RUNNING HEAD: THE ROLE OF THE EYES FOR FACE RECOGNITION

The role of the eye region for neural correlates of familiar face recognition: The N250r reveals no evidence for eye-centred face representations.

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Abstract

Humans are highly accurate at recognising familiar faces, which is based on the efficient activation of long-term face representations. However, it is unclear precisely what information is stored in these representations. While some suggest an important role of the eye region, other evidence has shown that faces are processed as integrated wholes. Here, we examined the role of the eye region in activating familiar face representations by measuring the N250r, an event-related potential correlate of repetition priming. In three experiments, we presented blur chimeras, i.e. spatially low-pass filtered faces with unfiltered eye regions, and observed a clear N250r that was not found for fully blurred faces (Experiments 1 and 2). However, we observed a similar N250r for chimeras with unfiltered eye or mouth regions (Experiment 3), indicating that the effect is not exclusive to the eyes. We conclude that fast and efficient activation of familiar face representations is not specifically facilitated by detailed information from the eye region, and that face representations are not centred around the eyes.

Keywords: face recognition, repetition priming, event-related potentials, blur chimeras, N250r

The role of the eye region for neural correlates of familiar face recognition: The N250r reveals no evidence for eye-centred face representations.

Familiar face recognition is typically highly accurate and efficient, which sharply contrasts with our substantially reduced ability to recognise or even match unfamiliar faces (Bruce et al., 1999; Burton, Wilson, Cowan, & Bruce, 1999; Wiese, Tüttenberg, et al., 2019; Young & Burton, 2018). We know what the people we are familiar with look like, and we, therefore, recognise them from a wide range of images, including pictures we have never seen before. At the same time, such knowledge is not available for faces we see for the first time. In other words, we have long-term memory representations for familiar but not unfamiliar faces, and accessing these representations is crucial for successful recognition. However, the specific properties of familiar face representations remain largely unclear. The present experiments examined one as yet unanswered question about these properties, namely whether face representations contain information about the eye region in finer detail relative to the rest of the face.

Face recognition is typically conceptualised as a serial process, which distinguishes early perceptual from subsequent representational stages (Bruce & Young, 1986; Bruce & Young, 2012; Schweinberger & Neumann, 2016). More specifically, when a face is detected in the visual field, a perceptual process known as structural encoding forms an internal code of the stimulus. This code is then compared to our stored long-term visual representations of known faces, and, in the case of a match, we recognise the face as familiar. However, precisely what information is stored in these visual face representations is not clear. It is often believed that faces are processed holistically (Tanaka & Farah, 1993; Young, Hellawell, & Hay, 1987). According to this view, parts of faces are integrated into a whole (or Gestalt) during perceptual processing (Maurer, Grand, & Mondloch, 2002), and therefore cannot be manipulated independently from each other (for alternative views, see Gold, Mundy, & Tjan, 2012; Sekuler, Gaspar, Gold, & Bennett, 2004). While most of the research on holistic processing has used unfamiliar face stimuli, and may therefore not be directly relevant to familiar face recognition (see Burton, 2013), it has been suggested that identity processing of known faces is based on integrated wholes rather than collections of individual parts (Bruce & Young, 2012; DeGutis, Wilmer, Mercado, & Cohan, 2013; Young et al., 1987).

However, at some variance with this holistic view, other evidence suggests that the eye region appears to be particularly important for face recognition. Studies isolating individual features have highlighted the eye region as the most informative facial component in making accurate identity judgements (Butler, Blais, Gosselin, Bub, & Fiset, 2010; Vinette, Gosselin, & Schyns, 2004), and greater reliance on the eye region during face perception tasks has been shown to correspond with increased recognition ability (Royer et al., 2018). Moreover, masking the eyes and eyebrows reduces recognition more substantially than masking other regions of the face (McKelvie, 1976; Sadr, Jarudi, & Sinha, 2003). In an attempt to identify specific critical features for recognition, Abudarham and colleagues (Abudarham, Shkiller, & Yovel, 2019) reported that three out of five of these features are located in the eye region (eye colour, eye shape, and eyebrow thickness); the other two (lip thickness and hair) are not.

Further results from the examination of so-called contrast chimeras (Gilad, Meng, & Sinha, 2009; Sormaz, Andrews, & Young, 2013) seem to suggest that a compromise between featural and holistic accounts of face recognition is possible. Contrast chimeras consist of contrast negative faces in which only the eye region is kept in normal, positive contrast. It has long been known that contrast reversal substantially impairs face recognition (Galper, 1970; Kemp, Pike, White, & Musselman, 1996; Russell, Sinha, Biederman, & Nederhouser, 2006). Interestingly, contrast chimeras are much easier to identify than full negative faces, with some experiments showing performance levels similar to unmanipulated, contrast positive faces (Gilad et al., 2009). While these findings may be initially seen as supporting a "critical feature" view, contrast chimeras are also clearly better recognised than isolated eyes, or eyes in otherwise dark silhouettes (Gilad et al., 2009; Quinn & Wiese, 2023; Sormaz et al., 2013). Moreover, a similar chimera advantage is not observed when other regions of the face, including the mouth, are presented in positive contrast (Sormaz et al., 2013). These findings suggest that the chimera advantage is specific to the eye region. Critically, they also show that the effect is not driven by information from the eye region alone, but that cues from the contrast-negative rest of the face become available when presented together with positive eyes. On the one hand, the eye region seems more important than other parts of the face (in line with a "critical feature" account), while on the other hand information from the rest of the face needs to be integrated (in line with a "holistic" account). It thus appears plausible to assume that face representations are *centred* around the eyes, containing relatively coarse information about the whole face while the eye region is represented in finer detail.

While behavioural findings seem to suggest such eye-centred face representations, eye-tracking research suggests that participants foveate just below the eyes, as this allows for greater amounts of information to be processed (Peterson & Eckstein, 2012). In other words, rather than directly fixating a region with potentially high informational value (i.e. the eye region), humans appear to integrate information across the whole face, which seems well in line with a holistic view. Critically, while this mechanism may represent an optimal strategy to gain as much information as possible, it does not inform us whether some regions within the field of vision contain relatively more informative cues than others. One might argue that fixation close to the eyes ensures that these are always well-represented, while avoiding other regions (such as the mouth) from losing too much acuity. Accordingly, the study by Peterson and Eckstein (2012) can be integrated with the view that the eye region is *relatively* more

important - but also with the alternative that it is not (as fixation below the eyes allows maximum information intake across the whole face).

Importantly, neither behavioural nor eye-tracking research directly indicates the processing level at which the chimera effect occurs. Alternative to locating the advantage elicited by a positive eye region at the representational level, it seems equally possible that chimeras facilitate structural encoding, and therefore perceptual processing. Here, we used event-related brain potentials (ERPs) to examine the locus of the chimera effect more directly.

