Is the rapid adaptation paradigm too rapid? Implications for face and object processing

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Abstract

Rapid adaptation is an adaptation procedure in which adaptors and test stimuli are presented in rapid succession. The current study tested the validity of this method for early ERP components by investigating the specificity of the adaptation effect on the face-sensitive N170 ERP component across multiple test stimuli. Experiments 1 and 2 showed identical response patterns for house and upright face test stimuli using the same adaptor stimuli. The results were also identical to those reported in a previous study using inverted face test stimuli (Nemrodov and Itier, 2011). In Experiment 3 all possible adaptor–test combinations between upright face, house, chair and car stimuli were used and no interaction between adaptor and test category, expected in the case of test-specific adaptation, was found. These results demonstrate that the rapid adaptation paradigm does not produce category-specific adaptation effects around 170–200 ms following test stimulus onset, a necessary condition for the interpretation of adaptation results. These results suggest the rapid categorical adaptation paradigm does not work.

Introduction

Face perception is an important and widely investigated function of the human visual system. Imaging methodologies have revealed brain areas with signal patterns highly sensitive to face processing, such as the middle fusiform gyrus (Kanwisher and Yovel, 2006) in functional magnetic resonance imaging (fMRI) studies, and early face-sensitive markers such as the N170 component in event-related potential (ERP) studies (e.g. Bentin et al., 1996; Itier et al., 2006b) and the M170 in magneto-encephalographic (MEG) studies (e.g. Halgren et al., 2000; Harris and Nakayama, 2008; Itier et al., 2006a). However, these techniques do not provide reliable information regarding the neuronal populations underlying the studied activity. The search for tools that would allow more detailed characterization of these populations has recently attracted attention to the phenomenon of *repetition suppression* (Grill-Spector and Malach, 2001; Naccache and Dehaene, 2001).

Measures as diverse in terms of spatial scales as firing rates of neurons in single-cell recordings (Desimone, 1996; Sobotka and Ringo, 1994), hemodynamic changes in fMRI (Buckner et al., 1998; Sayres and Grill-Spector, 2006; Vuilleumier et al., 2002) and voltage or magnetic changes in electrophysiological studies (Harris and Nakayama, 2008; Henson et al., 2004; Kovács et al., 2006) have often showed reductions in response to repetitive presentations of the same or similar stimuli. These changes have been referred to as *adaptation effect* or *repetition suppression effect* (Grill-Spector et al., 2006). It is not clear whether these effects at different spatial scales reflect the same mechanism or the widely

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studied effect of *cognitive priming* (Henson, 2003). In some cases, however, repetition of stimuli has been reported to result in an increased activity, producing an *enhancement effect* (Eimer et al., 2010; for discussion see Henson, 2003), rather than a response decrease.

Brain imaging researchers used repetition suppression as a tool for tagging populations of neurons sensitive to certain stimulus characteristics. For example, in fMRI studies a usual imaging procedure may not yield a discriminative pattern of activation because it reflects averaged activation of the populations within a voxel (Grill-Spector et al., 2006; Henson, 2003). To overcome this issue, subjects are presented with a certain stimulus type (adaptor) and then again with the same stimulus type (test or T1) in order to establish the extent of response adaptation/ suppression. Then, a second test stimulus (T2), which varies from T1 along the dimension of interest, is presented preceded by the same adaptor. If T2 shows a recovery from adaptation (compared to T1), the researchers conclude that it triggers, at least partially, some new nonadapted neuronal populations and that the voxel indeed contains neurons sensitive to the characteristic of interest. Thus, in the classic fMRI-adaptation method as it was proposed by Grill-Spector and Malach (2001), the comparison is made between responses to different test stimuli, adapted by the same adaptor stimuli.

This method has been adopted in electrophysiological studies which showed categorical adaptation of N170 for faces over a wide range of adaptation protocols (e.g. Amihai et al., 2011; Kloth et al., 2010; Maurer et al., 2008; Schweinberger et al., 2007). However, compared to fMRI studies, the logic behind the adaptation paradigm seems to have changed in electrophysiological studies, with two main variants of the method currently used in the literature. One variant, in accordance with the original fMRI method, compares varying test stimuli preceded by similar adaptors (e.g. Caharel et al., 2009, 2011); another variant compares the same test stimuli preceded by different adaptors (e.g. Eimer et al., 2011; Nemrodov and Itier, 2011). Thus, the difference between experimental conditions in the first variant comes late in the trial, at the level of the test stimulus (test level manipulation or TLM), whereas it comes early in the second variant, at the level of the adaptor stimulus (adaptor level manipulation or ALM).

The main advantage of the ALM design is that it compares responses to the same test stimuli which are assumed to be identical on average and to vary only according to the effects of the preceding adaptors. For example, since it was hypothesized that eye and inverted face stimuli trigger the response of the same neuronal populations sensitive to eyes and faces, whereas upright faces trigger the response of face-sensitive neurons only (Itier et al., 2007), one may predict that presenting eyes as adaptors for inverted faces would yield a stronger reduction of signal to inverted faces (adaptation effect) than presenting upright faces as adaptors for inverted faces. However, the convenience of the adaptor level manipulation design comes at a price. Unlike TLM design, in ALM the differentiation occurs early at the level of adaptors, creating the possibility that late processes triggered by the presentation of different adaptors would affect the response to test stimuli. This point is especially important in view of the short SOA used in some adaptation studies (Eimer et al., 2010, 2011; Harris and Nakayama, 2007, 2008; Nemrodov and Itier, 2011; Vizioli et al., 2010). To address this concern, one needs to demonstrate that the effect obtained using the ALM is specific to the test stimulus used.

