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Research Report

The Thatcher illusion seen by the brain: An event-related brain potentials study

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Abstract

In "Thatcherized" faces, the eyes and mouth regions are turned upside-down. Only when presented upright they are perceived as severely distorted. Common theories explain this effect by the loss of configural information for inverted faces. We investigated neural correlates of Thatcherization using event related potentials (ERPs). Sixteen right-handed participants performed identity classifications on Thatcherized or original familiar faces, presented either for 34 ms or 200 ms at an orientation of either 0°, 90° or 180°. For the occipito-temporal N170, we found (1) strong non-linear effects of orientation and (2) interactions between Thatcherization and orientation: Thatcherization resulted in larger N170 for upright faces, but smaller N170 for inverted faces. The novel finding of N170 effects of Thatcherization in inverted faces suggests differences in the neural encoding of Thatcherized and original inverted faces, even though Thatcherization escapes subjective perception in inverted faces.

Theme: Neural basis of behavior/perception
Topic: Cognition

Keywords: Event-related potential; Face perception; Thatcher illusion; Matching; Early processing; Local processing, configural processing, EEG, electroencephalogram

1. Introduction

The so-called 'Thatcher illusion' [49] is an orientation-sensitive face illusion. A face in which the eyes and mouth regions are turned upside-down (i.e., inverted) relative to the rest of the face is perceived immediately as being strongly altered. However, this strong perceptual effect is lost when the whole Thatcherized face is inverted. This anisotropic effect is illustrated in Fig. 1.

It is obvious from the images of Fig. 1 that the upright versions look more different from each other than the faces rotated by 90°. Furthermore, inverted Thatcherized and normal faces are perceptually similar and the grotesqueness of inverted Thatcherized faces is almost completely lost [1,49].

The Thatcher illusion has been explained by at least three competing hypotheses, which are elaborately discussed in Bartlett and Searcy [1]. These hypotheses are (1) the expression disruption theory [51,52], (2) the frame-of-reference theory [33] and (3) the bulk of dual processing models of face recognition [2,20,27]. As there is considerable evidence supporting the dual processing theory as an explanation of the Thatcher illusion (e.g., [1,4,23,24,47]), this theoretical account will be further described in the following.

The dual processing account postulates that face recognition is mainly based on the processing of *local/featural*

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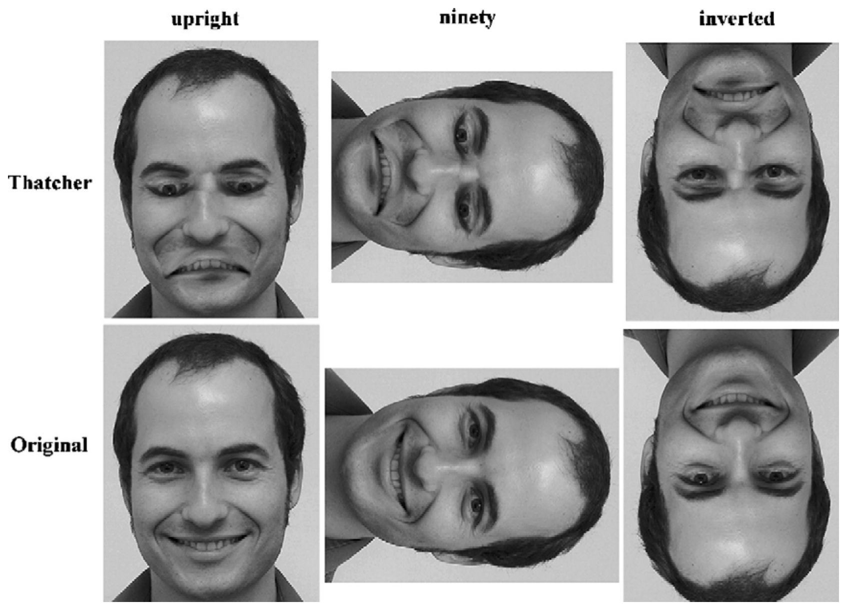

Fig. 1. Demonstration of the Thatcher illusion for the three used orientations, upright (0°), ninety (90°) and inverted (180°). The upper row shows the Thatcher versions, the lower shows the Original, thus unmanipulated, versions.

and *configural* information. Both types of information are not uniformly defined. Most commonly, local information is assumed to be information about locally circumscribed features such as the eyes, the eyebrows, the mouth or the nose [19]. Other authors define local information as pure local properties like feature distortions (e.g., gap in the teeth, [45]) or contrast and color [20] that do not change any micro- or macro-relations with respect to other features. The term "configural" information is also heterogeneously used in the face literature. One position claims that configural information covers the general spatial layout of the cardinal features with the eyes situated above nose and mouth. Humans are remarkably sensitive to detect faces based on first-order relations [30] and newborns show a preference towards stimuli that have face-like first-order relations [29]. Since this general relationship holds for all human faces and is therefore of little discriminative value, other authors define configural information as the specific spatial relationship between facial features, often known as second-order relations [10,20]: humans can detect deviations in these relations as small as 1 min of visual angle, which is very close to the absolute limits of visual acuity [6,15]. A third group stresses the holistic meaning of configural information [21,48]. Within this theoretical account, it is assumed that faces are processed and represented as *Gestalten*, for which part decomposition is severely limited [13]. An elaborate overview over all three definitions of configural information can be found elsewhere [26].

The perceived normality of inverted Thatcherized faces has been attributed to the dissociated disruption of local and configural information: whereas for inverted faces, *configural* processing is disrupted, *local* processing is still effective. For example, Searcy and Bartlett [45] demonstrated that the perception of an obvious local alteration of the face by blackening parts of the teeth persists when the whole face is inverted (see also [16] and [31]). In contrast, even strong configural changes are perceptually lost by rotating the face by 180° (e.g., [20,22]). Because in a Thatcherized face only the configuration of unaltered local features is changed, the manipulation is hardly detectable in the inverted presentation condition [1,9].

Stuerzel and Spillmann [47] and Murray et al. [31] determined the angular orientation at which a Thatcherized face turns from a normal looking face to a grotesque one. Stuerzel and Spillmann [47] identified a mean threshold at about 90° relative to the vertical and Murray et al. [31] found an apparent shift in processing mode between 90° and 120°. Moreover, Stuerzel and Spillmann [47] showed a relatively narrow zone of the changeover from a "pleasant" to a "grotesque" outlook. They suggested a neuronal step-tuning of hypothetical face cells in the human brain, underlying the holistic (for the upright version) versus componential processing (for the inverted version).

