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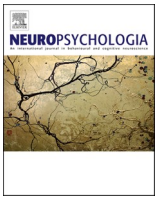

Adaptation in face animacy perception: An event-related potential study

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ABSTRACT

A real face differs from an artificial face mainly in the animacy. Nowadays, the perception boundaries between the real and artificial faces are becoming blurred in our life with the ubiquitous use of AI. Therefore, the perception of animacy causes increasing interests. Here, we used an adaptation paradigm to investigate the animacy perception in faces. We morphed a real and an artificial face to generate a continuum of face images, and asked participants to judge the animacy of those face images after they were exposed to a real face or an artificial face. We found that after adaptation to a real face, the subjects were apt to identify a subsequently ambiguous face to be inanimate, whereas after adaptation to an artificial face, the subjects were apt to identify a subsequently ambiguous face to be animate, i.e., the face animacy aftereffect (FAAE). We simultaneously recorded EEG during the task and analyzed the event-related potentials in response to the test faces, and found that adaptation to a face animacy suppressed the amplitude of LPP (late positive potential) and prolonged the latencies of N250r and LPP, in response to subsequent animacy-congruent faces. However, for subsequent animacy-incongruent faces, the amplitude was enhanced in LPP and the latencies were shortened in N250r and LPP. Those modulations of N250r and LPP activity act as a neural correlate of face animacy adaptation.

1. Introduction

With the rapid development of artificial intelligence (AI) technology, the human-like artificial entities become ubiquitous in our daily life and communicate with people frequently. Empirically, human is animate whereas artificial entities are inanimate. The human-like artificial entities appear to blur the animacy perceptual boundary between human and AI, but the knowledge of animacy perception and its underlying neural mechanism is still largely unknown. The perception of face animacy is a process that distinguishing an artificial face from a real face (Balas et al., 2017), and is referred to as the ability of our visual system to perceive "life" in a face (Koldewyn et al., 2014; Looser and Wheatley, 2010). Most previous studies explored the face animacy perception by judging a morph face image to be alive or not alive (Koldewyn et al., 2014; Looser and Wheatley, 2010). The animacy perception is shown to be categorical since the judgements of the face animacy exhibited a sigmoidal shape while the face stimuli were linear varies along the animate-inanimate axis (Balas et al., 2017; Looser and Wheatley, 2010).

Looser and Wheatley used several morphing continuums created from the animate (human) and inanimate (mannequin) faces, and found that the morph faces with more than 67% "life" property were more likely recognized as animate faces (Looser and Wheatley, 2010). The threshold for perceiving "life" in a face was varying due to the different characteristic of the face stimuli such as gender (Balas, 2013), expression (Bowling and Banissy, 2017) and racial (Krumhuber et al., 2015). Individual traits also modulate the perception of animacy. For instance, people who felt socially disconnected had lower thresholds in the judgment of whether a morph face to be alive (Powers et al., 2014). Besides, people inclined to judge in-group faces, but not out-group faces, as animate (Krumhuber et al., 2015).

Previous studies demonstrated that three face-sensitive temporal regions encoded the perceptions of face-animacy (real vs artificial) and face-form (human vs dog) in different ways. The IOG (inferior occipital gyrus) population responded prior to the face-form information than the latFG (lateral fusiform gyri) and STS (superior temporal sulcus). Whereas the latFG and STS populations responded prior to the face-animacy information. The human faces evoked a distinct pattern from the response patterns evoked by all other stimulus categories in latFG (Looser et al., 2013). However, the temporal stage of animacy perception is currently still under debate. Balas and Koldewyn (2013) found a larger peak amplitude of the P100 component in response to inanimate faces (human doll/dog doll) than to animate faces (real human/real dog), whereas there wasn't a significant difference between ERP responses evoked by the animate faces and inanimate faces at a later

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temporal stage from 400 ms to 900 ms (Balas and Koldewyn, 2013). Wheatley et al. (2011) found that the ERP responses to artificial faces and real faces were not significantly different at an early stage of face processing, but only the real faces elicited a significant LPP component (late positive potential, 400–1000 ms). Therefore, the authors proposed that the face animacy perception occurs at a late stage of face processing (Wheatley et al., 2011). Balas et al. (2017) also supported this view, and they found that animacy did not have an effect on the N170 or P100 component, thus they suggested that the animacy processing might occur at later stages of face processing.

In the present study, we employed an adaptation paradigm to investigate the face animacy perception. The adaptation aftereffect has been suggested to be the psychologist's microelectrode in the probe of the neural mechanism underlying face perception (Kovacs et al., 2006; Webster, 2011), such as facial expression (Wang et al., 2017), facial identity (Shen et al., 2017) and facial gender (Kloth et al., 2010). The neural response was attenuated following identical stimuli repetition, which was referred to as neural adaptation (Grill-Spector et al., 2006). In monkey single-cell recording studies, stimulus-specific neuronal population showed stronger activities to the first presented stimulus than to the repeat presented stimulus (Muller et al., 2009; Sobotka and Ringo, 1994). In a psychophysical view, the adaptation aftereffect was considered as an indicator of perceptual changes when comparing the responses to a test stimulus following different adaptation conditions. Specifically, after adapting to a pattern of stimuli, subjects would shift their response away from the adapted pattern more frequently, which was referred to as the adaptation aftereffect. For example, after adapting to a male face the subsequent neutral face was more likely judged to be female (Webster et al., 2004). Using a similar paradigm, Koldewyn et al. observed the animacy adaptation aftereffects, suggesting that the human visual system is fine-tuned to animacy (Koldewyn et al., 2014).