We previously reported an ERP study using an ALM adaptation paradigm and showed that adaptor stimuli (various face types presented upright and inverted) produced different modulations of the test stimuli (inverted faces) only when eyes were present in the adaptors (Nemrodov and Itier, 2011). Our focus was on the face-sensitive N170 component recorded in response to the test stimuli and the ISI between adaptors and tests was short (about 250 ms). Houses were used as a control category. The pattern of response was in accordance to

the expected pattern of adaptation effect as test stimuli preceded by houses always yielded larger amplitudes than test stimuli preceded by face stimuli, with the smallest amplitudes obtained for test stimuli preceded by the same adaptor category (inverted faces). Given these results, we assumed adaptation was the underlying mechanism (i.e. inverted faces were adapted by inverted faces but not by houses). However, since we used inverted faces as the only test stimuli, results could not be fully validated.

In Experiment 1 of the present study we intended to validate these results by using houses as our new test category with the same adaptors as used in our previous study. We expected to find an adaptation pattern different from the pattern found in Nemrodov and Itier (2011) that would indicate that the results found in that study were specific to inverted face test stimuli. However, contrary to our expectation the results did not conform to the predictions derived from the adaptation mechanism as houses (test stimuli) preceded by houses (adaptors) again yielded the largest amplitudes, not the smallest as adaptation would predict. Moreover the response modulations of the test stimuli as a function of the adaptor category were virtually identical to the ones reported in our previous study.

In view of the results reported by Eimer et al. (2010) showing adaption-like patterns for upright faces we decided to replicate our experiment once again with upright faces as test stimuli. Experiment 2 used the same design as Experiment 1 using upright faces as test stimuli. The results again deviated from the adaptation predictions and showed a strong similarity to the results obtained in Experiment 1 with houses as test stimuli and those obtained in Nemrodov and Itier (2011) with inverted faces as test stimuli. To examine systematically this invariance of the effects across different test stimuli, Experiment 3 employed a combined 4×4 adaption design with faces, chairs, cars and houses serving as both adaptors and test stimuli. This enabled us to compare adaptation effects of different categories across different categories of test stimuli in the same within-subjects design. If adaptation effects were specific to the category of test stimuli, we expected to find an interaction between categories of adaptors and tests. However, if adaptation effects were indeed invariant across test stimuli, we expected to find no interaction between the categories of adaptors and tests. This would suggest the paradigm employed, i.e. a rapid categorical adaptation, does not work.

Experiment 1

Materials and methods

Participants—Eighteen participants were paid $10/h or awarded course credits for their participation in the experiment. They gave signed, informed consent in accordance to the Research Ethic Board of the University of Waterloo prior to testing. All subjects had normal or corrected-to-normal visual acuity. Two participants were excluded from the final analysis due to an insufficient number of trials per condition after artefact rejection. The remaining 16 participants (6 males) were 18–25 years old (mean age 21 years). All, except one, participants were right-handed.

Stimuli and procedure—Greyscale images of whole faces, mouthless faces, eyeless faces, isolated mouths, isolated eyes, and houses presented upright and inverted, adapted from Itier et al. (2007), as well as flowers (13 categories total) as used in Nemrodov and Itier (2011), were used. Faces (half male, half female) were neutral in expression, showed part of the hair and were of Caucasian individuals. Faces were cropped so the eye region was exactly in the center of the stimuli. Isolated eye images were prepared by cropping the eye region (including eye brows) from faces so that the center of the rectangular eye region was approximately the center of the eyes. Isolated mouths were created by excising a rectangle around the mouth. Eyeless and mouthless faces were produced by substituting eye or mouth

regions with skin-like texture. The images were equated in luminance and contrast by adding pixelized background noise. The SHINE toolbox (Willenbockel et al., 2010, www.mapageweb.umontreal.ca/gosselif/shine) was used to match Fourier amplitude spectra.

Subjects were seated 60 cm in front of a computer 17 in. CRT monitor in a dimly lit room. At this distance, stimuli subtended ~3.8°×10.9° of visual angle. Stimuli were presented using Presentation software (Neurobehavioral Systems, http://www.neurobs.com) which also recorded behavioral responses from a Nintendo game controller. In each trial, two stimuli were presented in quick succession. Participants were instructed to press one button following the second picture presentation, if either the first or the second picture was a sunflower and another button if no sunflower was shown. Response buttons were counterbalanced across subjects.

The research design was an exact replication of our previous adaptation study using inverted face test stimuli (Nemrodov and Itier, 2011), except the test stimuli were now images of upright houses. Each adaptor category contained 44 different images presented twice, 88 times in total. On each trial, the adaptor and test stimuli were presented successively for 200 ms each, separated by one of three equiprobable intervals of 234, 250, and 267 ms, to reduce anticipation of test stimuli (see Fig. 1). Participants were given on average 1500 ms to respond (range 1300–1700 ms) before the next trial started. Only houses and flowers served as tests. During the experiment, 8 pictures from each category were followed by a sunflower thus excluded from further analysis. In addition, sun-flowers appeared 96 times as an adaptor stimulus and were also excluded from analysis. The sunflower image appeared as an adaptor or test with equal probability. Of the 1152 trials presented during the experiment, 960 trials were sunflower free and were kept in the analysis (80 trials for each of the 12 categories). Pictures were presented in random order in four blocks interspaced with self-paced breaks (of 264 pairs of stimuli, 240 containing no flowers and 24 pairs of stimuli containing flowers either as adaptors or tests).

EEG recording and data analysis—The electroencephalogram (EEG) was recorded from 64 Ag/AgCl active electrodes.

(BioSemi Active Two system, the Netherlands: http://www.biosemi.com) mounted on a flexible cap according to the extended international 10/20 system. A Common Mode Sense (CMS) active electrode and Driven Right Leg (DRL) passive electrode serving as ground were used. Eight additional electrodes were added to the standard montage: four electrodes recorded horizontal and vertical eye movements and were placed at the outer canthus and under the center of each eye. Two additional electrodes were placed on the posterior part of the cap on the left and right sides (CB1 and CB2, respectively) and two more electrodes were placed on the left and right mastoids (TP9 and TP10). EEG was digitized at a sampling rate of 512 Hz.

