

The Thatcher illusion in humans and monkeys

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Primates possess the remarkable ability to differentiate faces of group members and to extract relevant information about the individual directly from the face. Recognition of conspecific faces is achieved by means of holistic processing, i.e. the processing of the face as an unparsed, perceptual whole, rather than as the collection of independent features (part-based processing). The most striking example of holistic processing is the Thatcher illusion. Local changes in facial features are hardly noticeable when the whole face is inverted (rotated 180°), but strikingly grotesque when the face is upright. This effect can be explained by a lack of processing capabilities for locally rotated facial features when the face is turned upside down. Recently, a Thatcher illusion was described in the macaque monkey analogous to that known from human investigations. Using a habituation paradigm combined with eye tracking, we address the critical follow-up questions raised in the aforementioned study to show the Thatcher illusion as a function of the observer's species (humans and macaques), the stimulus' species (humans and macaques) and the level of perceptual expertise (novice, expert).

Keywords: Thatcher illusion; monkey; face recognition; holistic perception

1. INTRODUCTION

Figure 1 shows two inverted pictures of the same human individual. When these pictures are viewed right-side up (upper two pictures), a striking difference between the faces emerges that was not apparent when inverted, that is, when the eyes and mouth of an upright face are inverted, the face appears grotesque. Importantly, grotesqueness is reduced when the distorted face is turned upside down. This effect has been referred to as the Thatcher illusion (Thompson 1980). The Thatcher illusion is an impressive example of how the perception of a face can be changed by changing its orientation. The effect is commonly explained by a disruption of holistic processing (Rock 1973; Bartlett & Searcy 1993): in order to differentiate between faces, we rely not only on the facial parts themselves but also on their configuration—this ability is called holistic processing. By means of inversion, also referred to as face inversion, holistic processing is impaired, thus leaving local feature inversions undetected. In humans, the Thatcher illusion has been investigated extensively with psychophysical measurements of ratings (Parks *et al.* 1985; Bartlett & Searcy 1993; Murray *et al.* 2000), recognition (Rhodes *et al.* 1993), habituation (Bertin & Bhatt 2004) and perceptual comparison tasks (Bartlett & Searcy 1993; Searcy & Bartlett 1996; Leder *et al.* 2001; Edmonds &

Lewis 2007), as well as neurophysiological measurements (Milivojevic *et al.* 2003; Carbon *et al.* 2005; Boutsen *et al.* 2006; Gu *et al.* 2007) and functional magnetic resonance imaging (Rotshtein *et al.* 2001).

In general, the most prevalent paradigm for studying holistic face processing in non-human primate species is the face inversion effect, i.e. the fact that inverted faces seem to be processed differently than upright faces owing to a lack of sensitivity to holistic information (Rosenfeld & Van Hoesen 1979; Tomonaga 1994). Recent studies on face inversion in monkeys described systematic modulations of eye movement patterns that were dependent on whether faces were presented upright or inverted (Dahl *et al.* 2009; Gothard *et al.* 2009). In addition, one study found highly similar face processing strategies in humans and monkeys, in that conspecific faces elicited different viewing patterns than non-conspecific faces in both species. In addition, viewing patterns for conspecific faces were also highly similar for upright, inverted and blurred faces (Dahl *et al.* 2009). The data supported the assumption that macaques—much like humans—develop holistic processing strategies for conspecific faces. However, this view has been challenged by findings interpreted as lack of expertise in face processing (Parr *et al.* 2008). Besides numerous studies in non-human species on face inversion, the Thatcher illusion has only recently been studied in macaques (Adachi *et al.* 2009). Adachi *et al.* used a habituation paradigm to demonstrate the Thatcher illusion in the macaque monkey. This work illustrates the main effect of the Thatcher illusion as a function of dishabituation

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to a thatcherized face in upright and inverted conditions: the prediction from holistic processing is that thatcherized faces in the inverted condition elicit *less* dishabituation than those in the upright condition relative to the baseline, non-thatcherized faces: indeed, this pattern of responses was observed in the experiments. The main limitations of that study are the constrained set of stimuli (restricted to conspecific faces only, i.e. macaque faces) and the lack of a *direct* comparison with human participants using the same experimental protocol. Here, we answer the critical question that Adachi *et al.* (2009) phrased at the end of their article: ‘... it will be of interest to determine the extent to which the Thatcher effect reflects species-specific specializations of face perception. This question can best be addressed by ‘crossed’ comparative studies in which two different species are tested with thatcherized faces of both their own and the other species’.

We applied feature manipulations identical to those of ‘thatcherization’ to conspecific faces as well as to non-conspecific faces and determined the degree of grotesqueness as a function of dishabituation and viewing times for observers of both species (monkey and human). A habituation–dishabituation paradigm was used in combination with a preferential looking paradigm (Dahl *et al.* 2007), which allowed us to detect changes of interest in the grotesque-looking face. Moreover, eye gaze was investigated using eye tracking methods. According to the hypothesis that the processing of spatial relations of facial features in a thatcherized face is disrupted by inversion (Bartlett & Searcy 1993; Rakover & Teucher 1997), we hypothesize that with upright faces observers pay more attention to the manipulated facial parts than with inverted faces. Thus, viewing times for these parts are assumed to increase during the presentation of upright faces, while viewing times for inverted faces stay relatively low. Moreover, we hypothesize that this enhancement is stronger for conspecific than for non-conspecific faces as a result of the expertise effect (Dahl *et al.* 2009). Along the same line, we hypothesize that observers show a greater difference in dishabituation for *thatcherized upright* faces versus *normal upright* faces than for *inverted thatcherized* faces versus *inverted normal* faces. This difference indicates a greater perceptual dissimilarity between the thatcherized version of a face and the normal version when both are right-side up and a smaller perceptual dissimilarity when they are upside down. Taken together, these results would demonstrate the counterpart in monkeys to the Thatcher illusion in humans and provide the critical cross-species comparison (Adachi *et al.* 2009).

