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Search Asymmetries for Threatening Faces in Chimpanzees (*Pan troglodytes*)

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For primates, the ability to efficiently detect threatening faces is highly adaptive; however, it is not clear exactly how faces are detected. This study investigated whether chimpanzees show search asymmetries for conspecific threatening faces featuring scream and bared teeth expressions. Five adult female chimpanzees participated in a series of touchscreen matching-to-sample visual search tasks. In Experiment 1, search advantages for scream versus neutral targets and scream versus bared teeth targets were found. A serial search strategy indicated greater difficulty in disengaging attention from scream versus neutral distractors. In Experiments 2a and 2b, search advantages for scream versus neutral targets remained when the mouth was darkened, suggesting that the brightness contrast of the mouth was not critical for the efficient detection of scream targets. In Experiments 3a and 3b, search advantages for inverted scream versus neutral targets disappeared, indicating configural processing. Together, exclusion of the brightness contrast of the mouth as a low-level perceptual confound, and evidence of configural processing, suggested the scream faces may have been perceived as threatening. However, the search advantage for scream faces is most likely explained by the presence of teeth, independently of threat. The study provides further support that an attentional bias toward threatening faces is a homologous trait, which can be traced back to at least the last common ancestor of Old World monkeys and apes.


Keywords: search asymmetry, visual search, facial expression, threat, chimpanzees


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Faces are one of the most important social stimuli for primates; they convey information about identity, age, sex, attention, and other social information (Adachi & Tomonaga, 2017). Facial expressions signal emotion, motivation, and intention and function to establish and maintain social relationships (Ekman, 1997; Parr et al., 2002; Parr & Waller, 2006; van Hooff, 1967). As mammals have evolved, expanding group size has led to a complex social world. This has driven the enlargement of the neocortex and the

selection of behaviors that strengthen group cohesion (Barton & Aggleton, 2000; Dunbar, 1993; Sawaguchi & Kudo, 1990; Waller & Micheletta, 2013). These behaviors include facial expressions, and corresponding perceptual mechanisms, which enable the observer to predict the actions of others and thus reduce uncertainty (Waller et al., 2016).

In many primate societies, conflicts play a significant role in social relations (Muller & Mitani, 2005). Dominance hierarchies

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develop as a result of intragroup competition over limited resources but also serve to maintain group cohesion through affiliative bonding, social tolerance, and reconciliation after aggressive conflicts (de Waal, 1986). Social dominance is established through agonistic encounters during which ritualized facial expressions are displayed as signals of dominance or submission (Parr et al., 2002; Tinbergen, 1952). For example, in chimpanzees, the bared teeth expression signals submission and is often displayed by individuals experiencing fear, whereas the scream expression signals protest and is often shown by individuals who have been attacked (Parr et al., 2002). The bared teeth expression functions to solicit support from others and facilitate reconciliation, whereas the scream expression functions to recruit support during conflict and elicit consolation (Parr et al., 2002). Both expressions are likely to be perceived as threatening and generate fear in those observing. This may occur through reflexive emotional contagion, in which the observer experiences the same psychological state as the sender (Waller et al., 2017).

The ability to efficiently detect and respond to evolutionarily fear-relevant stimuli, such as threatening faces and predators, reduces the potential for injury and predation and is thus highly adaptive. Öhman (1986) proposed that two behavioral systems have evolved to respond to fear-relevant stimuli in animals: the *predatory defense system* to avoid predators such as snakes and, as group size expanded, the *social submissive system* to escape attack from dominant conspecifics. For this purpose, Öhman and Mineka (2001) proposed that animals have evolved a *fear module*, “a device for activating defensive behavior (e.g., immobility or flight) and associated psychophysiological responses and emotional feelings to threatening stimuli” (Öhman & Mineka, 2001, p. 485). When critical stimulus features reach the thalamic and midbrain structures, information is transferred automatically to the amygdala to produce the fear response (Öhman & Mineka, 2001). This thalamus–amygdala link is critical for fear learning and explains why fear can be easily conditioned to fear-relevant stimuli, even when they are masked from awareness (Esteves et al. 1994; LeDoux, 1996; Öhman & Soares, 1994) and why the response to fear-relevant stimuli is resistant to cognitive control (Hugdahl & Öhman, 1977; Soares & Öhman, 1993).

The predatory defense and social submissiveness systems are thought to rely on the same fear module neural system (Öhman & Mineka, 2001). However, although the amygdala plays a central role in the automatic response to predatory fear, increasing group size has driven the enlargement of both the amygdala and prefrontal cortex to allow greater cognitive control over the response to social fear (Adolphs, 2002; Öhman et al., 2012). It has been suggested that for larger primates such as humans and great apes, aggressive encounters during social conflict pose a greater threat to survival than predatory encounters (Öhman, 2009). Therefore, involvement of the prefrontal cortex in the strategic processing of threatening faces may be particularly important in these species. To understand how the fear module may be activated in response to threatening faces, it is first necessary to understand how faces are processed. In the following text, we provide an overview of face processing in primates, before considering experimental evidence for and against an attentional bias toward threatening faces during visual search.

Faces are special stimuli for the primate visual system. Face-selective regions in the brain have been identified in humans,

chimpanzees, and macaques (Parr et al., 2009; Tsao et al., 2008; Yovel & Freiwald, 2013). In the temporal lobe, the inferior temporal cortex and the superior temporal sulcus play a central role in processing faces (Tate et al., 2006). In humans, faces are mainly processed holistically. *Holistic processing* encodes information about all parts of the face as a unified whole and is crucial for identifying individual faces (Farah et al., 1998). In prosopagnosia, damage to areas of the brain involved in holistic processing (i.e., the right anterior temporal lobe, right inferior occipital cortex, and fusiform gyrus) leads to an inability to perceive and recognize faces (Busigny et al., 2014). In addition, *featural processing* encodes information about facial features (i.e., eyes, nose, and mouth) and their fixed position in relation to each other, whereas *configural processing* encodes information about the spatial relationship between features (Diamond & Carey, 1986). Single-cell recording studies in macaques demonstrate that inferior temporal cortex and superior temporal sulcus neurons respond selectively to individual facial features, configurations of features, and the distances between features (Perrett et al., 1982, 1992; Rolls et al., 1994; Yamane et al., 1988).

When faces are inverted, the ability to judge the spatial distances between features is impaired relative to nonface stimuli. This phenomenon is known as the “face inversion effect” (FIE) and provides evidence of configural processing. The FIE is consistently found in humans (Dernt et al., 2009; McKelvie, 1995; Prkachin, 2003; Tanaka & Farah, 1993; Valentine, 1988; Yin, 1969) and chimpanzees (Dahl et al., 2013; Parr, 2011; Parr & Heintz, 2006; Parr et al., 1998; Tomonaga, 1999a, 2007; Tomonaga & Imura, 2015; Weldon et al., 2013; Wilson & Tomonaga, 2018b), with some exceptions (Gao & Tomonaga, 2018; Kret & Tomonaga, 2016; Tomonaga et al., 1993). This suggests that humans and chimpanzees primarily use holistic and configural information for face recognition. In macaques, evidence is less consistent, with an equal number of studies providing support for (Dahl et al., 2007; Neiworth et al., 2007; Overman & Doty, 1982; Tomonaga, 1994; Vermeire & Hamilton, 1998) and against (Bruce, 1982; Ditrlich, 1990; Gothard et al., 2004; Parr et al., 1999; Rosenfeld & Van Hoesen, 1979) the FIE (Griffin, 2020). This suggests that macaques use a combination of holistic, configural, and featural information. Overall, the neuropsychological mechanisms of face processing are more similar between humans and chimpanzees than macaques (Parr et al., 2009).