The data were processed using the EEGLab toolbox (Delorme and Makeig, 2004) and ERPLAB toolbox (http://erpinfo.org/erplab) implemented in Matlab (Mathworks, Inc.). Only correct-response trials were analyzed. EEG was epoched offline using a 100 ms pre-adaptor baseline until 400 ms after test stimulus onset. Then, trials were digitally band-pass filtered (0.01–30 Hz) and average referenced. Trials containing artefacts ($>\pm100\,\mu V$) were then rejected. Ocular artefacts were first removed using independent component analysis (ICA) decomposition as implemented in the ADJUST toolbox (Mognon et al., 2011). On average 73.9 (std=11.2; range: 49–80) trials were kept in each condition for each subject. Note that this method ensures an exact correspondence between the trials kept in the average of the adaptor and those kept in the average of the test preceded by this adaptor.

The EEG waveforms were averaged separately for adaptors and tests according to the adaptor category: once locked to the adaptor onset and relative to a 100 ms pre-adaptor baseline (−100 ms to +900 ms from adaptor onset) and once locked to test stimulus and relative to a 50 ms pre-test and 50 ms post-test baseline as done by Eimer et al. (2010) and Nemrodov and Itier (2011) (−50 ms to +500 ms from test onset). N170 components in response to adaptor stimuli were quantified within a 160–220 ms time interval after stimulus onset. The N170 components in response to test stimuli were quantified within a 200–250 ms time interval after stimulus onset. For adaptor and test stimuli, N170 was measured at lateral posterior electrodes CB1 (left hemisphere) and CB2 (right hemisphere), where the amplitudes were maximal for both adaptors and tests; in addition, for test stimuli, N170 was also measured at P7 (left hemisphere) and P8 (right hemisphere) electrodes in order to compare with Eimer et al. (2010).

No adaptor category effect on accuracy was found. For ERP measures of the adaptors three-way repeated-measures analyses of variance (ANOVAs) were performed on N170 peak amplitudes with the factors adaptor category (6), adaptor orientation (2), and laterality (2). For test stimuli, a four-way analysis was performed, which, in addition to the three aforementioned factors, included an electrode pair factor contrasting CB1/2 and P7/8. When the adaptor category by adaptor orientation interaction was significant a further repeated-measures ANOVA was performed for each orientation separately to test for category effects (i.e., adaptor category (6)×laterality (2)) and for each adaptor category separately to test for orientation effects (i.e., adaptor orientation (2)×laterality (2)). For all analyses and in all subsequent experiments, Greenhouse–Geisser corrections to the degrees of freedom were performed where appropriate and Bonferroni corrections were used for multiple comparisons.

Results

Adaptor stimuli analysis—An initial analysis conducted on ERP peak amplitudes revealed an interaction of adaptor category with orientation ($F(5,75)=11.64$, $p<0.001$) (see Fig. 2A). Follow-up analyses of upright adaptors showed a main effect of adaptor category ($F(5,75)=28.89$, $p<0.001$) due to amplitudes decreasing in the following order: eyes followed by mouth, mouthless faces, whole faces, eyeless faces and houses. Post hoc tests revealed that houses elicited lower amplitudes than all the other categories ($p<0.002$ for all comparisons). Isolated eyes elicited higher amplitudes than both whole faces and eyeless faces ($p<0.05$). No other difference between the categories was found. A main effect of adaptor category was also found for inverted stimuli ($F(5,75)=44.62$, $p<0.001$), with amplitudes decreasing in the following order: mouthless faces, whole faces, eyes, eyeless faces, mouth and houses. Post hoc comparisons showed again that houses elicited lower amplitudes than all other stimuli ($p<0.001$ for all comparisons). Mouths also elicited smaller amplitudes than mouthless faces ($p<0.05$). Finally eyeless faces elicited smaller amplitudes than whole faces and mouthless faces (both comparisons at $p<0.05$). When each adaptor category was analyzed separately, only whole faces and mouthless faces showed an inversion effect ($p<0.001$ for both).

Peak latency analysis of the adaptors showed a main effect of orientation ($F(1, 10)=50.09$, $p<0.001$) and a main effect of adaptor category ($F(5,50)=4.46$, $p=0.025$). Inverted stimuli (mean=205.2; S.E.=2) tended to peak later than upright stimuli (m=200; ±2.23). The latency for adaptor categories decreased in the following order: mouths, eyeless faces, eyes, houses, mouthless faces and whole faces. Post hoc comparisons showed a delayed latency for mouth (significantly compared to whole faces, $p=0.02$ and mouthless faces, $p=0.047$). Latencies for eyeless faces were also delayed compared to whole faces ($p=0.018$).

Test stimuli (upright houses) analysis according to preceding adaptor categories—A four-way ANOVA on peak amplitudes in response to upright houses yielded a main effect of electrode pair ($F(1,15)=6.17$, $p=0.025$), with CB1/2 showing larger peak amplitudes than P7/8 electrodes. In addition, main effects of orientation ($F(1,15)=24.72$, $p=0.011$) and adaptor category ($F(5,75)=12.86$, $p<0.001$) were found (see Figs. 2 and 3). Smaller (less negative) amplitudes were found for upright house test stimuli adapted by inverted ($-1.36\,\mu V \pm 053$) than by upright adaptors ($-1.72\,\mu V \pm 0.51$). The largest amplitudes were found for house-adapted test stimuli ($p<0.015$ for all comparisons, except for isolated mouths), followed by mouth-adapted test stimuli (significantly compared to eyes, $p=0.005$) with the smallest amplitudes seen for test stimuli adapted by the other categories.