2. MATERIAL AND METHODS

(a) *Participants*

In this study, three male rhesus macaques (*Macaca mulatta*, 5–7 years old, 10–13 kg) and 22 human observers (12 females and 10 males aged 18–35 years) participated. Each monkey was implanted with a custom-designed, form-fitting titanium head post (Logothetis *et al.* 2002) under sterile conditions.

The macaques were housed with one to three conspecifics in the same cage and were from a colony of 20 to 30 individuals. Macaques had a direct and/or visual contact with their cage mates over a period of years. Contact with humans was

restricted to a few individuals who constantly wore face masks and protective clothing. Similarly, the human participants did not have explicit knowledge or expertise with macaques, nor were they familiar with the Thatcher illusion.

(b) *Stimuli*

Forty digital colour pictures of neutral rhesus macaque and human faces were used as stimulus material in the experiment. The faces were cut out, normalized for luminance and placed on a mid-grey background creating an image of 300×300 pixels (13.3° of visual angle). The stimulus set contained two manipulations: (i) an unaltered face (*upright normal*) was modulated by rotating the eyes and the mouth 180° in the image plane, leaving the remaining face intact (*upright thatcherized*). (ii) The entire images of both versions were then turned upside down (inverted normal and inverted thatcherized) (figure 1). We used a mid-grey blank square as well as a grey outline marking a frame of the same size as the face stimulus. Five additional human participants determined the main facial parts (eyes, nose and mouth) of all human and macaque faces using the `roi_poly` function in Matlab (Mathworks Inc., Natick, MA, USA). The mean of each area was calculated across participants by calculating the probability of each pixel being assigned to that area. Pixels with probabilities higher than 0.5 were included in the area templates.

(c) *Adaptation procedure and eye tracking*

Monkeys were seated in a primate chair inside a darkened sound-attenuating booth measuring $1.7 \times 2.0 \times 2.1$ m ($l \times w \times h$; inner dimension) during the experiment with its head restrained. Stimuli were presented on a 21-inch colour monitor (Digital, model: VRC21-HA) at a viewing distance of approximately 94 cm. Stimuli were presented with custom-written software controlled by the QNX real-time operating system (QNX Software Systems, Ontario, Canada). Human participants were seated in front of a 21-inch colour monitor (Model: Iiyama Vision Master Pro 21) at a viewing distance of 39 cm inside a darkened experimental room. They were head restrained using a chin rest and forehead and side cushions. The setups were such that both species viewed the stimuli at similar visual angles and under identical lighting conditions.

Eye movements of the macaques were recorded by an iView infrared eye tracking system (SensoMotoric Instruments (SMI), Teltow/Berlin, Germany) and sampled at 200 Hz. Human eye movements were recorded by an iView X Hi-Speed infrared eye tracking system and sampled at 200 Hz. The eye tracking systems had a *minimum* spatial resolution of 0.05° (human) and 0.1° (monkey).

Prior to the actual experiment, macaques were calibrated using a nine-point fixation task. During the experiment, the monkey was rewarded with juice for 300 ms in an inter-trial interval of 5000 ms, *regardless* of task behaviour. The order of trials was arranged such that upright normal or inverted normal trials were followed by upright thatcherized or inverted thatcherized trials, resulting in trial pairs of normal and manipulated faces. The macaques did about 20 ± 3 trial pairs per condition (upright and inverted \times human and monkey), split up into 8–10 days of experimental testing sessions per macaque. Thus, in one testing session, a stimulus sequence of 20 images, or 10 trial pairs, was presented. Statistics were calculated across sessions.

