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Electrophysiological individual face adaptation effects with fast periodic visual stimulation resist long interruptions in adaptation

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ABSTRACT

This study used fast periodic visual stimulation (FPVS) and electroencephalography (EEG) to investigate whether the reduction of face adaptation effects over time is due to the introduction of a novel stimulus. In adapting sequences, one individual face was presented at a rate of 6 Hz over 60 s. In testing sequences this adapted face was alternated with a novel individual face at the same rate for 20 s, so that face identity was repeated at a frequency of 3 Hz (i.e. 6 Hz/2). Testing sequences started immediately or 9–15 s after adapting sequences. Identity adaptation produced a selective response at 3 Hz over the right occipito-temporal cortex both with and without delay after adapting sequences. These results suggest that the adaptation effect persists for several seconds, and that the decay of the adaptation effect is due to the introduction of a novel face stimulus.

1. Introduction

Individualizing people by their faces is crucial for human social interactions. Despite the high similarity between faces, humans are highly accurate and fast (i.e., a single glance) at distinguishing individuals based on their faces (Hsiao & Cottrell, 2008; Jacques, d'Arripe, & Rossion, 2007), such that humans can be considered as face experts. However, measuring and comparing this process in all populations can be challenging, with explicit behavioral tasks involving many processes (e.g., attentional, decisional) beyond individual face perception.

Paradigms of adaptation—a reduction in neuronal activity in response to repeated compared with unrepeated stimuli—in fMRI or event-related potentials (ERP) have contributed greatly to the understanding of how different facial identities are encoded at the neuronal level. In particular, adaptation paradigms in ERP have shown reductions in amplitude of the N170 component following immediate repetition of face identity (Caharel, d'Arripe, Ramon, Jacques, & Rossion, 2009; Caharel, Collet, & Rossion, 2015; Cao, Ma, & Qi, 2015; Itier & Taylor, 2004; Jacques et al., 2007; Vizioli, Rousselet, & Caldara, 2010). The N170 is a negative component with maximal amplitude 130–190 ms after stimulus onset over occipito-temporal electrodes. This component is larger for faces than for other categories of visual objects (Bentin, Allison, Puce, Perez, & McCarthy, 1996) and may reflect the activation of a mechanism specialized in initial stages of face structural encoding, contributing to further individual identification (Bentin et al., 1996; Bentin, Golland, Flevaris, Robertson, & Moscovitch, 2006; Eimer, 2000). Facial identity repetition effects also occur at other time points, most notably on the N250r component, which peaks at 230–330 ms over the occipito-temporal cortex. The N250r is larger for repeated than for non-repeated faces (Herzmann, Schweinberger, Sommer, & Jentzsch, 2004; Schweinberger, Pfütze, & Sommer, 1995) and may reflect the transient activation of mental representations for recognizing individual faces (Schweinberger & Burton, 2003). Adaptation effects on the N250r can be long-lasting and persist after presentation of intervening faces (Tanaka, Curran, Porterfield, & Collins, 2006).

Recent studies used a simple adaptation paradigm with fast periodic visual stimulation (FPVS) in electroencephalography (EEG) to identify and quantify an implicit individual face discrimination response (Retter & Rossion, 2016b; Retter & Rossion, 2017). FPVS relies on the exact synchronization of the brain to a visual stimulus repeated at a periodic rate (i.e. a steady-state visual evoked potential; (Regan, 1982, 1989) and is suitable to study face processing (Liu-Shuang, Norcia, & Rossion, 2014; Rossion & Boremanse, 2011); for a review see (Rossion, 2014). In the study of Retter and Rossion (2016b), during a baseline adaptation of 10 s, one face was presented at a fixed rate of 6 Hz, only changing the size to avoid low-level visual adaptation (Fig. 1). Immediately afterwards, this adapted face was alternated with a novel face identity at the same frequency, such that face identity repetition occurred at a rate of 6 Hz/2 = 3 Hz. Compared with a stimulation sequence without an adaptation period, adaptation to the identity of this face produced a response at a differential identity repetition rate (i.e. 3 Hz) in the EEG

