (2006) found shallower search slopes for angry faces than happy faces when faces included only the mouth but not only the eyes. In contrast, Fox and Damjanovic (2006) found that angry faces were detected faster than happy faces when only the

eyes were presented but not only the mouth. In chimpanzees, Kano and Tomonaga (2009) found they fixated more on the mouth for scream expressions and more on the eyes for neutral faces. To reveal to what extent the mouth or eyes are responsible for more efficient search of scream and bared teeth faces in our chimpanzees, it would be useful to systematically remove or artificially darken these areas. If search asymmetries subsequently disappear, it may be concluded that these features are critical. Although it may be argued that the display of relatively bright teeth has evolved as a salient signal of threat, it is possible that bright areas on *any* part of the face may effectively draw attention. Therefore, a useful manipulation would be to artificially brighten areas of the face not associated with threat (e.g. the forehead). If search is just as efficient for such faces, this would suggest that low-level properties (i.e. brightness) rather than signals of threat facilitate biases (Hansen and Hansen 1988; Purcell et al. 1996). In addition, it would also be useful to test for the face inversion effect to determine whether threatening faces are processed holistically. The presence of an inversion effect would imply holistic processing, whereas the absence of an effect would support featural processing (e.g. Tomonaga and Imura 2015). To date, human visual search studies have found mixed evidence for the inversion effect for facial expressions. Some studies have found an inversion effect (e.g. Fox and Damjanovic 2006) whilst others have not (e.g. Williams et al. 2005; Horstmann and Bauland 2006; Lipp et al. 2009; Savage and Lipp 2014). Finally, general limitations of this study include the relatively small sample size and number of stimuli presented.

In conclusion, this study provides evidence for a threat-superiority effect during visual search for threatening facial expressions in chimpanzees. In addition, search was more efficient for facial expressions categorised as having higher than lower threat intensity. A serial search strategy suggested that the chimpanzees had difficulty in disengaging from threatening faces and processed them strategically rather than automatically. This provides partial support for the later evolution of a social submissiveness system to respond to social threat in chimpanzees.

Appendix IX: Individual data

Homogeneous distractors (mean response times in ms)

	Bared teeth-neutral		Scream-neutral		Scream-bared teeth	
Chimpanzee	Bared teeth target	Neutral target	Scream target	Neutral target	Scream target	Bared teeth target
Ai	717	859	722	828	1064	997
Chloe	1358	1504	1403	1371	1396	1335
Cleo	1246	1203	1113	1248	1180	1296
Pal	1039	1157	926	1114	1336	1550
Pendensa	1427	1555	1342	1469	1372	1740

Heterogeneous distractors (mean response times in ms)

	Bared teeth-neutral		Scream-neutral		Scream-bared teeth	
Chimpanzee	Bared teeth target	Neutral target	Scream target	Neutral target	Scream target	Bared teeth target
Ai	717	859	722	828	1064	997
Chloe	1385	1395	1445	1385	1390	1479
Cleo	1214	1330	1179	1240	1334	1539
Pal	1138	1181	1075	1169	1252	1493
Pendensa	1382	1446	1302	1577	1409	1513

Homogeneous distractors (mean percentage of errors)

	Bared teeth-neutral		Scream-neutral		Scream-bared teeth	
Chimpanzee	Bared teeth target	Neutral target	Scream target	Neutral target	Scream target	Bared teeth target
Ai	6	01	1	0	57	75
Chloe	13	40	17	38	28	40
Cleo	13	18	1	11	21	24
Pal	06	14	4	10	24	59
Pendensa	38	26	11	13	19	42

Heterogeneous distractors (mean percentage of errors)

	Bared teeth-neutral		Scream-neutral		Scream-bared teeth	
Chimpanzee	Bared teeth target	Neutral target	Scream target	Neutral target	Scream target	Bared teeth target
Ai	1	1	4	0	61	76
Chloe	28	56	22	49	53	53
Cleo	13	24	13	17	42	44
Pal	14	22	8	14	39	76
Pendensa	39	36	17	25	39	46

CHAPTER 5

GENERAL DISCUSSION

5.1. Summary of main findings

This thesis explored whether attentional biases towards threatening faces can be measured in chimpanzees using two well-established attentional tasks from human psychological research, the visual dot probe task and the visual search task. Prior to these attentional tasks, I demonstrated that our chimpanzees could successfully discriminate the threatening stimuli set (neutral, bared teeth and scream faces) in a touchscreen MTS task. Although the non-threatening stimuli (chimpanzee, baboon and orangutan faces) were not presented together in the same condition, all faces were discriminated above chance and so it may be inferred that they can be discriminated from each other. In both studies, perceptually different faces (i.e. baboon versus gorilla or orangutan faces, and neutral versus bared teeth or scream faces) were significantly easier to discriminate than perceptually similar faces. This is consistent with previous MTS studies on discrimination of facial expressions in chimpanzees (e.g. Parr et al. 1998). In addition, discrimination performance was better when the sample was a threatening face and the distractor was a neutral face (for identical and categorical matching) and when the sample was a scream face (higher threat intensity) and the distractor was a bared teeth face (lower threat intensity) than vice versa (for identical matching). This suggested that threatening and higher threat intensity faces were more salient and captured attention to a greater extent than neutral or lower threat intensity faces. Subsequently, the attentional component of these asymmetries was investigated in a MTS visual search task.

In the visual dot probe task the stimuli were presented for 150 ms, a duration thought optimal for threat detection in humans. In the preliminary experiments using non-threatening stimuli, biases were found for chimpanzee versus baboon faces (perceptually more different) but not chimpanzee versus orangutan faces (perceptually more similar), consistent with performance in the discrimination studies. In the main experiment, biases were found for threatening versus scrambled faces but not neutral faces. In addition, no significant difference

in response times was found between bared teeth (lower threat intensity) and scream faces (higher threat intensity) when paired separately with scrambled faces. The lack of a bias towards threatening versus neutral faces cannot be explained by a failure to visually discriminate the stimuli, as the chimpanzees successfully discriminated them in the previous MTS experiments. Rather, it suggests a bias towards faces in general, and larger perceptual differences between faces, rather than threatening faces specifically.

In the visual search task, the chimpanzees showed attentional biases (more efficient search) for threatening faces targets amongst neutral face distractors and scream face targets (higher threat intensity) amongst bared teeth face distractors (lower threat intensity) than vice versa, indicating a threat-superiority effect. As the number of distractors increased, search became less efficient, indicating serial search and strategic rather than automatic processing. The threatening face distractors were likely more difficult to disengage from than neutral face distractors, leading to slower response times to detect the neutral than threatening face targets. Overall, attentional biases specifically towards threatening faces appear to be absent at an earlier stage of processing in the visual dot probe task, but present at a later stage of processing in the visual search task. Next, I will relate these findings to previous studies in human and non-human primates.