To understand whether threatening faces are given attentional priority and how they are processed, we turn our attention to the visual search task. In the task, a target stimulus is presented among a set of “distractor” stimuli, and the aim is to detect the target as quickly as possible (Treisman & Gelade, 1980). If the target expression influences attentional priority then search efficiency, indicated by response time (RT) and accuracy to detect the target, differs between expressions (Frischen et al., 2008). Search asymmetries occur when, for example, search is more efficient for an angry face target among neutral face distractors than vice versa (Treisman & Souther, 1985; Wolfe, 2018). Visual search typically involves either *parallel search*, in which the target is detected rapidly and automatically irrespective of the number of distractors (set size), or *serial search*, in which attention is focused on each item until the target is found, so RTs increase linearly with set size (Treisman & Gelade, 1980). Serial search can also depend on working memory processes; the more items that are required to be

remembered, the longer it takes to find the target item (Sternberg, 1966).

In humans, several visual search studies have found search advantages for schematic threatening faces (Öhman, 2009; Öhman et al., 2001). However, studies using photographs of real faces are more inconsistent; some studies have found an angry face superiority effect (Fox & Damjanovic, 2006; Horstmann & Bauland, 2006; Lipp et al., 2009), whereas others have found a happy face superiority effect (Becker et al., 2011; Calvo & Marrero, 2009; Calvo & Nummenmaa, 2008; Horstmann et al., 2012). These mixed findings may be explained by the number of stimuli and exemplars, low-level or expression-related perceptual features, relative uniformity of expressions, and similarity between the target and distractors (Becker et al., 2011; Frischen et al., 2008; Savage & Lipp, 2015).

Several of these studies have further examined the role of configural and featural processing using face inversion. Fox and Damjanovic (2006) found an inversion effect for angry faces, supporting configural processing. In contrast, Horstmann and Bauland (2006), Lipp et al. (2009), and Savage and Lipp (2015) showed no inversion effect for angry or happy faces, supporting featural processing. Calvo and Nummenmaa (2008) found that search advantages for happy, surprised, or disgusted faces over angry, fearful, and sad faces were unimpaired by inversion, supporting featural processing. These inconsistencies may be explained by the different stimuli sets used between studies (Savage & Lipp, 2015).

In nonhuman primates, most visual search studies with faces have been conducted with monkeys and chimpanzees. Only one study has investigated visual search for threatening faces in monkeys; three Japanese macaques were faster to detect conspecific threatening face targets among neutral face distractors than vice versa (Kawai et al., 2016). In chimpanzees, the FIE (for neutral faces) has been studied extensively by Tomonaga and colleagues. An adult chimpanzee showed an inversion effect for human, chimpanzee, and dog faces but not houses, hands, and chairs (Tomonaga, 1999b, 2007). In contrast, the same chimpanzee showed no inversion effect for human faces with a direct gaze versus averted gaze (Tomonaga & Imura, 2010). Finally, three adult chimpanzees showed an inversion effect for chimpanzee faces versus nonface objects (Tomonaga & Imura, 2015). Overall, chimpanzees, similar to humans, show a consistent search advantage for faces and process them in a configural manner.

To date, no studies have examined visual search for facial expressions in chimpanzees. The aims of this study were to investigate whether chimpanzees (a) show a search advantage for threatening faces in a visual search task, (b) process them automatically or strategically, and (c) process them in a featural or configural manner. Examining how chimpanzees detect threatening faces may give us greater insight into how an attentional bias toward social threat may have evolved. In particular, a serial search strategy would suggest cognitive control over the detection of and response to social fear, supporting the evolution of a social submissiveness system to escape attack from dominant conspecifics (Öhman, 1986).

In Experiment 1, we investigated visual search for conspecific threatening faces (Wilson, 2019). We predicted a more efficient search for threatening targets (bared teeth or scream expressions) among neutral distractors than vice versa. Chimpanzee scream

expressions signal protest, often after being attacked, and are mainly associated with anger, whereas bared teeth expressions signal submission and are mainly associated with fear (Parr et al., 2002). Angry faces provide information about both the presence and source of threat and so are considered a more direct threat to the observer. Fearful faces provide information about the presence of threat, but less information about its source, and so are considered more ambiguous and an indirect threat (Davis & Whalen, 2001; Grillon & Charney, 2011). Therefore, we predicted more efficient search for scream targets among bared teeth distractors than vice versa. In Experiments 2a and 2b, we investigated whether asymmetries depended on low-level perceptual features, specifically, the brightness contrast of the mouth. Chimpanzees pay most attention to the mouth of scream faces and use the mouth to discriminate between scream and bared teeth faces (Kano & Tomonaga, 2009; Parr et al., 2008). If brightness contrast was critical for detection, we expected asymmetries would disappear when the mouth was darkened. Finally, in Experiments 3a and 3b, we examined the role of configural and featural information in detecting threatening faces using face inversion. If the chimpanzees rely more on configural information, we expected asymmetries to disappear when the faces were inverted. On the other hand, if they rely more on featural information, we expected asymmetries to remain when the faces were inverted. In addition, if we observed search asymmetries, with parallel search for one condition (e.g., scream targets–neutral distractors) and serial search for another condition (neutral targets–scream distractors), we expected a set size–target asymmetry interaction; if distractor homogeneity facilitated search efficiency, we expected interactions of distractor type effect with the other effects.

General Method

Participants

Five adult female chimpanzees (*Pan troglodytes*) participated in the study at the Primate Research Institute, Kyoto University, Japan (Watanuki et al., 2014; Table 1). The chimpanzees were members of a social group of 11 individuals living in an environmentally enriched facility consisting of an open-air outdoor enclosure (700 m²), two mesh outdoor enclosures (250 m² and 280 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 & Hayashi, 2011). The experimental protocol was approved by the Animal Welfare and Care Committee of the Primate Research Institute, Kyoto University, and the Animal Research Committee of Kyoto University (2018-125, 2019-064) and followed the *Guidelines for the Care and Use of Laboratory Primates* of the Primate Research Institute, Kyoto University (Version 3, 2010). No food or water deprivation was used in the study. The chimpanzees had extensive experience participating in cognitive touchscreen tasks, including visual search and matching-to-sample tasks (Tomonaga & Imura, 2015; Wilson & Tomonaga, 2018b).

Apparatus

The experiment was conducted in an experimental booth (1.80 × 2.15 × 1.75 m) inside a testing room. The chimpanzees voluntarily

Table 1
Basic Information About the Five Chimpanzees

Name	GAIN ID number	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

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

walked to the booth through an overhead walkway connected to the living rooms. A 17-in. touch-sensitive LCD monitor (1280 × 1024 pixels) encased inside Plexiglas was used to present visual stimuli at a distance of approximately 40 cm. Food reward (8-mm apple cubes) were delivered via a universal feeder device. All experimental events were controlled by a personal computer and the computer task was programmed using Microsoft Visual Basic 2010 (Express Edition).

Stimuli

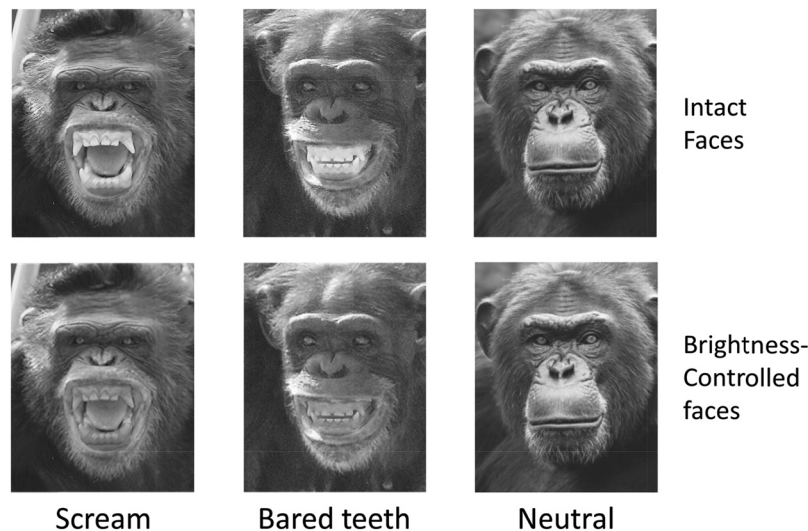
Facial stimuli consisted of cropped photographs (200 × 250 pixels) of unfamiliar chimpanzees obtained from Kumamoto Sanctuary, Kyoto University, and personal collections. Chimpanzee faces featured threatening (scream and bared teeth) and neutral expressions (Figure 1). As the social context of the expressions could not be reliably determined from all the still images, the experimenter, a certified Chimpanzee Facial Action Coding System coder, categorized scream and bared teeth expressions based on their physical features alone. Chimpanzee scream expressions were 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” (Parr et al., 2007, p. 176), and bared teeth expressions were defined as “an open mouth with lips parted, a raised upper lip, and retracted lip corners functioning to expose the teeth” (Parr et al., 2007, p. 175). 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 overall differences in color hue and luminance, which may inadvertently bias attention (Wilson & Tomonaga, 2018a). Images featuring 30 different individuals were presented, consisting of 10 different individuals per expression. The same stimuli sets were presented in all experiments.