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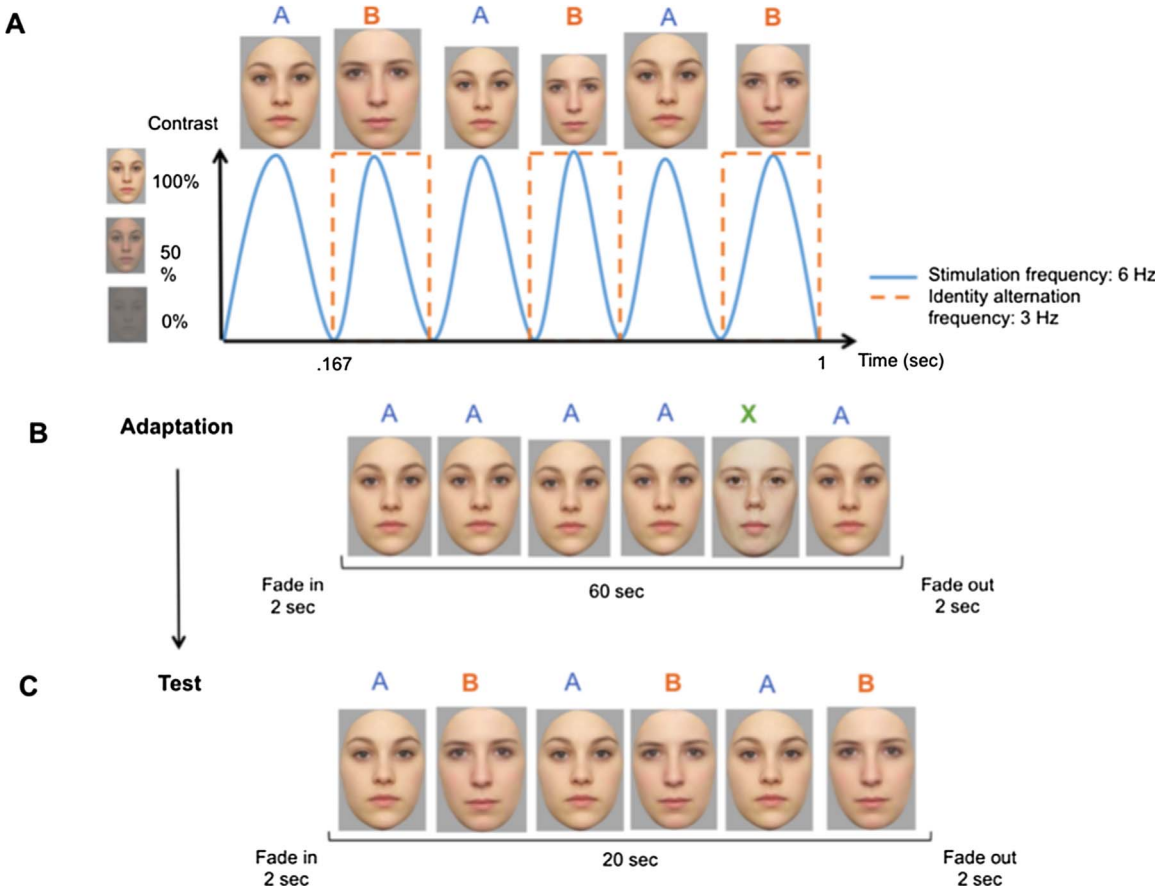

Fig. 1. (Color; 2 columns) Experimental procedure. **A.** Face stimuli were presented at a constant rate of 6 Hz through sinusoidal contrast modulation from 0% to 100%. During each stimulus presentation cycle, the size of the image varied randomly between 80% and 120% in 10% steps relative to the original presentation size. **B.** In adapting sequences, one face identity was presented continuously during a 60 s sequence. Every fifth stimulus, different oddball face identities were presented, resulting in a sequence of AAAABAAAAC... **C.** In testing sequences, the facial identity presented during encoding sequences was alternated with the presentation of a novel face identity during a 20 s sequence of stimulation. The repetition frequency for one face identity was 3 Hz (i.e. 6 Hz/2). In the adapted-no delay condition, a testing sequence immediately followed an adapting sequence. In the adapted-delay condition, a testing sequence started 9–15 s after an adapting sequence. In the control group, only testing sequences were presented.

spectrum, reflecting a difference in the responses to adapted and unadapted faces.