In the present study, we generated a morphed continuum as test faces ranging from a human face to an artificial face. We then compared the categorical difference between the two adaptation conditions (human face and artificial face as adaptors) and the baseline condition (no adaptor). Subjects were asked to judge a test face to be animate or inanimate. EEG data was collected simultaneously when subjects completing the psychophysical task. We expected to observe the face animacy adaptation at the behavioral level as well as the neural level. By analyzing the ERP features induced in different adaptation conditions, we hope to explore the neural mechanism of animacy perception.

2. Materials and methods

2.1. Subject

Twenty-six subjects (9 males, 19.8 ± 1.9 years) with no history of neurological or psychiatric impairment were recruited from Southwest University. They were all right-handed and had normal or corrected-to-normal vision. Four subjects were excluded from our analysis, since one subject showed a bad behavioral performance and three subjects showed excessive EEG artifacts. Thus, data of 22 subjects (8 males, 20.0 ± 1.9 years) were sent to final analysis. The protocols and experimental procedures were approved by the Internal Review Board (IRB) of Southwest University. All subjects signed the written informed consent before the experiment and were paid for their participation.

2.2. Stimuli

Two real face images were taken from the "Japanese and Caucasian Facial Expressions of Emotion (JACFEE) and Neutral Faces (JACNeuF)" database (Matsumoto and Ekman, 1988), and two artificial face images were taken from the internet. All faces were female. Faces were cropped to oval contour leaving only internal facial features except for ears and hair. All images were converted to grayscale using Photoshop CS5.1. They were grouped into two pairs of images. Each pair contained a real face and an artificial face. One pair of faces were used as adaptors with one as the animate adaptor (real face) and the other one as the inanimate adaptor (artificial face). The other pair of faces were used to create the test stimuli. FantaMorph software (Version 5; Abrosoft Co., Beijing, China) was used to generate 9 face images along the animate-inanimate axis with 0.125 increment. These face images with different animacy strength were used as the test stimuli. To minimize the possible image-level adaptation effects, we made the size of adaptors (9.3° × 8.2°) to be larger than that of the test stimuli (8.8° × 7.9°) (Fig. 1a).

2.3. Procedure

Stimuli were presented on an LED monitor (60 Hz refresh rate, a resolution of 1920 × 1080 pixels) at a viewing distance of 57 cm. The whole stimuli and procedure were run in E-prime 2.0 software (Psychology Software Tools, Pittsburgh, PA). Subjects sat in a dimly lit and sound-attenuated room. They were instructed to fixate on a centrally presented cross laid against a gray background. Stimuli were shown on the right side of the fixation cross.

In the adaptation condition, the adaptor was presented for 4 s and then a test face for 0.2 s. The inter-stimulus-interval (ISI) between the adaptor and the test face was 0.5 s. Subjects were asked to categorize a test face as to "animate" or "inanimate" by pressing a key ("1" for animate and "2" for inanimate) as accurately and quickly as possible (Fig. 1b). In the baseline condition, the procedure was identical to that of the adaptation condition except that there was no preceding adaptor. Each condition was carried out in a separate block. Overall, there were 3 blocks: the animate adaptation block, the inanimate adaptation block and the baseline block.

The baseline block was always presented before the adaptation blocks. The animate adaptation block and inanimate adaptation block were randomly presented across subjects. There were 135 trials in each block with 15 repetitions for each test stimulus. These test stimuli were presented randomly. There were 2 short practice sessions for each subject, before both the baseline block and the first adaptation block (27 trials for the baseline condition and 9 trials for the first adaptation condition). The subjects had a 3-min break after the baseline condition and a 12-min break between two adaptation blocks to avoid carryover of the aftereffects to the next block. During the break time, the subjects had no other task.

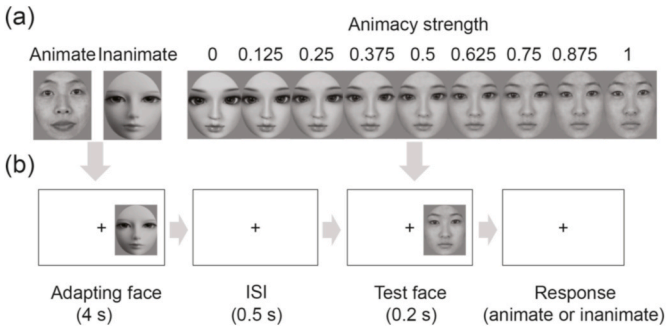

Fig. 1. Face stimuli and the experimental design. (a) Two faces (animate, inanimate) were used as adapting faces in the animate adaptation condition and in the inanimate adaptation condition respectively. Nine morphed faces were used as test faces with the proportion of animacy strength from 0 (inanimate) to 1 (animate) in steps of 0.125. Adapting faces and test faces were from different identities. (b) In the adaptation phase, the adapting face was presented for 4 s followed by a test face for 0.2 s. The inter-stimuli-interval (ISI) was 0.5 s. Participants judged the test face as animate or inanimate by pressing the response button.

2.4. Data recording and analysis

2.4.1. Psychophysical data

We chose 9 face images as test stimuli with animacy strength to be 0, 0.125, 0.25, 0.375, 0.5, 0.625, 0.75, 0.875 and 1. Data from each block were sorted into the fraction of "animate" response to each test stimulus. We then plotted the fraction of animate response as a function of the proportion of animacy strength of the test faces. The resulting psychometric curve was fitted with a sigmoidal function in the form of $f(x) = 1/(1 + 10^{(\log x0 - x) \times p})$, where p determined the hill slope and logx0 gave the test-stimulus parameter corresponding to 50% of the psychometric function, the point of subjective equality (PSE). We used a two-tailed paired *t*-test to compare subjects' PSEs for different conditions. We defined an aftereffect as the difference between the PSE of an adaptation condition (animate adaptor and inanimate adaptor) and the PSE of the corresponding baseline condition (no adaptor).