Procedure

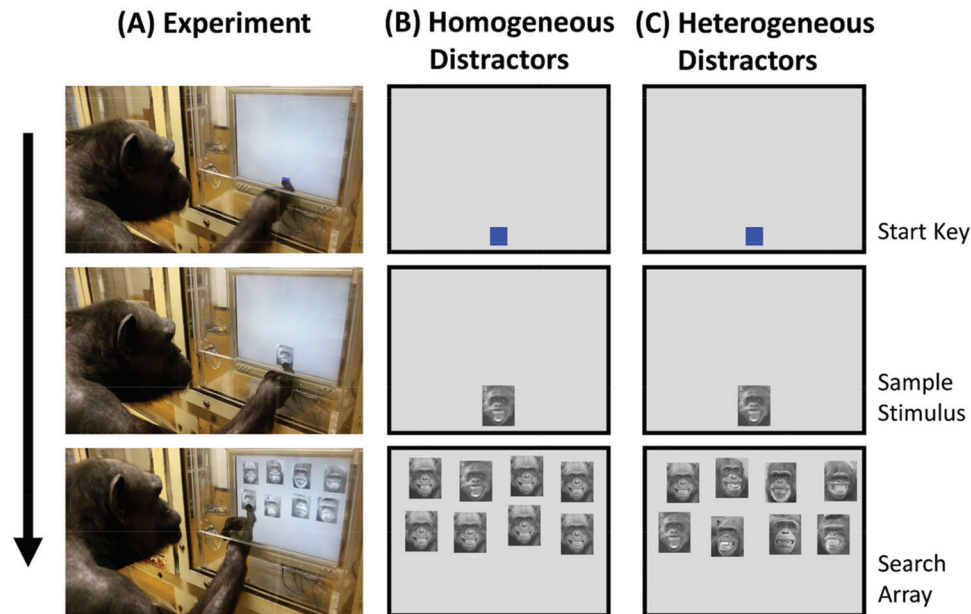
The chimpanzees participated in a matching-to-sample visual search task (cf. Tomonaga, 1993; Figure 2). Testing sessions took place for 2 hr either in the morning or the afternoon. During each testing session, the chimpanzees completed several other unrelated perceptual experiments that did not feature facial stimuli. To begin each trial the chimpanzees touched a blue start key followed by a sample stimulus (face) at the bottom of the screen. When the sample stimulus was touched, it disappeared and sets of three, five, or eight comparison stimuli appeared in the top half of the screen at

Figure 1
Examples of the Chimpanzee Scream, Bared Teeth, and Neutral Expressions Used as Stimuli



Note. All faces were presented in grayscale, and the average luminance of each face was scaled to the average luminance of all faces in each experiment.

Figure 2
Schematic Diagram of the Matching-to-Sample Visual Search Task



Note. (A) Chimpanzee ‘Ai’ participating in the experiment. (B) Homogeneous distractor trial: a scream face target is presented among identical bared teeth face distractors. (C) Heterogeneous distractor trial: A scream face target is presented among non-identical bared teeth face distractors. See the online article for the color version of this figure.

random locations. The stimuli were presented at random locations to prevent anticipatory responding to the images at fixed locations. The comparison stimuli consisted of the target face (identical to the sample) presented among several distractor faces with a different facial expression. Variable target search was used so that the target expression for each stimuli pair (scream–neutral, bared teeth–neutral, scream–bared teeth) varied from trial to trial (Savage et al., 2013). The stimuli remained on the screen until a stimulus was touched or 5 s had elapsed, after which time the image may not have been retained. On homogeneous distractor trials the distractor faces were identical to each other, while on heterogeneous distractor trials the distractor faces featured different individuals with the same expression. Homogeneous distractors were used to measure baseline performance, whereas heterogeneous distractors were used to simulate a more natural visual search situation and to reduce the effect of low-level perceptual confounds (Becker et al., 2011). Homogeneous and heterogeneous distractor presentation was alternated on each trial, and set size was randomized across trials. When a correct choice was made (the target was touched), a chime sound was played and a food reward was 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 target stimulus was presented again without any distractor stimuli. This was to maintain motivation during the task and prevent the development of idiosyncratic error response patterns. The intertrial interval was 2 s. The RTs (ms) and number of errors were recorded by a personal computer. Trial order was randomized within and across sessions.

Data Analysis

Trials with RTs of 5 s or longer were excluded from the analysis (0.4% of total trials averaged across participants and across experiments) as the chimpanzees were likely to be distracted, which would result in guessing behavior (cf. Wilson & Tomonaga, 2018b). The chimpanzees showed more errors when RTs became longer, indicating no speed–accuracy trade-off (Chittka et al., 2009; see Table S1 and Figure S1 in Supplementary File_S1 in the online supplemental materials). Although RTs on incorrect trials may also include useful information for cognitive processes in chimpanzees (cf. Tomonaga, 2007; Tomonaga & Matsuzawa, 1992), RTs on correct trials only were analyzed (Tomonaga & Imura, 2015). Generalized linear mixed model analyses were conducted using the *lmerTest* package in R, Version 4.1.1 (R Core Team, 2021). For the raw data and R analysis codes, see Supplementary File_S2 in the online supplemental materials. The *lmer* function (with Gaussian distribution) was used to analyze the logarithmically transformed and normally distributed RT data, and the *glmer* function (with binomial distribution and logit link function) was used to analyze the accuracy data. For each data set, fixed effects of distractor type (DT), target asymmetry (TA), and set size (SS) were included in the models. DT included homogeneous or heterogeneous distractors, TA included scream–neutral (S–N/N–S), bared teeth–neutral (B–N/N–B), or scream–bared teeth (S–B/B–S) stimuli pairs, and SS included three, five, or eight stimuli. Target asymmetry was determined by the assumption that targets that are more threatening are detected more efficiently (S–N, B–N, S–B) than vice versa (N–S, N–B, B–S; Davis & Whalen, 2001; Grillon & Charney, 2011). We prepared all possible

models (random intercept only models) combining fixed effects and their interactions including a null model (for summary tables, see Supplementary File_S3 in the online supplemental materials). For each model, random effects were Chimpanzee and Session, where the session was nested in Chimpanzee. We adopted a model-averaging approach using the *MuMIn* package. All models were sorted with Akaike's information criteria using the *dredge* function. We then calculated model-averaged coefficients using the *model.avg* function, where we applied the "full average" mode. Coefficient estimates for the RT data were evaluated with Satterthwaite's *t* tests, whereas those for accuracy data were evaluated with the Wald's method. Confidence intervals (CIs) were calculated using the *confint* function. For model averaging results tables, see Supplementary File_S3 in the online supplemental materials.