Since ERP studies have shown that adaptation effect can be long-lasting, it is likely that adaptation effects in FPVS might also be resistant to delay. However, in that study, adaptation was most pronounced during the first 2 s of the testing sequence, thereafter showing a rapid decay and becoming insignificant after 5 s. This is inconsistent with the longer duration of adaptation found in ERP studies. One explanation for this result is that the adaptation effect disappeared quickly because of the introduction of a novel face immediately after the 10-s adaptation baseline. The present short study aimed to test whether the rapid decay of the adaptation response in FPVS is due to the introduction of a novel face and to specifically evaluate the delay between adaptation and testing.

To do this, we conducted an adaptation paradigm using FPVS-EEG. We compared two adaptation conditions: in the first, participants were adapted to one face presented at a rate of 6 Hz over 60 s. Immediately afterwards, the adapted face stimulus was presented in alternation with an entirely novel face for 20 s at a rate of 6 Hz. Identity repetition frequency was therefore 3 Hz. In another condition, adaptation and testing occurred in different sequences separated by a blank delay of 9–15 s. This delay was longer than the delays tested in previous EEG studies (Neumann & Schweinberger, 2008; Schweinberger et al., 2002; Shen et al., 2017), so if the adaptation effect is limited in time, it should not be significant after a 9–15 s delay. A third, control group did not include any adaptation, thereby controlling for the physical difference between stimuli in the adaptation response. If the adaptation effect is limited in time, the individual face discrimination response should be significant when there is no delay between adaptation and testing, but should not be significant after a 9–15 s delay following adaptation stimulation. If, however, the decay in adaptation response is due to the introduction of a novel face stimulus, individual face adaptation responses should still be observed in delayed and non-delayed conditions.

2. Methods

2.1. Participants

Three groups of 14 participants each were recruited for this study. These groups included an adapted-no delay (seven females; mean age = 22.27 ± 2.02 years), an adapted-delay (seven females; mean age = 23.72 ± 3.32 years) and a control (eight females; mean age = 21.91 ± 1.57 years) group. All participants reported normal or corrected-to-normal vision and were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). All performed the Benton Face Recognition Test (BFRT; Benton & Van Allen, 1968) prior to the EEG session and all showed results in the normal range (mean = 84.88 ± 5.25; range = 74.07–96.30). All subjects received monetary compensation for participation in the study. All participants provided written informed consent before participation, in accordance with the requirements of the Biomedical Ethical Committee of the University of Louvain, which approved the study protocol.

2.2. Stimuli

In a "face space" framework (Leopold, O'Toole, Vetter, & Blanz, 2001), face identities are represented by vectors in a space with the average of all faces at the center. Faces lying on an axis from an original face to the mean, but on the other side of the mean (i.e an "anti-face") are perceived as entirely different individuals, and the transition across the average face between a face and its anti-face represents a point of discontinuity in perceived identity (Blanz et al., 2000). Thus, in this study, face pairs were designed to contain one face stimulus that was 80% an original identity and another that was 80% its anti-face. This ensures discrimination between face identities while keeping the distance to the average face identical.

Faces were prepared from seventy-two face stimuli. Using JPsychoMorph software (Tiddeman, 2005), three randomly selected faces of the same sex, each selected only once, were averaged together to make twenty-four novel identities. Then, all 12 female and 12 male face stimuli were averaged separately to create an average face for each gender category.

Twelve of the 24 novel identities were used to create 12 face pairs. The second face in each pair was created by morphing the shape and texture of the first face stimulus of the pair from the average face towards its anti-face in a theoretical face space (Leopold et al., 2001).

The oddball face stimuli presented in the adaptation sequences (see Section 2.3) consisted of 50 stimuli (half male). These stimuli came from the same face set as the one used to prepare the face pairs, but were not used to prepare the face pairs.

All face stimuli consisted of full-front color photographs of Caucasian faces (half male) with neutral expressions, cropped to exclude external features, standardized by height (250 pixels) and equalized by mean pixel luminance (183/255).

Stimuli were displayed on a monitor with 1920 by 1080 pixel resolution at a distance of 80 cm, and subtended at approximately 5.0 ° of vertical visual angle at the original presentation size.