2.4.2. Electrophysiological data

Continuous EEG was simultaneously recorded (SynAmps 2, Neuro-Scan) during the experiment. The whole scalp was covered by a cap with 64 Ag/AgCl electrodes using the International Standard 10–20 system. The reference electrode was placed on the tip of the nose, and the ground electrode was on the forehead. Bipolar electrodes were used to measure the electrooculography (EOG). The vertical electrodes were attached above and below the left eye, and the horizontal electrodes were attached laterally to the outer canthus of each eye. Impedances were kept below 5 kΩ. The data were collected with a band-pass of 0.05–100 Hz and a sampling rate of 1024 Hz. We corrected EOG artifacts with a regression-based procedure (Semlitsch et al., 1986) and rejected the contaminated trials identified by visual inspection. We used the Scan 4.3 software (NeuroScan) to perform the off-line analysis. We filtered the recording data offline (30 Hz low-pass, 24 dB/octave) with a finite impulse response filter. The EEG was segmented for each trial, starting 100 ms before and ending 900 ms after the onset of the test stimulus. Epochs were rejected if potential values fluctuated over ±75 μV at any channel except the EOG channels. The ERPs were corrected relative to the baseline (100-ms pre-test-stimulus mean amplitude). We averaged the ERP evoked by each test face from all 15 trials of each block. To increase the SNR, we averaged the ERPs of two faces at each end of the continuum as the ERP response to artificial test faces (animacy strength: 0 and 0.125) and the ERP response to real test faces (animacy strength: 1 and 0.875).

We explored 4 ERP components (P100, N170, N250r and LPP) by analyzing their mean amplitudes and latencies. The P100, N170 and N250r ERP components showed a parieto-occipital topography, whereas the LPP showed a central-parieto topography (Fig. 4). Accordingly, we analyzed the typical parieto-occipital electrodes over the scalp for the P100, N170 and N250r, and analyzed the typical central-parieto electrodes over the scalp for the LPP. Specifically, for the P100, N170 and N250r, the average of 6 electrodes from the left parieto-occipital region (P3, P5, P7, PO5, PO7, CB1) and 6 electrodes from the right parieto-occipital region (P4, P6, P8, PO6, PO8, CB2) were analyzed. The time windows for the P100, N170 and N250r were 108–148 ms, 168–208 ms and 248–288 ms, respectively. These time segments were defined by the intervals of ±20 ms placed around the peak latency of the ERP component. For the LPP, the average of 6 electrodes from the parieto-occipital region (PO3, POZ, PO4, O1, OZ, O2) and 9 electrodes from the central-parieto region (C1, CZ, C2, CP1, CPZ, CP2, P1, PZ, P2) were analyzed, due to a central-parieto maximum topography. The time window for the LPP was 420–520 ms. The time segment was defined by the intervals of ±50 ms placed around the peak latency of the LPP. Those specific electrodes and time intervals we selected were also in line with the parameters we used in our previous face adaptation studies (Gao and Wang, 2020; Wang et al., 2017). For the ERP analysis, we performed a two-way repeated measures Analysis of Variance (ANOVA) with Adaptor type (animate and inanimate) and Brain region (left and right parieto-occipital regions for P100, N170 and N250r; parieto-occipital region and central-parieto region for LPP) as within-subject factors for the mean amplitudes and latencies of the P100, N170, N250r and LPP separately.

3. Results

3.1. Behavioral results

We defined an aftereffect as a significant difference between the PSE of an adaptation condition (animate adaptor, inanimate adaptor) and the PSE of the baseline condition. Fig. 2a and b showed the average data of all the subjects. Compared to the baseline condition (black curve), the response curve of the inanimate adaptation condition shifted to the left side (blue curve), whereas the curve of the animate adaptation condition shifted to the right side (red curve) (Fig. 2a). That was, after viewing an artificial face for a while the subsequent ambiguous face was recognized as to be animate more likely, and vice versa, reflecting the FAAE. Fig. 2b showed the magnitude of the aftereffects. Both the animate adaptor and the inanimate adaptor induced significant adaptation aftereffects, since the PSE value under the animate adaptor condition was significant higher than that under the baseline condition ($t(21) = 4.61$, $p < 0.001$), whereas the PSE value under the inanimate adaptor condition was significant lower than that under the baseline condition ($t(21) = -4.481$, $p < 0.001$).

We fitted B-spline curves for the response time (RT) data. As shown in Fig. 2c, the RT curves showed an inverted U-shape. There was a longest RT for the most ambiguous test face, and a shortest RT for the unambiguous test face. We analyzed the two ends of the RT curves by conducting a 2 × 2 repeated ANOVA, with different animacy strength of the test faces (artificial test faces: 0, 0.125; real test faces: 1, 0.875) and adaptation conditions (animate; inanimate) as within-subject factors and found reversal effects of RTs for the two extremes of each end of the morph continua (Fig. 2c), i.e., there was an interaction between the two factors ($F(1, 21) = 23.54$, $p < 0.001$, $\eta^2_p = 0.53$). We observed a main effect of 'animacy strength of the test faces' ($F(1, 21) = 7.72$, $p = 0.01$, $\eta^2_p = 0.27$). Post-hoc pairwise contrasts showed that the RT for the real test faces (443.81 ms) was longer than that for the artificial test faces (391.95 ms) ($p = 0.01$). Furthermore, post-hoc pairwise contrasts showed that the RT for the real test face was longer when under the animate adaptation condition (476.34 ms) than when under the inanimate adaptation condition (411.29 ms) ($p = 0.04$).