Milivojevic et al. [28] investigated neural mechanisms mediating these processes by using event-related potentials (ERP). Participants performed a non-speeded gender decision task for Thatcherized and normal faces presented for 1000 ms in one of six different orientations (0°–300° in steps of 60°). Mean amplitudes were analyzed for 8 posterior electrodes and for each of four different time segments, which corresponded to P1, N170, P250 and late components. Milivojevic et al. [28] observed strong effects of Thatcherization for upright faces in the P1 and N170 components. Specifically, N170 amplitudes were increased for Thatcherized relative to normal faces when presented upright. By contrast, no effects of Thatcherization were seen for inverted faces in any of these 4 components. Milivojevic and co-workers concluded that the ERPs paralleled the perceptual illusion. Thus, differences between Thatcherized and normal faces when inverted were interpreted to be absent not only with respect to the perception of these faces, but also with respect to brain responses to these stimuli.

Rotshtein et al. [37] used functional magnetic resonance imaging (fMRI)[1] to investigate whether emotional attributes interact with sensory–perceptual properties of face stimuli. To avoid confounding of emotional attributes with facial feature alterations, they used Thatcherized faces. In the lateral occipital complex, they found a differential effect of inverted normal and inverted Thatcherized faces: upright faces elicited larger effects of Thatcherization in right than in left lateral occipital complex. By contrast, Thatcherization effects for inverted faces were not lateralized but were significant overall. Thus, these fMRI effects of Thatcherization for inverted faces are in some contrast to the ERP results by Milivojevic et al. [28] and suggest that (1) neural effects of Thatcherization for inverted faces may *not* parallel the perceptual illusion and that (2) such effects may be seen in the lateral occipital complex. The results of these two studies may thus be seen as somewhat discrepant, particularly when considering evidence that the scalp-recorded N170 may be generated in lateral occipito-temporal brain areas (for an overview see [39], e.g., [41]).

The aim of the present study was to reassess ERP correlates for the Thatcher effect while implementing a number of modifications relative to the Milivojevic et al. [28] study. We used a leaner design with only three orientations, and because rotation studies with human faces have shown symmetric effects for clockwise and anti-clockwise rotations (e.g., [28] and [47]), we only used clockwise rotations. Moreover, we varied the presentation time (PT) between a very short PT of only 34 ms and a relatively long PT of 200 ms (cf. [9]). The short PT was taken to investigate processes based on very limited presentation constraints. The long PT was used to investigate supraliminal processes for the perception of faces and to make the results comparable to the bulk of studies on the Thatcher illusion, which tended to use long presentation times. Milivojevic et al. [28] used a gender decision task, which did not require the processing of facial identity. As we were interested in the cognitive processes that mediate face *recognition*, we used an identity-decision task instead.

Based on recent evidence from fMRI data [37] that Thatcherization in inverted faces affects activation in the lateral occipital complex, we investigated whether the present design would reveal ERP effects of Thatcherization in inverted faces as well. The recent study by Milivojevic et al. [28] did not find such an effect in a gender decision task. We consider that the N170 component has been related to the structural encoding of faces and has been suggested to be generated in lateral occipito-temporal areas [41]. Furthermore, as demonstrated by Eimer [11], the N170 is tightly correlated with featural aspects of a face (see also [38] and [44]). With respect to the abovementioned findings, we therefore predicted that any ERP effects of Thatcherization in inverted faces would most likely show up in the N170 component.

2. Method

2.1. Participants

Sixteen participants (11 women and 5 men) aged between 18 and 27 years (M = 20.1 years, SD = 2.4 years) were paid £ 15 to contribute data to this study. All participants were undergraduate students at the University of Glasgow, Scotland. They all reported normal or corrected-to-normal visual acuity and were right-handers as measured by the Edinburgh Inventory [32].

2.2. Stimuli and apparatus

Photographs of eight female celebrities[2] were used in the experiment. The celebrities had been selected on the basis of high familiarity ratings in an earlier study [9]. For each celebrity, two different exemplars were used, one version for the familiarization phase and one for the test phase. This was done to prevent purely picture-based familiarity effects. Additionally, the faces of two celebrities (Penelope Cruz [actress] and Britney Spears [singer]) were used for practice trials. Faces were obtained from different sources but were all software-edited using Adobe Photoshop™. They were converted to grayscale and each face was framed within an area 180 pixels wide × 220 pixels high, corresponding to 5.8 × 7.1 cm on the screen. Using ERTS™ (Experimental Run Time System, Berisoft), the stimuli were presented in a dimmed room at a distance of about 85 cm at a screen resolution of 800 × 600 pixels.

All pictures were further manipulated in two ways. First, we used the unmanipulated faces (Original) to produce Thatcherized faces (Thatcher) by turning the areas of the eyes and the mouth by 180°. The resulting edges of these areas were smoothed to remove graphical inconsistencies or artificial local saliencies in the pictures. Second, in addition to the upright versions (upright), all faces were also rotated clockwise by 90° (ninety) and by 180° (inverted).

In total, there were 8 (celebrities) × 2 (class: Thatcher vs. Original) × 3 (orientation: up, ninety, inv) = 48 different test

[1] In fact, they used an adapted fMRI (fMR-A) routine in which the signal change between repeated and non-repeated conditions was compared to enhance fMRI resolution. This fMR-A approach evaluates the extent of signal decay that is attributable to stimulus repetition and is particularly sensitive to changes in the high-order visual cortex.

[2] Julia Roberts, Cameron Diaz, Gwyneth Paltrow, Marilyn Monroe and Pamela Anderson (actresses), Claudia Schiffer, Cindy Crawford (super models), Princess Diana (royal).

face versions and 2 × 2 × 3 = 12 different practice face versions.

2.3. Procedure

Before the experiment started, participants performed a verbal identification decision task on all celebrities presented in the study to ensure familiarity. To this means, we presented typical non-manipulated pictures, which were different to those used in the experiment. As a participation criterion, participants had to identify at least 8 of 10 faces.

The experiment consisted of a practice phase using the two practice faces and a test phase using pictures of eight different celebrities.

Each trial began with the presentation of a fixation cross in the center of the screen for 500 ms. Then, a question about the identity of a succeeding face was presented for 500 ms (e.g., "Is this 'Julia Roberts'?") followed by a second fixation cross visible for 1000 ms. Text was presented in white on a black background and all names were derived from the celebrities included in the face set. After that, the picture of a celebrity was presented either for 34 ms (short presentation time, PT) or 200 ms (long PT) and participants judged whether the face matched the previously presented name by pressing one of two response buttons. For face–name matches, the 'same' button had to be pressed irrespective of orientation or Thatcherization. For non-matches, the "different" button had to be pressed. Index fingers of both hands were used for responding. Both speed and accuracy were stressed. The face stimulus was masked by a random dot pattern for 366 ms or 200 ms for the short and long presentation time, respectively. Note that these different mask durations provided the same offset of visual stimulation for both target presentation times at 400 ms after face stimulus onset. The interval between mask-offset and the onset of the next trial was 2000 ms. The time course of a trial is illustrated in Fig. 2.