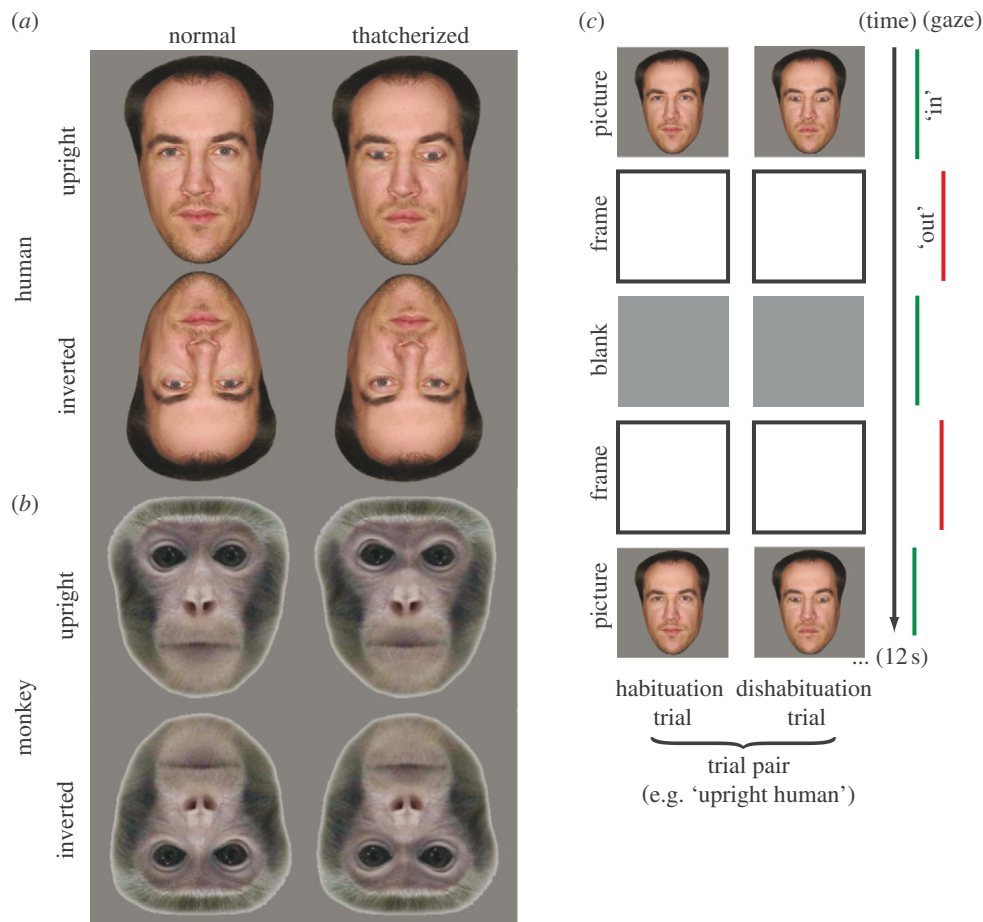


Figure 1. The Thatcher illusion. Shown are two pictures of the same individual. A striking difference between the two upper two faces becomes obvious that is not at all evident in the inverted orientation. (a,b) Normal and thatcherized stimuli. Face stimuli of (a) humans and (b) macaques were placed on a grey background and manipulated such that eyes and mouth were locally inverted (thatcherized). The adaptation procedure is shown in (c). The observer actively controls on- and offset of the stimuli by entering and leaving a centrally presented image frame. Directing the eye gaze into the image frame elicits the presentation of either blank or a picture. The trial is completed after a total time of 12 s looking at blank and picture.

Humans were calibrated prior to every trial using the same nine-point fixation task to minimize spatial distortions due to head movements. They were financially compensated at the end of the experiment. The human participants did 20 trials per condition (upright and inverted \times human and monkey) and statistics were calculated across participants.

(d) Habituation task

Participants could actively control the onset and offset of the stimuli by entering and leaving a centrally presented image frame. By directing the eye gaze into the image frame, the participant elicited the presentation of either blank (every first inwards gaze) or a picture (every other inwards gaze). The trial was automatically completed after a total time of 12 s spent on blank and picture. A behavioural measurement was obtained by determining the ratio of time the observer spent looking at the picture over the total time spent looking at the picture and the blank. This ratio provides information about the observer's preference for the picture over the blank at each point in time during a trial. Over the course of a trial, viewing results in a habituation to the presented picture. However, by comparing the time course or an average time span to habituation of a *normal* trial with a subsequent *thatcherized* trial, one can determine the dishabituation to that second picture after having observed the first picture. In other words, it is the *rebound of interest* in that second picture that

reflects the perceived degree of similarity between the two pictures: thus, a small rebound would indicate similarity, while a great rebound would indicate dissimilarity. We contrasted the preference ratios of each trial pair (normal–thatcherized).

(e) Data analysis

Viewing preference was measured as the ratio of time spent looking at the picture to the total time looking at the picture and the blank square combined (12 s). Eye movements were also determined by recording the total number of fixations and the viewing time. Fixation periods were extracted as a function of velocity, including eye movement samples that were no faster than 20° s^{-1} within a time period of at least 100 ms. The average position of samples containing one fixation period was taken as the final eye position of that fixation period. To statistically evaluate the fixation frequency and density of single facial parts (*eyes*, *nose* and *mouth*), the number of fixations and viewing time for single parts were normalized to the total number of fixations and the viewing time in that trial. Furthermore, the proportion of the area of a particular facial part relative to the whole image was subtracted from the proportion of data samples for a particular facial part and the total number of samples in that trial. Any difference in viewing time from zero means that this particular facial area was looked at more or less than would be predicted by a uniform looking strategy. Dependent variables

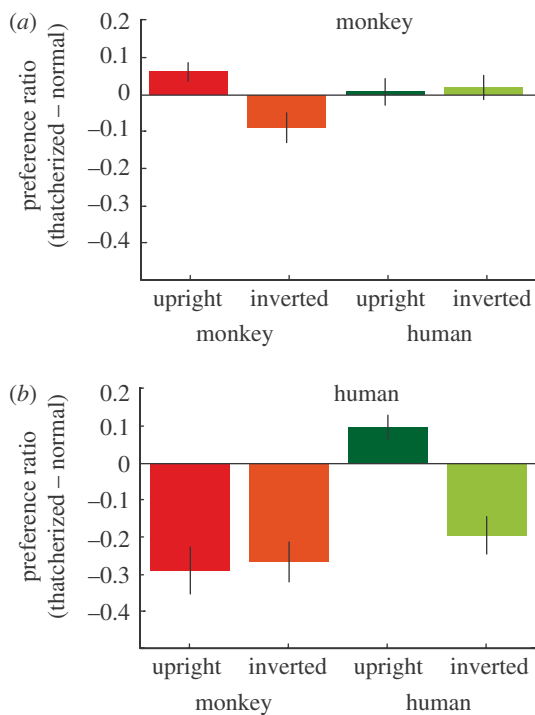


Figure 2. Preference for the face picture above the blank (preference ratio). (a,b) The grand mean of the difference in preference ratio for thatcherized versus normal (y -axis) conditions as a function of stimulus species (human versus monkey) and presentation condition (upright versus inverted) (x -axis). Titles indicate the species affiliation of the observers.