A four-way ANOVA on peak latency yielded a main effect of electrode pair ($F(1,15)=4.59$, $p=0.049$), with CB1/2 electrodes yielding earlier peaks than P7/8 sites (223.9 ms ±2.86 vs. 227 ms ±2.97 respectively). In addition, a main effect of adaptor category ($F(5,75)=3.03$, $p=0.025$) was found. Post hoc analyses revealed that the responses to house tests preceded by house adaptors peaked slightly earlier than the responses to house tests preceded by mouthless face adaptors (222.17 ms ±2.94 vs. 227.77 ms ±2.87, respectively).

Discussion

Analysis of the adaptors showed the classic pattern of sensitivity to faces, with larger N170 responses to facial stimuli than to houses (Bentin et al., 1996; Itier and Taylor, 2004). Eyes also elicited larger responses than other facial stimuli, conforming to the well-established pattern (Bentin et al., 1996; Itier et al., 2006b, 2007b, 2011). Finally, the inversion effect was confined to whole faces and mouthless faces and not present for eyeless faces (Itier et al., 2007, 2011).

However, the results at the test level were inconsistent with the predictions of the adaptation method according to which the response to houses preceded by house adaptors should have yielded maximum adaptation (i.e. smallest amplitudes). In contrast, largest amplitudes (or smallest adaptation) were found for house test stimuli adapted by houses, which could reflect an enhancement mechanism. One possible explanation for this result is that, because N170 is not preferentially sensitive to houses, it does not follow the same adaptation pattern for houses as for faces. Experiment 2 tested this possibility, using upright faces as test stimuli. Based on the results reported by Eimer et al. (2010) we expected to find an adaptation pattern, with upright face adaptors yielding the strongest adaptation response.

Experiment 2

Materials and methods

Participants—Twenty three participants were paid $10/h or participated for course credits and gave signed, informed consent as approved by the Research Ethic Board of the University of Waterloo prior to testing. All subjects had normal or corrected-to-normal visual acuity. Seven participants were excluded from the final analysis due to an insufficient number of trials per condition after artefact rejection (since the N170 amplitude for S2 was diminished, we ensured that all conditions had a minimum of 60 trials, which resulted in 7 participants being eliminated). The remaining 16 participants (11 males) were 19–22 years old (mean age 20 years). All participants were right-handed except for one left handed.

Stimuli and procedure—The EEG recordings and pre-processing, stimuli and procedure were identical to Experiment 1 and to Nemrodov and Itier (2011), except that test stimuli were now upright faces. The same analyses were used as in Experiment 1 except the time

window of the N170 component was 150–210 ms for both adaptor and test level analyses (defined after inspection of the data). There were 78 (std=3.4; range 64–80) trials on average per condition per subject. No effects of adaptor on accuracy were found.

Results

Adaptor stimuli analysis—Omnibus analysis of the N170 amplitude (see Fig. 2) showed a main effect of laterality ($F(1,15)$=4.77, p=0.045), due to larger amplitudes at CB1 than CB2 electrodes. Laterality did not interact with any of the other factors. An interaction between orientation and adaptor category ($F(5,75)$=7.7, p<0.001) was found so post hoc analyses were performed for each adaptor category and each orientation separately. A main effect of orientation was found for eyeless faces ($F(1,15)$=5.98, p=0.027), mouthless faces ($F(1,15)$=15.53, p<0.001) and whole faces ($F(1,15)$=25.42, p<0.001) but not for isolated eyes, isolated mouths and houses. When inverted faces were analyzed separately a main effect of adaptor category was found ($F(5,75)$=22.81, p<0.001). Post hoc comparisons revealed that all facial adaptor categories elicited larger amplitudes than houses (p <0.005 for all comparisons), but did not differ significantly between themselves. The analysis of upright faces also revealed a main effect of the adaptor category ($F(5,75)$=22.19, p <0.001), with amplitudes decreasing in the following order: eyes, mouths, eyeless faces, mouthless faces, whole faces and houses. Houses elicited smaller amplitudes than all upright facial stimuli (p <0.002 for all comparisons). The N170 was also larger for isolated eyes than eyeless faces (p =0.007), mouthless faces (p <.0001) and upright whole faces (trend, p =0.062) which did not differ.

Omnibus analysis of the N170 peak latency yielded an interaction between orientation and adaptor category ($F(5,75)$=8.29, p<0.001). Post hoc analyses showed that inversion delayed the N170 peak for all stimuli (p<0.004) except mouths and houses.

Test stimuli (upright faces) analysis according to preceding adaptor categories—A four-way ANOVA on peak amplitudes in response to upright face tests yielded a main effect of electrode pair ($F(1,15)$=7.66, p=0.014), with CB1/2 electrodes showing the largest peak amplitudes. In addition, main effects of orientation ($F(1,15)$=10.35, p=0.006) and adaptor category ($F(5,75)$=12.78, p=0.003) were found. Post hoc comparisons showed that amplitudes to upright face test stimuli were largest when they were adapted by houses than by any other adaptor category (p<0.009 for all comparisons) (Figs. 2 and 3). No other comparisons were significant. Finally, a two-way interaction between electrodes and orientation ($F(1,15)$=8.99, p=0.009) was found. Post hoc analyses revealed amplitudes to upright face tests were larger when preceded by upright than inverted adaptors and this difference was more pronounced for CB1/2 than P7/8 electrodes.

The N170 peak latency analysis yielded a significant interaction between orientation and category ($F(5,75)$=3.02, p=0.028). A separate analysis of test stimuli preceded by face adaptors did not yield a significant effect of orientation. Upright face test stimuli adapted by houses in contrast, produced a significant orientation effect (p=0.049), with earlier N170 peaks for test stimuli preceded by inverted than upright house adaptors (193 ms ±4.24 vs. 196 ms ± 4.44 respectively).