Experiment 1: Intact Face

Method

Search asymmetries between three facial expression pairs were explored (Wilson, 2019). Scream or bared teeth targets were presented among neutral distractors and vice versa (scream-neutral condition and bared teeth-neutral condition), and scream targets were presented among bared teeth distractors and vice versa (scream-bared teeth

condition). The chimpanzees completed 24 trials for each condition (72 trials \times 12 sessions = 864 trials).

Results

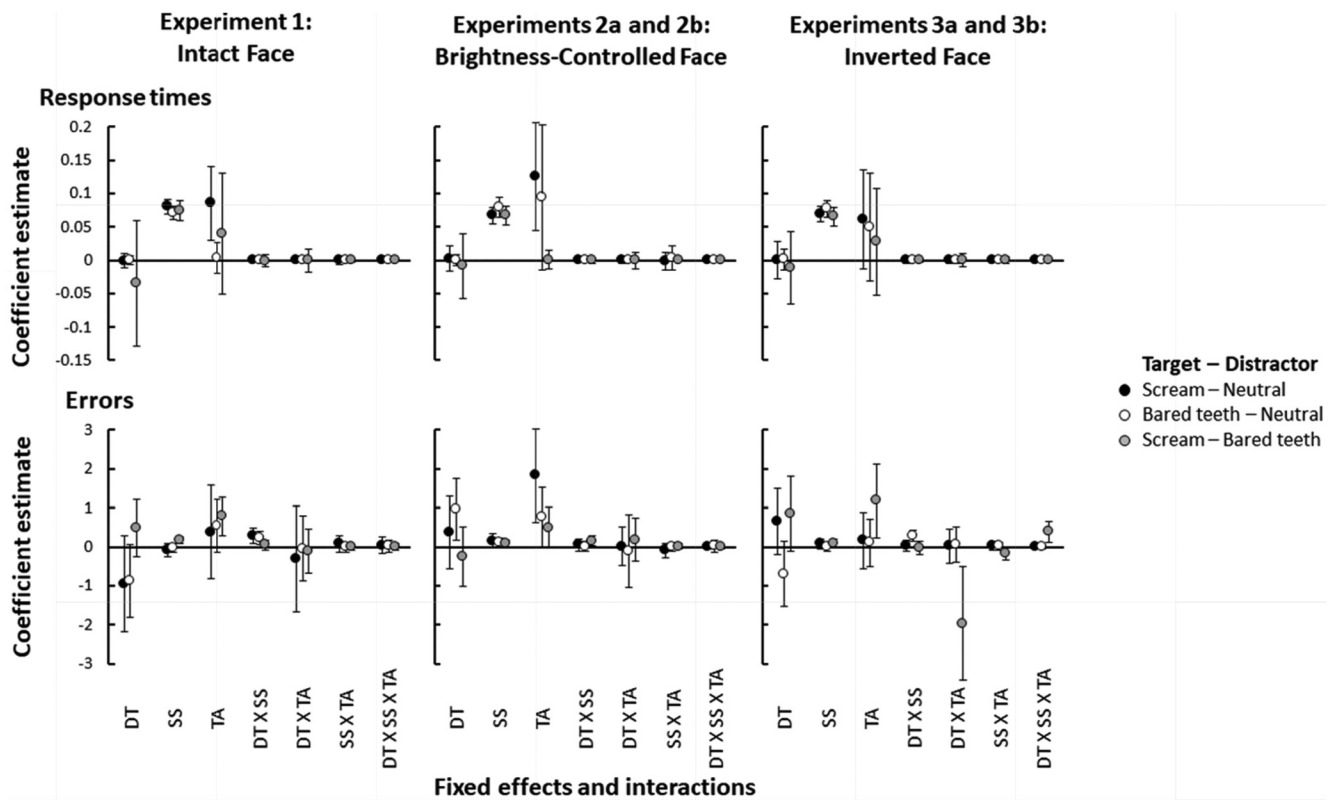
Figure 3 shows a summary of the coefficient estimates for the averaged models in each experiment. Figure 4 shows the mean percent incorrect choices and mean RTs as a function of set size for each stimuli pair target in Experiment 1.

Accuracy

In the scream-neutral condition, accuracy for homogeneous distractors was $M = 7\%$ incorrect for scream targets and $M = 14\%$ incorrect for neutral targets, and for heterogeneous distractors was $M = 13\%$ incorrect for scream targets and $M = 21\%$ incorrect for neutral targets. In the full-averaged model, estimates for the main effects of distractor type, set size, and target asymmetry were not significant. A significant interaction between distractor type and set size was found ($\beta = 0.29$, $SE = .11$, $Z = 2.77$, $p < .01$, 95% CI [0.08, 0.50]) showing that accuracy decreased as set size increased on heterogeneous distractor trials. No other interactions were found.

In the bared teeth-neutral condition, accuracy for homogeneous distractors was $M = 15\%$ incorrect for bared teeth targets and $M = 20\%$ incorrect for neutral targets, and for heterogeneous distractors was $M = 19\%$ incorrect for bared teeth targets and $M = 28\%$

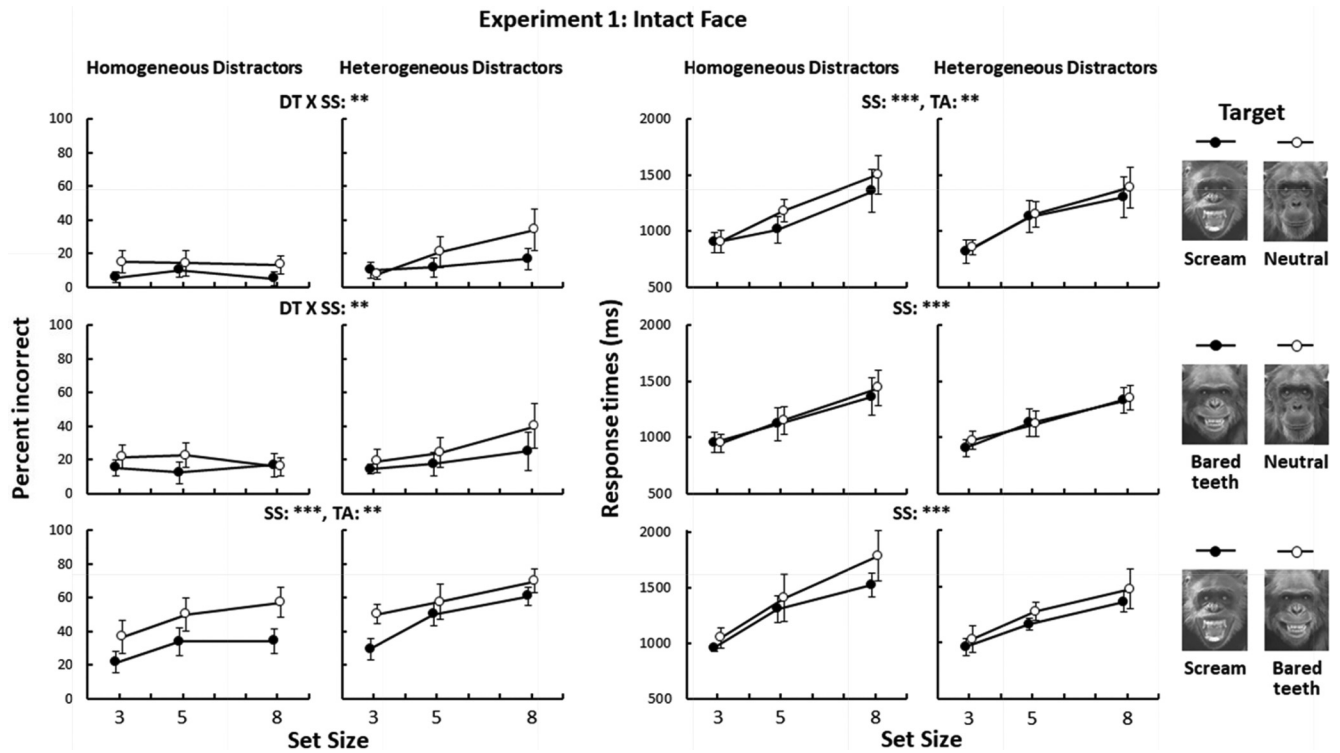
Figure 3
Summary of the Coefficient Estimates for the Averaged Models in Each Experiment



Note. DT = distractor type; TA = target asymmetry; SS = set size; X = interaction. Error bars indicate 95% confidence intervals.