ERPs reflect voltage changes in the human scalp-recorded EEG time-locked to an event, such as the presentation of a visual stimulus (Luck, 2014). They consist of positiveand negative-going waveforms (so-called components) which reflect summed post-synaptic potentials (Jackson & Bolger, 2014). The first ERP component sensitive to face processing is the N170, a negative peak approximately 170 ms after stimulus onset at occipito-temporal channels (Bentin, Allison, Puce, Perez, & McCarthy, 1996). Most researchers agree that the N170 reflects the detection of a face-like visual object or structural encoding (Eimer, 2011; Schweinberger & Burton, 2003), i.e. a perceptual stage prior to the processing of individual identity (e.g. Andrews, Burton, Schweinberger, & Wiese, 2017; Bentin & Deouell, 2000; but see Caharel & Rossion, 2021). Interestingly, contrast negative faces elicit an increased N170 (Itier & Taylor, 2002, 2004), reflecting enhanced demands on perceptual processing. Previous research has also examined the N170 for contrast chimeras, which has produced somewhat mixed findings. While an initial study reported a comparable N170 for contrast chimeras and positive faces (Gandhi, Suresh, & Sinha, 2012), these results are difficult to judge as no figure of the ERP data is presented. A further study (Fisher, Towler, & Eimer, 2016) found similar N170 amplitudes for contrast chimeras and full positive faces only when the fixation cross preceding the stimulus was presented at the location of the eye region of the upcoming faces, while larger amplitudes for contrast chimeras were observed when the fixation cross was presented over the mouth region. Finally, in a previous study from our lab (Wiese, Chan, & Tüttenberg, 2019), the N170 was consistently larger for contrast chimeras relative to positive faces (and similar to negative faces) in a series of three experiments. As an increased N170 is typically interpreted as reflecting more difficult processing, it appears at least questionable that the chimera advantage occurs at this early perceptual level.

Alternatively, as suggested above, the chimera advantage might be located at the level of familiar face representations, which can be examined using the N250r effect (Begleiter, Porjesz, & Wang, 1995; Schweinberger, Pfütze, & Sommer, 1995). The N250r is observed in immediate repetition priming experiments, in which a target face is directly preceded by a prime which can either show the face of the same (repetition condition) or of a different identity (non-repetition condition). Targets in the repetition condition elicit a more negative waveform relative to non-repetitions starting approximately 200 ms after target onset at occipito-temporal channels, even when different images of the same familiar identity are used as primes and targets in the repetition condition (Bindemann, Burton, Leuthold, & Schweinberger, 2008; Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002). Accordingly, the N250r reflects facilitated access to visual long-term representations of familiar faces.

In a previous study (Wiese, Chan, et al., 2019), we examined an N250r following priming by contrast chimeras to test whether familiar face representations are centred around the eye region. If this was indeed the case, contrast chimeras should prime familiar faces similarly efficiently as positive primes, and the N250r should be stronger following chimera relative to full negative primes, which do not contain easily accessible information about the eyes. However, in a series of three experiments, the N250r tended to be larger for priming from full positive faces relative to contrast negative and chimera primes, which elicited similar effects. We therefore did not detect convincing evidence for eye-centred face representations. As noted above, contrast chimera (and fully negative) primes also elicited larger N170 amplitudes relative to unmanipulated faces. This suggests that chimeras were not processed as efficiently as positive primes at the perceptual stage, which in turn might have affected later processing. Familiar face representations might have been activated less in the chimera condition – but not because they are not particularly sensitive to information from the eye region. Instead, difficulties at the perceptual level may have resulted in less activation being passed on to the representational stage.

Interestingly, a further ERP study seems to support the idea of eye-centred face representations. Mohr and colleagues (Mohr, Wang, & Engell, 2018) examined the N250r with prime faces that were spatially low-pass filtered (or blurred), except for either the eye or the mouth region, which was presented with full frequency spectrum information. Moderate to severe blurring (below approximately eight cycles per image; cpi) is known to reduce face recognition accuracy (Costen, Parker, & Craw, 1996; Nasanen, 1999; Parker & Costen, 1999). However, similar to the above-described contrast chimera effect, leaving the eye region unfiltered, and thus creating blur chimeras, substantially improves recognition (Quinn & Wiese, 2023). Of particular interest, Mohr and colleagues (2018) observed a clear N250r for blur chimeras with unfiltered eyes, but no corresponding effect when the mouth was unfiltered. The authors interpreted this finding as reflecting the importance of the eye region for face recognition but argued that the effect emerged from processing the eyes as isolated facial features. This suggestion is in line with neuroimaging studies on macaques, in which the presentation of isolated eyes elicited a comparable response in face-selective neurons to that of the presentation of full faces (Issa & DiCarlo, 2012).

Behavioural evidence, however, shows that blur chimeras with unfiltered eyes (but not unfiltered mouths) are easier to recognise than eyes in dark silhouettes, which points to a contribution from the blurred area of the face (Quinn & Wiese, 2023). Regardless of this, contrary to our previous results (Wiese, Chan, et al., 2019), a clear N250r for blur chimeras appears well in line with the idea of eye-centred face representations.

A critical difference between the study by Mohr and colleagues (2018) and our previous work may lie in the processing of the prime stimuli. As noted above, fully contrast negative faces and, in our study at least, contrast chimeras elicit larger N170 amplitudes relative to unmanipulated faces, and this increased processing difficulty could hamper the down-stream activation of familiar face representations. Interestingly, spatially low-pass filtering of a face has been found to either decrease (Halit, de Haan, Schyns, & Johnson, 2006) or not have any significant effect on the N170 amplitude (Flevaris, Robertson, & Bentin, 2008). Accordingly, blur chimeras, unlike contrast chimeras, might not elicit difficulties at a processing level prior to individual face recognition. If so, they would be well-suited to further examine the suggestion of eye-centred face representations.

Using the N250r, the present series of experiments investigated whether familiar face representations are centred around the eyes. Experiment 1 tested whether a basic imageindependent N250r effect for blur chimeras could be established. In Experiment 2, we aimed at replicating an initial positive result and contrasting it to priming from contrast chimeras. Finally, Experiment 3 tested the specificity of the observed blur chimera effect for the eye region by examining priming from blurred stimuli with unfiltered eyes or unfiltered mouths, as well as a combination of the two.

Experiment 1: Priming from blur chimeras

In our first experiment, we aimed to establish an N250r for blur chimeras, i.e. for spatially-low pass filtered face images in which only the eye region was presented with full

frequency spectrum information. Therefore, our main research question was whether we would find significantly more negative ERP amplitudes for repeated versus non-repeated blur chimera targets during the N250r time range. We further tested for corresponding repetition priming effects in unmanipulated faces (to ensure that our experiment produced the standard effect) and in fully blurred faces (to test whether low-pass filtering effectively restrained the N250r). With respect to prime stimuli, and as a further important experimental control, we tested whether the N170 for fully blurred faces and blur chimeras would either be less negative or similar relative to unmanipulated faces. Particularly in the latter case, this finding would suggest no deficit at the N170 level prior to accessing familiar face representations.