5.2. Comparison with human and non-human primate studies

The failure to find an attentional bias towards threatening versus neutral faces presented at 150 ms in the current dot probe task with chimpanzees is inconsistent with human studies which tend to find biases at around 100 ms (e.g. Cooper and Langton 2006; Holmes et al. 2005; Stevens et al. 2009). Kret et al. (2018) also failed to show a bias towards threatening human and chimpanzee fearful (scream) and angry (bulging lip) whole-body expressions in the dot probe task presented at 33 ms (subliminal presentation) and 300 ms (supraliminal presentation) in the same group of chimpanzees. However, human participants did show biases towards

human and chimpanzee threatening bodies at both presentation times. The authors speculate that the chimpanzees may take longer than humans to process the emotional significance of the expressions in the images. Similarly, in the present dot probe task, it is possible that the stimuli were not presented for sufficiently long for the chimpanzees to process their emotional meaning and therefore form threat-specific biases. However, Kret et al. (2016) did find biases towards emotional versus neutral scenes featuring whole-bodies presented at 300 ms in a dot probe task with a closely related species, bonobos. The stimuli were more complex and naturalistic than those used in Kret et al. (2018) and presented in colour, which may have helped to facilitate biases. The fact that two dot probe studies in the same group of chimpanzees failed to find biases towards threat may be significant. Our chimpanzees have many years of experience participating in touchscreen cognitive tasks featuring faces and bodies as stimuli and therefore may have become habituated to them, reducing their overall emotional salience. In future, it would be useful to conduct similar experiments with chimpanzees with little or no exposure to such stimuli for comparison.

There have only been two dot probe studies in monkeys which have presented threatening faces as stimuli. King et al. (2012) found biases towards threatening versus neutral faces presented for 1,000 ms and Parr et al. (2013) found biases towards threatening versus scrambled but not neutral versus scrambled faces presented for 500 ms. However, it is important to note that at SOAs above 200 ms (the duration of an eye saccade) attention can shift between the two stimuli during presentation. Therefore, the responses in these two studies do not necessarily provide information about initial orientation towards threat (Bourne 2006; Bradley et al. 2000). In addition, threatening versus neutral faces were not presented in the study by Parr et al. (2013), so it is difficult to know how specific these biases are to threatening faces. Whilst acknowledging such limitations, these experiments in monkeys suggest biases towards threatening faces are present at later stages of processing (i.e. involve strategic rather

than automatic processing). To confirm if biases also develop at later stages of processing in chimpanzees longer SOAs should be tested (e.g. 500 ms and above). Conversely, to confirm if biases are also present at earlier stages of processing, shorter SOAs should be tested in monkeys.

In the visual search task, the chimpanzees were more efficient in searching for threatening face targets amongst neutral face distractors than vice versa. This result is consistent with some human visual search studies which have found biases towards real threatening faces (e.g. Fox and Damjanovic 2006; Hansen and Hansen 1988; Horstmann and Bauland 2006). However, caution should be exercised in interpreting these biases as strictly related to threat or involving automatic processing (e.g. Hansen and Hansen 1988). Some studies have found that low-level perceptual cues (e.g. dark areas) may be responsible for parallel search for threatening faces (e.g. Purcell et al. 1996) whilst others have found more efficient search for happy face targets amongst angry face distractors than vice versa (e.g. Byrne and Eysenck 1995; Juth et al. 2005).

The present results in chimpanzees are also consistent with those in visual search with monkeys. Kawai et al. (2016) found that Japanese macaques were more efficient in searching for conspecific threatening faces amongst neutral face distractors than vice versa. In this study, no difference in response times to detect non-face targets (pictures of computers) amongst neutral or threatening face distractors was found, suggesting that the threatening face target facilitated faster detection. On the other hand, our chimpanzees appeared to have difficulty in disengaging from threatening face distractors, as indicated by decreasing search efficiency with increasing set size. This is in contrast to some human visual search studies with snakes which demonstrate parallel search for snake targets but serial search for non-threatening mushrooms or flowers targets, providing evidence of automatic processing of threat (e.g. Lipp 2006; Öhman et al. 2001). Japanese macaques also show more efficient search for snake targets

amongst flowers or fear-irrelevant animal distractors than vice versa (Kawai and Koda 2016; Shibasaki and Kawai 2009). However, Kawai et al. (2016) and Kawai and Koda (2016) did not vary the set size in their studies, so it was not clear to what extent automatic processing may have been involved. Shibasaki and Kawai (2009) found more efficient search for snake than flower targets. However, efficiency to detect either target type did not vary with set size (i.e. parallel search) suggesting automatic processing was not specific to threat

Overall, in the present set of studies the presence of a bias towards threatening faces in the visual search task, involving difficulty in disengagement, and the absence of a bias in the visual dot probe task, involving facilitated attention, suggests that biases towards threatening faces are formed at a relatively later stage of processing in chimpanzees. These findings provide partial support for the later evolution of a *social submissiveness system* and implicate greater involvement of the prefrontal cortex and strategic processing of threatening faces in chimpanzees (**see Figure 5**). To provide more direct evidence for the earlier evolution of a *predatory defence system* involving the amygdala and automatic processing, it would be useful to test snake, or other predatory stimuli, in the dot probe and visual search tasks with chimpanzees. The presence of biases towards snake stimuli in the dot probe task presented for 150 ms or less, and evidence of parallel search in the visual search task, would provide stronger support for the evolution of these two behavioural systems put forward by Öhman et al. (1985).

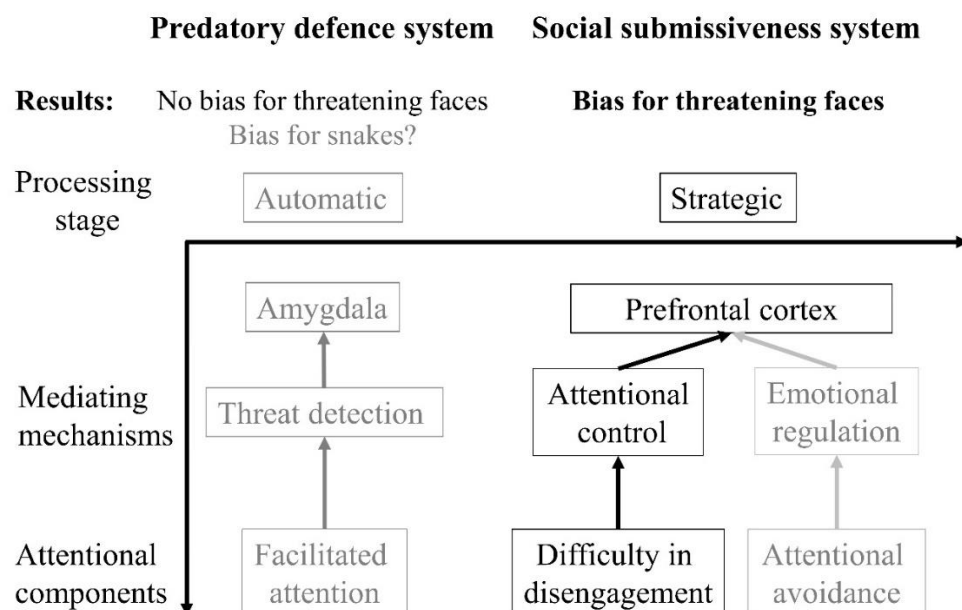


Figure 5. Main thesis findings in the context of frameworks of attentional bias towards threat (Cisler and Koster 2010) and the predatory defence and social submissiveness systems (Öhman et al. 1985). Chimpanzees showed evidence of difficulty in disengagement from threatening faces in the visual search task (relevant areas highlighted in black) but not facilitated attention towards threatening faces in the visual dot probe task.