were therefore the preference ratio for each trial pair and the total viewing time during image presentation. To compare the two experiments, analyses of variances were conducted for the stimulus groups (*monkey* versus *human*) as well as for the two stimulus manipulations *orientation* (upright versus inverted) and *thatcherization* (thatcherized versus normal). In all cases, corrections for multiple comparisons (α/n) (Bonferroni correction) were applied if required. We report the corresponding α -level of a single comparison (e.g. $p = 0.05$ (reported) is equivalent to $p = 0.0167$ (tested) for $n = 3$ comparisons).

3. RESULTS

(a) Preference ratio

(i) The Thatcher illusion in monkeys

To test the Thatcher illusion in monkeys, three adult male rhesus macaques (*M. mulatta*) performed the non-reinforced passive viewing task. Figure 2 illustrates the rebound of interest (measured as preference ratio) for the thatcherized condition relative to the normal condition (i.e. a subtraction of normal from thatcherized conditions). Figure 2a shows the grand mean of the preference ratio (data acquisition of 12 s) for the conditions 'monkey upright', 'monkey inverted', 'human upright' and 'human inverted'. The zero line (0 on the y -axis) indicates no additional interest for the thatcherized condition, with positive values denoting increased interest and negative values denoting disinterest, respectively. As indicated by the coloured bars, the rebound of interest for the human stimuli is relatively constant, i.e. the relative rebound is independent of orientation (upright

versus inverted) of the face ($t(27) = -0.28$; $p = 0.78$; s.d. = 0.22). However, the monkey upright condition showed a large rebound of interest over the entire 12 s of trial duration (electronic supplementary material, figure S1a). In contrast the 'monkey inverted' condition caused a disinterest in the thatcherized stimulus. Statistically, the rebound of interest between the monkey conditions is highly significant ($t(21) = 4.30$, $p < 0.001$, s.d. = 0.17). The rebound of interest for the monkey upright condition is presumably caused by the perceived dissimilarity between the upright normal and the upright thatcherized face, which reflects the sensitivity to holistic information for upright faces. In contrast, the inverted condition of monkey faces and both conditions of human faces elicited no rebound of adaptation, which is indicative of a relatively high perceived similarity. Thus, by means of adaptation, monkeys show sensitivity to holistic information only for faces when they are right-side up and conspecific.

(ii) The Thatcher illusion in humans

To investigate the Thatcher illusion in humans, 22 human participants performed the same non-reinforced passive viewing task as the macaques did. The identical face stimuli with neutral facial expression of rhesus macaques and humans in upright normal, upright thatcherized, inverted normal and inverted thatcherized versions were presented and analysed in the same fashion as above. Figure 2b shows the grand mean of preference ratio for the experimental conditions. As indicated by the coloured bars, the rebound of interest for the monkey conditions is relatively equal, i.e. the relative rebound does not depend on the orientation (upright versus inverted) of the face ($t(21) = -0.64$, $p = 0.53$, s.d. = 0.17). In contrast, the human upright condition showed a rebound of interest over the entire 12 s of trial duration (electronic supplementary material, figure S1b), while the human inverted condition caused a disinterest in the thatcherized stimulus. A t -test shows that the rebound of interest between the human conditions is significantly different ($t(22) = 5.26$, $p < 0.001$, s.d. = 0.27). Sensitivity to holistic information, again, is only provided when conspecific faces are presented right-side up, thus causing a high degree of rebound of adaptation given the extent to which the participant perceives the two images as different.

Adaptation in humans (as well as in monkeys) therefore reveals a consistent and robust response pattern that is dependent on the species affiliation of the stimuli.

(b) Differences in preference ratios between human and monkey observers

To gain more insight into the response characteristics of human and monkey observers, preference ratios were compared using a mixed-factor analysis of variance (ANOVA): figure 2 clearly shows that the overall effect size of preference ratio is greater for humans than for monkeys, while the critical difference between conspecific upright and conspecific inverted faces, as well as the critical similarity of upright non-conspecific and inverted non-conspecific faces is apparent in both humans and monkeys. Accordingly, quantifying the effect size of preference ratio across participant groups yields a main

effect of preference ratio for *observer* (human versus monkey) ($F_{1,346} = 107.8, p < 0.001$), showing that *overall* the two participant groups look differently. The interactions between the factors *observer* and *stimulus* (human versus monkey) ($F_{1,346} = 24.26, p < 0.001$) as well as the interaction between the factors *observer* and *stimulus* with respect to viewer's species (conspecific versus non-conspecific) ($F_{1,346} = 36.22, p < 0.001$) were significant. Thus, the way the two participant groups look at the two groups of faces differs. This is due to the fact that for human participants the preference ratio drops considerably when they believe they are seeing the same picture for a second time, i.e. for non-conspecific faces and conspecific inverted faces. Thus, in this condition, the habituation (first) stimulus (mean: 0.85; s.d.: 0.17) is statistically significant in preference ratio from the dishabituation (second) stimulus (mean: 0.60; s.d.: 0.24): $t(66) = 7.72, p < 0.001$. This broad tendency was not apparent for monkey participants (habituation (first) stimulus (mean: 0.44; s.d.: 0.13)—dishabituation (second) stimulus (mean: 0.42; s.d.: 0.13): $t(77) = 0.66, p = 0.51$). However, this *does not* indicate that humans are less interested in these pictures than monkeys; they simply start at a much higher level of preference for the first picture shown.