2.3. Procedure

Participants were seated in a quiet, dimly lit room in front of a computer screen and keyboard. The experimental procedure is summarized in Fig. 1. Face stimuli were presented at a constant rate of 6 Hz (i.e., 6 images/sec) through sinusoidal contrast modulation from 0% to 100% using software running over Java (Sinstim). At a screen refreshing rate of 120 Hz, each complete 6 Hz image presentation cycle consisted of 20 frames (i.e., 120 Hz/6 Hz) (i.e., from 0% to 100% to 0% contrast); the contrast at each frame corresponded to the percent contrast of the 6 Hz sinusoidal contrast function at that time. To reduce the potential impact of low-level adaptation, the size of the image during each stimulus presentation cycle was varied randomly between 80% and 120%, in 10% steps, of the original presentation size (Dzhelyova & Rossion, 2014; Rossion & Boremanse, 2011). Each sequence started with a 2 s fade-in, during which the maximum stimulus contrast presentation gradually increased from zero to full contrast, and finished with a 2 s fade-out.

Adaptation and testing sequences alternated throughout the experiment. In adaptation sequences, the first face of one pair was presented continuously during a 60 s sequence. Every fifth stimulus, different faces were presented, resulting in the sequence: AAAABAAAAC... These face stimuli differed from those used in the 12 pairs of face identities, thus avoiding overlap between oddball faces presented during adaptation and novel faces presented during testing sequences. Therefore, the second face presented during testing sequences was entirely novel to the subjects. Different faces were presented during adaptation sequences to make stimuli less monotonic and most importantly to maintain high amplitude responses throughout the duration of adaptation (i.e. 60 s), as the response at the stimulation frequency was shown to be lower for presentation of the same compared to different face identities during a stimulation sequence (Nemrodov, Jacques, & Rossion, 2015; Rossion & Boremanse, 2011).

In testing sequences, the two facial identities of each pair were presented in an alternating fashion over a 20 s stimulation sequence. At a presentation rate of 6 Hz, the repetition frequency for each individual face was 3 Hz (i.e. 6 Hz/2). Only one pair of faces was presented during each testing sequence.

In total, there were 12 adapting and 12 testing sequences. Each adaptation sequence containing the first face of the pair was followed by the testing sequence containing both faces.

Subjects in the adapted-no delay group were presented adaptation sequences, followed immediately by testing sequences; subjects in the adapted-delay group were presented adaptation and testing sequences separated by an interval of 9–15 s; and subjects in the control group were presented only testing sequences, thus viewing two alternating, novel face identities, like in the previous study (Rossion, 2016a,b;), to ensure that the response at the face identity repetition frequency (i.e. at 3 Hz) could not be explained by physical differences between the two faces rather than by only one of the two faces being previously presented. Therefore, if the adaptation baseline produces a different response to the adapted than to the unadapted face (i.e. an adaptation effect), the response at 3 Hz would be greater in the two adapted groups than in the control group.

Participants were asked to look at the face stimuli displayed on the computer screen while fixating on a centrally presented fixation cross, and to press the space bar when the cross briefly changed color (from black to red). Color changes occurred randomly for 200 ms throughout the face sequences. Eight changes occurred during the adaptation sequences (60 s) and three changes during the testing sequences (20 s). This task ensures that participants stay focused throughout the experiment.

2.4. Electroencephalography (EEG)

EEG was recorded using a 128-channel BioSemi Active 2 system (BioSemi, Amsterdam, Netherlands), with electrodes at standard 10–20 system locations as well as at intermediate positions, and sampled at 512 Hz. Electrode offset was held below 50 mV. Eye movements were monitored using four electrodes placed at the outer canthi of the eyes and above and below the right orbit.

2.5. Analyses

2.5.1. Preprocessing

EEGs were processed using *Letswave 5* (http://nocions.webnode.com/letswave). First, changes in offset due to pauses in the recording between trials were corrected by aligning the offset for each channel at the start of a recording with the offset prior to the pause. EEG data were band-pass filtered (0.1–100 Hz zero-phase Butterworth filter, 24 dB/octet slope), with a Fast-Fourier Transform (FFT) multi-notch filter applied to remove electrical noise at three harmonics of 50 Hz, with widths of 0.5 Hz. EEG data were down-sampled to 256 Hz and segmented by trial with two extra seconds at the start and end of each stimulation sequence (i.e. −2 s to 66 s for adaptation sequences and −2 s to 26 s for testing sequences). Ocular artifacts were removed by independent component analysis (ICA) with square mixing matrix. All channels were re-referenced to the common average reference (excluding ocular channels).