Half of all trials were match trials. The other half were non-match trials which were included to create the task demands. All factors, class (Original vs. Thatcherized), orientation and presentation time (pt), and the celebrities who were presented, were fully balanced. Every celebrity was repeated 4 times per condition, resulting in a total of 2 (match) × 2 (class) × 3 (orientation) × 2 (pt) × 8 (celebrity) × 4 (repetitions) or 768 trials. We were only interested in match trials for which the face presented corresponded to the face that was expected as a result of the question, and we therefore exclusively analyzed responses to match trials. In the test phase, short breaks were allowed every 80 trials.

The practice phase consisted of 24 practice trials, in which feedback was provided after every trial. Feedback consisted in the visual presentation of the letter strings "correct" (for correct answers within the time limits, "wrong" (for wrong answers within the time limits), "too fast" (for responses earlier than 300 ms after face onset) or "too slow" (for responses later than 2000 ms after face onset).

The order of the trials within each of the two experimental phases was fully randomized for each participant and the assignment of left and right response keys to match and non-match trials was counterbalanced across participants. The experiment lasted about 80–90 min including the verbal identification task, the practice and the test phase and a final block of trials in which participants performed blinks (30 trials). These trials served as an individual calibration used for the correction of ocular contributions to the EEG (see below). Furthermore, the participants were instructed to avoid eye movements and withhold blinking while the stimuli were presented.

2.4. Behavioral results

Responses were scored as correct if the correct key was pressed within a time window lasting from 300 to 2000 ms after target onset. Errors of omission (no key press), of commission (wrong key) and of time limitation (too slow and too fast) were recorded separately. Mean reaction times

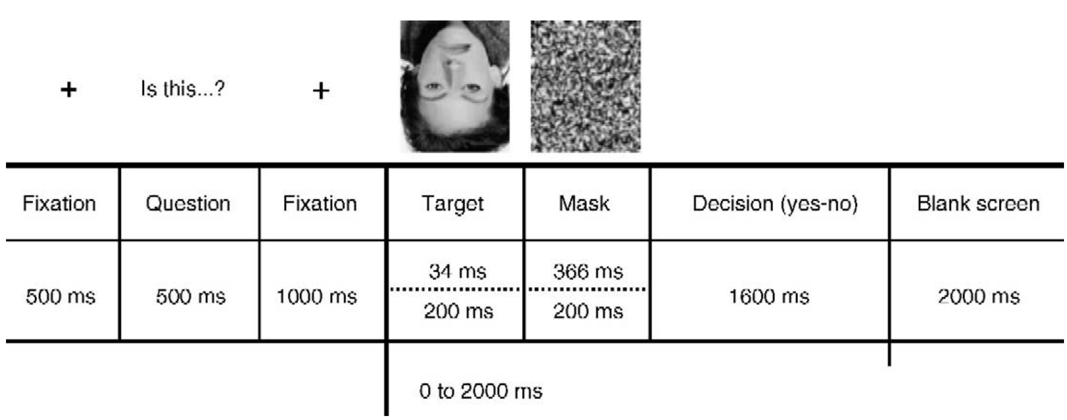

Fig. 2. Schematic display of the trial structure in this study. Participants responded to the target face, which was presented for 34 ms or 200 ms, respectively. The subsequent visual mask was presented for 366 or 200 ms, respectively, in order to obtain a standardized overall presentation time of target + mask for 400 ms.

were calculated only for correct matching responses with a measurement accuracy of <1 ms (timing accuracy of the response button device: M = 0.6 ms; SD < 0.01). Furthermore, for the calculation of mean RTs, we only considered those responses that were within a symmetric range of ±2.5 SD values from the averaged RT of the individual subject matched over all conditions (see [46]).

2.5. Event-related potentials

The electroencephalogram (EEG) was recorded with sintered Ag/AgCl electrodes mounted in an electrode cap (Easy-Cap™) at the scalp positions F_z, C_z, P_z, I_z, Fp_1, Fp_2, F_3, F_4, C_3, C_4, P_3, P_4, O_1, O_2, F_7, F_8, T_7, T_8, P_7, P_8, FT_9, FT_{10}, P_9, P_{10}, PO_9, PO_{10}, F_9', F_{10}', TP_9 and TP_{10}.

Note that the T_7, T_8, P_7 and P_8 locations are equivalent to T_3, T_4, T_5 and T_6 in the old nomenclature [34]. The F_9' electrode was positioned 2 cm anterior to F_9 at the outer canthus of the left eye, and the F_{10}' electrode was positioned 2 cm anterior to F_{10} at the outer canthus of the right eye. The positions TP_9 and TP_{10} refer to inferior temporal locations over the left and right mastoids, respectively. The TP_{10} (right upper mastoid) electrode served as initial common reference, and a forehead electrode (AF_z) served as the ground. All impedances were kept below 10 kΩ and were typically below 5 kΩ. The horizontal electrooculogram (EOG) was recorded from F_9' and F_{10}' at the outer canthi of both eyes. The vertical EOG was monitored from an electrode above the right eye against an electrode below the right eye. All signals were recorded with a band pass from 0.05 Hz to 40 Hz (−6 dB attenuation, 12 dB/octave) and sampled at a rate of 250 Hz.

Offline, epochs were generated lasting 2000 ms and starting 300 ms before target onset. Automatic artifact detection software was run for an initial sorting of trials, and all trials were then visually inspected for artifacts of ocular (e.g., blinks, saccades) and non-ocular origin (e.g., channel blocking or drifts). Trials with non-ocular artifacts, trials with saccades and trials with incorrect behavioral responses were discarded. For all remaining trials, ocular blink contributions to the EEG were corrected [12]. ERPs were averaged separately for each channel and for each experimental condition. Each averaged ERP was low-pass filtered at 10 Hz with a zero phase shift digital filter and recalculated to average reference excluding the vertical EOG channel.

3. Results

3.1. Familiarity

In the verbal identification task, all participants were familiar with the practice faces and a mean of 7.8/8 (97.2%) test faces were recognized as familiar.

3.2. Performance

Performance results for all conditions, in terms of mean percentages of correct responses (match trials only) and the corresponding mean reaction times (RTs), are shown in Table 1.

3.2.1. Accuracy

The percentage of incorrect reactions was low (M = 6.5%) and did not exceed 10.2% in any condition (see Table 1). In order to ensure that the participants had not used any artificial response strategies, the percentage correct for mismatch trials was also checked. A high recognition rate of 95.1% for mismatch trials indicated that participants performed very well for this response type, too. However, in the following, we will only report match trials.