Discussion

As in Experiment 1 the adaptor results showed the classic larger N170 amplitudes for faces than houses, for inverted than upright faces and for eyes than faces. Although at first glance, the larger amplitude for face tests preceded by houses than by face-related stimuli seems compatible with an adaptation effect, a closer look suggests otherwise. The test stimuli results showed a strikingly similar pattern of results as that found in Experiment 1 and a lack

of specific adaptation advantage for upright faces as amplitudes to upright face tests were larger rather than smaller, when preceded by upright than inverted face adaptors, in contrast to what the adaptation paradigm would predict. In fact, a visual comparison of the results between the three experiments (the first two of the present paper and the study reported by Nemrodov and Itier, 2011) showed a striking similarity in the pattern (see Fig. 3), which could not be accounted for by chance and which is inconsistent with any known model of face processing.

In the previous experiments (Experiments 1, 2 and in Nemrodov and Itier, 2011) face-related stimuli were presented more frequently than house stimuli, which may have caused a cumulative effect of increased adaptation to the face-related category of stimuli. In order to address this problem and in view of the results' pattern, a third experiment was run which combined features of ALM and TLM and allowed comparing adaptation results between different adaptors across different test stimuli. If the test results reflected category-specific adaptation or enhancement mechanisms, we expected to find an interaction between the adaptor and test categories. If, however, as suspected, there was no specific effect of adaptors on the response to different test stimuli, we expected to find only main effects for the adaptors and for the test stimuli.

Experiment 3

Materials and methods

Participants—Seventeen participants were paid $10/h or participated for course credits and gave signed, informed consent as approved by the Research Ethic Board of the University of Waterloo prior to testing. All subjects had normal or corrected-to-normal visual acuity. One participant was excluded from the final analysis due to too many ocular artifacts. The remaining 16 participants (10 males) were 18–23 years old (mean age 20.7 years). All participants were right-handed, except for one left handed.

Stimuli and procedure—Stimuli consisted of upright faces, houses and the sunflower picture used in the previous experiments, as well as gray-scale images of chairs and cars. Chairs were all in three-quarter right views while cars were all in front views. Forty images of each category were equated in luminance and contrast by adding pixelized background noise. The SHINE toolbox (Willenbockel et al., 2010, www.mapageweb.umontreal.ca/gosselif/shine) was used to match Fourier amplitude spectra.

The EEG recordings and pre-processing, task, experimental settings and trial composition were as in the two previous experiments. The experimental design contained 16 combinations of stimulus categories (faces, chairs, cars and houses) in adaptor and test positions, varied orthogonally. Each combination was presented 72 times. Each image was presented in pseudorandom order about 15 times during the experiment. A sunflower picture was presented 128 times during the experiment either as an adaptor or test stimulus (16 catch trials with each stimulus category). A total number of 1280 trials were presented in 8 blocks. It was ensured that each adaptor and test shared a similar number of faces of each gender. The number of trials per category and number of catch trials were equal in each block. A short training session was performed prior to the beginning of the experiment, which contained a different, but similarly manipulated set of stimuli. The time window for analysis of the N170 recorded to the adaptors was 180–240 ms post-stimulus onset and 150–250 ms post stimulus onset for the test stimuli. At the test stimulus level CB1/2 pair yielded the strongest amplitudes. At the adaptor level CB1/CB2 pair yielded the second strongest amplitude after P9/P10 pair. However, amplitudes or latencies at these electrodes were not significantly different compared to the other electrodes and the same pattern of activation was seen. Thus, for consistency with the test-level analysis in this experiment and with all

the analyses in the other experiments, CB1/2 were chosen for the adaptor analysis and CB1/2 and P7/8 pairs for the test analysis. On average the number of trials per condition per participant was 60.8 (std=9.3, range 34–72).

No significant differences were found in accuracy analysis. The analyses of ERP measures used a 2 laterality (left hemisphere, right hemisphere)×4 adaptor categories (faces, houses, cars, chairs) ANOVA for adaptor stimuli and a 2 electrodes (CB1/2, P7/8)×2 laterality (left hemisphere, right hemisphere)×4 adaptor categories (faces, houses, cars, chairs)×4 test categories (faces, houses, cars, chairs) ANOVA for the test stimuli.

Results

Adaptor stimuli analysis—Analysis of N170 amplitudes (see Fig. 4A) showed a main effect of adaptor category ($F(3,45)=25.22$, $p<0.001$) with faces and cars yielding larger amplitudes than chairs and houses ($p<0.009$ for all comparisons) which did not differ. The interaction between laterality and adaptor category ($F(3,45)=5.76$, $p=0.014$) was also significant. Post hoc analyses revealed that the laterality effect was found only for chairs and houses with larger amplitudes at CB1 than CB2 ($p<0.02$). In addition, amplitudes for faces tended to be larger than for cars ($p=0.062$) at CB1 and CB2 ($p=0.034$).

Latency analysis of N170 peak yielded a significant main effect of adaption category ($F(3,45)=31.59$, $p<0.001$) and a significant main effect of laterality ($F(3,15)=5.5$, $p=0.033$). N170 peaked earlier at CB1 (209.3 ms ±3.53) than at CB2 (213.7 ms ±2.89). Cars triggered later peaks than any other category ($p<0.001$ for all comparisons). N170 peaks were later for houses than faces and chairs ($p<0.002$ for all comparisons) which did not differ. Thus the contrasts revealed the following pattern of N170 latencies: faces=chairs<houses<cars.

Test-stimuli analysis according to preceding adaptors—The analysis of the amplitudes recorded to the test stimuli showed a main effect of electrode pair ($F(1,15)=6.98$, $p=0.019$), with CB1/2 showing larger N170 amplitudes than P7/8 (−4.15 μV ±0.51 vs. −3.46 μV ±0.53). A main effect of adaptor category ($F(3,45)=33.95$, $p<0.001$) was found (Figs. 4A–B). When comparing the amplitude in response to test stimuli according to the preceding adaptor categories, the following pattern was found: house>chair>face>car ($p<0.04$ for all comparisons). That is, test stimuli (regardless of the category) yielded larger amplitudes when preceded by houses than by chairs, faces or cars. A main effect of test category ($F(3,45)=22.05$, $p<0.001$) was also found. The largest test amplitudes were triggered by test cars and faces (which did not differ), followed by houses and chairs which did not differ ($p<0.015$ for all comparisons). Most importantly, no interaction between adaptor and test category was found ($p=0.9$).