Methods

Participants

Power calculation using G*Power (Faul, Erdfelder, Lang, & Buchner, 2007) was based on the late N250r (300-400 ms) effect size for unmanipulated faces in Experiment 3 of Wiese et al. (2019), which suggested that a sample of N = 21 would be required (paired samples *t*-test, two-sided, $1-\beta = .8$, dz = 0.66). We planned with 24 participants for counterbalancing reasons, which resulted in an estimated achieved power of .87. The tested sample consisted of 25 Durham University undergraduate students, one of whom was excluded due to insufficient familiarity with the celebrities used as stimuli (with < 15 recognised faces in the unmanipulated condition). The remaining participants (16 female, eight male; mean age = 20.5 years, SD = 1.1) reported normal or corrected-to-normal vision, no known neurological conditions, did not take psychoactive medication, and were righthanded according to a modified version of the Edinburgh Handedness Inventory (Oldfield, 1971). All participants received course credit or a monetary compensation of £8/h and provided written informed consent. The experiment was approved by the ethics committee of Durham University's Psychology Department.

Stimuli

We collected 252 images showing the faces of 42 celebrities (actors, musicians, politicians etc.), with six images per identity. A full list of the celebrity identities used across the present experiments can be found in the supplementary material. To avoid image priming effects, images were selected to show a variety of different angles, expressions and lighting conditions, representative of naturalistic differences found in ambient faces. Faces were cropped from the background, converted to greyscale, and pasted onto a light grey background. Prime stimuli were standardised to 190 x 285 pixels, and targets to 228 x 342 pixels. Image manipulations were carried out using GIMP (version 2.8.14; www.gimp.org). To create stimuli for the blurred condition, images were filtered using FourierImage (2017 version; Dr Risto Nasanen, personal communication, see https://nasanen.com/) using a lowpass Butterworth filter (with a filter exponent of 5 and a cut-off frequency of 7cpi; please note that this filter does not completely isolate all frequencies below the cut-off). For the blur chimera condition, a lemniscate around the eyes (including the eyebrows and outer canthi) was selected from the unfiltered image and overlayed onto the matching blurred face. Borders between blurred and unfiltered face regions were smoothed to reduce sharp edges. Examples are provided in Figure 1.



Figure 1. Example stimuli as used in Experiments 1-3. Columns from left to right show unmanipulated faces (Experiments 1-3), blurred faces (Experiment 1), blur (eye) chimeras (Experiments 1-3), contrast chimeras (Experiment 2), mouth chimeras (Experiment 3), and eye+mouth chimeras (Experiment 3). Images of the celebrities are reproduced here under creative commons licence. Joe Biden, Source: <u>https://www.flickr.com/photos/58993040@N07/13978713242</u>, Attribution: U.S. Embassy Kyiv, Ukraine, public domain mark. Boris Johnson Source: <u>https://www.flickr.com/photos/148748355@N05/48790940708</u>, Attribution: Trump White House Archived, public domain mark.

Stimuli were grouped into prime/target pairs, such that unfiltered, blurred or chimera primes were always followed by a target from the same manipulation condition. Primes and targets in each trial could either show different pictures of the same identity (repetition condition) or a different identity (non-repetition condition). Target stimuli were increased in size by approximately 20%.

Procedure

Participants were seated in a sound-attenuated, electromagnetically shielded cabin with their heads in a chin rest 85 cm away from an LCD monitor. Accordingly, primes subtended to 3.63° by 5.44° of visual angle, and targets subtended to 4.34° by 6.52° of visual angle. The experiment consisted of four experimental blocks with 60 trials each, half of which were repetition and the other half non-repetition trials in the unfiltered, fully blurred and blur chimera conditions, respectively. Each of the six images of 40 identities was used once as a target and once as a prime in two different of the six experimental conditions, such that no targets were repeated within the experiment. Assignment of stimuli to specific conditions was counterbalanced across participants. Images of the two remaining celebrities were used for practice trials which were presented before the experiment and excluded from data analysis.

Each trial started with a red fixation cross, displayed for 1,000 ms, followed by the prime, presented for 500 ms, a green fixation cross, presented for 500 ms, and the target. Participants were instructed to maintain fixation on the location of the cross for the duration of stimulus presentation. Both prime and target faces were positioned so that uniformly, their vertical and horizontal centre-point (typically slightly below the eyes) aligned with the location of the prior fixation cross. Once the target was on the screen for 1,000 ms an additional text box appeared, asking the participant to respond with a keypress. The task was to indicate the familiarity with the target face (1 = unfamiliar, 2 = appears familiar, but no identity-specific information available, 3 = clearly familiar and identity-specific information available. The delay between target presentation and the availability of response options was introduced to not compromise ERP measures with motor activity. The target (plus text box) remained on the screen until a key was pressed, which initiated the next trial. *EEG recording and data analysis*

During the experiment, 64-channel EEG was recorded from sintered Ag/AgCl electrodes mounted in elastic caps using an ANT Neuro EEGo amp (ANT Neuro, Enschede, The Netherlands; DC-120Hz, 1024 Hz sampling frequency). AFz served as ground, while CPz was used as the recording reference. Blink artefacts were corrected using the algorithm implemented in BESA 6.3 (Graefelfing, Germany; www.besa.de). EEG was segmented from -200 to 500 ms relative to prime onset and from -200 to 1,000 ms relative to target onset, with the first 200 ms as the baseline, respectively. Artefact rejection was conducted using an amplitude threshold of 100 μ V and a gradient criterion of 75 μ V. For targets, only trials in which participants reported to have unambigiously identified the faces (response options 3 or

4) were analysed based on previous studies having indicated that such ratings induce a clear N250r (Wiese et al., 2019). The remaining trials were recalculated to the common average reference and then averaged according to experimental conditions. Mean number of trials for prime stimuli were 75.9 (SD = 5.2, min = 59) in the unmanipulated, 76.1 (SD = 4.2, min = 68) in the blurred, and 80.0 (SD = 5.4, min = 58) in the blur chimera conditions, respectively. For targets, mean number of trials were 34.8 (SD = 5.2, min = 20) in the unmanipulated repetition, 35.1 (SD = 5.1, min = 21) in the unmanipulated non-repetition, 32.4 (SD = 5.8, min = 20) in the blur repetition, 32.0 (SD = 5.8, min = 17) in the blur non-repetition, 32.8 (SD = 6.4, min = 15) in the blur chimera repetition, and 32.3 (SD = 6.5, min = 15) in blur chimera non-repetition conditions, respectively.