The accuracy data were analyzed in a repeated measurement ANOVA with the within-subjects factors class (Original vs. Thatcherized), pt (pt-short vs. pt-long) and orientation (upright, ninety, inverted). The main factor orientation, $F(2,30)$ = 10.72, P = 0.0003, η_p^2 = 0.417, and the main factor *pt*, $F(1,15)$ = 11.85, P = 0.0036, η_p^2 = 0.441, were significant. Furthermore, there were trends for the main factor class, $F(1,15)$ = 4.01, P = 0.0637, n.s., and for the interaction between orientation and pt, $F(2,30)$ = 3.30, P = 0.0506, n.s. No other effects were significant. Bonferroni-adjusted pairwise comparisons on the factor orientation revealed significant differences between upright and ninety, P = 0.0230, and between upright and inverted, P < 0.0001. Furthermore, the

Table 1
Mean reaction times (RT, in ms) and percentages of correct trials (match trials only) for all analyzed conditions

Condition	RT			Percentage correct		
	Original 0°	Original 90°	Original 180°	Original 0°	Original 90°	Original 180°
pt-short 34 ms	631.6 (125.6)	662.3 (170.7)	669.1 (141.4)	0.961 (0.039)	0.918 (0.091)	0.900 (0.070)
pt-long 200 ms	610.3 (113.3)	615.6 (115.7)	628.3 (128.8)	0.971 (0.037)	0.949 (0.057)	0.943 (0.046)

Condition	RT			Percentage correct		
	Thatcher 0°	Thatcher 90°	Thatcher 180°	Thatcher 0°	Thatcher 90°	Thatcher 180°
pt-short 34 ms	636.8 (121.3)	676.1 (126.4)	688.3 (151.5)	0.930 (0.065)	0.898 (0.069)	0.902 (0.066)
pt-long 200 ms	650.6 (128.8)	642.6 (128.6)	641.8 (133.8)	0.953 (0.066)	0.949 (0.047)	0.951 (0.062)

Standard deviations are in parentheses.

strong trend for an interaction between orientation and pt was tested by analyzing the simple main effects of orientation. The factor orientation was only significant for pt-short, $F(2,14) = 10.92$, $P < 0.0001$, but not for pt-long, $F(2,14) = 1.96$, n.s. Pair-wise comparisons on the simple main effect orientation for the pt-short condition revealed significant differences between upright and ninety, $P = 0.0122$, and between upright and inverted, $P < 0.0001$. Due to possible ceiling effects and to cross-check the found effects, we also analyzed the reaction times (RTs).

3.3. Reaction times (RTs)

Table 1 gives an overview of the RTs for all conditions. A three-way ANOVA with repeated measures on class, orientation and pt was performed. The main factor class, $F(1,15) = 8.47$, $P = 0.0108$, $\eta_p^2 = 0.361$, orientation, $F(2,30) = 6.74$, $P = 0.0038$, $\eta_p^2 = 0.310$, and pt, $F(1,15) = 16.04$, $P = 0.0011$, $\eta_p^2 = 0.517$, were significant. Furthermore, there was an interaction between orientation and pt, $F(2,30) = 5.85$, $P = 0.0071$, $\eta_p^2 = 0.281$. No other effects were significant.

Bonferroni-adjusted pair-wise comparisons on the factor orientation revealed significant differences between upright and ninety, $P = 0.0233$, and between upright and inverted, $P = 0.0475$. Furthermore, the interaction between orientation and pt was tested by analyzing the simple main effects of orientation. The factor orientation was only significant for pt-short, $F(2, 14) = 7.89$, $P < 0.0051$, but not for pt-long, $F(2, 14) < 1$, n.s. Pair-wise comparisons on the simple main effect orientation for the pt-short condition revealed significant differences between upright and ninety, $P = 0.0062$, and between upright and inverted, $P = 0.0011$.

3.4. Event-related brain potentials

Mean ERP amplitudes to target faces were analyzed for the time segments 100–140 ms, 170–190 ms, 200–300 ms and 300–500 ms, relative to a 200-ms prestimulus baseline. The first two segments were chosen to capture the P1 and N170, respectively. The 200–300 ms time segment was chosen for a comparison with the P250 as reported by Milivojevic et al. [28]. Finally, the 300–500 ms time

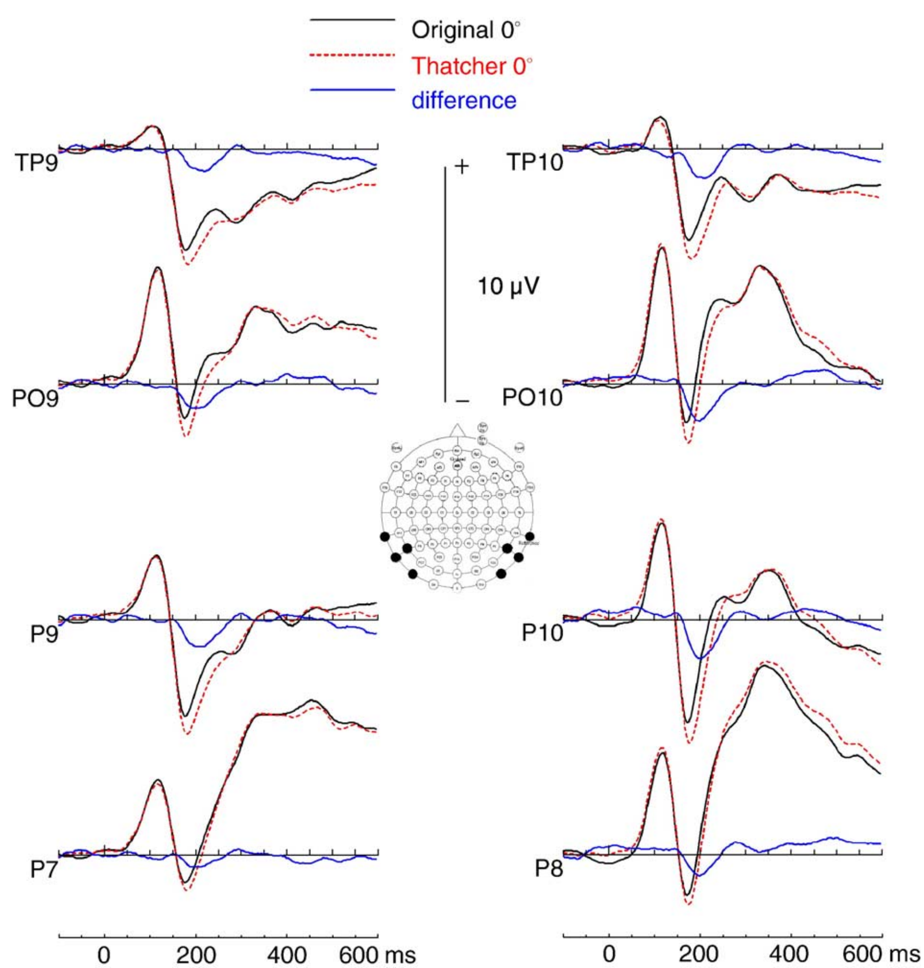

Fig. 3. Event-related potentials of the upright (0°) orientation condition for Original and Thatcherized faces for selected electrode sites. Additionally, the difference curve is plotted. The position of selected electrodes is indicated by the black circles in the EEG set-up in the center of the figure.

segment was chosen arbitrarily and will be called the "late component" in the following.