For N170 latency, a main effect of electrode pair was found ($F(1,15)=4.68$, $p=0.047$), such that CB1/CB2 showed later peaks than P7/8 (215.4 ms ±3.14 vs. 210.9 ms ±2.9). In addition, an interaction between adaptor and test categories was found ($F(9,135)=2.79$, $p=0.024$). When car tests were analyzed separately, a main effect of the adaptor category was found ($F(3,45)=9.68$, $p=0.001$) such that car test stimuli adapted by cars yielded a significantly earlier N170 peak than car test stimuli adapted by the other categories ($p<0.011$ for all comparisons). A separate analysis of house test stimuli also yielded a main effect of adaptor category ($F(3,45)=5.1$, $p=0.006$) such that house test stimuli adapted by chairs yielded a delayed N170 peak compared with house test stimuli adapted by cars and houses ($p<0.025$ for all comparisons). For chairs and face test stimuli no main effect of adaptor category was found.

As it appeared from inspection of the waveforms that the P1 component might also show adaptation effects, we analyzed this component at the test level. The analysis of P1

amplitudes (see Fig. 4C) yielded a main effect of adaptor category ($F(3,45)=15.57$, $p<0.001$) and an interaction between adaptor and test categories ($F(9,135)=3.67$, $p=0.006$). Separate post hoc analyses revealed that car-adapted test stimuli yielded larger amplitudes than house-adapted test stimuli regardless of the test categories ($p<0.026$ for all). Car-adapted stimuli also yielded significantly larger amplitudes than chair-adapted stimuli for all tests stimuli except cars ($p<0.012$ for chair, house and face tests). Face-adapted stimuli yielded larger amplitudes than house- and chair-adapted stimuli for car and chair test stimuli but not for house and face test stimuli for which the difference between face, house and chair-adapted stimuli was not significant.

Discussion

These results confirm our previous conclusion that adaptors do not affect the N170 amplitude in response to test stimuli in a specific and differentiating way. The pattern showed main effects of test and adaptor categories which did not interact. Particularly, house-adapted stimuli produced the largest N170 amplitudes, as was also found in Experiments 1 and 2 and in some previous studies (Eimer et al., 2010; Nemrodov and Itier, 2011) irrespective of the test category.

Interestingly, the analysis of P1 component in Experiment 3 did show an interaction effect between adaptor and test stimuli. The results (see Fig. 4C) indicated that the three object test stimuli shared similar adaptation patterns while face test stimuli differed because of reduced amplitudes for face-adapted stimuli. However this interaction does not reflect a true face specific adaptation at the P1 level. In order to have a true face specific adaptation, amplitudes for face test stimuli should have been even smaller (i.e. maximally adapted) when preceded by face adaptors than chairs or house adaptors, which was not the case. The overall pattern of adaptation for face tests was very similar to that of the other object tests. These results thus confirm the lack of category specific adaptation seen at the N170 level and will not be discussed further.

General discussion

In the current study we aimed at validating the rapid categorical adaptation method that we used previously with inverted face test stimuli (Nemrodov and Itier, 2011), in order to test a model of the neuronal populations involved in early face processing (Itier et al., 2007). Since this method manipulates adaptors (adaptor level manipulation or ALM) and measures responses to test stimuli presented at a later stage, it is essential to ensure that the results do not only differ as a function of adaptor category, but that they also are test-stimulus specific. We thus presented two kinds of test stimuli (houses in Experiment 1 and upright faces in Experiment 2), using the same adaptors as used previously with inverted face test stimuli (Nemrodov and Itier, 2011). As expected, these experiments showed different response amplitudes to different test stimuli (see Fig. 3), with overall larger responses for face tests than for house test stimuli. However, contrary to the expectations of the adaptation method, the qualitative pattern elicited by different adaptors was not test stimulus specific but rather identical across the different test stimuli, i.e. inverted faces (used in Nemrodov and Itier, 2011), houses and upright faces. Specifically, face-related adaptors produced stronger amplitude reductions at the test level than house adaptors, regardless of the test category used. Because face and face-related stimuli were more numerous than object (house) stimuli, we were concerned that the overall adaptation advantage for these stimuli might be due to these differences in proportions rather than to true adaptation effects.

In order to explore further this lack of specificity of adaption effects and to ensure the proportion of face-related stimuli was not an issue, we employed a combined method consisting of a number of adaptors and tests (houses, faces, cars and chairs) in a within-

subject paradigm (Experiment 3). We expected that adaptor categories would interact with test categories. In contrast, the results showed main effects of adaptor and test stimuli without their interaction. The main effect of test category showed the classic larger amplitudes for face-related stimuli compared with object stimuli. The main effect of adaptor category showed the surprising and consistently larger amplitudes of test stimuli in response to houses compared to the other adaptor categories, a result that was also found in Experiments 1 and 2, in Nemrodov and Itier (2011) and in Eimer et al. (2010). The lack of interaction effect at the N170 level in this third experiment indicates that the adaptation effect is not specific to a given test stimulus, hence the method cannot serve as a basis to draw conclusions regarding the involvement of neuronal populations in face processing. Importantly, this noninteractive pattern of results was found for a variety of test stimuli and adaptor stimuli, both face and object categories (see Fig. 4).