5.3. Methodological limitations and future directions

In this section I will consider the main methodological limitations of my studies and make recommendations for how these may be addressed in future. I will broadly divide them into stimuli limitations (i.e. threatening properties and threat intensity) and procedural limitations (i.e. SOA duration, measurement of attentional components and manual responding). Finally, I will consider the influence of multimodal cues and anxiety on attentional bias towards threat.

5.3.1. Stimuli limitations

One major limitation of using faces to investigate attentional biases towards threat is that it is impossible to determine if biases are towards threat per se, or the visual properties of the face (Adolphs 2008; Koster et al. 2004a). Thus, it is also possible to discuss biases towards faces in the present studies purely in the context of their relative perceptual similarity to each other, or the presence or absence of certain facial features. For example, in the visual search task, more

efficient search for scream than neutral face targets could simply be explained by an additional visual feature (e.g. the mouth and teeth) (Treisman and Souther 1985). However, it can also be argued that the display of teeth has evolved as a signal of threat *because* it effectively draws attention at a low-level of visual processing. One way to confirm if the mouth and teeth are responsible for more efficient search for scream faces relative to neutral faces is to artificially darken these areas. If biases disappear after such a manipulation, this would suggest the mouth is a key feature in facilitating attention towards scream faces and an important signal of threat.

In the dot probe task, an important moderating factor for measuring attentional biases towards threat is the stimulus threat intensity (Cisler and Koster 2010; Yiend 2010; van Rooijen et al. 2017). It is possible that chimpanzees show attentional biases towards threatening faces at an SOA of 150 ms or less, but that the threat intensity of the stimuli was too weak to facilitate them. Although chimpanzees can discriminate facial expressions presented in greyscale (e.g. Parr 2003) it is possible that greyscale presentation may have reduced their threat intensity somewhat. As noted above, Kret et al. (2016) found biases towards stimuli presented in colour in bonobos, but Wilson and Tomonaga (2018b) and Kret et al. (2018) failed to find biases towards stimuli presented in greyscale in chimpanzees. Therefore, it would be useful to test the stimuli in colour with our chimpanzees. Although the categorisation of higher (scream) and lower (bared teeth) threat intensity faces was used as a way to investigate threat intensity, the degree of intensity expressed (e.g. jaw stretch, lip corner pull, eye tightening) varied between faces to some extent. Ideally, expression intensity should be more tightly controlled. The use of morphing techniques may help to address this problem in future studies (e.g. Wilson and MacLeod 2003). In addition, although the stimuli size was typical for dot probe and visual search studies, presenting a more realistic face size may help to increase threat intensity.

On an issue related to stimuli threat intensity, it is possible that chimpanzees may also rely on other types of cue for threat detection (e.g. vocal calls or actions) (Kawai et al. 2016;

Parr 2004). In humans, auditory threat signals enhance visual processing (Carlson et al. 2018; Brosch et al. 2008a, 2009; Zeelenberg and Bocanegra 2010) and vice versa (Harrison and Woodhouse 2016; Selinger et al. 2013). Moreover, animal studies suggest that responses to multimodal signals are faster, more accurate and occur at less intensity than unimodal signals (Parr 2004; Rowe 1999, 2001). This would be interesting to investigate in chimpanzees, as typically in agonistic social interactions visual threat signals (e.g. scream facial expressions) are accompanied by auditory threat signals (e.g. scream vocalisations). Parr (2004) found that chimpanzees prefer to discriminate pant-hoot faces using the auditory modality and scream faces using the visual modality. Whilst this would suggest that the visual modality is more important for discrimination of scream faces, multimodal cues should also be investigated in attentional experiments using the dot probe and visual search task with chimpanzees.

5.3.2. Procedural limitations

Although the present studies point towards difficulty in disengaging from, rather than facilitated attention towards threatening faces in chimpanzees, the current methodology is somewhat limited in measuring these attentional components. In the dot probe task, the inclusion of baseline neutral-neutral trials (two neutral expression faces) to compare with threatening-neutral trials is recommended (Koster et al. 2004b). Facilitated attention is indicated by faster response times to respond to the dot replacing threatening faces (congruent presentation) on threatening-neutral trials relative to neutral-neutral trials, whereas difficulty in disengagement is indicated by slower response times to neutral faces (incongruent presentation) on threatening-neutral trials relative to neutral-neutral trials. Similarly, in the visual search task, facilitated attention is indicated by faster response times to detect threatening face targets amongst neutral face distractors than neutral stimuli (non-face) targets amongst neutral face distractors, and difficulty in disengagement indicated by slower response times to detect neutral face targets amongst threatening face distractors than neutral stimuli

targets amongst neutral face distractors (Cisler et al. 2009; Kawai et al. 2016). It would be useful to incorporate these procedural designs into future dot probe studies with chimpanzees.

In the dot probe task, another important moderating factor for attentional biases towards threat is the SOA duration. Although SOAs of 150 ms (Wilson and Tomonaga 2018b), 33 ms and 300 ms (Kret et al. 2018) appear to be appropriate for facilitating attention towards threat in humans, they may not be optimal in chimpanzees. Therefore, additional SOAs should be tested to examine the timeline at which attentional biases towards threatening faces emerge.

The type of response method used may also be important. In human dot probe studies, computer keys or buttons are typically used to respond to the probe, whereas non-human primates use touchscreens due to ease of manipulation. Whilst the chimpanzees in the present studies showed clear biases towards some stimuli through touchscreen responses, it is possible that manual movement may mask more subtle biases for threatening stimuli. In humans, Kret et al. (2018) found no difference in response times using buttons and touchscreens in the dot probe task. However, it would be useful to use more direct measures of attention such as eye tracking to determine if gaze location corresponds directly to motor responses in the task. Finally, anxious states may be important for measuring facilitated attention towards threat in chimpanzees. In human dot probe studies, biases towards threat are typically not observed in non-anxious people (Bar-Haim et al. 2007). Failure to observe biases towards threatening faces is often attributed to low trait anxiety or failure to induce a high state of anxiety experimentally (Bradley et al. 1997; Gotlib et al. 2004; Pineles and Mineka 2005). Behaviourally, our chimpanzees appeared to be in a relaxed state during the tasks. Moreover, when the appetitive motivational system is activated (e.g. when the chimpanzees receive food rewards during experiments) the aversive motivational system is inhibited and vice versa (Dickinson and Dearing 1979; Dickinson and Pearce 1977; Konorski 1967). The appetitive motivational system may have inhibited the threat detection system in our chimpanzees, preventing biases

from occurring (Cisler and Koster 2010). In future, it would be interesting to examine the relationship between personality and attentional bias. For example, do more submissive or neurotic chimpanzees show stronger biases towards threatening stimuli? Establishing such a link may be helpful in predicting how certain individuals are likely to react to specific stimuli. Taking measures to limit exposure to such stimuli could help prevent stress for the animal and injury to caretakers.