We quantified ERPs for eight electrodes situated in the temporal–occipital areas (P_7, P_8, TP_9, TP_{10}, P_9, P_{10}, PO_9, PO_{10}). For every time segment, ANOVAs were performed with repeated measures on the within-subjects factors hemisphere (LH vs. RH), site (P_7/P_8, TP_9/TP_{10}, P_9/P_{10}, PO_9/PO_{10}), presentation time (pt; short: 34 ms vs. long: 200 ms), class (Original vs. Thatcherized) and orientation (up, ninety, inv). This kind of analysis will be referred to as region-specific analysis below.

Furthermore, as we were particularly interested in the N170 component, we analyzed the data for this time window in more detail. If we found any interactions of the factor site with any of the experimental factors for the N170, we analyzed the data for each symmetric pair of electrodes. This kind of analysis will be referred to as electrode-specific analysis below.

3.4.1. Effects on the N170 component (170–190 ms)

The present study particularly focused on the N170 component which has been related to face perception [3] and which has recently been reported to be sensitive to Thatcherization [28]. Therefore, we will analyze and discuss this component more in detail than the other components.

3.4.1.1. Effects of Thatcherization (factor class). The region-specific analysis for the time window of 170–190 ms revealed no main effect of class, $F(1,15) = 2.67$, $P = 0.1233$, n.s., but an interaction between the factor orientation and class, $F(2,30) = 9.47$, $P = 0.0006$, $\eta_p^2 = 0.387$. This interaction is a crucial result and is therefore analyzed in some detail. We analyzed the simple main effects class for all orientation conditions. The factor class was significant for upright, $F(1,15) = 23.47$, $P < 0.0001$, $\eta_p^2 = 0.610$, but not for ninety, $F(1,15) < 1$, n.s. Most importantly, there was also an effect of class for the inverted orientation, $F(1,15) = 4.86$, $P = 0.0434$, $\eta_p^2 = 0.245$. Figs. 3 and 4 illustrate these findings by showing the ERPs of the ROIs for the upright and the inverted condition, respectively.

Most importantly, as compared to Original faces, Thatcherized faces appeared to elicit larger N170 amplitudes for upright faces but smaller amplitudes for inverted faces (see Figs. 3 and 4, respectively).

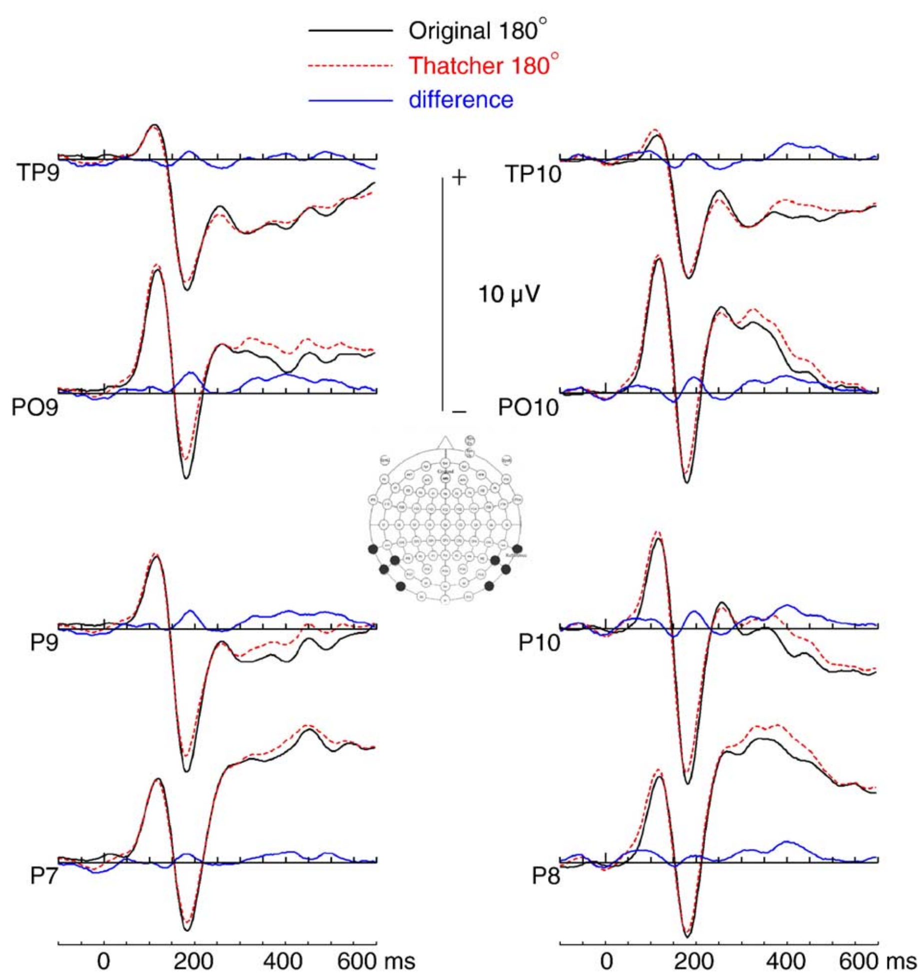

Fig. 4. Event-related potentials of the inverted (180°) orientation condition for Original and Thatcherized faces for selected electrode sites. The difference curve is also plotted.

3.4.1.2. Effects of orientation. In addition to the interaction with class (see above), the main effect orientation was also significant, $F(2,30) = 26.53$, $P < 0.0001$, $\eta_p^2 = 0.639$. Bonferroni-adjusted pair-wise comparisons on the factor orientation revealed significant differences between upright and ninety, $P < 0.0001$, and between upright and inverted, $P < 0.0001$.