(c) Eye tracking analysis

(i) Monkey

The viewing time during image presentation was analysed and the saliency for two experimental variables (*species* (stimulus) and *facial parts*) and for the manipulation *conditions* (upright and inverted) was determined. In the following, we describe the main interaction of unmanipulated upright and inverted monkey and human faces (i.e. the first stimulus of each trial pair) by a multi-factor ANOVA. For monkey participants, an interaction of the three factors facial parts (eyes, nose and mouth), orientation (upright and inverted) and stimulus (human and macaque) was significant ($F_{2,288} = 5.2, p < 0.001$), which is analysed in the following.

To examine the effects of thatcherization, viewing times for macaque and human faces were compared. Stimulus manipulation (thatcherization) was, by definition, restricted to eyes and mouth of the face. Thus, we compared these parts for thatcherized and normal faces. Monkey observers showed a tendency to look longer at 'thatcherized eyes' than at 'normal eyes' when the face of a monkey was presented in upright orientation ($t(21) = 3.10, p < 0.01, s.d. = 0.20$) (figure 3a). Moreover, an increase in viewing time was also observed for the 'thatcherized mouth' as opposed to the 'normal mouth' ($t(21) = 2.03, p < 0.05, s.d. = 0.16$). In contrast, the (unchanged) nose region was visited equally often in the thatcherized version as in the normal version ($t(21) = -0.85, p = 0.40, s.d. = 0.17$). Interestingly, when the monkey face was inverted by 180°, the increased viewing times for nose and mouth decrease significantly with upright faces (eyes: $t(21) = -0.65, p = 0.52, s.d. = 0.24$; nose: $t(21) = -3.90, p < 0.001$ (normal > thatcherized), s.d. = 0.16; mouth: $t(21) = -3.73, p < 0.001$ (normal > thatcherized), s.d. = 0.17), reflecting a typical habituation effect, as seen when two identical pictures are shown in succession (figure 3c). The tendency to

look longer at thatcherized eyes than at normal eyes in upright monkey faces was not observed with human faces ($t(27) = -0.33, p = 0.74, s.d. = 0.26$) (figure 3b), nor was it observed with the thatcherized mouth as opposed to the normal mouth in human faces ($t(27) = -3.69, p < 0.001$ (normal > thatcherized), s.d. = 0.19) or the 'thatcherized nose' versus the 'normal nose' ($t(27) = -6.67, p < 0.001$ (normal > thatcherized), s.d. = 0.17). Inverting the human face 180° elicited a similar decrease in time spent viewing eyes and mouth (eyes: $t(27) = -2.88, p < 0.01, s.d. = 0.19$; nose: $t(27) = -5.61, p < 0.001, s.d. = 0.15$; mouth: $t(27) = -5.75, p < 0.001, s.d. = 0.13$; while all normal conditions > thatcherized conditions) (figure 3d). Thus, the response patterns of viewing time closely resemble the patterns revealed in the previous study by Dahl *et al.* (2009), indicating the strong nature of thatcherization for conspecific upright faces, but not for inverted or non-conspecific faces. Moreover, the time course as a function of number of fixation can be seen in figures S2a–d in the electronic supplementary material: these plots show that the eyes of an upright monkey face are not only looked at more frequently overall, but that this happens already from the first fixation onwards. In addition, this tendency is even stronger for the eyes of the thatcherized version of the upright monkey faces. Interestingly, the mouth region also attracts the gaze starting with the first fixation. We hypothesized that observers pay more attention to manipulated facial parts in upright faces than in inverted faces. Accordingly, viewing times for these parts were increased during the presentation of upright faces, while viewing times for inverted faces were relatively low. This enhancement was stronger for conspecific than for non-conspecific faces.

(ii) Human

The ANOVA on part viewing times revealed the same interaction for normal faces for human observers as previously found for monkey observers: facial parts (eyes, nose and mouth) × orientation (upright and inverted) × stimulus (human and macaque): $F_{2,258} = 9.64, p < 0.001$.

Effects of thatcherization were determined by comparing time spent viewing macaque and human faces. We compared eyes, nose and mouth for thatcherized and normal faces, assuming that changes in viewing behaviour occur at the manipulated facial parts. Human observers looked longer at thatcherized eyes than at normal eyes when the face of a human was presented upright ($t(22) = 4.25, p < 0.001, s.d. = 0.26$) (figure 3f). An increase in viewing time was also observed for the thatcherized mouth as opposed to the normal mouth ($t(22) = 3.55, p < 0.001, s.d. = 0.15$). In contrast, the unaltered nose region was looked at as often in the thatcherized version as in the normal version ($t(22) = 0.53, p = 0.60, s.d. = 0.12$). However, inversion of human faces caused a decrease in time spent viewing eyes and mouth, as well as nose, of manipulated faces as opposed to normal faces (eyes: $t(22) = -2.21, p < 0.05, s.d. = 0.16$; nose: $t(22) = -8.94, p < 0.001, s.d. = 0.11$; mouth: $t(22) = -3.96, p < 0.001, s.d. = 0.16$, while all normal conditions > thatcherized conditions), reflecting a