5.4. General Conclusion

In conclusion, this set of studies used two well-established experimental paradigms from human psychological research to measure attentional biases towards threatening faces in chimpanzees. The visual dot probe study was the first to investigate attentional biases towards threatening faces in chimpanzees. The study improved on similar non-human primate studies by using a more appropriate stimuli presentation time for threat detection and by examining the issue of stimuli threat intensity. The visual search task provided the first demonstration in chimpanzees of a bias towards threatening faces, which helps to bridge the gap in knowledge between findings in humans and macaques. This provides further support that biases towards threatening faces are a homologous trait which can be traced back to at least the last common ancestor between old-world monkeys and apes. Together, the experiments revealed that chimpanzees perceive similarity in faces in a similar way to humans and give attentional priority to threatening faces over neutral faces at a relatively later stage of processing. This attentional priority was reflected in difficulty to disengage from threatening faces, rather than facilitated attention towards them, consistent with human research. The studies provide partial support for the later evolution of a social submissiveness system in response to social threat expressed by threatening faces. Overall, this thesis provides a foundation on which to further investigate the factors important for attentional bias towards threatening faces in chimpanzees and to understand more about how this bias has developed as an evolutionary adaptation.

REFERENCES

- Adachi I, Tomonaga M (2017) Face perception and processing in nonhuman primates. In: Call J, Burghardt GM, Pepperberg IM, Snowdon CT, Zentall T (eds.) *APA Handbook of Comparative Psychology: Perception, Learning, and Cognition*, vol 2. American Psychological Association, Washington, pp 141–161
- Adolphs R (2002) Recognizing emotion from facial expressions: psychological and neurological mechanisms. *Behav Cognit Neurosci Rev* 1(1):21–62
- Adolphs R (2008) Fear, faces, and the human amygdala. *Curr Opin Neurobiol* 18(2):166–172
- Alcantarilla PF, Nuevo J, Bartoli A (2011) Fast explicit diffusion for accelerated features in nonlinear scale spaces. *IEEE Trans Patt Anal Mach Intell* 34(7):1281–98
- Ales JM, Farzin F, Rossion B, Norcia AM (2012) An objective method for measuring face detection thresholds using the sweep steady-state visual evoked response. *J Vis* 12:1–18
- Allritz M, Call J, Borkenau P (2016) How chimpanzees (*Pan troglodytes*) perform in a modified emotional Stroop task. *Anim Cogn* 19(3):435–449
- Barton RA, Aggleton JP (2000) Primate evolution and the amygdala. In: Aggleton JP (ed) *The amygdala: A functional analysis*. Oxford University Press, New York, pp 479–508
- Bar-Haim Y (2010) Research review: attention bias modification (ABM): a novel treatment for anxiety disorders. *J Child Psychol Psychiatry* 51:859–870
- Bar-Haim Y, Lamy D, Pergamin L, Bakermans-Kranenburg MJ, van IJzendoorn MH (2007) Threat-related attentional bias in anxious and nonanxious individuals: A meta-analytic study. *Psychol Bull* 133:1–24
- Beck AT, Clark DA (1997) An information processing model of anxiety: Automatic and strategic processes. *Behav Res Ther* 35:49–58
- Bethell EJ, Holmes A, MacLarnon A, Semple S (2012) Evidence that emotion mediates social attention in rhesus macaques. *PLoS One* 7(8):e44387. doi:10.1371/journal.pone.0044387
- Bethell EJ, Holmes A, MacLarnon A, Semple S (2016) Emotion evaluation and response slowing in a non-human primate: New directions for cognitive bias measures of animal emotion? *Behav Sci* 6(1):2. doi:10.3390/bs6010002
- Bourne VJ (2006) The divided visual field paradigm: Methodological considerations. *Laterality* 11:373–393
- Bourne VJ, Hole GJ (2006) Lateralized repetition priming for familiar faces: evidence for Asymmetric Interhemispheric Cooperation. *Q J Exp Psychol* 59:1117–1133
- Bradley BP, Mogg K, Falla SJ, Hamilton LR (1998) Attentional bias for threatening facial expressions in anxiety: Manipulation of stimulus duration. *Cogn Emot* 12:737–753
- Bradley BP, Mogg K, Millar N, Bonham-Carter C, Fergusson E, Jenkins J, Parr M (1997) Attentional biases for emotional faces. *Cogn Emot* 11:25–42
- Bradley BP, Mogg K, Millar NH (2000) Covert and overt orienting of attention to emotional faces in anxiety. *Cogn Emot* 14(6):789–808

- Brothers L (1990) The social brain: a project for integrating primate behaviour and neurophysiology in a new domain. *Concepts neurosci* 1:27–51
- Brosch T, Grandjean D, Sander D, Scherer KR (2008) Behold the voice of wrath: Crossmodal modulation of visual attention by anger prosody. *Cognition* 106(3):1497–1503
- Brosch T, Grandjean D, Sander D, Scherer KR (2009) Cross-modal emotional attention: Emotional voices modulate early stages of visual processing. *J Cognitive Neurosci* 21(9):1670–1679
- Bruce V, Young A (1986) Understanding Face Recognition. *Br J Psychol* 77(3):305–327
- Burton AM, Wilson S, Cowan M, Bruce V (1999) Research article evidence from security surveillance. *Psychol Sci* 10:243–248
- Byrne A and Eysenck MW (1995) Trait anxiety, anxious mood, and threat detection. *Cogn Emot* 9(6):549–562
- Calcutt SE, Rubin TL, Pokorny JJ, de Waal FBM (2017) Discrimination of emotional facial expressions by tufted capuchin monkeys (*Sapajus apella*). *J Comp Psychol* 131:40–49
- Calvo MG, Marrero H (2009) Visual search of emotional faces: The role of affective content and featural distinctiveness. *Cogn Emot* 23(4):782–806
- Calvo MG, Nummenmaa L (2008) Detection of emotional faces: Salient physical features guide effective visual search. *J Exp Psychol Gen* 137:471–494
- Campbell R, Pascalis O, Coleman M, Wallace SB, Benson PJ (1997) Are faces of different species perceived categorically by human observers? *Proc Biol Sci* 264:1429–1434
- Carlson JM, Conger S, Sterr J (2018) Auditory distress signals potentiate attentional bias to fearful faces: Evidence for multimodal facilitation of spatial attention by emotion. *J Nonverbal Behav* 42(4):417–426
- Chen Y, Ehlers A, Clark D, Mansell W (2002) Patients with generalized social phobia direct their attention away from faces. *Behav Res Ther* 40:677–687
- Chevalier-Skolnikoff S (1973) Facial expression of emotion in nonhuman primates. In: Ekman P (ed) *Darwin and Facial Expression: A Century of Research in Review*. Academic Press, New York, pp 11–98
- Cisler JM, Bacon AK, Williams NL (2009) Phenomenological characteristics of attentional biases towards threat: A critical review. *Cognitive Ther Res* 33(2):221–234
- Cisler JM, Koster EHW (2010) Mechanisms of attentional biases towards threat in anxiety disorders: An integrative review. *Clin Psychol Rev* 30:203–216
- Coleman K, Pierre PJ (2014) Assessing anxiety in nonhuman primates. *ILAR J* 55:333–346
- Cooper RM, Langton SRH (2006) Attentional bias to angry faces using the dot-probe task? It depends when you look for it. *Behav Res Ther* 44:1321–1329
- Dahl CD, Chen C-C, Rasch MJ (2014a) Own-race and own-species advantages in face perception: a computational view. *Sci Rep* 4:6654. doi:10.1038/srep06654