Interestingly, the peak of the RT curve shifted towards right after exposing to the animate face adaptor (red curve) and towards left after exposing to the inanimate face adaptor (blue curve), compared to the baseline condition. This could be interpreted as that after adapting to an animate face, subjects recognized the ambiguous faces more likely to be inanimate, consequently the most ambiguous faces in this situation should became more than 50% (of animacy strength), i.e., 65% animacy strength (Fig. 2c, red curve). Likewise, after adapting to an inanimate face, subjects recognized the ambiguous faces more likely to be animate, therefore the most ambiguous faces became < 50% (of animacy strength), i.e., 46% animacy strength (Fig. 2c, blue curve).

3.2. ERP results

We analyzed the amplitude and the latency of the P100, N170, N250r and LPP components elicited by the real test faces and artificial test faces respectively. The main significant effects were shown in the following. More results of amplitude and latency were shown in Tables 1 and 2.

3.2.1. P100–N170 complex

The ERPs in response to all the test faces showed a robust P100–N170 complex. We observed main effects of the factor 'Brain region', for the P100 latency in response to the artificial test faces ($F(1, 21) = 14.07$, $p = 0.001$, $\eta^2_p = 0.401$), and the real test faces ($F(1, 21) = 6.372$, $p = 0.02$,

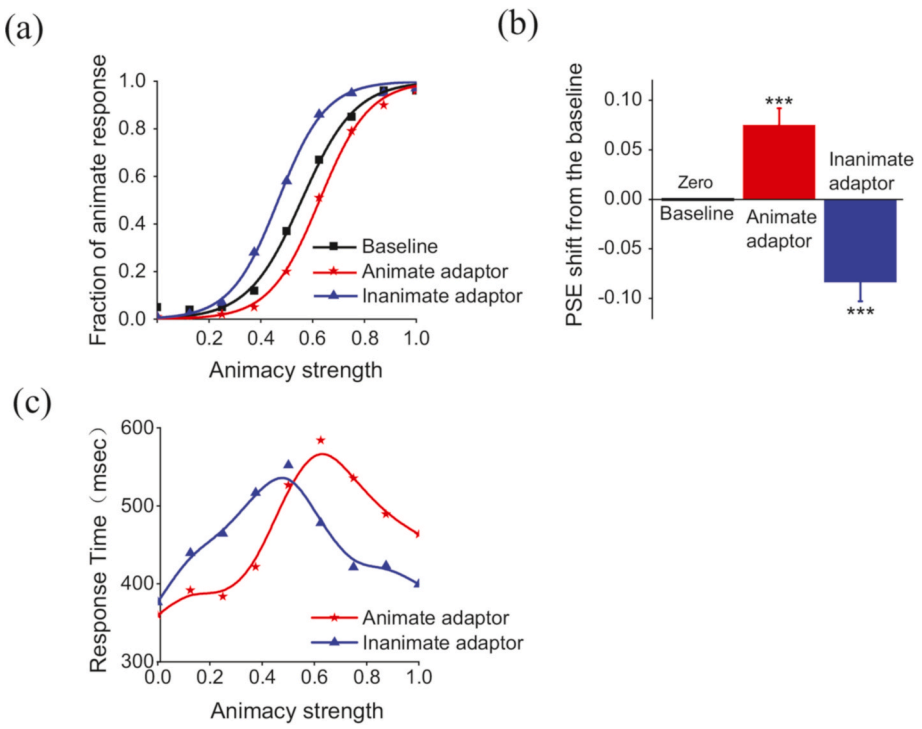

Fig. 2. Aftereffect in face animacy judgment. (a) Average psychometric functions from all participants (n = 22) under the following conditions: baseline condition (black), animate adaptation condition (red) and inanimate adaptation condition (blue). For each condition, the fraction of animate response was plotted as a function of the animacy strength of the morphed test faces. The shift of an adaptation curve relative to the baseline curve (black) indicated an adaptation aftereffect. (b) The average PSE shift relative to the baseline condition (no adaptor). (c) Response time (RT) at each test face morph level following the animate and inanimate adaptors, the reversal of the relativity of the left and right ends of the two RT curves, as well as the shift of peak of curves can also roughly represent the magnitude of FAAE. The error bars indicate SEMs. The *** indicate significance level $p < 0.001$. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
The ANOVA analysis results of the amplitude.

Factor	Artificial test faces				Real test faces			
	df	*F*	*p*	η^2_p	*df*	*F*	*p*	η^2_p
A. P100 results								
Adaptor type	*1,21*	*2.24*	*0.15*	*0.10*	*1,21*	*0.56*	*0.46*	*0.03*
Brain region	*1,21*	*0.28*	*0.60*	*0.01*	*1,21*	*0.10*	*0.75*	*0.01*
Adaptor type × brain region	*1,21*	*2.75*	*0.11*	*0.12*	*1,21*	*1.11*	*0.31*	*0.05*
B. N170 results								
Adaptor type	*1,21*	*0.96*	*0.34*	*0.04*	*1,21*	*0*	*0.99*	*0*
Brain region	*1,21*	*3.23*	*0.09*	*0.13*	*1,21*	*3.87*	*0.06*	*0.16*
Adaptor type × brain region	*1,21*	*3.88*	*0.06*	*0.16*	*1,21*	*0*	*0.96*	*0*
C. N250r results								
Adaptor type	*1,21*	*0.55*	*0.47*	*0.03*	*1,21*	*0.04*	*0.85*	*0*
Brain region	*1,21*	*6.11*	***0.02****	*0.23*	*1,21*	*5.08*	***0.04****	*0.20*
Adaptor type × brain region	*1,21*	*0.14*	*0.71*	*0.01*	*1,21*	*0.37*	*0.55*	*0.02*
D. LPP results								
Adaptor type	*1,21*	*9.85*	***0.005****	*0.32*	*1,21*	*15.49*	***0.001****	*0.43*
Brain region	*1,21*	*22.25*	***<0.001****	*0.52*	*1,21*	*2.71*	*0.12*	*0.11*
Adaptor type × brain region	*1,21*	*0.88*	*0.36*	*0.04*	*1,21*	*2.79*	*0.11*	*0.12*