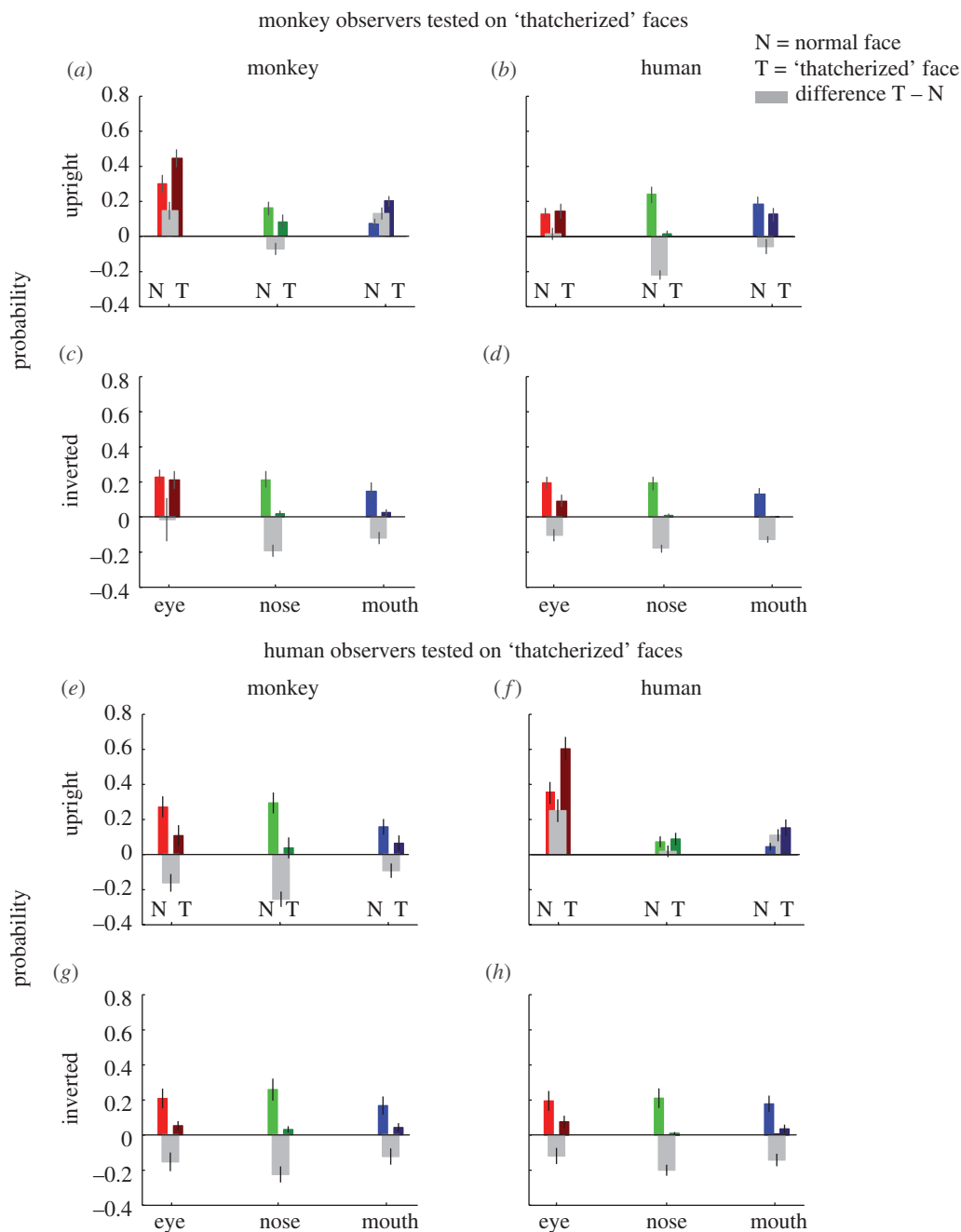


Figure 3. Monkeys and humans tested on thatcherized faces. This figure shows the grand mean of looking time, i.e. the time that the observer spent looking at a specific part (normalized to the overall looking time and the size of the specific parts) for (a–d) monkey and for (e–h) human observer. The bars indicate the probability of looking at eyes (red), nose (green) and mouth (blue). ‘N’ stands for the normal face, ‘T’ for the thatcherized face. The grey bars show the difference between thatcherized and normal faces. (a,b) The upright and (c,d) the inverted presentation condition. The titles indicate the species of the stimuli. The zero line indicates a random gaze distribution. Values above 0 are of higher probability than random; everything below 0 is of lower probability than random.

habituation effect (figure 3h). The longer viewing times for thatcherized eyes compared with normal eyes found in upright human faces, however, were not reproduced when observers looked at monkey faces ($t(21) = -2.99$, $p < 0.01$ (normal > thatcherized), s.d. = 0.17) (figure 3e), nor were they seen with the thatcherized mouth as opposed to the normal mouth of monkey faces ($t(21) = -1.57$, $p = 0.13$, s.d. = 0.16) or the thatcherized nose as opposed to the normal nose ($t(21) = -10.75$, $p < 0.001$ (normal > thatcherized), s.d. = 0.12). Inversion of monkey faces elicited a similar decrease in time spent viewing eyes and

mouth (eyes: $t(21) = -5.42$, $p < 0.001$, s.d. = 0.13; nose: $t(21) = -6.07$, $p < 0.001$, s.d. = 0.16; mouth: $t(21) = -4.08$, $p < 0.001$, s.d. = 0.15, while all normal condition > thatcherized conditions) (figure 3g). To illustrate this point, figures S2e–h in the electronic supplementary material show the response patterns of viewing times as a function of number of fixation. Humans, too, show an enhanced probability of looking at the eyes and mouth of an upright conspecific face from the first fixation onwards. We therefore find a systematic modulation of viewing times with orientation and species affiliation of the face in human observers.