Mean amplitudes at occipito-temporal electrodes P9/P10/TP9/TP10 were calculated for prime N170 from 140-180 ms, as well as for an earlier (240-300 ms) and later (300-400 ms) N250r time window. We note that the onset of the repetition effect varies to some extent across experiments, and that we adjust the early boundary of the N250r analysis time window correspondingly. The 300-400 ms time window is identical to the one used in our previous study (Wiese, Chan, et al., 2019). A priori hypotheses of repetition priming for chimera and unmanipulated faces, but not in the fully blurred condition, were tested using repeatedmeasures *t*-tests. Additional exploratory analyses are reported in the supplementary material. Following an estimation approach (Cumming, 2012), measures of effect size and confidence intervals are reported throughout. Repeated-measures Cohen's d was bias-corrected (d_{unb}.) and calculated using the mean standard deviation rather than the standard deviation of the difference as the denominator (Cumming, 2012). Data and analysis code will be available in a publicly accessible repository (https://osf.io). Face stimuli of celebrities cannot be published for copyright reasons. The study design and hypotheses were not pre-registered.

Results

Planned comparisons yielded significantly less negative N170 amplitudes for blurred relative to both unmanipulated, $M_{diff.} = 0.87 \mu V$, 95% CI [0.32, 1.41], t(23) = 3.26, p = .003, $d_{unb.} = 0.29$, 95% CI [0.10, 0.50], and blur chimera primes, $M_{diff.} = 0.86 \mu V$, 95% CI [0.52, 1.20], t(23) = 5.30, p < .001, $d_{unb.} = 0.29$, 95% CI [0.16, 0.44]. Unmanipulated faces and blur chimeras did not differ, $M_{diff.} = 0.01 \mu V$, 95% CI [-0.38, 0.39], t(23) = 0.03, p = .979, $d_{unb.} = 0.002$, 95% CI [-0.12, 0.13].



Figure 2. ERP results for prime faces in Experiment 1. (a) Grand average ERPs at left and right occipito-temporal electrodes. (b) Mean and individual N170 amplitudes at P9/P10/TP9/TP10. Error bars show 95% CIs.

Testing our main hypothesis, planned comparisons for the 240-300ms time window revealed a trend for more negative amplitudes for repeated relative to non-repeated faces in the blur chimera condition, $M_{diff.} = 0.45 \mu V$, 95% CI [-0.05, 0.96], t(23) = 1.85, p = .073, d_{unb}. = 0.14, 95% CI [-0.02, 0.31]. At the same time, significant priming effects, were observed in the unmanipulated condition, $M_{diff.} = 0.67 \mu V$, 95% CI [0.03, 1.31], t(23) = 2.18, p = .040, $d_{unb.} = 0.20$, 95% CI [0.01, 0.41], but not in the fully blurred condition, $M_{diff.} = 0.35 \mu V$, 95% CI [-0.14, 0.83], t(23) = 1.48, p = .153, $d_{unb.} = 0.12$, 95% CI [-0.05, 0.30].



Figure 3. Effects of repetition priming in Experiment 1. (a) Illustration of priming conditions and sample stimuli. Images of the celebrities are reproduced here under create commons licence. For copyright information, see Figure 1, except for Joe Biden 2 (Prime)

Source: <u>https://www.flickr.com/photos/58993040@N07/13958019726</u>, Attribution: U.S. Embassy Kyiv, Ukraine, public domain mark. (b) Grand average ERPs to target stimuli at left and right occipito-temporal

electrodes P9/P10 and TP9/TP10. Vertical lines show the two analysed time windows. (c) Mean and individual priming effects at electrodes P9/P10/TP9/TP10. Error bars reflect 95% CIs.

Critically, planned comparisons revealed a significant N250r for blur chimeras in the 300-400ms time window, $M_{diff.} = 0.63 \ \mu\text{V}$, 95% CI [0.08, 1.19], t(23) = 2.36, p = .027, $d_{unb.} = 0.21$, 95% CI [0.03, 0.41]. Moreover, a significant priming effect was observed for unmanipulated faces, $M_{diff.} = 0.96 \ \mu\text{V}$, 95% CI [0.43, 1.49], t(23) = 3.75, p = .001, $d_{unb.} = 0.32$, 95% CI [0.13, 0.53], but not for fully blurred faces, $M_{diff.} = 0.33 \ \mu\text{V}$, 95% CI [-0.22, 0.87], t(23) = 1.24, p = .229, $d_{unb.} = 0.12$, 95% CI [-0.08, 0.32].

Discussion

To test the hypothesis of eye-centred face representations, Experiment 1 investigated ERP correlates of immediate repetition priming for unmanipulated, fully blurred, and blur chimera faces. We observed a clear N250r, both in the earlier and later time window for unmanipulated faces, and a significant effect in the later time window for blur chimeras, while only a trend was observed in the earlier one. Importantly, no N250r was observed in the fully blurred condition. While prime N170 was smaller for fully blurred relative to both unmanipulated and blur chimera faces, the latter two conditions did not differ. Together, these results seem to provide initial evidence that blur chimera primes facilitate access to visual face representations, while fully blurred faces do not.

In line with our pre-experimental assumptions, blur chimeras elicited an N170 of comparable amplitude to the one generated by unmanipulated faces, and, critically, at the same time also elicited repetition priming. Accordingly, our previous failure to observe a comparable pattern for contrast chimeras (Wiese, Chan, et al., 2019) may have been related to processing difficulties at the perceptual level, prior to accessing long-term face representations. As blur chimeras did not elicit a similar N170 effect, these stimuli may be

better suited for testing the suggestion of eye-centred face representations. However, this interpretation can only be tentative, as it is based on a comparison across experiments. Accordingly, we will examine both blur and contrast chimeras in Experiment 2.

Experiment 2: Blur versus contrast chimeras

Experiment 1 generated initial evidence for a blur chimera N250r, and thus for the idea of eye-centred face representations. However, it remained somewhat unclear whether blur chimeras are indeed superior at eliciting the N250r relative to contrast chimeras. In Experiment 2, we therefore presented and analysed ERP responses to both types of chimeras. Our main research question was whether we could replicate the blur chimera effect in the N250r, as observed in Experiment 1. We predicted that we would detect significantly more negative amplitudes for repeated as compared to non-repeated blur chimeras in the N250r time range. At the same time, while we also expected a clear N250r for unmanipulated faces, in line with our previous results, we predicted no such effect for contrast chimeras. Moreover, if face representations were centred around the eyes, and our previous failure to find support for this suggestion from contrast chimeras was related to processing difficulties at perceptual stages, we would expect a similar N170 for blur chimeras and unmanipulated primes, while contrast chimeras should elicit larger amplitudes.