$\eta^2_p = 0.233$), indicating an earlier P100 response in the left parieto-occipital region than in the right. The N170 component showd the same effect, i.e., we observed main effects of the factor 'Brain region', for the N170 latency in response to the artificial test faces ($F(1, 21) = 10.249$, $p = 0.004$, $\eta^2_p = 0.328$), and the real test faces ($F(1, 21) = 23.136$, $p < 0.001$, $\eta^2_p = 0.524$), indicating an earlier N170 response in the left parieto-occipital region than in the right. No other main effects or interactions were found to be significant (Tables 1 and 2). In our experimental design, the stimuli were presented on the right side of the fixation cross. This probably accounted for the earlier P100–N170 ERP response in the left parieto-occipital region than in the right. On the whole, our results indicated that the P100 or N170 was not responsible for the face animacy adaptation.

3.2.2. N250r

For the N250r amplitude, we observed a main effect of 'Brain region' in response to the artificial test faces ($F(1, 21) = 6.105$, $p = 0.022$, $\eta^2_p = 0.225$) and the real test faces ($F(1, 21) = 5.075$, $p = 0.035$, $\eta^2_p = 0.195$), i.e., the N250r amplitude was more negative in the left parieto-occipital region than in the right. For the N250r latency, we observed a main effect of 'Adaptor type' in response to the artificial test faces ($F(1, 21) = 6.254$, $p = 0.021$, $\eta^2_p = 0.229$). Post-hoc pairwise contrasts showed that the N250r latency was earlier in the animate adaptation condition than in the inanimate adaptation condition ($L_a = 261.591$ ms vs. $L_i = 270.318$ ms). We also found a main effect of 'Adaptor type' in response to the real test faces ($F(1, 21) = 10.831$, $p = 0.003$, $\eta^2_p = 0.340$). Post-hoc pairwise contrasts showed that the N250r latency was earlier in the inanimate adaptation condition than that in the animate adaptation condition ($L_a = 271.545$ ms vs. $L_i = 260.818$ ms) (Fig. 3a). The latency effects of N250r in response to the two categories of test faces (artificial and real) between the two adaptation conditions (animate and inanimate) were shown in Fig. 5 (lower right panel).

In brief, adaptation to an animate face shortened the N250r latency to subsequent artificial test faces, but prolonged that to subsequent real

Table 2
The ANOVA analysis results of the latency.

Factor	Artificial test faces				Real test faces			
	df	*F*	*p*	η^2_p	*df*	*F*	*p*	η^2_p
A. P100 results								
Adaptor type	1,21	*1.42*	*0.25*	*0.06*	1,21	*1.11*	*0.31*	*0.05*
Brain region	1,21	*14.07*	***0.001*** **	*0.40*	1,21	*6.37*	***0.02*** *	*0.23*
Adaptor type × brain region	1,21	*2.87*	*0.11*	*0.12*	1,21	*1.33*	*0.26*	*0.06*
B. N170 results								
Adaptor type	1,21	*0.83*	*0.37*	*0.04*	1,21	*0.69*	*0.41*	*0.03*
Brain region	1,21	*10.25*	***0.004*** **	*0.33*	1,21	*23.14*	***<0.001*** ***	*0.52*
Adaptor type × brain region	1,21	*0.93*	*0.35*	*0.04*	1,21	*0.38*	*0.54*	*0.02*
C. N250r results								
Adaptor type	1,21	*6.25*	***0.02*** *	*0.23*	1,21	*10.83*	***0.003*** **	*0.34*
Brain region	1,21	*0.43*	*0.52*	*0.02*	1,21	*0.01*	*0.93*	*0*
Adaptor type × brain region	1,21	*0.12*	*0.74*	*0.01*	1,21	*0.37*	*0.55*	*0.02*
D. LPP results								
Adaptor type	1,21	*16.80*	***0.001*** **	*0.44*	1,21	*6.95*	***0.02*** *	*0.25*
Brain region	1,21	*1.18*	*0.29*	*0.05*	1,21	*1.12*	*0.30*	*0.05*
Adaptor type × brain region	1,21	*0.90*	*0.35*	*0.04*	1,21	*0.28*	*0.60*	*0.01*