(d) Differences in viewing times between human and monkey observers

The same statistical comparisons as those applied to the preference ratio were made with respect to viewing times to further describe the characteristics of eye tracking. Using a mixed-factor ANOVA, a main effect of viewing times for observer (human versus monkey) was significant ($F_{1,1038} = 17.39$, $p < 0.001$), indicating an overall difference between the two participant groups that can be best described by a greater effect size of viewing times in humans compared with monkeys. However, the critical differences between conspecific upright and conspecific inverted faces, as well as the critical similarity of upright non-conspecific and inverted non-conspecific faces (seen as a modulation in preference ratio) are maintained in both human and monkey observers. The interactions between the factors observer and stimulus (human versus monkey) ($F_{1,1038} = 3.85$, $p < 0.05$) as well as the interaction between the factors observer and stimulus with respect to viewer's species (conspecific versus non-conspecific) ($F_{1,1038} = 13.52$, $p < 0.001$) were significant. This trend was discussed in the previous paragraph about differences in preference ratios. Human observers initially pay more attention (and as a result show longer viewing times) to the first-presented stimulus of a pair, with the decrease in viewing time for the second stimulus being much more pronounced than in monkey observers. This could result from the task instruction given to the human observers to view the stimuli as normally as possible.

4. DISCUSSION

The Thatcher illusion is an interesting paradigm for dissociating processing of local features from global/configural processing. While configural processing is affected for inverted faces (in other words, a change in the configuration of facial parts is hard to detect when the face is inverted), local feature processing is still intact (i.e. an obvious featural manipulation of the face, for example, occlusion of facial parts, makes a face look grotesque or bizarre, but is still noticeable even when the face has been turned upside down (Searcy & Bartlett 1996; Hancock *et al.* 2000; Murray *et al.* 2000). On the other hand, a configural manipulation of facial parts is detectable when the face is presented right-side up, but completely lost when the face is upside down (Eimer 2000; Freire *et al.* 2000; Leder & Bruce 2000). In thatcherized faces, only the configuration of facial parts is changed, while local facial features are unaltered, making the manipulation hard to detect when inverted (Bartlett & Searcy 1993).

(a) The Thatcher illusion in humans

As mentioned earlier, the Thatcher illusion has been shown psychophysically using rating tasks (Parks *et al.* 1985; Bartlett & Searcy 1993; Murray *et al.* 2000), recognition rates (Rhodes *et al.* 1993), habituation (Bertin & Bhatt 2004) and perceptual comparison tasks (Bartlett & Searcy 1993; Searcy & Bartlett 1996; Leder *et al.* 2001; Edmonds & Lewis 2007) and has become an important tool for the exploration of processing strategies. A continuous rotation along the image-plane axis induces a shift from holistic and part-based processing to part-based processing strategies. Lewis (2001)

investigated the Thatcher illusion in children and adults ranging from 6 to 75 years and found no effect of age, i.e. young children showed the same effect as adult humans. Sjöberg & Windes (1992) showed an increase in reaction times, although not a linear increase, with increasing angle of rotation from the vertical upright position when observers were asked to decide whether a face was thatcherized or not. Stuerzel & Spillmann (2000) and Murray *et al.* (2000) determined the point of rotation at which the percept turns from a normal into a grotesque appearance. Both revealed a mean threshold at 90–120° relative to the vertical. Owing to a relatively narrow degree of 'appearance change', Stuerzel and Spillmann suggested a neural step tuning in face cells that reflects a change from holistic processing (in the case of upright faces) to featural processing (in the case of inverted faces). Based on these findings, experiments (Milivojevic *et al.* 2003; Carbon *et al.* 2005; Boutsen *et al.* 2006; Gu *et al.* 2007) have been conducted to explore the underlying neurophysiological mechanisms. Most prominently, event-related potentials such as the face-sensitive N170 were analysed to track down changes in the neural code when thatcherized faces were turned upside down. In the study by Boutsen *et al.* (2006), the N170 component over the occipito-temporal cortex was delayed for thatcherized faces, but not for thatcherized houses. This modulation was more prominent in upright than inverted faces, thus matching the illusion and supporting the notion that both the effect of face inversion and the effect of 'feature inversion' (thatcherization) are distinguishable at both the functional and neural level.