- Dahl CD, Logothetis NK, Hoffman KL (2007) Individuation and holistic processing of faces in rhesus monkeys. *Proc R Soc London Ser B-Biological Sci* 274(1622):2069–2076
- Dahl CD, Rasch MJ, Chen CC (2014b) The other-race and other-species effects in face perception - A subordinate-level analysis. *Front Psychol* 5:1–9
- Dahl CD, Rasch MJ, Tomonaga M, Adachi I (2013a) Laterality effect for faces in chimpanzees (*Pan troglodytes*). *J Neurosci* 33:13344–13349
- Dahl CD, Rasch MJ, Tomonaga M, Adachi I (2013b) Developmental processes in face perception. *Sci Rep* 3:1044. doi:10.1038/srep01044
- Dahl CD, Rasch MJ, Tomonaga M, Adachi I (2013c) The face inversion effect in non-human primates revisited - an investigation in chimpanzees (*Pan troglodytes*). *Sci Rep* 3(2):2504. doi:10.1038/srep02504
- Darwin C (1872) *The Expression of the Emotions in Man and Animals*. John Murray, London
- Davis M, Whalen PJ (2001) Vigilance and emotion. *Mol Psychiatry* 6:13–34
- de Valk JM, Wijnen JG, Kret ME (2015) Anger fosters action. Fast responses in a motor task involving approach movements toward angry faces and bodies. *Front Psychol* 6:1240. doi:10.3389/fpsyg.2015.01240
- Demaria C, Thierry B (1988) Responses to animal stimulus photographs in stump-tailed macaques (*Macaca arctoides*). *Primates* 29:237–244
- Dhum M, Herwig U, Opialla S, Siegrist M, Brühl AB (2017) Evolutionary and modern image content differentially influence the processing of emotional pictures. *Front Hum Neurosci* 11:415. doi:10.3389/fnhum.2017.00415
- Diamond R, Carey S (1986) Why faces are and are not special: an effect of expertise. *J Exp Psychol Gen* 115(2):107–117
- Dickinson A, Dearing MF (1979) Appetitive–aversive interactions and inhibitory processes. In: Dickinson A, Boakes A (eds.) *Mechanisms of Learning and Motivation: A Memorial Volume to Jerzy Konorski*. Erlbaum, Totawa, NJ, pp 203–231
- Dickinson A, Pearce JM (1977) Inhibitory interactions between appetitive and aversive stimuli. *Psychol Bull* 84:690–711
- Dufour V, Pascalis O, Petit O (2006) Face processing limitation to own species in primates: A comparative study in brown capuchins, Tonkean macaques and humans. *Behav Processes* 73(1):107–113
- Ekman P (1973) Cross-cultural studies of facial expressions. In: Ekman P (ed) *Darwin and Facial Expressions: A Century of Research in Review*. Academic Press, New York, pp 169–222
- Ekman P, Friesen WV (1971) Constants across cultures in the face and emotion. *J Pers Soc Psychol* 17:124–129
- Eldar S, Ricon T, Bar-Haim Y (2008) Plasticity in attention: implications for stress response in children. *Behav Res Ther* 46:450–461

- Eysenck MW, Derakshan N, Santos R, Calvo MG (2007) Anxiety and cognitive performance: Attentional control theory. *Emotion* 7:336–353
- Fashler SR, Katz J (2016) Keeping an eye on pain: investigating visual attention biases in individuals with chronic pain using eye-tracking methodology. *J Pain Res* 9:551–561
- Fox E (2002) Processing emotional facial expressions: the role of anxiety and awareness. *Cogn Affect Behav Neurosci* 2:52–63
- Fox E, Damjanovic L (2006) The eyes are sufficient to produce a threat-superiority effect. *Emotion* 6:534–539
- Frischen A, Eastwood JD, Smilek D (2008) Visual search for faces with emotional expressions. *Psychol Bull* 134:662–676
- Fujita K (1987) Species recognition by five macaque monkeys. *Primates* 28(3):353–366
- Fujita K (1990) Species preference by infant macaques with controlled social experience. *Int J Primatol* 11:553–573
- Fujita K (1993a) Role of some physical characteristics in species recognition by pigtail monkeys. *Primates* 34(2):133–140
- Fujita K (1993b) Development of visual preference for closely related species by infant and juvenile macaques with restricted social experience. *Primates* 34(2):141–150
- Fujita K, Watanabe K (1995) Visual preference for closely related species by Sulawesi macaques. *Am J Primatol* 37:253–261
- Ge L, Zhang H, Wang Z, Quinn PC, Pascalis O, Kelly D, Slater A, Tian J, Lee K (2009) Two faces of the other-race effect: Recognition and categorisation of caucasian and chinese faces. *Perception* 38(8):1199–1210
- Gilboa-schechtman E, Foa EB (2010) Attentional biases for facial expressions in social phobia: The face-in-the-crowd paradigm. *Cogn Emot* 13:305–318
- Goldstein AG (1965) Learning of inverted and normally oriented faces in children and adults. *Psychon Sci* 3:447–448
- Goodall J (1968) A preliminary report on expressive movements and communication in the Gombe Stream chimpanzees. In: Jay PC (ed) *Primates: Studies in Adaptation and Variability*. Holt, Rinehart and Winston, New York, pp 313–519
- Gothard KM, Brooks KN, Peterson MA (2009) Multiple perceptual strategies used by macaque monkeys for face recognition. *Anim Cogn* 12:155–167
- Gotlib IH, Kasch KL, Traill S, Joormann J, Arnow BA, Johnson SL (2004) Coherence and specificity of information-processing biases in depression and social phobia. *J Abnorm Psychol* 113:386–398
- Grillon C, Charney DR (2011) In the face of fear: anxiety sensitizes defensive responses to fearful faces. *Psychophysiology* 48:1745–1752

- Hansen CH, Hansen RD (1988) Finding the face in the crowd: An anger superiority effect. *J Pers Soc Psychol* 54:917–924
- Harrison NR, Woodhouse R (2016) Modulation of auditory spatial attention by visual emotional cues: Differential effects of attentional engagement and disengagement for pleasant and unpleasant cues. *Cogn Process* 17(2):205–211
- Hirata S, Matsuda G, Ueno A, Fukushima H, Fuwa K, Sugama K, Kusunoki K, Tomonaga M, Hiraki K, Hasegawa T (2013) Brain response to affective pictures in the chimpanzee. *Sci Rep* 3:srep01342. doi:10.1038/srep01342
- Holmes A, Green S, Vuilleumier P (2005) The involvement of distinct visual channels in rapid attention towards fearful facial expressions. *Cogn Emot* 19:899–922
- Horstmann G (2007) Preattentive face processing: What do visual search experiments with schematic faces tell us? *Vis Cogn* 15:799–833
- Horstmann G, Bauland A (2006) Search asymmetries with real faces: Testing the anger-superiority effect. *Emotion* 6:193–207
- Humphrey N (1974) Species and individuals in the perceptual world of monkeys. *Perception* 3:105–114
- Isbell LA (2006) Snakes as agents of evolutionary change in primate brains. *J Hum Evol* 51:1–35
- Izumi A, Kojima S (2004) Matching vocalizations to vocalizing faces in a chimpanzee (*Pan troglodytes*). *Anim Cogn* 7(3):179–184
- Juth P, Lundqvist D, Karlsson A, Öhman A (2005) Looking for foes and friends: Perceptual and emotional factors when finding a face in the crowd. *Emotion* 5:379–395
- Kanazawa S (1996) Recognition of facial expressions in a Japanese monkey (*Macaca fuscata*) and humans (*Homo sapiens*). *Primates* 37:25–38
- Kano F, Tanaka M, Tomonaga M (2008) Enhanced recognition of emotional stimuli in the chimpanzee (*Pan troglodytes*). *Anim Cogn* 11:517–524
- Kano F, Tomonaga M (2009) How chimpanzees look at pictures: A comparative eye-tracking study. *Proc R Soc B Biol Sci* 276:1949–1955
- Kano F, Tomonaga M (2010a) Face scanning in chimpanzees and humans: continuity and discontinuity. *Anim Behav* 79:227–235
- Kano F, Tomonaga M (2010b) Attention to emotional scenes including whole-body expressions in chimpanzees (*Pan troglodytes*). *J Comp Psychol* 124:287–294
- Kawai N, Koda H (2016) Japanese monkeys (*Macaca fuscata*) quickly detect snakes but not spiders: Evolutionary origins of fear-relevant animals. *J Comp Psychol* 130:299–303
- Kawai N, Kubo K, Masataka N, Hayakawa S (2016) Conserved evolutionary history for quick detection of threatening faces. *Anim Cogn* 19:655–660
- King HM, Kurdziel LB, Meyer JS, Lacreuse A (2012) Effects of testosterone on attention and memory for emotional stimuli in male rhesus monkeys. *Psychoneuroendocrinology* 37:396–409