These findings underscore the necessity of validating adaptation results by employing control test stimuli. The classic formulation of the adaptation method assumes a decrease in the signal following repetitive presentation of the same stimulus and a signal recovery following presentation of the same adaptors with different test stimuli (Grill-Spector and Malach, 2001; Grill-Spector et al., 2006). However, in electrophysiological studies, adaptation is sometimes measured as a decrease in response to test stimuli preceded by the same stimulus compared to the response to the same test stimuli preceded by a different (control) adaptor stimulus (e.g. Eimer et al., 2010, 2011; Harris and Nakayama, 2008; Nemrodov and Itier, 2011). In this case the choice of the control category is critical, since it validates the adaptation effect and sometimes serves as a basis for measuring the amount of adaptation obtained with the other adaptor categories (Eimer et al., 2011). The results of the current study cast doubt on the validity of using houses as a control category for categorical adaptation studies (Eimer et al., 2010, 2011; Harris and Nakayama, 2008; Nemrodov and Itier, 2011).

The reason for the lack of interactive effects between adaptors and test stimuli in the current study is not clear. Category specific adaptation effects, especially for the face stimuli, have been shown in a number of studies (e.g. Amihai et al., 2011; Kloth et al., 2010; Kovács et al., 2006; Maurer et al., 2008). However, these studies differed from the current study in terms of procedure (e.g. two adaptors in Amihai et al., 2011 or block presentation in Maurer et al., 2008) and used longer SOA (ranging from 1128 ms to 5000 ms) between adaptor and test stimuli than in the present set of studies. Shorter SOA, as employed in the rapid adaptation paradigm, may lead to an adaptor-locked interference at the test stage. The SOA between adaptor and test presentations in the current experiments was about 450 ms on average (with 16 ms jitter). This means that the N170 component in response to a test stimulus was recorded around 400–450 ms following the N1/N170 response to the adaptor, which makes the interference between the processes likely. In fact, the visible baselines in the studies employing this paradigm are often not aligned horizontally suggesting a non-random effect (Amihai et al., 2011; Eimer et al., 2010; Nemrodov and Itier, 2011; Werheid et al., 2005), as also found in the present studies (Figs. 2 and 4). To the best of our knowledge this interference effect was directly investigated in only one MEG study by Harris and Nakayama (2007) who concluded that the S2 response is not dependent on S1 amplitude. However in their study only the adaptors varied, while the test stimuli remained the same (faces), so they were unable to test the specificity of their effects. Their results, coupled with the results of the current study, make it clear that the adaptation should be assessed not only in terms of adaptor (ALM) effects, but also in terms of test stimulus (TLM) specificity.

The interference explanation views the possible carry-over response from adaptors as an artifact at the test level. However, an alternative explanation to the lack of category

specificity but involving true adaptation mechanisms could be considered. Researchers employing the adaptation paradigm focus on the populations of neurons recruited and often neglect the intensity of the response. It is well known that many neurons in the visual system are tuned to the optimal presentation of stimulus properties (Desimone et al., 1984; Kayaert et al., 2005). Assuming that the neurons are sensitive to all the categories of stimuli presented in the current experiments (rather than being category specific), but have different tuning properties for these categories, it would be expected that all test stimulus categories are affected by the adaptors approximately to the same degree. For example, if the neuronal populations involved in the generation of the N170 are sensitive to both faces and houses, the N170s to both faces and houses at test would be affected by earlier presentation of these stimuli as adaptors and the extent of the effect would be directly proportional to the neurons' tuning to these categories. This tuning mechanism may underlie the lack of categorical specificity of the adaptation effect.

Grill-Spector et al. (2006) have proposed three models to account for the adaptation effects: neuronal fatigue, which reflects a reduction in firing rates of the affected population; sharpening, which reflects a sparser representation of repeated stimuli; and facilitation which reflects a shorter duration of neural firing periods for repeated stimuli. If indeed the results we report stem from the differentiated excitability of the same neuronal population in response to different stimulus categories, the neuronal fatigue would provide a suitable model to account for the reduction of the signal at the test level. Specifically the hyperpolarization of the membrane potential due to changes in ion currents upon repetitive presentation may serve as a potential neuronal mechanism for such fatigue (Gollisch and Herz, 2004). A short time scale of these changes may also account for the discrepancy between our results and the results of the studies employing longer SOA, which may rely on different adaptation mechanisms (sharpening or facilitation). Our results provide indirect support for the neuronal fatigue adaptation mechanism in a category-tuned neuronal population: cars and faces, which showed a larger activation at the adaptor level than chairs and houses thus presumably triggering a larger neuronal fatigue, also showed stronger adaptation potential at the test level. The possible existence of separate adaptation mechanisms at short and long time scales needs to be further investigated.

How justified is, then, the use of the rapid adaptation method? It has two important advantages. First, it uses short SOAs, which presumably increases the chance that adaptors will adapt test stimuli (Harris and Nakayama, 2007). Second, it conveniently reduces the length of the trials, so more conditions can be presented during the same session. However, this comes with the risk for contamination of test activity with adaptor activity or confound of the results and poor baseline that makes the interpretation of adaptation results difficult. Longer exposure to stimuli (which thus increases the adaptor–test SOA) may also produce more valid repetition suppression effects. The current results suggest that while rapid stimulus presentation may or may not lead to adaptation effects, the paradigm should not be used without prior validation, both in terms of response suppression and in terms of specificity of the effects. In any case, it should be kept in mind that short and long term exposure may produce different adaptation effects (Harris and Nakayama, 2007; Kovács et al., 2007; Pavan et al., 2010; Weiner et al., 2010) and this needs to be further investigated.

Our conclusions are naturally limited to the particular temporal parameters used in the current experiments. The temporal characteristics of methods used for repetition priming/ adaptation may vary in accordance to stimulus presentation times and SOA. Some studies used a comparatively short presentation time, but a long inter-stimulus interval, resulting in a longer SOA (e.g. Campanella et al., 2011; Schweinberger et al., 2002), others used a longer exposure time for the adaptor stimuli (e.g. Caharel et al., 2009; Jacques and Rossion, 2007; Kovács et al., 2006). Rapid adaptation methods range from short 250 ms SOA

(Werheid et al., 2005) to 550 ms (Vizioli et al., 2010) with many studies using SOAs between 400 and 500 ms (Eimer et al., 2010, 2011; Harris and Nakayama, 2007, 2008; Nemrodov and Itier, 2011). Competition paradigms, where the prime (context) stimulus stays on during the presentation of the test stimulus, are usually performed with SOA around 600 ms (e.g. Jacques and Rossion, 2004, 2006; Jacques et al., 2007; Rossion et al., 2004; Sadeh and Yovel, 2010) and may also be problematic. There is an urgent need to check to what extent different time scales of rapid adaptation methods share the problematic pattern of results of the current study.