Furthermore, there were two two-way interactions, one of hemisphere by orientation, $F(2,30) = 4.63$, $P = 0.0177$, $\eta_p^2 = 0.236$, and one of site by orientation, $F(6,90) = 11.09$, $P < 0.0001$, $\eta_p^2 = 0.425$. These effects simply appear to reflect the fact that orientation effects on the N170 were largest at those electrodes at which N170 showed up most clearly.

3.4.1.3. Effects independent of class and orientation. The region-specific analysis revealed several effects that were independent of the factor class or orientation. There were main effects of site, $F(3,45) = 18.18$, $P < 0.0001$, $\eta_p^2 = 0.548$, and *pt*, $F(1,15) = 8.20$, $P = 0.0118$, $\eta_p^2 = 0.353$. The N170 was the earliest ERP component which was sensitive to the presentation time. As the subsequent analyses of the later components show, this effect was even more pronounced for the P250 and the later component. In contrast, the early ERP component P1 was equally sensitive to subliminally/liminally presented as well as to supraliminally presented ones. Fig. 5 summarizes these findings by showing the amplitudes for both presentation times for all time windows.

Moreover, the following interactions were significant: hemisphere by pt, $F(1,15) = 9.14$, $P < 0.0086$, $\eta_p^2 = 0.379$, site by pt, $F(3,45) = 5.50$, $P = 0.0026$, $\eta_p^2 = 0.268$, and site by hemisphere by pt, $F(3,45) = 4.10$, $P = 0.0118$, $\eta_p^2 = 0.214$.

Due to significant interactions of the experimental factors with the factor site, we analyzed the ERP data further in four separate electrode-specific ANOVAs. The results of these electrode-specific ANOVAs are listed in Table 2. For significant effects, the partial effect size calculated as partial

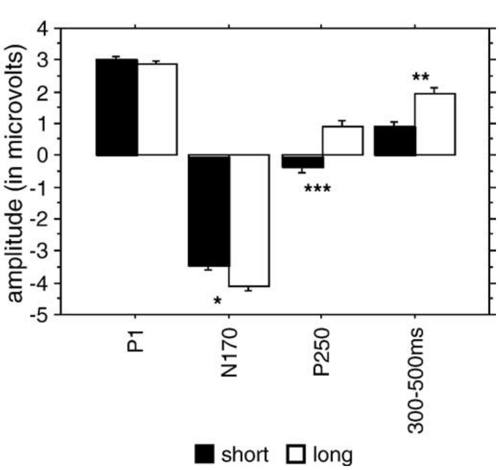

Fig. 5. Amplitudes (in microvolts) of both presentation times for the different time windows. Asterisks indicate significant simple main effects of the factor presentation time (short vs. long). Error bars are standard errors of the mean.

Table 2
Significant effects for the time window 170–190 ms

Effect	P_7, P_8	P_9, P_{10}	PO_9, PO_{10}	TP_9, TP_{10}
pt	–	$F(1,15) = 13.81$, $P = 0.0021$, $\eta_p^2 = 0.479$, L > S	$F(1,15) = 10.28$, $P = 0.0059$, $\eta_p^2 = 0.570$, L > S	$F(1,15) = 11.93$, $P = 0.0035$, $\eta_p^2 = 0.443$, L > S
Orientation	$F(2,30) = 29.22$, $P < 0.0001$, $\eta_p^2 = 0.661$, U < N, U < I	$F(2,30) = 19.87$, $P < 0.0001$, $\eta_p^2 = 0.570$, U < N, < I	$F(2,30) = 20.73$, $P < 0.0001$, $\eta_p^2 = 0.580$, U < N, U < I	$F(2,30) = 11.49$, $P < 0.0001$, $\eta_p^2 = 0.434$, U < I, N < I
Class	–	–	–	$F(1,15) = 5.63$, $P = 0.0314$, $\eta_p^2 = 0.273$, T > O
Orientation by class	–	$F(2,30) = 12.48$, $P < 0.0001$, $\eta_p^2 = 0.454$	$F(2,30) = 11.92$, $P < 0.0001$, $\eta_p^2 = 0.443$	$F(2,30) = 4.15$, $P = 0.0256$, $\eta_p^2 = 0.217$
Hemi by orientation	$F(2,30) = 4.37$, $P = 0.0216$, $\eta_p^2 = 0.226$	$F(2,30) = 4.93$, $P = 0.0141$, $\eta_p^2 = 0.247$	$F(2,30) = 5.00$, $P = 0.0134$, $\eta_p^2 = 0.250$	–
Hemi by class	–	–	–	$F(1,15) = 5.01$, $P = 0.0409$, $\eta_p^2 = 0.250$
Hemi by pt	$F(1,15) = 13.80$, $P = 0.0021$, $\eta_p^2 = 0.479$	$F(1,15) = 7.29$, $P = 0.0165$, $\eta_p^2 = 0.327$	–	$F(1,15) = 5.99$, $P = 0.0272$, $\eta_p^2 = 0.285$

For main effects, also the relation of the levels of the respective factor is given in the last row (in respect to absolute amplitudes). Factor pt: (S)hort vs. (L)ong, orientation: (U)pright vs. (N)inety vs. (I)nverted, class: (T)hatcher vs. (O)riginal. Only these effects are reported for which significance was obtained for at least one of the four electrode pairs.

eta-square (η_p^2) will be given. For main effects, the relation of the factor levels will also be indicated.

Since all main effects and interactions were already provided in Table 2, we will focus on the most interesting simple main effects of class on the different factor levels of orientation. With the exception of P_7/P_8, all other electrode pairs revealed significant interactions between orientation and class. Therefore, we further analyzed the simple main effects of class on orientation for these three electrode pairs only.

For the P_9, P_{10} electrode pair, Thatcherization yielded significant main effects not only for the upright condition, $F(1,15) = 25.55$, $P < 0.0001$, $\eta_p^2 = 0.630$, but also for the inverted version, $F(1,15) = 8.18$, $P = 0.0119$, $\eta_p^2 = 0.353$. A similar pattern was evident at PO_9 and PO_{10} (upright: $F(1,15) = 19.66$, $P < 0.0001$, $\eta_p^2 = 0.567$; inverted: $F(1,15) = 6.02$, $P = 0.0262$, $\eta_p^2 = 0.286$), but not at TP_9 and TP_{10} (upright: $F(1,15) = 13.39$, $P = 0.0023$, $\eta_p^2 = 0.472$; inverted: $F(1,15) = 2.54$, $P = 0.1317$, *n.s.*). All tests for simple main effects and the attached amplitude data are shown graphically in Fig. 6.