- Klumpp H, Amir N (2009) Examination of vigilance and disengagement of threat in social anxiety with a probe detection task. *Anxiety Stress Copin* 22:283–296
- Koda H, Sato A, Kato A (2013) Is attentional prioritisation of infant faces unique in humans?: Comparative demonstrations by modified dot-probe task in monkeys. *Behav Processes* 98:31–36
- Kojima S, Izumi A, Ceugniet M (2003) Identification of vocalizers by pant hoots, pant grunts and screams in a chimpanzee. *Primates* 44(3):225–230
- Konorski J (1967) *Integrative Activity of the Brain: An Interdisciplinary Approach*. The University of Chicago Press, Chicago, IL
- Koster EH, Crombez G, Van Damme S, Verschuere B, De Houwer J (2004a) Does imminent threat capture and hold attention? *Emotion* 4(3):312–317
- Koster EH, Crombez G, Verschuere B, De Houwer J (2004b) Selective attention to threat in the dot probe paradigm: Differentiating vigilance and difficulty to disengage. *Behav Res Ther* 42(10):1183–1192
- Koster EHW, Crombez G, Van Damme S, Verschuere B, De Houwer J (2005) Signals for threat modulate attentional capture and holding: Fear-conditioning and extinction during the exogenous cueing task. *Cogn Emot* 19:771–780
- Koster EHW, Crombez G, Verschuere B, Van Damme S, Wiersema JR (2006) Components of attentional bias to threat in high trait anxiety: Facilitated engagement, impaired disengagement, and attentional avoidance. *Behav Res Ther* 44:1757–1771
- Kret ME, Jaasma L, Bionda T, Wijnen JG (2016) Bonobos (*Pan paniscus*) show an attentional bias toward conspecifics' emotions. *Proc Natl Acad Sci* 113:3761–3766
- Kret ME, Muramatsu A, Matsuzawa T (2018) Emotion processing across and within species: A comparison between humans (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *J Comp Psychol* 132: 395–409
- Kret ME, Tomonaga M, Matsuzawa T (2014) Chimpanzees and humans mimic pupil-size of conspecifics. *PLoS One* 9:e104886. doi:10.1371/journal.pone.0104886
- Kuniecki M, Pilarczyk J, Wichary S (2015) The color red attracts attention in an emotional context. An ERP study. *Front Hum Neurosci* 9:212. doi:10.3389/fnhum.2015.00212
- Lacreuse A, Schatz K, Strazzullo S, King HM, Ready R (2013) Attentional biases and memory for emotional stimuli in men and male rhesus monkeys. *Anim Cogn* 16:861–871
- LeDoux JE (1996) *The Emotional Brain: The Mysterious Underpinnings of Emotional Life*. Simon and Schuster, New York
- Levin DT (1996) Classifying faces by race: The structure of face categories. *J Exp Psychol Learn Mem Cogn* 22:1364–1382
- Levin DT (2000) Race as a visual feature: Using visual search and perceptual discrimination tasks to understand face categories and the cross-race recognition deficit. *J Exp Psychol Gen* 129:559–574

- Lipp OV (2006) Of snakes and flowers: Does preferential detection of pictures of fear-relevant animals in visual search reflect on fear-relevance? *Emotion* 6(2):296–308
- Lipp OV, Price SM, Tellegen CL (2009a) No effect of inversion on attentional and affective processing of facial expressions. *Emotion* 9:248–259
- Lipp OV, Price SM, Tellegen CL (2009b) Emotional faces in neutral crowds: Detecting displays of anger, happiness, and sadness on schematic and photographic images of faces. *Motiv Emot* 33:249–260
- MacLeod C, Rutherford E, Campbell L, Ebsworthy G, Holker L (2002) Selective attention and emotional vulnerability: assessing the causal basis of their association through the experimental manipulation of attentional bias. *J Abnorm Psychol* 111:107–123
- MacLeod CM, Mathews A, Tata P (1986) Attentional bias in emotional disorders. *J Abnorm Psychol* 95:15–20
- Mansell W, Clark DM, Ehlers A, Chen YP (1999) Social anxiety and attention away from emotional faces. *Cogn Emot* 13:673–690
- Marsh HL, MacDonald SE (2008) The use of perceptual features in categorization by orangutans (*Pongo abelli*). *Anim Cogn* 11(4):569–585
- Martin-Malivel J, Mangini MC, Fagot J, Biederman I (2006) Do humans and baboons use the same information when categorizing human and baboon Faces? *Psychol Sci* 17:599–607
- Martin-Malivel J, Okada K (2007) Human and chimpanzee face recognition in chimpanzees (*Pan troglodytes*): role of exposure and impact on categorical perception. *Behav Neurosci* 121(6):1145–1155
- Marzouki Y, Gullstrand J, Goujon A, Fagot J (2014) Baboons' response speed is biased by their moods. *PloS one* 9:e102562. doi:10.1371/journal.pone.0102562
- Matsuzawa T (2006) Sociocognitive Development in chimpanzees: A synthesis of laboratory work and field work. In: Matsuzawa T, Tomonaga M, Tanaka M (eds.) *Cognitive Development in Chimpanzees*. Springer-Verlag, Tokyo, pp 3–33
- Matthews A, Mackintosh B (1998) A cognitive model of selective processing in anxiety. *Cognitive Ther Res* 22:539–560
- Mogg K, Bradley BP (1998) A cognitive-motivational analysis of anxiety. *Behav Res Ther* 36:809–848
- Mogg K, Bradley BP (1999) Orienting of attention to threatening facial expressions presented under conditions of restricted awareness. *Cogn Emot* 13:713–740
- Mogg K, Bradley BP (2002) Selective orienting of attention to masked threat faces in social anxiety. *Behav Res Ther* 40:1403–1414
- Mogg K, Philippot P, Bradley BP (2004) Selective attention to angry faces in clinical social phobia. *J Abnorm Psychol* 113:160–165
- Monk CS, Telzer EH, Mogg K, Bradley BP, Mai X, Louro HM, Chen G, McClure-Tone EB, Ernst M, Pine DS (2008) Amygdala and ventrolateral prefrontal cortex activation to