Figure 4

Mean Percent Incorrect Choices and Mean Response Times as a Function of Set Size for Each Stimuli Pair Target in Experiment 1



Note. DT = distractor type; SS = set size; TA = target asymmetry; X = interaction. Error bars indicate the standard error of the mean (*SEM*) across participants. * $p < .05$. ** $p < .01$. *** $p < .001$.

incorrect for neutral targets. In the full-averaged model, estimates for the main effects of distractor type, set size, and target asymmetry were not significant. A significant interaction between distractor type and set size was found ($\beta = 0.23$, $SE = .08$, $Z = 2.80$, $p < .01$, 95% CI [0.07, 0.39]) showing that accuracy decreased as set size increased on heterogeneous distractor trials. No other interactions were found.

In the scream–bared teeth condition, accuracy for homogeneous distractors was $M = 30\%$ incorrect for scream targets and $M = 48\%$ incorrect for bared teeth targets, and for heterogeneous distractors was $M = 47\%$ incorrect for scream targets and $M = 59\%$ incorrect for bared teeth targets. In the full-averaged model, estimates for the main effects of set size ($\beta = 0.17$, $SE = .05$, $Z = 3.67$, $p < .001$, 95% CI [0.08, 0.26]) and target asymmetry ($\beta = 0.79$, $SE = .26$, $Z = 3.08$, $p < .01$, 95% CI [0.29, 1.29]) were significant. No main effect of distractor type and no interactions were found.

Response Time

In the scream–neutral condition, RTs for homogeneous distractors were $M = 1,089$ ms for scream targets and $M = 1,196$ ms for neutral targets, and for heterogeneous distractors were $M = 1,083$ ms for scream targets and $M = 1,131$ ms for neutral targets. In the full-averaged model, estimates for the main effects of set size ($\beta = 0.08$, $SE = .01$, $t(1180) = 15.10$, $p < .001$, 95% CI [0.07, 0.09]) and target asymmetry ($\beta = 0.09$, $SE = .03$, $t(1190) = 3.02$, $p < .01$,

95% CI [0.03, 0.14]) were significant. No main effect of distractor type and no interactions were found.

In the bared teeth–neutral condition, RTs for homogeneous distractors were $M = 1,144$ ms for bared teeth targets and $M = 1,178$ ms for neutral targets, and for heterogeneous distractors were $M = 1,120$ ms for bared teeth targets and $M = 1,146$ ms for neutral targets. In the full-averaged model, estimates for the main effect of set size were significant ($\beta = 0.07$, $SE = .01$, $t(1090) = 13.63$, $p < .001$, 95% CI [0.06, 0.08]). No main effects of distractor type and target asymmetry and no interactions were found.

In the scream–bared teeth condition, RTs for homogeneous distractors were $M = 1,265$ ms for scream targets and $M = 1,431$ ms for bared teeth targets, and for heterogeneous distractors were $M = 1,163$ ms for scream targets and $M = 1,260$ ms for bared teeth targets. In the full-averaged model, estimates for the main effect of set size were significant ($\beta = 0.07$, $SE = .01$, $t(726) = 9.68$, $p < .001$, 95% CI [0.06, 0.09]). No main effects of distractor type and target asymmetry and no interactions were found.

Discussion

RTs indicated more efficient search for scream versus neutral targets in the heterogeneous distractor condition. This result is comparable with the threatening face superiority effect found in Japanese macaques by Kawai et al. (2016). In addition, accuracy indicated more efficient search for scream versus bared teeth targets in the homogeneous distractor condition. In all conditions, RTs progressively

slowed as set size increased, which indicated inefficient search and a serial search strategy. Serial search suggested that scream distractors were more difficult to disengage attention from than neutral distractors, resulting in slower RTs to detect neutral targets (Wolfe, 2018). The relatively larger bright area of the scream mouths may have held attention for longer than bared teeth or neutral mouths. The extent to which this low-level perceptual feature accounts for these threatening face superiority effects was subsequently investigated.

Experiments 2a and 2b: Brightness-Controlled Face

In Experiments 2a and 2b, the possibility that low-level perceptual features were responsible for the search advantages for scream versus neutral faces, and scream versus bared teeth faces, in Experiment 1 were examined. Specifically, we focused on the mouth of the scream and bared teeth faces, as this was the most conspicuous area of brightness contrast. In addition, chimpanzees pay most attention to the mouth of scream faces and use the mouth to discriminate between scream and bared teeth faces (Kano & Tomonaga, 2009; Parr et al., 2008).

Method

In Experiments 2a and 2b, stimuli consisted of modified versions of the scream and bared teeth faces, and neutral faces presented in Experiment 1. The brightness of the mouth area of the scream and bared teeth faces were manipulated to reduce the contrast with the

surrounding face (Figure 1). Brightness contrast effects were achieved using customized application software written in Microsoft Visual Basic Version 6.0. First, the average brightness (RGB) value of the mouth area and its *SD* was calculated. Second, the average RGB value of the surrounding upper face area and its *SD* was calculated. Finally, the RGB value of each pixel of the mouth area was changed to match the RGB value and *SD* of the upper face area. Final adjustments were made in Photoshop Elements 15. In Experiment 2a (scream–neutral and bared teeth–neutral conditions), scream or bared teeth targets were presented among neutral distractors and vice versa. The chimpanzees completed 24 trials for each condition (48 trials \times 12 sessions = 576 trials). In Experiment 2b (scream–bared teeth condition), scream targets were presented among bared teeth distractors and vice versa. The chimpanzees completed 24 trials (24 trials \times 12 sessions = 288 trials).