Methods

Participants

The tested sample consisted of 26 Durham University undergraduate students, two of whom were excluded due to insufficient familiarity with the celebrities (see Experiment 1). Twenty-three of the 24 remaining participants (19 female, five male; mean age = 19.8

years, SD = 1.4) were right-handed. All ERP measures of the left-handed participant were within 1 SD of the respective group means and therefore well within the range of expected variability. All other inclusion/exclusion criteria, participant compensation, and ethics procedures were analogous to Experiment 1.

Stimuli

A new set of 42 celebrity identities (e.g., actors, politicians, musicians) was used. Images for the unmanipulated and blur chimera conditions were edited analogously to Experiment 1. Contrast chimeras were created by rendering the faces into negative contrast and then overlaying the same lemniscate shape used for blur chimeras, leaving the eye region in positive contrast. Example stimuli are shown in Figure 1.

Procedure, EEG recording, and data analysis

All experimental procedures, EEG recording, and analysis parameters were analogous to Experiment 1, except that after visual inspection of the grand averages the time window for the early N250r was widened to 200-300 ms to capture the full repetition effect. For prime stimuli, mean number of trials were 76.2 (SD = 5.4, min = 56) in the unmanipulated, 75.9 (SD = 5.1, min = 57) in the contrast chimera, and 76.5 (SD = 5.0, min = 58) in the blur chimera conditions, respectively. For targets, mean number of trials were 35.5 (SD = 3.8, min = 27) in the unmanipulated repetition, 35.1 (SD = 4.0, min = 26) in the unmanipulated non-repetition, 33.4 (SD = 4.9, min = 23) in the contrast chimera repetition, 32.9 (SD = 5.2, min = 21) in the contrast chimera non-repetition, 34.4 (SD = 4.2, min = 26) in the blur chimera repetition, and 34.0 (SD = 4.5, min = 25) in the blur chimera nonrepetition conditions, respectively.

Results

While contrast chimera primes elicited clearly more negative N170 amplitudes than unmanipulated prime faces, $M_{diff.} = 1.16 \ \mu\text{V}$, 95% CI [0.57, 1.76], t(23) = 4.04, p = .001, $d_{unb.} = 0.39$, 95% CI [0.17, 0.63], a corresponding trend was also observed for blur chimera primes, $M_{diff.} = 0.41 \ \mu\text{V}$, 95% CI [-0.08, 0.90], t(23) = 1.75, p = .094, $d_{unb.} = 0.15$, 95% CI [-0.03, 0.33]. Contrast chimeras were significantly more negative than blur chimeras, $M_{diff.} = 0.75 \ \mu\text{V}$, 95% CI [0.23, 1.26], t(23) = 3.01, p = .006, $d_{unb.} = 0.27$, 95% CI [0.08, 0.47].



Figure 4. ERP results for prime faces in Experiment 2. (a) Grand average ERPs at left and right occipito-temporal electrodes. (b) Mean and individual N170 amplitudes at P9/P10/TP9/TP10. Error bars show 95% CIs.

Testing our main hypothesis, planned comparisons for target stimuli in the early N250r time range (200-300 ms) yielded significant priming for blur chimeras, $M_{diff.} = 0.50$

 μ V, 95% CI [0.04, 0.96], t(23) = 2.27, p = .033, $d_{unb.} = 0.16$, 95% CI [0.01, 0.31], but, critically, not for contrast chimeras, $M_{diff.} = 0.17 \mu$ V, 95% CI [-0.19, 0.53], t(23) = 1.00, p = .329, $d_{unb.} = 0.05$, 95% CI [-0.05, 0.14]. Unmanipulated faces elicited a significant N250r, $M_{diff.} = 0.78 \mu$ V, 95% CI [0.38, 1.17], t(23) = 4.07, p < .001, $d_{unb.} = 0.20$, 95% CI [0.09, 0.31].



Figure 5. Effects of repetition priming in Experiment 2. (a) Illustration of priming conditions and sample stimuli. Images of the celebrities are reproduced here under creative commons licence. For copyright information, see Figures 1 and 2. (b) Grand average ERPs to target stimuli at left and right occipito-temporal electrodes P9/P10 and TP9/TP10. Vertical lines show the two analysed time windows. (c) Mean and individual priming effects at electrodes P9/P10/TP9/TP10. Error bars reflect 95% CIs.

In the 300-400ms time window, planned comparisons revealed significant priming for blur chimeras, $M_{diff.} = 1.06 \ \mu V$, 95% CI [0.22, 1.12], t(23) = 3.10, p = .005, $d_{unb.} = 0.29$, 95% CI [0.09, 0.50], and contrast chimeras, $M_{diff.} = 0.39 \ \mu\text{V}$, 95% CI [0.03, 0.75], t(23) = 2.25, p = .034, $d_{unb.} = 0.16$, 95% CI [0.01, 0.32]. Moreover, a significant N250r was observed for unmanipulated faces, $M_{diff.} = 1.15 \ \mu\text{V}$, 95% CI [0.55, 1.76], t(23) = 3.93, p = .001, $d_{unb.} = 0.42$, 95% CI [0.18, 0.68],

Discussion

To test whether blur chimeras are more efficient at activating familiar face representations than contrast chimeras, Experiment 2 measured ERP correlates of repetition priming for these two stimulus categories. In line with our predictions, we observed significant priming effects for both unmanipulated faces and blur chimeras, but not contrast chimeras in the early N250r time window. In the later time window, priming was observed in all conditions. Moreover, Experiment 2 replicated our previous finding of clearly enhanced N170 amplitudes for contrast chimeras, while blur chimeras elicited somewhat larger N170 amplitudes than unmanipulated faces but clearly smaller amplitudes than contrast chimeras. These findings suggest that blur chimeras activate familiar face representations more efficiently, presumably because they do not require enhanced processing at perceptual stages.

ERPs in the early N250r time window demonstrated priming for blur but not contrast chimeras, and effect sizes were substantially bigger for the former than for the latter condition in the later time range. It therefore appears that, as the eye region is identical, information from the manipulated part of the face can be used more effectively to activate familiar face representations in the blur relative to the contrast chimera condition. A potentially important difference between blur and contrast chimeras lies in the insertion of a local edge and thus additional high spatial frequency information around the eye region in the latter but not the former stimuli. While it is possible that this local edge might hamper efficient processing and therefore the early N250r, it remains remarkable that contrast chimeras are recognized nearly as accurately as full positive faces even with very harsh local edges around the eyes (Sormaz et al., 2013). We further note that contrast chimeras elicited a significantly more negative N170 relative to blur chimeras in the present study, but very similar N170 amplitudes relative to full contrast negative faces in our previous experiments (Wiese, Chan, et al., 2019). Contrast chimeras and fully negative faces therefore elicit similar difficulties at early perceptual processing stages, and it seems unlikely that the additional local edge in the chimera stimuli plays a major role in inducing these difficulties. In addition, when creating stimuli for the present study, we applied a graded border around the lemniscate (see methods section of Experiment 1), which presumably mitigated potential effects resulting from the addition of high frequency information. Independent of the specific reason why contrast chimeras do not produce clear ERP priming effects, the findings of our first two experiments provide evidence for priming from blur chimeras, which may be seen as supportive of the idea of eye-centred familiar face representations.