- masked angry faces in children and adolescents with generalized anxiety disorder. *Arch Gen Psychiatry* 65:568–576
- Morris JS, Öhman A, Dolan RJ (1998) Conscious and unconscious emotional learning in the human amygdala. *Nature* 393:467–470
- Muller MN, Mitani JC (2005) Conflict and cooperation in wild chimpanzees. *Advances in the Study of Behavior* 35:275–331
- Öhman A (1996) Preferential preattentive processing of threat in anxiety: Preparedness and attentional biases. In: Rapee RM (ed) *Current Controversies in the Anxiety Disorders*. The Guilford Press, New York, pp 253–290
- Öhman A (2008) Fear and anxiety. In: Lewis M, Haviland-Jones JM, Barrett LF (eds.) *Handbook of Emotions*. The Guilford Press, New York, pp 709–729
- Öhman A (2009) Of snakes and faces: An evolutionary perspective on the psychology of fear. *Scand J Psychol* 50(6):543–552
- Öhman A, Dimberg U, Öst LG (1985) Animal and social phobias: Biological constraints on learned fear responses. In: Reiss S, Bootzin RR (eds.) *Theoretical Issues in Behavior Therapy*. Academic Press, Orlando, FL, pp 123–178
- Öhman A, Flykt A, Esteves F (2001) Emotion drives attention: detecting the snake in the grass. *J Exp Psychol Gen* 130(3):466–478
- Öhman A, Mineka S (2001) Fears, phobias, and preparedness: toward an evolved module of fear and fear learning. *Psychol Rev* 108(3):483–522
- Öhman A, Soares SC, Juth P, Lindström B, Esteves F (2012) Evolutionary derived modulations of attention to two common fear stimuli: Serpents and hostile humans. *J Cogn Psychol* 24(1):17–32
- OpenCV Development Team (2014) Feature matching. URL https://docs.opencv.org/3.0-beta/doc/py_tutorials/py_feature2d/py_matcher/py_matcher.html. Accessed 21 November 2017
- Parr LA (2001) Cognitive and physiological markers of emotional awareness in chimpanzees (*Pan troglodytes*). *Anim Cogn* 4:223–229
- Parr LA (2003) The discrimination of faces and their emotional content by chimpanzees (*Pan troglodytes*). *Ann Ny Acad Sci* 1000(1):56–78
- Parr LA (2004) Perceptual biases for multimodal cues in chimpanzee (*Pan troglodytes*) affect recognition. *Anim Cogn* 7(3):171–178
- Parr LA (2011) The evolution of face processing in primates. *Philos Trans R Soc Lond B Biol Sci* 366(1571):1764–1777
- Parr LA, Cohen M, De Waal F (2005) Influence of social context on the use of blended and graded facial displays in chimpanzees. *Int J Primatol* 26(1):73–103
- Parr LA, Dove T, Hopkins WD (1998) Why faces may be special: evidence of the inversion effect in chimpanzees. *J Cogn Neurosci* 10(5):615–622

- Parr LA, Heintz M (2009) Facial expression recognition in rhesus monkeys, *Macaca mulatta*. *Anim Behav* 77:1507–1513
- Parr LA, Hopkins WD, deWaal FBM (1998) The perception of facial expressions by chimpanzees, *Pan Troglodytes*. *Evol Commun* 2:1–23
- Parr LA, Modi M, Siebert E, Young LJ (2013) Intranasal oxytocin selectively attenuates rhesus monkeys' attention to negative facial expressions. *Psychoneuroendocrinology* 38:1748–1756
- Parr LA, Waller BM (2006) Understanding chimpanzee facial expression: insights into the evolution of communication. *Soc Cogn Affect Neurosci* 1(3):221–228
- Parr LA, Waller BM, Heintz M (2008) Facial expression categorization by chimpanzees using standardized stimuli. *Emotion* 8(2):216–231
- Parr LA, Waller BM, Vick SJ, Bard KA (2007) Classifying chimpanzee facial expressions using muscle action. *Emotion* 7:172–181
- Parr LA, Winslow JT, Hopkins WD, de Waal FBM (2000) Recognizing facial cues: Individual discrimination by chimpanzees (*Pan troglodytes*) and Rhesus monkeys (*Macaca mulatta*). *J Comp Psychol* 114(1):47–60
- Pascalis O, Bachevalier J (1998) Face recognition in primates: a cross-species study. *Behav Process* 43(1):87–96
- Pascalis O, Wirth S (2011) Recognizing the faces of other species: What can a limited skill tell us about face processing? In: Calder AJ, Rhodes G, Johnson MH, Haxby JV (eds.) *The Oxford Handbook of Face Perception*, Oxford University Press Inc., New York, pp 719–730
- Piepers DW, Robbins RA (2012) A review and clarification of the terms “holistic,” “configural,” and “relational” in the face perception literature. *Front Psychol* 3(559):1–11
- Pine DS, Helfinstein SM, Bar-Haim Y, Nelson E, Fox NA (2009) Challenges in developing novel treatments for childhood disorders: Lessons from research on anxiety. *Neuropsychopharmacology* 34:213–228
- Pineles SL, Mineka S (2005) Attentional biases to internal and external sources of potential threat in social anxiety. *J Abnorm Psychol* 114:314–318
- Pinkham AE, Griffin M, Baron R, Sasson NJ, Gur RC (2010) The face in the crowd effect: Anger superiority when using real faces and multiple identities. *Emotion* 10:141–146
- Pishyar R, Harris LM, Menzies RG (2004) Attentional bias for words and faces in social anxiety. *Anxiety Stress Copin* 17:23–36
- Pouget P, Arita J, Woodman GF (2012) How studies of monkeys have shaped theories of selective visual processing. In: Lazareva OF, Shimizu T, Wasserman EA (eds.) *How animals see the world: Comparative Behavior, Biology, and Evolution of Vision*. Oxford University Press Inc., New York, pp 335–350
- Preuschoft S, van Hooff JARAM (1995) Homologizing primate facial displays: a critical review of methods. *Folia Primatol* 65:121–137