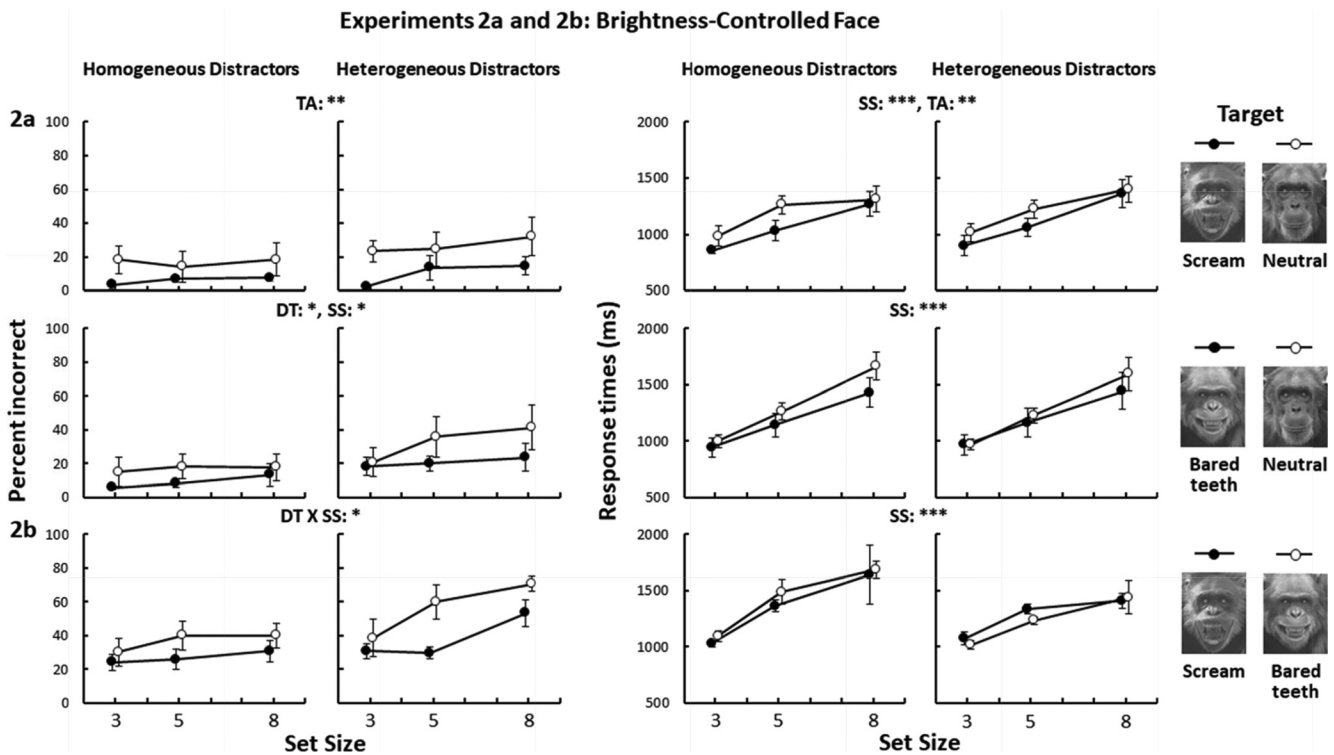
Results

Figure 5 shows the mean percent incorrect choices and mean RTs as a function of set size for each stimuli pair target in Experiments 2a and 2b.

Accuracy

In the scream–neutral condition, accuracy for homogeneous distractors was $M = 6\%$ incorrect for scream targets and $M = 17\%$ incorrect for neutral targets, and for heterogeneous distractors was $M = 10\%$ incorrect for scream targets and $M = 27\%$ incorrect for

Figure 5
Mean Percent Incorrect Choices and Mean Response Times as a Function of Set Size for Each Stimuli Pair Target in Experiments 2a and 2b



Note. DT = distractor type; SS = set size; TA = target asymmetry; X = interaction. Error bars indicate the standard error of the mean (*SEM*) across participants. * $p < .05$. ** $p < .01$. *** $p < .001$.

neutral targets. In the full-averaged model, estimates for the main effect of target asymmetry were significant ($\beta = 1.84$, $SE = .61$, $Z = 3.00$, $p < .01$, 95% CI [0.64, 3.04]). No main effects of distractor type and set size and no interactions were found.

In the bared teeth–neutral condition, accuracy for homogeneous distractors was $M = 9%$ incorrect for bared teeth targets and $M = 17%$ incorrect for neutral targets, and for heterogeneous distractors was $M = 21%$ incorrect for bared teeth targets and $M = 33%$ incorrect for neutral targets. In the full-averaged model, estimates for the main effects of distractor type ($\beta = 0.95$, $SE = .41$, $Z = 2.35$, $p < .05$, 95% CI [0.16, 1.75]) and set size ($\beta = 0.12$, $SE = .06$, $Z = 2.03$, $p < .05$, 95% CI [0.00, 0.23]) were significant. No main effect of target asymmetry and no interactions were found.

In the scream–bared teeth condition (Experiment 2b), accuracy for homogeneous distractors was $M = 27%$ incorrect for scream targets and $M = 37%$ incorrect for bared teeth targets, and for heterogeneous distractors was $M = 38%$ incorrect for scream targets and $M = 56%$ incorrect for bared teeth targets. In the full-averaged model, estimates for the main effects of distractor type, set size, and target asymmetry were not significant. A significant interaction between distractor type and set size was found ($\beta = 0.15$, $SE = .06$, $Z = 2.40$, $p < .05$, 95% CI [0.03, 0.28]) showing that accuracy decreased as set size increased on heterogeneous distractor trials. No other interactions were found.

Response Time

In the scream–neutral condition, RTs for homogeneous distractors were $M = 1,053$ ms for scream targets and $M = 1,188$ ms for neutral targets, and for heterogeneous distractors were $M = 1,108$ ms for scream targets and $M = 1,215$ ms for neutral targets. In the full-averaged model, estimates for the main effects of set size ($\beta = 0.07$, $SE = .01$, $t(1156) = 10.79$, $p < .001$, 95% CI [0.06, 0.08]) and target asymmetry ($\beta = 0.13$, $SE = .04$, $t(1160) = 3.05$, $p < .01$, 95% CI [0.05, 0.21]) were significant. No main effect of distractor type and no interactions were found.

In the bared teeth–neutral condition, RTs for homogeneous distractors were $M = 1,172$ ms for bared teeth targets and $M = 1,309$ ms for neutral targets, and for heterogeneous distractors were $M = 1,192$ ms for bared teeth targets and $M = 1,264$ ms for neutral targets. In the full-averaged model, estimates for the main effect of set size were significant ($\beta = 0.08$, $SE = .01$, $t(1134) = 10.69$, $p < .001$, 95% CI [0.07, 0.09]). No main effects of distractor type and target asymmetry and no interactions were found.

In the scream–bared teeth condition (Experiment 2b), RTs for homogeneous distractors were $M = 1,344$ ms for scream targets and $M = 1,423$ ms for bared teeth targets, and for heterogeneous distractors were $M = 1,273$ ms for scream targets and $M = 1,231$ ms for bared teeth targets. In the full-averaged model, estimates for the main effect of set size were significant ($\beta = 0.07$, $SE = .01$, $t(828) = 9.20$, $p < .001$, 95% CI [0.05, 0.08]). No main effects of distractor type and target asymmetry and no interactions were found.

Discussion

In Experiment 2a, RT and accuracy data indicated more efficient search for scream targets with darkened mouths than neutral targets in both homogeneous and heterogeneous distractor conditions. Therefore, the brightness contrast of the scream mouths did

not appear to be responsible for the asymmetries observed in Experiment 1. Instead, the chimpanzees may have relied simply on the relatively large open mouth shape for detection, irrespective of the brightness contrast of the mouth (Horstmann et al., 2012; Treisman & Souther, 1985). In Experiment 2b, the search advantage for scream versus bared teeth targets in the homogeneous distractor condition disappeared, suggesting that the brightness contrast between the scream and bared teeth mouths facilitated more accurate search for scream versus bared teeth targets in Experiment 1. Comparing Experiments 2a and 2b, overall search was least efficient for scream versus bared teeth targets, suggesting that these expressions were most difficult to discriminate.

Experiments 3a and 3b: Inverted Face

In Experiments 3a and 3b, the role of configural and featural processing in the search advantages for scream versus neutral faces, and scream versus bared teeth faces, in Experiment 1 was examined.

Method

Stimuli consisted of inverted versions of the original scream, bared teeth, and neutral faces presented in Experiment 1. In Experiment 3a (scream–neutral and bared teeth–neutral conditions), scream or bared teeth targets were presented among neutral distractors and vice versa. The chimpanzees completed 24 trials for each condition (48 trials \times 12 sessions = 576 trials). In Experiment 3b (scream bared–teeth condition), scream targets were presented among bared teeth distractors and vice versa. The chimpanzees completed 24 trials (24 trials \times 12 sessions = 288 trials). Both the sample and comparison (target) images were presented in the same orientation (cf. Tomonaga, 1999b).

Results

Figure 6 shows the mean percent incorrect choices and mean RTs as a function of set size for each stimuli pair target in Experiments 3a and 3b.