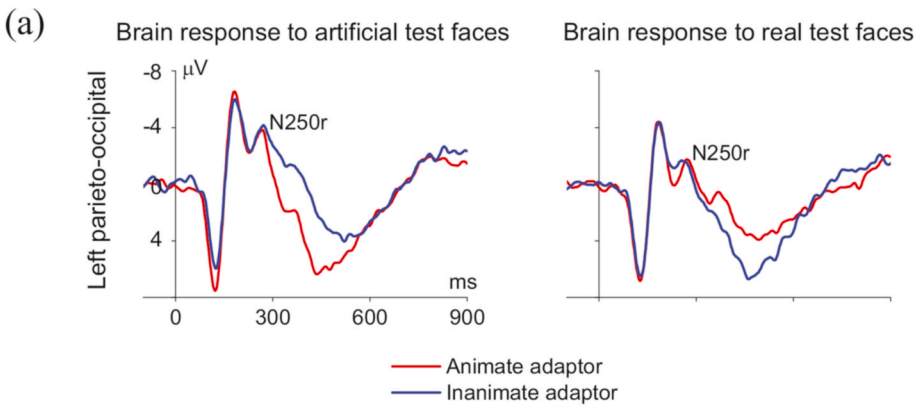

Fig. 3. Animacy adaptation revealed by ERPs. Grand averages of the N250r and the LPP components in response to the artificial test faces (animacy strength = 0, 0.125; left panel) and to the real human test faces (animacy strength = 0.875, 1; right panel) preceded by the inanimate adaptor (blue) and the animate adaptor (red). (a) The N250r (~268 ms) in the left parieto-occipital region (average of electrodes P3, P5, P7, PO5, PO7, and CB1). After adapting to the animate adaptor, the latency of the N250r was shortened in response to subsequent artificial test faces (left), but was prolonged to the real test faces (right). (b) The LPP (~420 ms) in the central-parieto (average of electrodes C1, Cz, C2, CP1, CPZ, CP2, P1, PZ, P2). After adapting to the animate adaptor, the latency was shortened in response to subsequent artificial test faces (left), but was prolonged to the real test faces (right). Whereas the amplitude was enhanced in response to subsequent artificial test faces (left), but was suppressed in response to real test faces (right). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

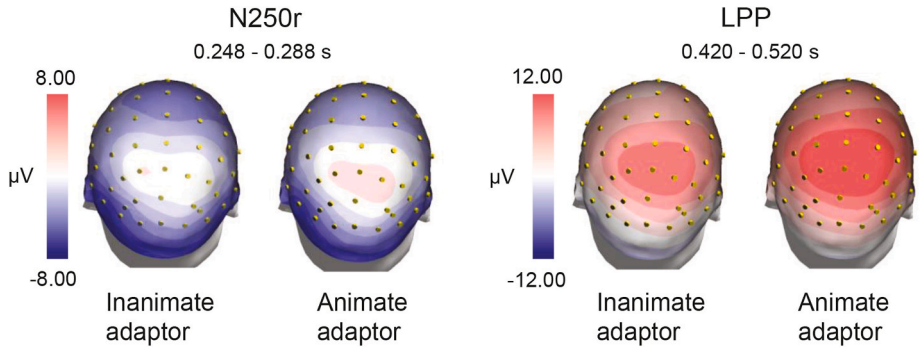

Fig. 4. Topographic maps of the N250r at 248–288 ms and the LPP at 420–520 ms. Here, we showed the ERP response to the artificial test faces (animacy strength = 0, 0.125) after adaptation to the animate and inanimate adaptors respectively.

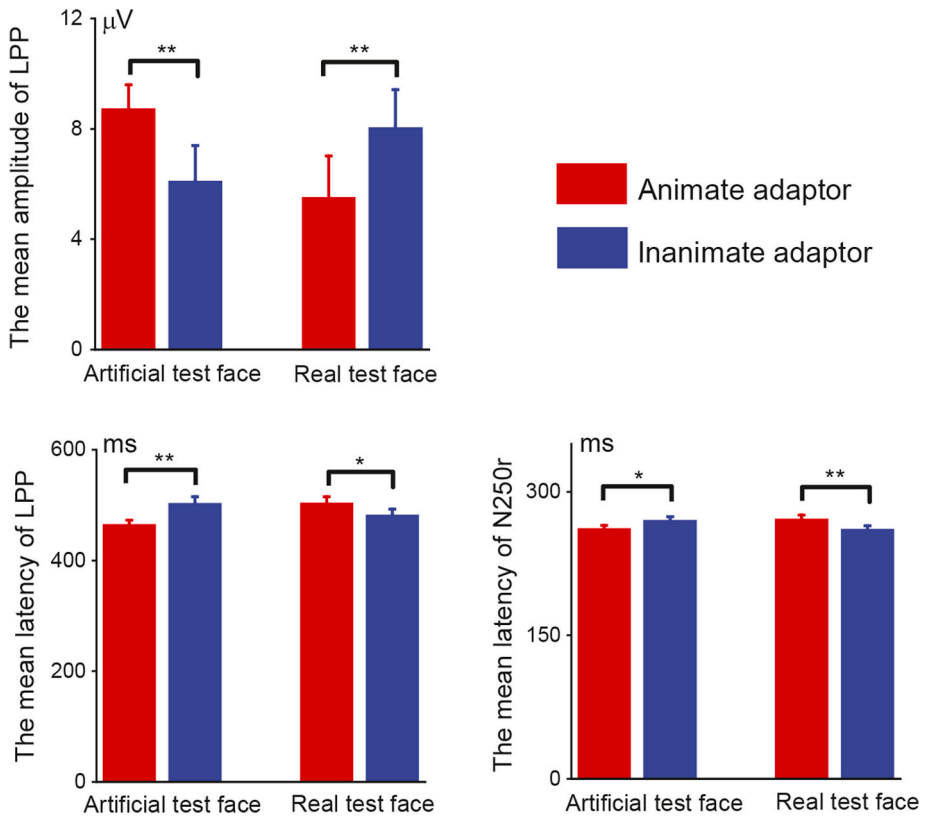

Fig. 5. The mean amplitude and the mean latency of the N250r and the LPP. * ** and *** indicate the significance level of $p < 0.05$, $p < 0.01$, $p < 0.001$ respectively.

test faces. Whereas adaptation to an inanimate adaptor prolonged the N250r latency to subsequent artificial test faces, but shortened that to subsequent real test faces.