2.5.2. Frequency-domain analyses

Sequences were averaged within condition for each participant. A FFT was computed to represent the data of each channel as a normalized amplitude spectrum (μV) in the frequency domain (range from 0 to 256 Hz), with a frequency resolution of 0.04 Hz (i.e. the inverse of the sequence length in seconds, 1/25). Two different methods of baseline correction were applied to data from individual participants: a baseline-

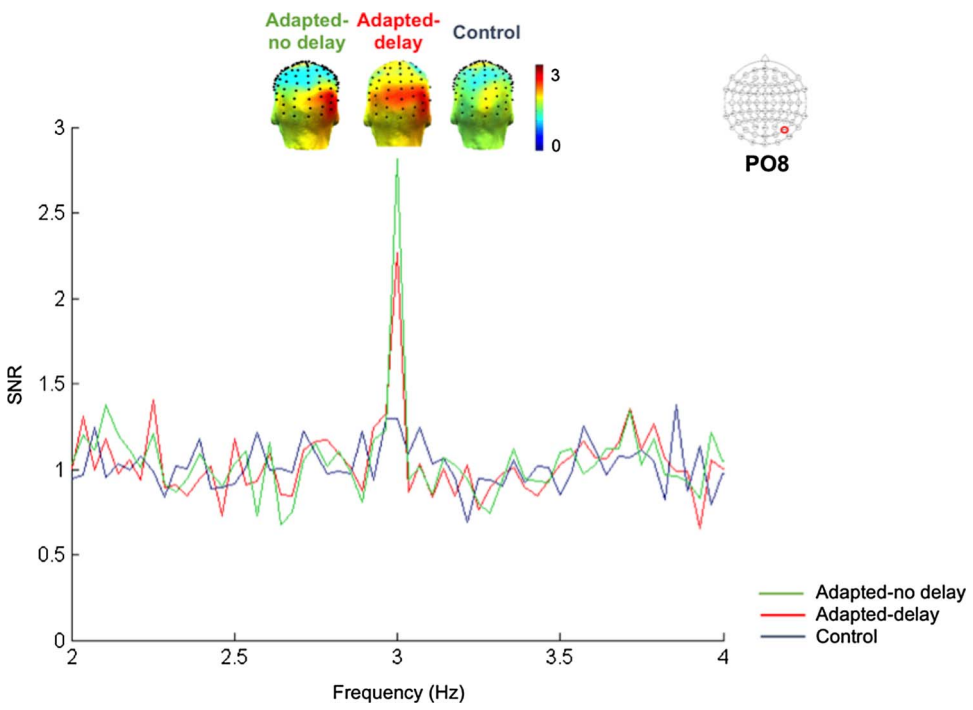

Fig. 2. (Color; 2 columns) Signal-to-noise (SNR) spectra of EEG channel PO8 and scalp topographies of the responses at 3 Hz in the adapted-no delay (green line), adapted-delay (red line) and control (black line) groups. The adapted-no delay and adapted-delay groups, but not the control group, showed a significant response at 3 Hz in the right occipito-temporal cortex. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

subtraction and a signal-to-noise (SNR) transform. The average of the 20 bins surrounding the bin of interest was used to define the baseline (Rossion, Hanseeuw, & Dricot, 2012; Srinivasan, Russell, Edelman, & Tononi, 1999), which corresponds to a 1/20 (5%) chance of a signal being significantly above the baseline. The maximum bin was excluded to prevent the signal from being included when calculating the baseline of noise bins near the signal (Retter & Rossion, 2016b). The minimum bin was excluded for balance. In the baseline-subtraction method, the baseline was subtracted from the amplitude at the bin of interest, whereas in the SNR method, the signal of interest was divided by the baseline. The baseline subtraction method was used to quantify the signals in μV, whereas the SNR method was used to display responses (Retter & Rossion, 2016a).