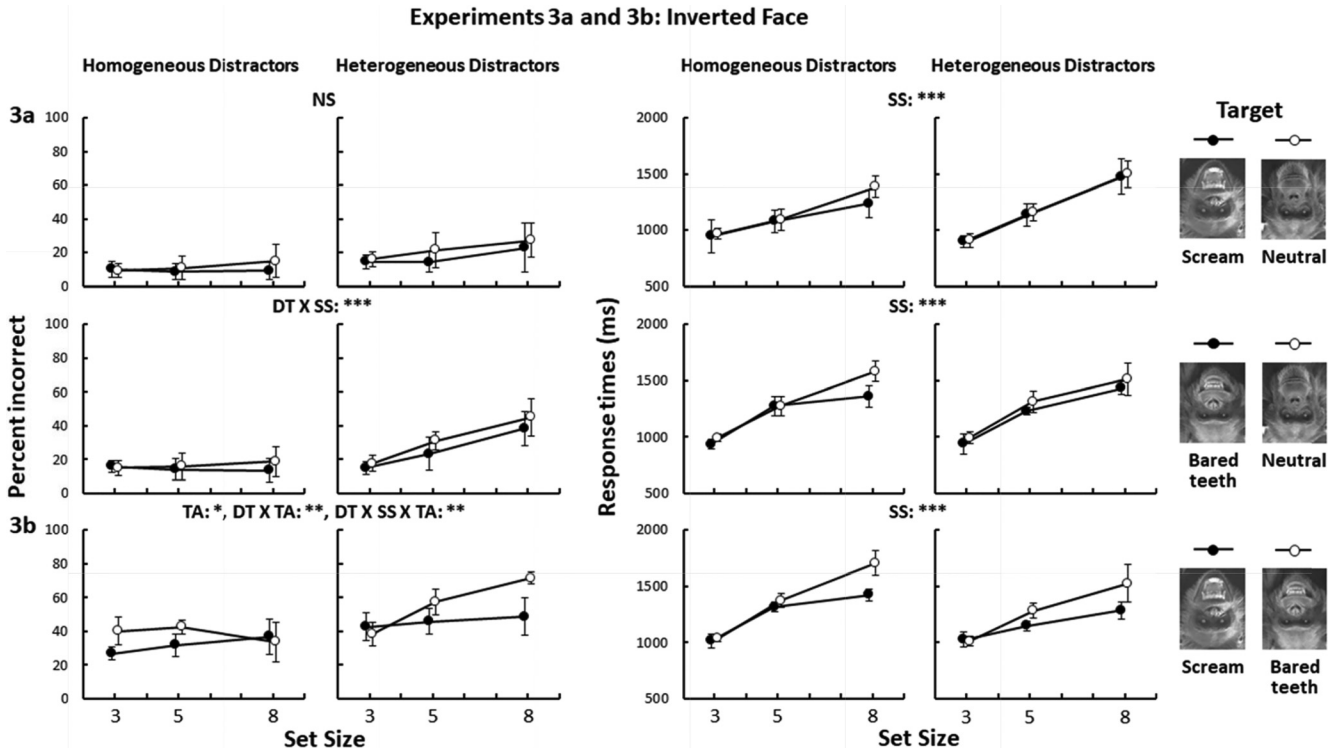
Accuracy

In the scream–neutral condition, accuracy for homogeneous distractors was $M = 9%$ incorrect for scream targets and $M = 12%$ incorrect for neutral targets, and for heterogeneous distractors was $M = 17%$ incorrect for scream targets and $M = 22%$ incorrect for neutral targets. In the full-averaged model, estimates for the main effects of distractor type, set size, and target asymmetry were not significant and no interactions were found.

In the bared teeth–neutral condition, accuracy for homogeneous distractors was $M = 14%$ incorrect for bared teeth targets and $M = 16%$ incorrect for neutral targets, and for heterogeneous distractors was $M = 26%$ incorrect for bared teeth targets and $M = 31%$ incorrect for neutral targets. In the full-averaged model, estimates for the main effects of distractor type, set size, and target asymmetry were not significant. A significant interaction between distractor type and set size was found ($\beta = 0.27$, $SE = .07$, $Z = 3.89$, $p < .001$, 95% CI [0.14, 0.41]) showing that accuracy decreased as set size increased on heterogeneous distractor trials. No other interactions were found.

Figure 6

Mean Percent Incorrect Choices and Mean Response Times as a Function of Set Size for Each Stimuli Pair Target in Experiments 3a and 3b



Note. DT = distractor type; SS = set size; TA = target asymmetry; X = interaction. Error bars indicate the standard error of the mean (*SEM*) across participants. * $p < .05$. ** $p < .01$. *** $p < .001$.

In the scream–bared teeth condition (Experiment 3b), accuracy for homogeneous distractors was $M = 32\%$ incorrect for scream targets and $M = 39\%$ incorrect for bared teeth targets, and for heterogeneous distractors was $M = 46\%$ incorrect for scream targets and $M = 56\%$ incorrect for bared teeth targets. In the full-averaged model, estimates for the main effect of target asymmetry were significant ($\beta = 1.18$, $SE = .48$, $Z = 2.45$, $p < .05$, 95% CI [0.24, 2.13]). Significant interactions between distractor type and target asymmetry ($\beta = -1.97$, $SE = .74$, $Z = 2.67$, $p < .01$, 95% CI [-3.42, -0.52]) and distractor type, set size, and target asymmetry ($\beta = 0.39$, $SE = .13$, $Z = 2.91$, $p < .01$, 95% CI [0.13, 0.65]) indicated that on homogeneous distractor trials target asymmetry decreased as set size increased, whereas on heterogeneous distractor trials target asymmetry increased as set size increased. No other main effects or interactions were significant.

Response Time

In the scream–neutral condition, RTs for homogeneous distractors were $M = 1,088$ ms for scream targets and $M = 1,148$ ms for neutral targets, and for heterogeneous distractors were $M = 1,170$ ms for scream targets and $M = 1,187$ ms for neutral targets. In the full-averaged model, estimates for the main effect of set size were significant ($\beta = 0.07$, $SE = .01$, $t(1157) = 11.66$, $p < .001$, 95% CI [0.06, 0.08]). No main effects of distractor type and target asymmetry and no interactions were found.

In the bared teeth–neutral condition, RTs for homogeneous distractors were $M = 1,190$ ms for bared teeth targets and $M = 1,283$ ms for neutral targets, and for heterogeneous distractors were $M = 1,200$ ms for bared teeth targets and $M = 1,273$ ms for neutral targets. In the full-averaged model, estimates for the main effect of set size were significant ($\beta = 0.08$, $SE = .01$, $t(1060) = 12.57$, $p < .001$, 95% CI [0.07, 0.09]). No main effects of distractor type and target asymmetry and no interactions were found.

In the scream–bared teeth condition (Experiment 3b), RTs for homogeneous distractors were $M = 1,250$ ms for scream targets and $M = 1,370$ ms for bared teeth targets, and for heterogeneous distractors were $M = 1,152$ ms for scream targets, and $M = 1,273$ ms for bared teeth targets. In the full-averaged model, estimates for the main effect of set size were significant ($\beta = 0.07$, $SE = .01$, $t(807) = 9.17$, $p < .001$, 95% CI [0.05, 0.08]). No main effects of distractor type and target asymmetry and no interactions were found.

Discussion

In Experiment 3a, RT data showed that search asymmetries for scream versus neutral targets in Experiment 1 disappeared, indicating an inversion effect. This is consistent with human and chimpanzee studies (humans: Calvo & Nummenmaa, 2008; Fox & Damjanovic, 2006; chimpanzees: Tomonaga, 1999a, 2007; Tomonaga & Imura, 2015), suggesting that the stimuli were mainly processed configurally and perceived as whole faces.

In Experiment 3b, inverted scream face targets were detected with higher accuracy than inverted bared teeth targets. However, homogeneous distractors are more vulnerable to low-level perceptual confounds such as the brightness contrast of the mouth, as demonstrated in Experiment 2, which may account for the lack of an inversion effect. Comparing Experiments 3a and 3b, overall search was least efficient for scream versus bared teeth targets, suggesting that these expressions were most difficult to discriminate.