3.2.3. LPP

For the LPP amplitude, we observed a main effect of 'Adaptor type' in response to the artificial test faces ($F(1, 21) = 9.851$, $p = 0.005$, $\eta^2_p = 0.319$). Post-hoc pairwise contrasts showed that the LPP amplitude in response to the artificial test faces was larger after adapting to the animate adaptor than to the inanimate adaptor ($A_a = 8.741$ μV vs. $A_i = 6.106$ μV). Similarly, there was also a main effect of 'Adaptor type' in response to the real test faces ($F(1, 21) = 15.494$, $p = 0.001$, $\eta^2_p = 0.425$). Post-hoc pairwise contrasts showed that the LPP amplitude in response to the real test faces was larger after adapting to the inanimate adaptor than to the animate adaptor ($A_i = 8.049$ μV vs. $A_a = 5.523$ μV) (Figs. 3b and 5). There was also a significant main effect for the factor 'Brain region' ($F(1, 21) = 22.246$, $p < 0.001$, $\eta^2_p = 0.514$) for the LPP amplitude in response to the artificial test faces. The central-parietal region ($A_{cp} = 9.140$ μV) showed a stronger elicitation than the parieto-occipital region ($A_{po} = 5.707$ μV). No significant interactions were found.

For the LPP latency, there was a main effect of 'Adaptor type' ($F(1, 21) = 16.801$, $p = 0.001$, $\eta^2_p = 0.444$) in response to the artificial test faces. Post-hoc pairwise contrasts showed that the LPP latency in response to the artificial test faces was earlier after adapting to the animate faces than to the inanimate faces ($L_a = 465.318$ ms vs. $L_i = 503.545$ ms). We also found a main effect of 'Adaptor type' in response to the real test faces ($F(1, 21) = 6.948$, $p = 0.015$, $\eta^2_p = 0.249$). Post-hoc pairwise contrasts showed that the LPP latency in response to the real test faces was earlier after adapting to the inanimate faces than to the animate faces ($L_a = 503.636$ ms vs. $L_i = 481.955$ ms). No significant interactions were found. The amplitude and latency effects of LPP in response to the two categories of test faces (artificial and real) between the two adaptation conditions (animate and inanimate) were shown in Fig. 5 (left panel).

In brief, adaptation to an animate adaptor suppressed the amplitude and prolonged the latency of the LPP in response to subsequent real faces, but enhanced the amplitude and shortened the latency of the LPP in response to subsequent artificial faces. However, adaptation to an inanimate adaptor suppressed the amplitude and prolonged the latency of the LPP to subsequent artificial faces, but enhanced the amplitude and shortened the latency of the LPP to subsequent real faces. All in all, the amplitude of LPP was suppressed and the latency of LPP was prolonged when the adaptor and the test face were animacy-congruent, whereas the amplitude of LPP was enhanced and the latency of LPP was shortened when the adaptor and the test face were animacy-incongruent.

4. Discussion

In the present study, we found a robust FAAE in the behavioral experiment. We obtained three sigmoidal curves as a function of the proportion of the animacy strength of the test faces. The two adaptation curves (animate adaptation and inanimate adaptation) shifted to the opposite directions (Fig. 2a). After adapting to an animate face for a while, subjects were apt to judge the subsequent ambiguous faces as inanimate, and vice versa, reflecting the FAAE. The animacy aftereffect was in accordance with the face identity adaptation aftereffect (FIAE), i.e., the judgement of the identity of a subsequent face was biased away from the adaptor along the identity trajectory (Gao and Wang, 2020). The FAAE suggested that the previous visual experience could affect the perception boundary of the animacy category. Furthermore, we found that the animacy adaptation transferred across different identities (Fig. 1). This was in line with the study of Koldewyn et al. (2014) in which the authors found that the FAAE did not differ from a face identity congruent condition to a face identity incongruent condition (Koldewyn et al., 2014). Overall, like other face attributes, such as facial identity, expression, gender and racial, exposing to a face animacy also generated an aftereffect. The adaptation paradigm is a useful tool to explore the

face animacy perception.

In our experimental design, the adaptors were a real face and an artificial face. The test faces were a morph continua generated from another pair of a real face and an artificial face, whose identity were totally different from those of the adaptors. The cross-identity design between the adaptors and test faces basically guaranteed that the FAAE observed in the present study was a high-level effect. The parameters used here were adapted from previous face adaptation studies, in which the morph continua of the test stimuli generally consisted of 7–11 face images (Gao and Wang, 2020; Wang et al., 2017; Xu et al., 2008). However, the use of a relatively small number of morph continua might limit the potential generalizability of the stimuli somewhat.

We investigated the neural mechanism of the face animacy adaptation characterized by the P100, N170, N250r and LPP ERP components. We found that the amplitudes and latencies of the P100 or N170 elicited by a test face did not differ across the adaptation conditions. These results were consistent with our previous studies on face adaptation, which demonstrated that face identity adaptation (Gao and Wang, 2020) or face emotion adaptation (Wang et al., 2017) did not modulate the P100 and N170. We obtained an N250r component with a parieto-occipital scalp distribution peaking around 268 ms (Fig. 4). The N250r was suggested to be triggered by repeated faces (Schweinberger et al., 2002, 2004). It reflected the face recognition by matching the visual face to the face representation in memory (Zimmermann and Eimer, 2013). In our experiment, the N250r amplitude in response to the same test face in both the animacy-congruent condition and the animacy-incongruent condition did not differ, but the latency was significantly shorter when the test face was animacy-incongruent, than when the test face was animacy-congruent, with the preceding adaptor (Fig. 3a). In our paradigm the identities of the adaptor and the test face were completely different. We inferred that the modulation of N250r we observed was due to the animacy congruency.