To determine significance at the group level, grand-averaged amplitude spectra were generated for each channel. To quantify responses, amplitude spectra were pooled across all channels after conducting FFT for each individual participant, but separate analyses were also conducted on three regions of interest (ROI) defined according to scalp topographies and the previous study (Retter & Rossion, 2016b): the medial occipital (MO) and the right and left occipito-temporal (ROT and LOT, respectively). Each ROI included five channels: MO (PPOz, POz, POOz, Oz, and Oiz); ROT (PO10, P10, PO12, P8, PO8); and LOT (PO9, P9, PO11, P7, PO7). To determine whether responses at the frequency of interest were significant, Z-scores (Z = (X-baseline)/standard deviation of the baseline) were computed across the ROIs of the grand-averaged amplitude spectra. A response in a ROI was considered significant if $Z > 1.64$, i.e., when $p < 0.05$ (one-tailed, i.e., signal > noise). Face identity specific responses at the face alternation frequency (i.e. 3 Hz) were predicted to occur in the adapted-no delay and adapted-delay groups, but not in the control group, and maximally at the ROT ROI (Retter & Rossion, 2016b).

2.5.3. Statistical analyses

The magnitude of the response at the identity alternation frequency (i.e. 3 Hz) was compared among the adapted-delay, adapted-no delay and control groups. The effect of adaptation was expected only at a frequency of 3 Hz, independently of the response at base frequency (Ales, Farzin, Rossion, & Norcia, 2012; Ales & Norcia, 2009; Liu-Shuang, Ales, Rossion, & Norcia, 2015; Liu-Shuang, Ales, Rossion, & Norcia, 2015).

Adaptation responses were compared by repeated measures ANOVA, with adaptation conditions (adapted-delay, adapted-no delay, and control) as a between subject factor and *ROI* (MO, ROT, LOT) as a within subject factor. When ANOVA showed significant effects, Newman-Keuls post-hoc analyses were performed.

Between group adaptation responses when channels were averaged were compared by one-way ANOVA. A *p*-value < 0.05 was defined as statistically significant.

2.6. Behavioral data

Response times during the fixation cross task were compared in the three groups by one-way ANOVA, with a significance cutoff of $p < 0.05$.

3. Results

3.1. Alternation frequency responses

We quantified the response at 3 Hz after subtraction of baseline noise. We predicted that the adaptation would yield greater responses at 3 Hz in the adapted-no delay and adapted-delay groups than in the control group. Although one-way ANOVA failed to show a significant difference between groups when pooling across channels ($F[2;39] = 2.11$; $p = 0.134$; $\eta_p^2 = 0.10$), clear peaks at 3 Hz were observed under adapted-no delay and adapted-delay conditions focused over right occipito-temporal sites (Fig. 2).

We found that *Condition* had a primary effect on the amplitude of the 3 Hz response ($F[2;39] = 3.36$; $p = 0.045$; $\eta_p^2 = 0.15$). Although there was no significant effect of *ROI* ($F[2;39] = 2.46$; $p = 0.091$; $\eta_p^2 = 0.06$), we observed a significant interaction effect between *Condition* and *ROI* ($F[4;78] = 3.52$; $p = 0.011$; $\eta_p^2 = 0.15$; Fig. 3). Newman-Keuls post-hoc analyses showed that, in the ROT ROI, the response at 3 Hz was greater in the adapted-no delay ($p = 0.005$) and adapted-delay ($p = 0.034$) groups than in the control group, but did not differ between the adapted-no delay and adapted-delay groups ($p > 0.250$).

Assessment of the adapted-no delay group showed that a frequency

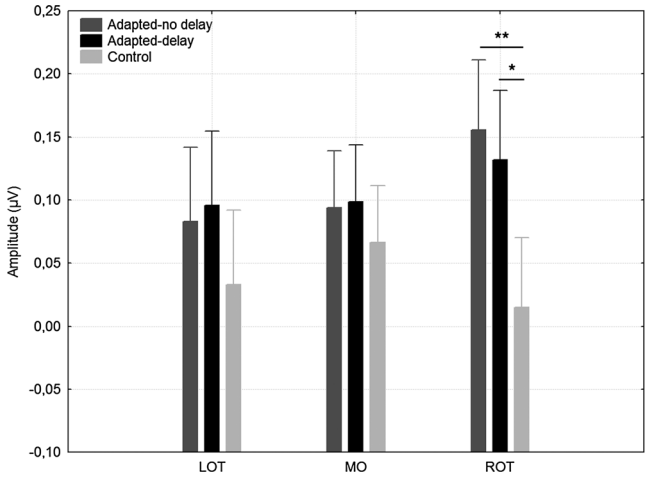

Fig. 3. (Black and white; 1.5 column) Amplitudes (µV) of the response at 3 Hz under adapted-no delay (dark grey bars), adapted-delay (black bars) and control (light grey bars) conditions over the left occipito-temporal (LOT), medial occipital (MO) and right occipito-temporal (ROT) cortices. * $p < 0.050$; ** $p < 0.010$.