Experiment 3: Specificity of the eye region

Experiments 1 and 2 yielded ERP priming effects for blur chimeras, but not control stimuli, as clear priming was neither evident for fully blurred faces nor contrast chimeras. Therefore, the N250r for blur chimeras seems to show that information from the blurred part of the stimulus can become available to some extent when presented in the context of an unfiltered eye region. The final question we address is whether this effect is specific to the eye region. In line with an eye-specific effect, previous behavioural studies have demonstrated no substantial recognition advantage for stimuli with unmanipulated face parts outside the eye region (Quinn & Wiese, 2023; Sormaz et al., 2013). In addition, a previous

ERP study has observed no priming from blurred faces with unfiltered mouth regions (Mohr et al., 2018).

The main research question for Experiment 3 was whether the chimera effects in Experiments 1 and 2 were specific to the eye regions, and, therefore, whether we would see an N250r for mouth chimeras. If the effect was specific, repeated mouth chimera targets should not elicit more negative amplitudes relative to the non-repeated condition. As experimental controls, we further tested whether we could again replicate the blur chimera effect, and whether the experiment would generate the standard effect for unmanipulated faces. Finally, in case mouth chimeras would not elicit an N250r, we were interested to see whether combined eye+mouth chimeras would, and therefore added a corresponding condition to the experiment.

Methods

Participants

The tested sample consisted of 28 Durham University undergraduate students, four of whom were excluded because of insufficient numbers of reported target identifications (see above). The final sample consisted of 20 female and four male participants (mean age = 20.1 years, SD = 1.9). All participants except for one were right-handed. All ERP measures of the left-handed participant were within 1 SD of the respective group means and therefore well within the range of expected variability. All inclusion/exclusion criteria, participant compensation, and ethics approval were analogous to Experiment 1.

Stimuli, procedure, EEG recording and data analysis

Facial identities used as stimuli were identical to those used in Experiment 2, but two additional images per identity were collected, such that eight different images per celebrity were available. Unmanipulated and eye chimera stimuli were created as described for Experiment 1. For mouth chimeras, eye chimera images were used as a template and the unfiltered lemniscate from the eye region was moved to the mouth region of each face. This was applied individually to each stimulus, assuring that mouth and eye chimeras retained the same number of unfiltered pixels. For combined eye+mouth chimeras, the resulting unfiltered mouth lemniscate region was copied into the respective original eye chimera image. Example stimuli are provided in Figure 1.

All experimental procedures were identical to Experiment 1. EEG analysis was analogous to Experiment 2, with an early N250r time window between 200-300 ms. For prime stimuli, mean number of trials were 76.7 (SD = 3.4, min = 66) in the unmanipulated, 77.0 (SD = 3.6, min = 67) in the eye chimera, 76.5 (SD = 3.9, min = 66) in the mouth chimera, and 76.1 (SD = 4.0, min = 63) in the eye+mouth chimera conditions, respectively. For targets, mean number of trials were 32.3 (SD = 4.1, min = 26) in the unmanipulated repetition, 31.7 (SD = 4.5, min = 21) in the unmanipulated non-repetition, 31.3 (SD = 4.4, min = 22) in the eye chimera repetition, 30.6 (SD = 4.3, min = 23) in the eye chimera non-repetition, 29.8 (SD = 4.8, min = 20) in the mouth chimera repetition, 28.8 (SD = 5.5, min = 20) in the mouth chimera non-repetition, 31.0 (SD = 4.3, min = 23) in the eye+mouth chimera non-repetition, and 30.7 (SD = 4.4, min = 23) in the eye+mouth chimera non-repetition, and 30.7 (SD = 4.4, min = 23) in the eye+mouth chimera non-repetition, and 30.7 (SD = 4.4, min = 23) in the eye+mouth chimera non-repetition, and 30.7 (SD = 4.4, min = 23) in the eye+mouth chimera non-repetition, and 30.7 (SD = 4.4, min = 23) in the eye+mouth chimera non-repetition, and 30.7 (SD = 4.4, min = 23) in the eye+mouth chimera non-repetition, and 30.7 (SD = 4.4, min = 23) in the eye+mouth chimera non-repetition conditions, respectively.

Results



Figure 6. ERP results for prime faces in Experiment 3. (a) Grand average ERPs at left and right occipito-temporal electrodes. (b) Mean and individual N170 amplitudes at P9/P10/TP9/TP10. Error bars show 95% CIs.

Analyses of N170 primes revealed no significant differences relative to unmanipulated faces in the eye chimera, $M_{diff.} = 0.11 \ \mu\text{V}$, 95% CI [-0.28, 0.50], t(23) = 0.58, p = .570, $d_{unb.} = 0.04$, 95% CI [-0.09, 0.17], mouth chimera, $M_{diff.} = -0.03 \ \mu\text{V}$, 95% CI [-0.53, 0.46], t(23) = -0.14, p = .891, $d_{unb.} = -0.01$, 95% CI [-0.17, 0.15], or combined eye+mouth chimera conditions, $M_{diff.} = -0.13 \ \mu\text{V}$, 95% CI [-0.51, 0.26], t(23) = -0.68, p = .505, $d_{unb.} = -$ 0.04, 95% CI [-0.18, 0.09]. Moreover, no significant differences were detected between eye and mouth chimeras, $M_{diff.} = -0.14 \ \mu\text{V}$, 95% CI [-0.51, 0.23], t(23) = -0.79, p = .437, $d_{unb.} = -$ 0.05, 95% CI [-0.17, 0.07], eye and eye+mouth chimras, $M_{diff.} = -0.24 \ \mu\text{V}$, 95% CI [-0.53, 0.06], t(23) = -1.63, p = .117, $d_{unb.} = -0.08$, 95% CI [-0.19, 0.02], as well as mouth and eye+mouth chimeras, $M_{diff.} = -0.09 \ \mu V$, 95% CI [-0.57, 0.39], t(23) = -0.40, p = .692, $d_{unb.} = -0.03$, 95% CI [-0.18, 0.12].