Our results showed that only the N250r latency, but not the amplitude, was modulated by the prior adaptation to face animacy. This indicates that, unlike the LPP, the N250r amplitude was not responsible for the face animacy adaptation. N250r is assumed to reflect a successful match between a perceptual face representation and the memory trace of the face (Zimmermann and Eimer, 2013). Indeed, the N250r amplitude was found to be sensitive to the adaptation of face emotion (Wang et al., 2017) and identity (Gao and Wang, 2020), in which the S1 (adaptor) and S2 (test face) were from the same identity. The N250r was always reported in face identity-repetition studies (Schweinberger et al., 2004; Zimmermann and Eimer, 2013). However, in the present study the N250r amplitude was not responsible for the face animacy adaptation, probably because the S1 (adaptor) and S2 (test face) were from different identities (Fig. 1). This notion received supportive evidence from our previous study on face adaptation, in which we found an effect of N250r amplitude in face identity adaptation. But the effect vanished when we used side view faces as the adaptor, suggesting that the N250r component is more sensitive to the configural information of a human face rather than the identity information of the face (Gao and Wang, 2020). From this point, there was a possibility that the N250r latency effect we observed in the present study was a result of some ramp-up to the LPP differences occurring in the N250r time window.

The LPP was suggested to be an index of mind perception or animacy perception (Wheatley et al., 2011), in this study the authors compared the ERP characteristics of three stimulus categories, and found that the LPP amplitude was sustained only for the human face but not for the doll face or the clock. In the present study, we compared the LPP elicited by the same test stimuli across different adaptation conditions. The LPP showed a central-parieto topographic distribution (Fig. 4). The LPP amplitude and latency were modulated by the animacy congruency between the adaptor and test stimulus, i.e., the amplitude was suppressed and the latency was prolonged when the adaptor and the test stimulus were animacy-congruent, whereas the amplitude was enhanced and the latency was shortened when the adaptor and the test stimulus were animacy-incongruent (Fig. 3b). In the neural level, the modulation of LPP could be explained by the fact that the neuronal population responsible for encoding the adapted stimulus would decrease their activities when the stimulus was repeatedly presented (Muller et al., 2009; Sobotka and Ringo, 1994). Therefore, we proposed that the modulation of LPP may act as a neurophysiological correlate of face animacy adaptation.

Up to now, the functional interpretation of the LPP component is still obscure. Some studies suggest that the LPP is related to the salience and significance of the stimuli in the environment (Hajcak and Foti, 2020; Schupp et al., 2000, 2012; Wheatley et al., 2011). For example, emotional stimuli (e.g. pleasant and unpleasant) elicited a larger LPP component relative to neutral expression stimuli (Schupp et al., 2000). In the study of Wheatley et al. (2011), they found that the animate faces elicited a more robust LPP component relative to the inanimate faces (Wheatley et al., 2011). The paradigm we chose could not rule out another interpretation which argued that the LPP is a P3-like component. The P3 component is considered to be a neural connection to contextual novelty (Kloth et al., 2010; Wang et al., 2017). Contextual novelty was referred to as the neural representation update when the novel stimuli insert into the current environment, which is characterized by the P3 component (Delplanque et al., 2005; Donchin and Coles, 1988; Polich, 2007). In the present study, after the 4-s adaptation period, the immediate memory represented the animacy information of the adaptor. Once the subsequent test face was animacy-incongruent with the adaptor, the mental representation would be refreshed and updated, reflecting the process of contextual novelty. Overall, we were cautious to conclude the functional interpretation of the LPP. More evidence is needed to give a full picture of the functional meaning of the LPP, such as whether the face animacy adaptation can be observed cross-species, as well as the functional localization of the LPP. Looser et al. demonstrated that the latFG and the STS region were involved in the face animacy process (Looser et al., 2013). Whether and how the LPP was associated with the activities in these regions need to be explored in future studies.

A worth noting question is that the two extremes of each end of the morph series were always 100% judged as inanimate (or animate) in both the animate adaptation condition and the inanimate adaptation condition. This likely indicates that the adaptation does not affect the animacy judgement of the extremes. However, we observed neural adaptation in these extremes, as revealed by the N250r/LPP modulations. Why does adaptation have an effect on the ERP, but not on the behavioral judgment, of the extremes of each end of the morph series? There might be two explanations. Firstly, the psychophysical indicator (PSE shift) and the electrophysiological indicator (ERP modulation) were not a causality relationship. Secondly, there might be other factors, but not the accuracy response of the extremes, that were affected by adaptation. For example, the RT effect. As shown in Fig. 2c, there was a reversal of the relativity of the left and right ends of the two RT curves. The RT for the real test face in the animate adaptation condition was longer compared to that in the inanimate adaptation (the right end of the morph continua). There was a reversal for that of the left end of the morph continua. These results showed that the RT modulation basing on the two extremes of each end of the morph continua, could also be used as an indicator of FAAE. The RT, however, was still not the key indicator of adaptation in our experiment. The subjects were asked to respond as accurately and quickly as possible, and therefore the accuracy always took precedence over RT, in their judgment. All in all, we found that the adaptation did not affect the accuracy response to the unambiguous stimuli. Yet, the RT for the unambiguous stimuli was somewhat affected by adaptation.

In summary, we explored the face animacy adaptation using psychophysical and electrophysiological methods. The two ERP components, N250r and LPP, were modulated by the animacy congruency between the adaptor and the test stimulus. The modulations of N250r and LPP activity act as a neurophysiological correlate of face animacy

adaptation.

Credit author contribution statement

Jinglan Xiang: Conduct and experiment, write the original paper. **Mi Tang:** Revise the paper. **Xiaodong Wang:** Design the experiment and revise the paper.

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