of 3 Hz produced a significant response in the ROT ($Z = 3.07$; $p = 0.001$), MO ($Z = 1.66$: $p = 0.049$) and LOT ($Z = 1.83$; $p = 0.034$) ROIs. Analysis of the adapted-delay group showed that the 3 Hz frequency produced significant responses in the ROT ($Z = 2.33$, $p = 0.010$) and MO ($Z = 1.74$, $p = 0.041$) ROIs, but not in the LOT ROI ($Z = 1.62$; $p = 0.053$). In the control group, the 3 Hz frequency did not produce significant responses in any ROI, including the ROT ($Z = 0.61$; $p > 0.250$), LOT ($Z = 0.79$; $p = 0.215$) and MO ($Z = 1.39$; $p = 0.082$) ROIs.

3.2. Fixation cross task

Response times to the fixation cross color changes did not differ in the three groups ($F[2;39] = 1.17$; $p > 0.250$; $\eta_p^2 = 0.03$).

4. Discussion

This study investigated whether the decay over time of the individual face adaptation response is due to the introduction of a novel face in testing sequences or to a natural decay of this effect. Consistent with previous results (Retter & Rossion, 2016b; Retter & Rossion, 2017), we observed an adaptation response at the identity alternation frequency (i.e. 3 Hz), mainly in the right occipito-temporal cortex, following adaptation to a single face identity. However, whereas the adaptation response declined rapidly in the original study, adaptation response persisted after a delay of 9–15 s following the adaptation sequence in the present study. These results suggest that (i) the ultimate decay of the adaptation effect observed in previous studies was likely due to the introduction of a novel face stimulus and (ii) the adaptation effect can persist for at least 15 s in the neural system.

Our hypotheses predicted that, if the adaptation effect is limited in time, adaptation responses should be observed under the “no delay” condition, but not in the “delay” condition. On the other hand, if the decay of adaptation effect is rather due to the introduction of a novel face, adaptation responses should be observed in both “delay” and “no delay” conditions. Our results showed a significant adaptation response in both “delay” and “no delay” conditions, suggesting that the decay of the adaptation response in the previous study was likely due to the introduction of a novel face in the testing sequences.

The amplitude of the adaptation effect did not differ between the two adapting conditions, suggesting that time alone does not explain the decay of the adaptation effect. This decay is rather due to the appearance of new stimulations of the neural system. In the absence of new stimulations, the adaptation effect might be long-lasting, and our results suggest that the duration of adaptation is on the order of 10–15 s at least.

However, these results do not allow excluding the hypothesis of a natural decay of the adaptation effect in time, since we did not test duration longer than 15 s. Therefore, adaptation effect may decline anyway after a certain period of time. Longer delays between adaptation and testing might be needed to more precisely quantify the duration of the adaptation effect.

Although comparing different approaches is difficult, our results are consistent with previous standard ERP studies showing an adaptation effect on N170 amplitude (Jacques et al., 2007; Jacques & Rossion, 2006) and on N250 amplitude (Tanaka et al., 2006), suggesting that adaptation effects might be long-lasting in FPVS as well as in ERP. The rapid decay of the adaptation effect in a previous study using FPVS (Retter & Rossion, 2016b) might not be explained by methodological particularities of FPVS.

Modifications of the paradigm presented here may be particularly appropriate to test individual face discrimination processes in clinical populations. For example, epileptic patients show mild impairment in face recognition, and a much more severe impairment in face recognition after a delay following resection of the right anterior temporal lobe (Milner, Taylor, & Sperry, 1968). Face processing is also impaired in patients with Alzheimer’s disease (Lavallee et al., 2016; Nguyen, Gillen, & Dick, 2014; Werheid & Clare, 2007), along with deficits in episodic and short-term memory, language and attention. Because FPVS provides an objective and quantifiable response without requiring a behavioral response, it may allow the testing of face discrimination processing in Alzheimer patients without the influence of other cognitive deficits due to the pathology.

Declaration of conflicting interests

The authors declare no conflicts of interest with respect to the authorship or publication of this article.

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