General Discussion

This study investigated search asymmetries for threatening faces in chimpanzees. In Experiment 1, a search advantage for scream versus neutral targets was found. This threatening face superiority effect is consistent with several studies in humans and monkeys (humans: Fox & Damjanovic, 2006; Horstmann & Bauland, 2006; Lipp et al., 2009; monkeys: Kawai et al., 2016). The RTs to detect scream targets slowed as set size increased, consistent with comparable human studies with angry faces in which set size was varied (Horstmann & Bauland, 2006; Horstmann et al., 2012; Lipp et al., 2009). This suggested that chimpanzees, similar to humans, adopt a serial search strategy for the detection of threatening faces and have greater difficulty in disengaging attention from threatening than neutral face distractors (Horstmann & Bauland, 2006; Horstmann et al., 2012). Serial search suggests involvement of the prefrontal cortex in the strategic processing of threatening faces. This implies a degree of cognitive control over the detection of and response to social threat from dominant conspecifics, which lends support to the evolution of a social submissiveness system (Öhman, 1986). The ability of the scream, but not bared teeth expressions, to hold attention longer than neutral expressions may be related to the social context in which it occurs and the perceived level of threat. The scream expression signals protest after being attacked and is associated with anger, whereas the bared teeth expression signals submission and is associated with fear (Parr et al., 2002). As the scream expression occurs in response to a more direct and less ambiguous threat than bared teeth faces, it may hold the attention of observers for longer. This may be adaptive by increasing the likelihood of support from allies, thus reducing the risk of further injury. However, in the scream–bared teeth condition, although accuracy was higher for scream versus bared teeth targets on homogeneous distractor trials, RTs did not significantly differ. This suggests scream faces do not signal a more direct threat than bared teeth faces (Davis & Whalen, 2001; Grillon & Charney, 2011).

In Experiments 2a and 2b, we examined whether low-level perceptual features can explain the search advantages found in Experiment 1. Specifically, we focused on the brightness contrast of mouth (Kano & Tomonaga, 2009; Parr et al., 2008). In Experiment 2a, the RT search advantage for scream versus neutral targets remained, indicating that the chimpanzees did not simply rely on the brightness contrast of the mouth for faster detection. In humans, Becker et al. (2011) found a search advantage for happy faces, even when the high contrast teeth were removed. The authors speculated that this was due to an understanding of the communicative intent of the smiling faces. Similarly, our chimpanzees may have understood the communicative intent of the scream faces. In Experiment 2b, the accuracy search advantage for

scream versus bared teeth targets disappeared, indicating that the brightness contrast of the mouth was more important for more accurate detection.

In Experiments 3a and 3b, we examined the role of configural and featural processing in the search asymmetries observed in Experiment 1. In Experiment 3a, the search advantage for scream versus neutral targets disappeared when the stimuli were inverted. This is consistent with some human and chimpanzee studies (humans: Calvo & Nummenmaa, 2008; Fox & Damjanovic, 2006; chimpanzees: Tomonaga, 1999a, 2007; Tomonaga & Imura, 2015) and indicated that the stimuli were mainly processed configurally and perceived as whole faces. This provides further evidence that the chimpanzees may have understood their threatening content to some extent (Becker et al., 2011; Calvo & Nummenmaa, 2008).

Together, the exclusion of the brightness contrast of the scream mouth as a low-level perceptual confound, and evidence of configural processing, suggested that the threatening content of the scream expressions may have biased attention in our chimpanzees. However, we must also consider alternative and simpler explanations for our findings. One possibility is that the search advantages were simply due to the presence of teeth in the scream faces (Horstmann et al., 2012; Treisman & Souther, 1985). Furthermore, as visual search involves the detection of a target that differs from the surrounding distractors, visual discrimination is a major factor in determining performance (Duncan & Humphreys, 1989). As search efficiency was consistently lower for scream versus bared teeth faces across experiments, they were likely perceived as more similar to each other. This may have forced the chimpanzees to focus attention on specific facial features for discrimination, rather than looking more globally at the whole face, slowing down overall detection time. For example, the larger surface area of the scream mouth relative to the bared teeth mouth may have been facilitated more accurate detection. Indeed, Parr et al. (2008) found that chimpanzee scream and bared teeth faces only differed in the dimension of the mouth opening in a multidimensional scaling analysis. This suggests that the mouth is the most important feature of discrimination.

Another possibility is that the relative novelty of the scream faces may have facilitated more efficient search (cf. Kawai et al., 2016). In their daily social interactions, chimpanzees encounter conspecific scream expressions less often than neutral expressions. In addition, our chimpanzees have less exposure to scream than neutral facial stimuli in an experimental context. However, bared teeth expressions did not facilitate faster detection than neutral faces despite also being relatively novel. In addition, evidence that chimpanzees pay more attention toward novelty in faces is mixed. For example, Tomonaga and Imura (2010) found that chimpanzees were faster to detect human faces with a direct gaze (more familiar) among those with an averted gaze (less familiar) in a visual search task. In contrast, Matsuda et al. (2016) reported that chimpanzees looked longer at novel faces than familiar or morphed “novel-familiar” faces in a preferential looking paradigm. However, in the visual search task, novelty is only considered to guide attention when the influence of more basic features has been ruled out (Wolfe, 2018). Therefore, the presence of teeth is a more likely explanation than novelty for the scream face search advantages we observed.

It is important to note that it is impossible to separate emotional features (the signal of threat) from expression-related perceptual

features (display of teeth) in scream faces, as they are fundamentally intertwined (Frischen et al., 2008; Horstmann et al., 2012). Therefore, it may be argued that the display of teeth is integral to the signal of threat, toward which primates have evolved an attentional bias (Becker et al., 2011). However, while the presence of teeth can explain our results, the signal of threat alone cannot. Therefore, we conclude that the display of teeth is the most likely explanation for the search advantages we found.

In future experiments, it would be useful to determine whether faster detection of threatening faces is more strongly linked to the emotional valence of the expression or the presence of teeth. This could be done by comparing search asymmetries for chimpanzee scream and play faces (controlled for the amount of teeth exposure) versus neutral faces. A search advantage for scream, but not play faces, would suggest that the negative valence of the scream expression facilitates faster detection than neutral faces. No difference in the search advantage for scream and play faces would suggest that the teeth facilitate faster detection than neutral faces, irrespective of positive or negative valence. Another important line of investigation is the role of multimodal cues in threat detection. In primate agonistic social interactions, scream expressions are typically accompanied by vocalizations. In humans, auditory threat signals enhance visual processing, and in animals, responses to multimodal signals are faster, are more accurate, and occur at less intensity than unimodal signals (Carlson et al., 2018; Parr, 2004). If scream vocalizations selectively enhance the detection of scream faces during visual search, this would provide stronger evidence that they do indeed signal a threat. It would also be useful to systematically examine the importance of the size and shape of the mouth and eyes in the detection of threatening faces by removing these features or presenting them in isolation (Fox & Damjanovic, 2006; Horstmann et al., 2012; Tomonaga, 2007).

Finally, we acknowledge the limitations of our study, including the small number of participants and stimuli used. Due to the difficulty in obtaining large numbers of high-quality images of chimpanzee facial expressions, the same stimuli set was used across experiments. This may limit our findings somewhat to the specific stimuli set we used. Therefore, the extent to which our results can be generalized to other chimpanzees should be assessed in future replication studies using comparable stimuli sets. In addition, more species should be tested to determine whether our findings generalize across primate species with similar hierarchical social structures. This will allow us to provide further support for the evolution of a social submissiveness system in response to social threat (Öhman, 1986).

In conclusion, this was the first visual search study to find a search advantage for threatening faces (scream expressions) in chimpanzees, which helps to bridge the gap in knowledge between human and macaque studies. A serial search strategy suggested that the chimpanzees had greater difficulty in disengaging attention from scream than neutral face distractors. The ability of the scream faces to hold attention for longer than neutral faces is most likely explained by the presence of the teeth. However, we do not rule out the possibility that the signal of threat may also have held attention to some extent. Overall, the study provides further support that an attentional bias toward threatening faces is a homologous trait, which can be traced back to at least the last common ancestor of Old World monkeys and apes.

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