Planned comparisons for targets in the early N250r time window (200-300 ms) revealed significant priming in the eye chimera, $M_{diff.} = 0.59 \ \mu\text{V}$, 95% CI [0.03, 1.16], t(23) =2.17, p = .040, $d_{unb.} = 0.17$, 95% CI [0.01, 0.35], and mouth chimera conditions, $M_{diff.} = 0.79$ μV , 95% CI [0.22, 1.37], t(23) = 2.85, p = .009, $d_{unb.} = 0.26$, 95% CI [0.07, 0.47]. While a clear N250r was observed in the unmanipulated condition, $M_{diff.} = 0.92 \ \mu\text{V}$, 95% CI [0.39, 1.46], t(23) = 3.58, p = .002, $d_{unb.} = 0.26$, 95% CI [0.10, 0.44], only a trend was detected in the combined eye+mouth chimera condition, $M_{diff.} = 0.48 \ \mu\text{V}$, 95% CI [-0.05, 1.02], t(23) =1.88, p = .073, $d_{unb.} = 0.16$, 95% CI [-0.01, 0.31].



Figure 7. Effects of repetition priming in Experiment 3. (a) Illustration of priming conditions and sample stimuli. Images of the celebrities are reproduced here under creative commons licence. For copyright information, see Figures 1 and 2. (b) Grand average ERPs to target stimuli at left and right occipito-temporal electrodes P9/P10 and TP9/TP10. Vertical lines show the two analysed time windows. (c) Mean and individual priming effects at electrodes P9/P10/TP9/TP10. Error bars reflect 95% CIs.

Similarly, planned comparisons in the 300-400ms time window revealed significant priming for both eye chimeras, $M_{diff.} = 0.67 \ \mu V$, 95% CI [0.05, 1.30], t(23) = 2.23, p = .036, $d_{unb.} = 0.20$, 95% CI [0.01, 0.40], and mouth chimeras, $M_{diff.} = 0.70 \ \mu V$, 95% CI [0.06, 1.34], t(23) = 2.26, p = .034, $d_{unb.} = 0.23$, 95% CI [0.02, 0.46]. Moreover, a significant N250r was detected in the unmanipulated, $M_{diff.} = 0.90 \ \mu V$, 95% CI [0.40, 1.39], t(23) = 3.74, p = .001, $d_{unb.} = 0.27, 95\%$ CI [0.11, 0.45], but not in the combined eye+mouth chimera condition, $M_{diff.} = 0.45 \ \mu\text{V}, 95\%$ CI [-0.11, 1.01], $t(23) = 1.68, p = .107, d_{unb.} = 0.15, 95\%$ CI [-0.03, 0.35].

Discussion

To test the specificity of the previously observed N250r results to the eyes, Experiment 3 examined ERP correlates of repetition priming for different types of blur chimeras, i.e., for blurred faces in which only the eye region, only the mouth region, or both were presented with full frequency spectrum information. Counter to the idea of eye-specific priming effects, we observed a clear N250r for both eye chimeras and mouth chimeras. Moreover, we did not observe clear evidence for priming in the combined eye+mouth condition. Prime N170 was again comparable across conditions, suggesting that differences at earlier perceptual processing stages are unlikely to have affected the observed pattern of ERP priming effects.

Most importantly, ERP repetition effects were evident not only for unmanipulated faces and eye chimeras, but also for mouth chimeras. Moreover, effect sizes provided no hint that the N250r was reduced for mouth relative to eye chimeras. Availability of full-spectrum information from the eye region, therefore, does not seem to provide a specific advantage for the efficient activation of familiar face representations as measured by the N250r. Previous research indicates that the mouth contains information about individual identity (Abudarham et al., 2019; McKelvie, 1976). It thus appears that full access to this information results in a similar advantage at the level of familiar face representations as accessing information from the eyes. At the same time, these results are somewhat at odds with previous results showing an N250r for eye but not mouth chimeras (Mohr et al., 2018). While future studies will have to show whether the effect observed here can be replicated or not, it appears noteworthy to

point out that the N250r for mouth chimeras in our experiment was particularly pronounced at electrodes TP9/TP10, and that these electrodes were not reported in the study by Mohr and colleagues.

Counterintuitively, no clear evidence for priming was observed in the combined eye+mouth chimera condition, which only yielded a trend in the early and a non-significant result in the later N250r time window. It thus appears that the full and simultaneous availability of information from two spatially separate face regions, which are both informative by themselves, does not facilitate the activation of a familiar face representation. While the mechanism underlying this finding remains unclear at present, it seems possible that the repeated change from filtered to unfiltered parts across the image hampers rather than facilitates the integration of low-frequency and full-spectrum information. Further experimental work will be necessary to understand this finding better.

General Discussion

The present series of experiments tested whether long-term, visual representations of familiar faces are centred around the eyes. Using the image-independent N250r as a measure of facilitated access to these representations, we observed clear ERP priming effects for spatially low-pass filtered faces in which only the eye region was presented with full frequency-spectrum information. Priming from these blur chimeras was observed in all three experiments. At the same time, either no or weaker N250r effects were observed for fully blurred faces (Experiment 1) and contrast chimeras (i.e. contrast-negative faces with positive eye regions; Experiment 2). While these findings initially seemed to support the idea of eye-centred representations, similar priming effects were observed for blurred stimuli with

unfiltered eye or mouth regions in Experiment 3, arguing against the specificity of the chimera N250r for the eye region. These findings are discussed in more detail below.

In the present series of experiments, we repeatedly observed significant N250r effects for blur chimeras with unfiltered eyes, and comparable effects were not found for fully blurred faces or contrast chimeras, neither in the present Experiment 2 nor in our previous work (Wiese, Chan, et al., 2019). This latter finding suggests that blurring might be preferable to contrast reversal as a manipulation to emphasise information from an unmanipulated eye region. Contrast reversal is known to result in difficulties at early perceptual processing stages (Itier & Taylor, 2002, 2004), and contrast chimeras elicited an increased prime N170 both in the present and our previous experiments. Blur chimeras, however, elicited N170 amplitudes similar to unmanipulated faces. This difference between chimeras supports the idea of canonical ordinal contrast patterns as particularly relevant during early face perception (Dakin & Watt, 2009; Ohayon, Freiwald, & Tsao, 2012). Ordinal contrast patterns are most consistently represented by the eyes, nostrils, and mouth (Sinha, 2002) as being darker relative to their surroundings, and the stability of these contrast relationships over different lighting conditions has been suggested as a reliable signal for face detection (Crouzet, Kirchner, & Thorpe, 2010; Halit et al., 2006), even over distance or in poor visibility conditions (Loftus & Harley, 2005). While these canonical contrast patterns are preserved in blur chimeras, contrast negation of the face outside of the eye region distorts a significant portion of these typically stable relationships in contrast chimeras. This in turn might explain the increased effort of processing contrast relative to blur chimeras at early perceptual processing stages reflected in the N170 and may result in reduced pre-activation of face representations by contrast chimera primes. Absent or reduced priming for contrast chimeras therefore appears to result from less activation carried forward from the N170 stage, and not from reduced sensitivity for these stimuli at the representational stage. Consequently,

absent, or reduced effects for contrast chimeras in the N250r do not provide strong arguments against, while the observed effects from blur chimeras could be seen as evidence for, eye-centred face representations.