Due to its central importance of the differential processing of inverted Thatcher and inverted Original versions, Fig. 7 also gives the topographic voltage for the N170. The topographic maps for the upright and the inverted presentations look very similar for the N170 component concerning the occipito-temporal and parietal areas. For both orientations, there was a pronounced difference between the Thatcher and the Original class in these areas, indicated by a light red coloration for the difference topographies (Thatcherized-Original).

In summary, we could demonstrate differential results for the N170 in comparison with the perceptual illusion, particularly for the P_9, P_{10} and PO_9, PO_{10} electrode pairs.

3.4.1.4. Effects on the P1 (100–140 ms), the P250 (200–300 ms) and the late component (300–500 ms). Analyses for the P1, the P250 and the late component (300–500 ms) were also performed but for the sake of brevity will not be reported in detail here. The main results from analyses of the P1 demonstrated that the Thatcherization of the faces had little influence on this early ERP component. For P250, we observed statistically significant but numerically small effects of both class and orientation, in addition to a strong effect of presentation time. Finally, for the late component, we observed strong effects of presentation time and orientation.

In summary, both the P250 (200–300 ms) and the late component (300–500 ms) were mainly sensitive to effects of presentation time, whereas Thatcherization had no influence on the amplitudes in the time segments following the N170. Moreover, the N170 and the late component (300–500 ms) were sensitive to orientation. Fig. 8 shows the influence of the factor orientation on the four temporal ROIs.

4. Discussion

This study investigated the effects of Thatcherization for brief presentation times (34 ms and 200 ms) and three different orientations (0°, 90° and 180°). First, we

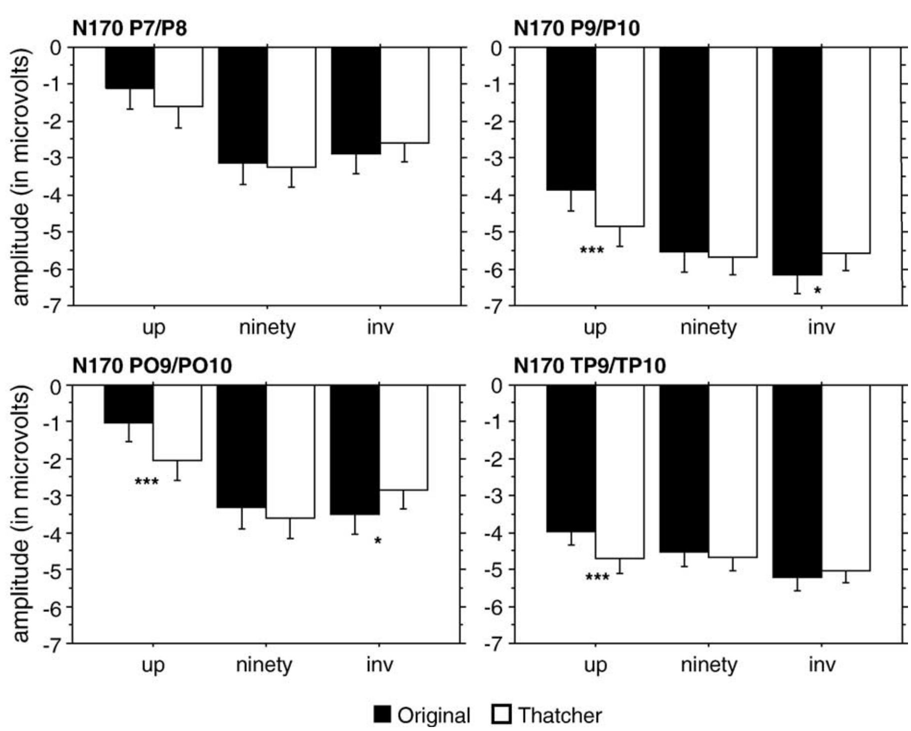

Fig. 6. Amplitudes (in microvolts) at selected electrodes for Original and Thatcherized faces and all orientations for the N170 component. Asterisks indicate significant simple main effects of the factor class (Original vs. Thatcherized face). Error bars are standard errors of the mean.

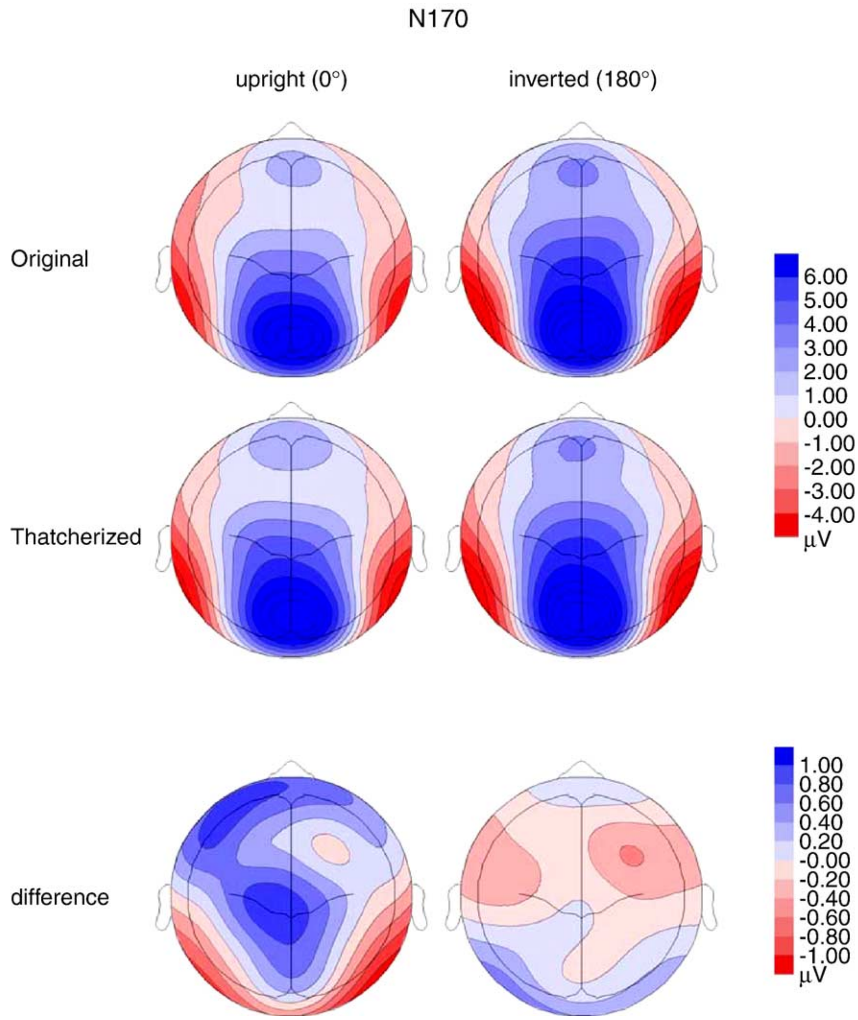

Fig. 7. Topographical voltage maps of the ERP amplitudes for Original (1st row) and Thatcherized faces (2nd row). The left maps show the data for the upright condition, the right maps show the data for the inverted condition. Additionally, the differences between Original and Thatcherized face amplitudes are given by maps in the bottom row. Maps show a 110° equidistant projection and were obtained using spherical spline interpolation. Negativity is red.