(b) The Thatcher illusion in monkeys

The only two studies that have addressed the Thatcher illusion in monkeys to date draw conflicting conclusions. Parron & Fagot (2007) tested baboons (*Papio papio*) and found no difference in recognition performance between thatcherized and normal faces. However, idiosyncratic response strategies have often been observed in explicit reinforcement paradigms, leaving the real nature of the Thatcher illusion—which must be understood as spontaneous behaviour—unclear: the matching-to-sample paradigm in the above study involved extensive pre-training with a very restricted set of stimuli. In this case, reliance on salient, low-level features seems a more likely explanation for the data than a strategy based on different face processing aspects, such as configuration and facial features. In contrast, the study of Adachi *et al.* (2009) used a habituation–dishabituation paradigm that enabled the participants to act as naturally as possible. The conception behind this study is along the same lines as the experiments conducted in the study presented here. Adachi *et al.* (2009) measured the dishabituation to a thatcherized monkey face after the subject viewed the same monkey face in a normal (non-thatcherized) version. As expected, dishabituation to the thatcherized faces was greater when the images were presented right-side up than upside down. As in an earlier study by Dahl *et al.* (2009), this experiment demonstrates that non-human primates rely on the same mechanism of face perception as humans do, i.e. holistic processing for upright faces. Moreover, these findings are fully in accordance with the presence of an inversion effect in monkeys.

Importantly, the experiments presented here replicate the findings by Adachi *et al.* (2009) and strongly support the notion that monkeys, or at least rhesus macaques, show the Thatcher effect. In the following, important aspects will be highlighted that allow more insights into the nature of the Thatcher effect in monkeys and humans.

(c) 'The eyes have it'

As in Dahl *et al.* (2009), we demonstrate that eye movement patterns are critically affected by species affiliation: viewing times show a fairly equal distribution across facial parts for non-conspecific faces as well as for inverted conspecific faces, while upright conspecific faces elicit a high degree of eye saliency. The eye saliency for upright conspecific faces has been interpreted as a critical component of a holistic face processing strategy (Dahl *et al.* 2009). As the brain is not holistically tuned to inverted and non-conspecific (non-expert) faces but rather has to rely on part-based scanning strategies, an equal distribution of viewing times across parts is indicative of part-based processing. Here again, it follows that holistic face processing reduces fixations to the most prominent and preferential features, the eyes (Keating & Keating 1982; Nahm *et al.* 1997; Barton *et al.* 2006). Scanning of further facial parts is not required since holistic processing is an obligatory stage of processing that implies an (upright) template to detect whole faces. Moreover, thatcherized expert processing is characterized by even stronger enhancement of viewing times for eyes and mouth, as will be discussed in the next paragraph.

(d) Thatcher illusion manifests in the preference ratio as well as in the viewing times

In the present study, the effect of thatcherization becomes apparent in a twofold manner. First, the rebound of adaptation is clearly enhanced for eyes and mouth when a conspecific face is presented in a thatcherized upright version when compared with the normal upright version. This enhancement is observed neither with inverted conspecific faces nor with non-conspecific faces in general. In other words, there is renewed interest in previously shown faces only when changes are noticed, i.e. manipulations of eyes and mouth; otherwise, it will be treated as the same face, resulting in a decrease of interest. Secondly, eye movements support the notion that the effect of thatcherization is driven by a configural change, i.e. observers spend more time looking at the manipulated facial features. Importantly, by definition, the proportion of time spent viewing a particular facial feature of the second stimulus shown in succession does not necessarily need to be higher than the corresponding proportion of viewing time in the first stimulus. A proportion of viewing time for the second stimulus that is equal to that for the first stimulus would be sufficient to indicate that the respective facial part is treated differently. However, the results show that time spent viewing the manipulated parts significantly exceeded that observed with the first stimulus. The Thatcher effect in monkeys as revealed by Adachi *et al.* (2009) has not only been replicated but substantially extended by dissociating monkey and human faces, supporting the notion of expertise processing for conspecific faces. Future work will extend the present experiments to determine whether the Thatcher effect is

related to effects occurring in changes in configuration of facial parts, that is, whether the preference ratio and viewing patterns change similarly in Thatcherized faces than in face, in which, for example, the distance between the eyes have been increased (a configural change).

(e) Perceptual learning process or genetic determination?

Here, as well as in Dahl *et al.* (2009), the aspect of expertise for faces is crucial. In both species of observers, the thatcherization effect is only evident if a conspecific face is presented. Non-conspecific faces, on the other hand, are handled in the same manner as faces that are turned upside down even exemplars of a generic object category (Dahl *et al.* 2009). Thus, it is only after extensive training with the species-relevant face that the observer becomes aware of configural manipulations such as thatcherization. Again, it is important to stress that the same set of stimuli was shown to both groups of observers, but was processed according to their own perceptual experience. Finally, in the case of rhesus macaques, genetic predisposition towards conspecific faces might also play a role as previous studies have shown that these macaques still retain preference for conspecific faces when raised by Japanese macaques (Fujita 1990, 1993). Interestingly, for Japanese macaques, this preference does not seem to exist as they become sensitive to human or macaque faces when exposed to either during early infancy (Sugita 2008). The reason for this might be that the conspecific bias serves as a perceptual barrier against interbreeding in the Rhesus macaque—a danger that Japanese macaques do not have to face. It remains to be seen which factors play a role in carving out conspecific, face-processing expertise in these primates.

This research adhered to the Association for the Study of Animal Behaviour/Animal Behaviour Society Guidelines for the Use of Animals in Research and the guidelines of the European Community (EU VD 86/609/EEC) for the care and use of laboratory animals under the approval of local authorities (Regierungspraesidium). This work was supported by the Max Planck Society and by the WCU (World Class University) programme through the National Research Foundation of Korea funded by the Ministry of Education, Science and Technology (R31-2008-000-10008-0).

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