- Purcell DG, Stewart AL, Skov RB (1996) It takes a confounded face to pop out of a crowd. *Perception* 25:1091–1108
- Quinn PC, Eimas PD (1996) Perceptual cues that permit categorical differentiation of animal species by infants. *J Exp Child Psychol* 63:189–211
- R Core Team (2015) R: A language and environment for statistical computing. R Foundation for statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>. Accessed 21 November 2017
- Roberts WA, Mazmanian DS (1988) Concept learning at different levels of abstraction by pigeons, monkeys, and people. *J Exp Psychol Anim Behav Process* 14:247–260
- Rowe C (1999) Receiver psychology and the evolution of multicomponent signals. *Anim Behav* 58:921–931
- Rowe C (2001) Sound improves visual discrimination learning in avian predators. *Proc R Soc Lond B* 269:1353–1357
- Savage RA, Lipp OV, Craig BM, Becker SI, Horstmann G (2013) In search of the emotional face: Anger versus happiness superiority in visual search. *Emotion* 13(4):758–768
- Savage RA, Lipp OV (2014) The effect of face inversion on the detection of emotional faces in visual search. *Cogn Emot* 29(6):972–991
- Sawaguchi T, Kudo H (1990) Neocortical development and social structure in primates. *Primates* 31(2):283–289
- Scapinello KF, Yarmey AD (1970) The role of familiarity and orientation in immediate and delayed recognition of pictorial stimuli. *Psychon Sci* 21:329–330
- Schmukle SC (2005) Unreliability of the dot probe task. *Eur J Pers* 19:595–605
- Seligman ME (1971) Phobias and preparedness. *Behav Ther* 2(3):307–320
- Selinger L, Dominguez-Borrás J, Escera C (2013) Phasic boosting of auditory perception by visual emotion. *Biol Psychol* 94(3):471–478
- Seyfarth RM, Cheney DL, Bergman T, Fischer J, Zuberbühler K, Hammerschmidt K (2010) The central importance of information in studies of animal communication. *Anim Behav* 80:3–8
- Shibasaki M, Kawai N (2009) Rapid detection of snakes by Japanese Monkeys (*Macaca fuscata*): An evolutionarily predisposed visual system. *J Comp Psychol* 123:131–135
- Spencer J, Quinn PC, Johnson MH, Karmiloff-Smith A (1997) Heads you win, tails you lose: evidence for young infants categorizing mammals by head and facial attributes. *Early Dev Parent* 6:113–126
- Sposari JA, Rapee RM (2007) Attentional bias toward facial stimuli under conditions of social threat in socially phobic and nonclinical participants. *Cognit Ther Res* 31:23–37
- Staugaard SR (2009) Reliability of two versions of the dot-probe task using photographic faces. *Psychol Sci Q* 51:339–350
- Staugaard SR (2010) Threatening faces and social anxiety: A literature review. *Clin Psychol Rev* 30:669–690

- Stevens S, Rist F, Gerlach AL (2009) Influence of alcohol on the processing of emotional facial expressions in individuals with social phobia. *Br J Clin Psychol* 48:125–140
- Tanaka M (2003) Visual preference by chimpanzees (*Pan troglodytes*) for photos of primates measured by a free choice-order task: implication for influence of social experience. *Primates* 44(2):157–165
- Tanaka M (2007) Development of the visual preference of chimpanzees (*Pan troglodytes*) for photographs of primates: Effect of social experience. *Primates* 48(4):303–309
- Tomonaga M (1993) Use of multiple-alternative matching-to-sample in the study of visual search in a chimpanzee (*Pan troglodytes*). *J Comp Psychol* 107:75–83
- Tomonaga M (1997) Precuing the target location in visual searching by a chimpanzee (*Pan troglodytes*): Effects of precue validity. *Jpn Psychol Res* 39:200–211
- Tomonaga M (1999) Inversion effect in perception of human faces in a chimpanzee (*Pan troglodytes*). *Primates* 40(3):417–438
- Tomonaga M (2007a) Visual search for orientation of faces by a chimpanzee (*Pan troglodytes*): Face-specific upright superiority and the role of facial configural properties. *Primates* 48(1):1–12
- Tomonaga M (2007b) Is chimpanzee (*Pan troglodytes*) spatial attention reflexively triggered by gaze cue? *J Comp Psychol* 121:156–170
- Tomonaga M, Imura T (2009) Faces capture the visuospatial attention of chimpanzees (*Pan troglodytes*): evidence from a cueing experiment. *Front Zool* 6:14. doi:10.1186/1742-9994-6-14
- Tomonaga M, Imura T (2010) Visual search for human gaze direction by a chimpanzee (*Pan troglodytes*). *PLoS One* 5(2):e9131. doi:10.1371/journal.pone.0009131
- Tomonaga M, Imura T (2015) Efficient search for a face by chimpanzees (*Pan troglodytes*). *Sci Rep* 5:11437. doi:10.1038/srep11437
- Torrence RD, Troup LJ (2017) Event-related potentials of attentional bias toward faces in the dot-probe task: A systematic review. *Psychophysiology*. doi:10.1111/psyp.13051
- Treisman A, Souther J (1985) Search asymmetry: A diagnostic for preattentive processing of separable features. *J Exp Psychol Gen* 114(3):285–310
- Treisman AM, Gelade G (1980) A feature-integration theory of attention. *Cogn Psychol* 12(1):97–136
- Valentine T (1991) A unified account of the effects of distinctiveness, inversion, and race in face recognition. *Q J Exp Psychol Sect A Hum Exp Psychol* 43(2):161–204
- van Rooijen R, Ploeger A, Kret ME (2017) The dot-probe task to measure emotional attention: A suitable measure in comparative studies? *Psychon Bull Rev* 24:1686–1717
- Watanuki K, Ochiai T, Hirata S, Morimura N, Tomonaga M, Idani G, Matsuzawa T (2014) Review and long-term survey of the status of captive chimpanzees in Japan in 1926–2013. *Primate Res* 30:147–156

- Weierich MR, Treat TA, Hollingworth A (2008) Theories and measurement of visual attentional processing in anxiety. *Cogn Emot* 22:985–1018
- Wells A, Matthews G (1994) *Attention and emotion: A clinical perspective*. Lawrence Erlbaum Associates, Hillsdale, NJ
- Williams JMG, Watts FN, MacLeod C, Mathews A (1988) *Cognitive psychology and emotional disorders*. John Wiley and Sons, Chichester
- Williams MA, Moss SA, Bradshaw JL, Mattingley JB (2005) Look at me, I'm smiling: Visual search for threatening and nonthreatening facial expressions. *Vis Cogn* 12:29–50
- Wilson DA, Tomonaga M (2018a) Visual discrimination of primate species based on faces in chimpanzees. *Primates* 59(3):243–251
- Wilson DA, Tomonaga M (2018b) Exploring attentional bias towards threatening faces in chimpanzees using the dot probe task. *PLoS ONE* 13(11):e0207378. doi:10.1371/journal.pone.0207378
- Wilson DA, Tomonaga M, Vick S-J (2016) Eye preferences in capuchin monkeys (*Sapajus apella*). *Primates* 57(3):433–440
- Wilson E, MacLeod C (2003) Contrasting two accounts of anxiety-linked attentional bias: Selective attention to varying levels of stimulus threat intensity. *J Abnorm Psychol* 112:212–218
- Wilson ML, Wrangham RW (2003) Intergroup relations in chimpanzees. *Annu Rev Anthropol* 32:363–392
- Wolfe JM (2018) Visual Search. In: Wixted JT, Thompson-Schill SL (eds.) *Stevens' Handbook of Experimental Psychology and Cognitive Neuroscience, Language and Thought* 4(3). John Wiley and Sons, Hoboken, NJ, pp 1–55
- Yamanashi Y, Hayashi M (2011) Assessing the effects of cognitive experiments on the welfare of captive chimpanzees (*Pan troglodytes*) by direct comparison of activity budget between wild and captive chimpanzees. *Am J Primatol* 73:1231–1238
- Yiend J (2010) The effects of emotion on attention: A review of attentional processing of emotional information. *Cogn Emot* 24:3–47
- Yin R (1969) Looking at upside-down faces. *J Exp Psychol Gen* 81:141–145
- Young AW (1982) Methodological and theoretical bases of visual hemifield studies. In: Beaumont JG (ed) *Divided visual field studies of cerebral organisation*. Academic Press, London, pp 11–27
- Zeelenberg R, Bocanegra BR (2010) Auditory emotional cues enhance visual perception. *Cognition* 115(1):202–206