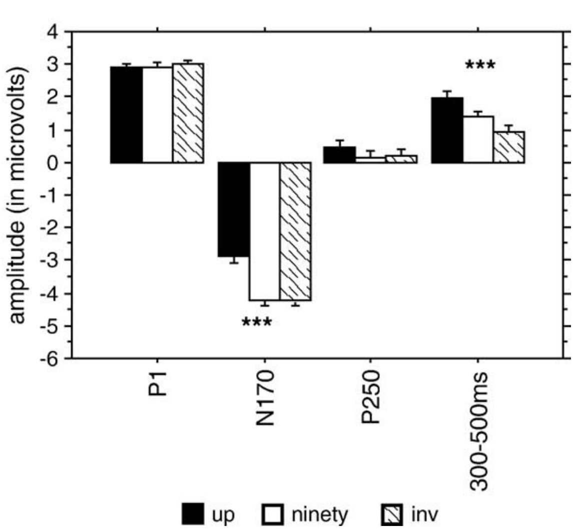

Fig. 8. Amplitudes (in microvolts) of orientation for the different time windows. Asterisks indicate significant simple main effects of the factor orientation. Error bars are standard errors of the mean.

demonstrated that a presentation time of only 34 ms is sufficient to recognize familiar faces at a high level with $P_{\text{short-pt}}$(correct) = 0.918 compared to $P_{\text{long-pt}}$(correct) = 0.953, replicating effects of briefly presented faces ([7], for fast face attractiveness processing, see [25]). Moreover, such a short presentation time is also sufficient to induce typical effects of the recognition of Thatcherized faces (cf. [9]).

Effects of Thatcherization were found for the N170 (170–190 ms), but not for the early P1 component (100–140 ms). This influence of Thatcherization on the N170 was independent of presentation time.

Moreover, there was a strong effect of orientation for the N170 and the late time window (300–500 ms), but not for the P1 and P250 component (200–300 ms). For Original faces, we found larger N170 amplitudes for inverted faces compared with upright faces. This is in accordance with a number of other ERP studies [17,36,38,42]. The current experiment extends the study by Milivojevic et al. [28] by employing a 90° rotation. Stuerzel and Spillmann [47] demonstrated a discontinuous and steep zone of changeover of the Thatcher effect at a rotation of about 90° (see also [31]). They suggested a neuronal step-tuning as the reason for this non-gradual transition. If rotation has a gradual and constant effect on recognition, then one might expect that the performance of the 90° condition would lie between that of the upright and the inverted condition. However, in our study, this was only partly the case. Whereas our behavioral data for the short presentation time indicated a monotonic increase of reaction times, being in line with a linear effect of orientation, there was no orientation effect for the longer presentation time. Thus, the data of the shorter presentation time are in accordance with the behavioral data of the Lewis [23] learning paradigm experiment, who found a gradual change for whole faces.

In addition, there was an interaction between orientation and class (Thatcherized vs. Original faces). First, we revealed a strong Thatcherization effect for upright faces. This parallels the perceptual effect of recognizing upright Thatcherized faces as odd and very differently looking from normal faces [49]. Moreover, our effects of Thatcherization for upright faces replicate those reported by Milivojevic et al. [28] and corroborate an increase of N170 amplitudes as a result of Thatcherization. These effects might reflect the increased difficulty to encode a Thatcherized face. However, Milivojevic et al. [28] also found a small effect of upright Thatcherization for the P1 ($P = 0.049$, $\eta_p^2 = 0.245$): Upright Thatcherized compared to upright normal faces resulted in some amplification of the P1—an effect that we were unable to replicate in the present study.

Most importantly, the present study is the first to demonstrate a Thatcherization effect on the N170 for inverted faces. This suggests an effect of Thatcherization on the neural encoding of inverted faces as well. Thus, the absence of a perceptual effect in inverted Thatcherized faces was not paralleled by ERP components. This contrasts the previous finding of Milivojevic et al. [28], which is to our knowledge the only study investigating the Thatcher effect by means of ERPs. However, our findings appear to be broadly in line with the fMRI data reported by Rotshtein et al. [37] who found that Thatcherization of inverted faces does affect neural activation in the lateral occipital complex. It is remarkable that the ERP effect we found was specific for the N170 component (which is thought to be generated by the same or similar areas in occipito-temporal cortex). This possible correspondence between metabolic and electrophysiological findings seems worth further exploration, particularly because a combination of these techniques would provide simultaneous information about both the timing and the anatomical origin of experimental effects.

The N170 effect of Thatcherization for inverted faces was especially found for the P_9/P_{10} and PO_9/PO_{10} electrode pairs (see Fig. 6), which roughly correspond to the electrodes 64/96 and 65/91, analyzed by Milivojevic et al. [28]. However, our study is not directly comparable with the Milivojevic et al. [28] study, as they used a gender-decision task which is not identity-based as the paradigm used here. According to the Bruce and Young [5] model, the pathways for analyzing facial identity are assumed to be parallel and independent from the processing of gender (but see [14,43,50]) and expression [8,40]. Despite some evidence that the N170 is relatively unaffected by changes in task demands (e.g., [44]), a reason for the discrepancy between the present data and those by Milivojevic et al. [28] could be different cognitive processes invoked by these two paradigms.

Importantly, there are evidences that the N170 effect documented here was not a simple reflection of inverted Thatcherized faces looking different to an inverted original. Recent research on early EEG components has revealed that especially the N170 is relatively insensitive to "looks different" manipulation but is sensitive to configural changes (e.g., [18,35]). Therefore, it seems consequent to think of having measured components that were correlated with the specific configural changes realized by Thatcherization (cf. [35]) but not due to unspecific "looks different" manipulations.

In summary, the present study showed a clear difference of N170 amplitudes between inverted Thatcherized and inverted Original faces. This demonstrates that inverted Thatcherized faces are processed differently compared to normal faces, although they perceptually look quite like normal faces. We suggest that these differences arise early in time at the initial encoding of faces and are probably mediated by brain areas in or near the lateral occipital complex. Further research should aim at solving this inconsistency between conscious perception and brain activity, especially why we perceive an inverted Thatcherized face as quite normal in spite of a grotesque facial configuration.

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