However, a substantial problem with this suggestion comes from our finding of a similar N250r for eye and mouth chimeras in Experiment 3, which indicates that information from at least one other region of the face can be used with similar effectiveness. The mouth region carries some identity information (Abudarham et al., 2019; McKelvie, 1976), and presenting this part of the face unfiltered might be more helpful relative to other regions (such as the forehead or the nose in frontal views; see Sormaz et al., 2013). In any case, our conclusion from the first two experiments has been that eye chimeras allow to access information within the filtered area of the stimulus, and it now appears as if a similar mechanism must be assumed for mouth chimeras, suggesting that the blur chimera N250r advantage is not specific to the eyes.

At first glance, these ERP findings seem to conflict with present and previous behavioural results, which have shown higher identification rates for eye relative to mouth chimeras (Quinn & Wiese, 2023; Sormaz et al., 2013). It should be noted, however, that the chimera advantage observed with behavioural measures and the ERP effects tested here presumably reflect different processes. The behavioural measure is an estimate of how likely a face is recognised in the various experimental conditions. In the present experimental paradigm, this is in principle possible without processing the prime at all. By contrast, the N250r only takes those trials into account in which the target faces have been successfully recognised, and then tests to what extent the prime influenced recognition. In repetition trials, target recognition is typically more efficient due to the pre-activation of the visual face representation by the prime, which is not possible in the non-repetition condition (for evidence from response times, see e.g. Schweinberger et al., 1995; Schweinberger, Pickering, Jentzsch, et al., 2002). Target faces in the non-repetition condition are therefore successfully recognised even though the underlying representation has not been pre-activated by the prime. In sum, the behavioural measure is about the probability of recognising a face, or effectiveness, while the N250r is about efficiency, and therefore the two measures are not necessarily related.

As noted above, the clear N250r effects for both eye and mouth chimeras suggest that the underlying face representations have initially been pre-activated with similar efficiency. This finding is in line with eye-tracking evidence indicating that the optimal fixation point during face recognition lies below the eyes (Linka, Broda, Alsheimer, de Haas, & Ramon, 2022; Peterson & Eckstein, 2012), as more centralised fixation allows other important features such as the mouth to not fall into the visual periphery. It is also in line with retinotopic mapping of the face-selective occipital gyrus in humans, in which clusters of faceselective neurons are attuned to both the eyes and mouth respectively (de Haas, Sereno, & Schwarzkopf, 2021). It therefore seems plausible that familiar face representations are similarly sensitive to eye and mouth chimeras, and thus not specifically centred around the eyes.

While our general conclusion is that face representations are not centred around the eye-region, we note that the eye region has never been tested in isolation in our experiments. However, we do not believe that examining the eye region in isolation is critical to this conclusion. Throughout the three experiments we found an N250r for blur chimeras, whereas no such effect was observed for contrast chimeras in Experiment 2 (or in our previous experiments, see Wiese et al., 2019). Critically, as the eye region itself is identical, the advantage of blur over contrast chimeras cannot be about the eyes per se. Accordingly, unfiltered access to the eye region allows for more efficient usage of information from the rest of the face in the former relative to the latter case. Moreover, our last experiment shows

no evidence for enhanced importance of the eye relative to the mouth region, as both eye and mouth chimeras elicit very similar N250r effects. Accordingly, detailed information from the mouth region also allows for increased usage of the filtered parts of the face. We believe this finding is not easy to integrate with the suggestion that representations of familiar faces, used for the recognition of individual identity are particularly centred around the eyes, and it appears unlikely that the presentation of isolated eyes could have changed the line of argument presented.

A potential limitation of the present experiments might be that face stimuli were not low-pass filtered strongly enough. As noted in the introduction, frequencies between eight and 16cpi seem to be most relevant for face recognition (Nasanen, 1999), and our filter cutoff at seven cpi clearly affected this frequency range. However, recognition deficits become stronger with increasingly lower cut-offs (Nasanen, 1999), and harsher filter settings might have put a stronger emphasis on the eyes. In addition, it is noteworthy that while the present study did not aim to assess laterality, and therefore comparisons were not made between ERPs generated by the left and right hemispheres, N250r ERPs appeared stronger in the left hemisphere than the right hemisphere in Experiments 1 and 2 (also see supplementary material). While this initially seems inconsistent with evidence indicative of righthemispheric dominance in face processing (e.g. Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Asgari, Gore, & McCarthy, 1996; Yovel, Tambini, & Brandman, 2008), it is noteworthy that some previous studies have demonstrated ERP effects of equal or greater magnitude in the left hemisphere (Deffke et al., 2007; Schweinberger, Pickering, Burton, & Kaufmann, 2002). We further note that previous studies have demonstrated left-lateralized N250r effects for written names (Pickering & Schweinberger, 2003). As the task in our present experiments may have shifted our participants' attention towards accessing name information for the targets, a pre-activation of name representations after presentation of the prime may explain the observed shift towards the left hemisphere. However, without a direct comparison between different tasks, this interpretation must remain speculative. Finally, with the task used in the present experiments it is not possible to objectively determine whether participants recognised the faces correctly. We have no reason to question our participants' motivation to categorise the faces to the best of their ability, but cannot exclude the possibility of honest mistakes. However, we think that such mistakes were unlikely, given that response speed was not emphasised and the instruction to respond with options 3 or 4 only if the faces were "clearly familiar" based on either identity-specific semantic or name information.

Finally, we note that the absence of a significant result is not evidence for the null hypothesis of no difference between two conditions (e.g., Cumming, 2012). For example, if we do not find a significant N250r for contrast chimeras, this does not mean that such an effect does not exist. At the same time, power calculations can estimate the probability of finding an effect of an a priori defined size. Given the power analysis provided in the present study, we had an 80% chance of finding an effect of the same (or larger) size than the N250r for unmanipulated faces (as estimated from a previous experiment, see methods), and we did not. Of course, this leaves us (i) with a 20% type 2 error rate, and (ii) the possibility that an N250r for contrast chimeras exists but is smaller than the a priori defined effect, in which case the analysis is insufficiently powered to detect it. To avoid such situations, we recommend that future studies should increase statistical power, particularly by adding more trials (see Boudewyn, Luck, Farrens, & Kappenman, 2018).

In conclusion, the present results are not easy to integrate with the suggestion of eyecentred face representations. While clear evidence for ERP priming effects were observed for blur chimeras, these effects were not specific to the eye region, but similarly elicited by unmanipulated mouth regions. We suggest that this observation is easiest to explain with a holistic account to face recognition, which suggests that faces are not only perceived but also represented as fully integrated wholes.

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