None of the studies employing rapid adaptation or priming methods reached conclusions similar to ours. Some did not compare different test stimuli (Harris and Nakayama, 2007, 2008; Jacques and Rossion, 2004). Others had adaptors undifferentiated at the level of prime presentation (e.g. identity priming, Vizioli et al., 2010). Werheid et al. (2005) employed a 2 (happy or angry test faces)×2 (happy or angry adaptors) design and did not find a significant interaction between test and adaptor variables, a result similar to ours in that their priming effect was not specific to a particular emotion valence at test. Finally, two studies employing a method very similar to the one employed in the present study yielded a different pattern of results (Eimer et al., 2010, 2011). In order to make our findings comparable to the results of these studies we analyzed peaks of N170 at the electrodes that were used in their study (P7/8) in addition to the electrodes that yielded maximum amplitudes in the current experiments (CB1/2). Unlike the present study, these studies reported an interaction between test and adaptor stimuli, suggesting that the adaptation effects found were category specific. There were, however, a number of minor dissimilarities between the methods. Eimer et al. (2010, 2011) used a slightly shorter (400 ms) and unjittered SOA. While stimuli in Eimer et al. (2010) were by and large similar to our face-related stimuli (although stimuli employed in the present study were equated in luminance and frequency content), the adaptors in Eimer et al. (2011) were schematic faces. A number of recent studies have shown that noisier stimuli tend to produce lower amplitudes in early components (Bankó et al., 2011; Jemel et al., 2003; Nasr and Esteky, 2009). It is possible that our results were somewhat affected by the noise introduced to equate stimuli in luminance, contrast and amplitude spectra. The latencies of the N170s at test were indeed a little delayed, a result consistent with the effect of noise-level increase (Jemel et al., 2003). However, N170 latencies and amplitudes at the adaptor level were in the normal range and showed a similar pattern to what has been reported by studies using the same stimuli but non-equated for low level contents (e.g. Itier et al., 2007, 2011). We thus do not believe that noise alone is the reason for the lack of category specific adaptation although this remains a possibility that awaits investigation.

In conclusion, the results of the current study highlight the necessity of including control test stimuli in the early manipulation method of adaptation in order to ensure that the adaptation effects are specific to the test categories. More importantly, the results cast doubt on the validity of the rapid adaptation paradigm for N170 measures. Note that we do not claim there is no adaption at all when using the rapid adaptation paradigm, but that this paradigm should not be used without prior validation that the effects seen are category specific. In addition, adaptation mechanism for different paradigms (different procedures, stimulus presentation, SOA etc.) may be considerably different. The implications of these findings are important for designing further ERP adaptation studies and suggest caution in the interpretation of previously published findings, including our own.

Acknowledgments

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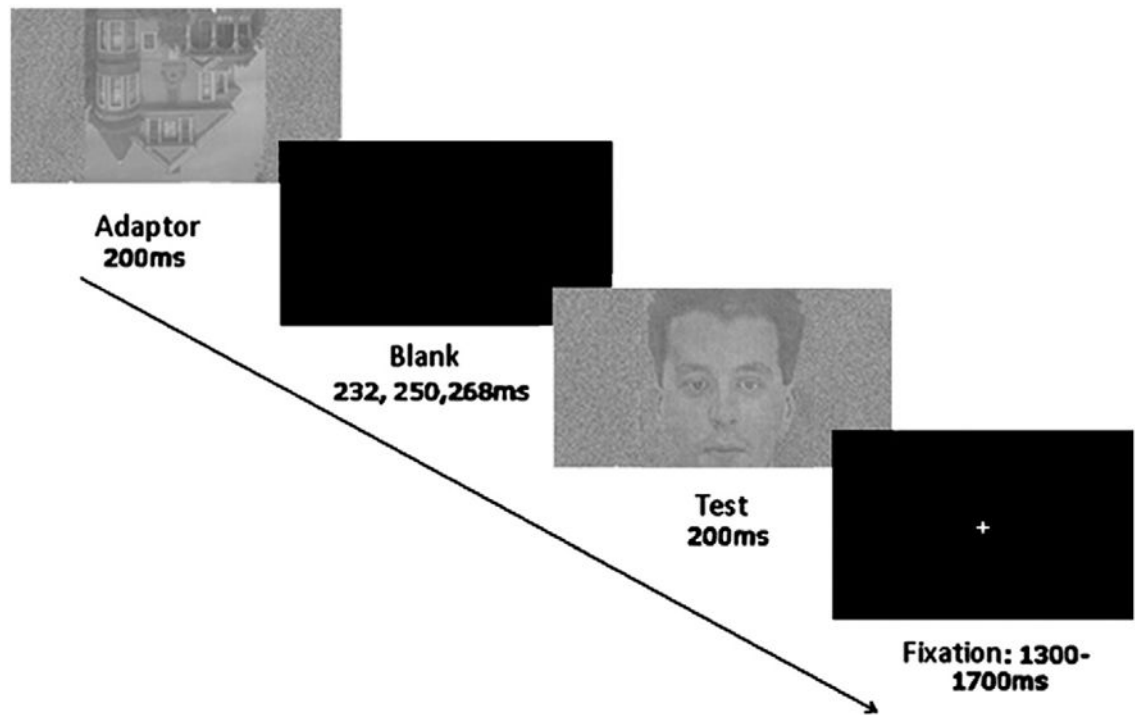
Fig. 1.
Example of a trial as used in the studies.
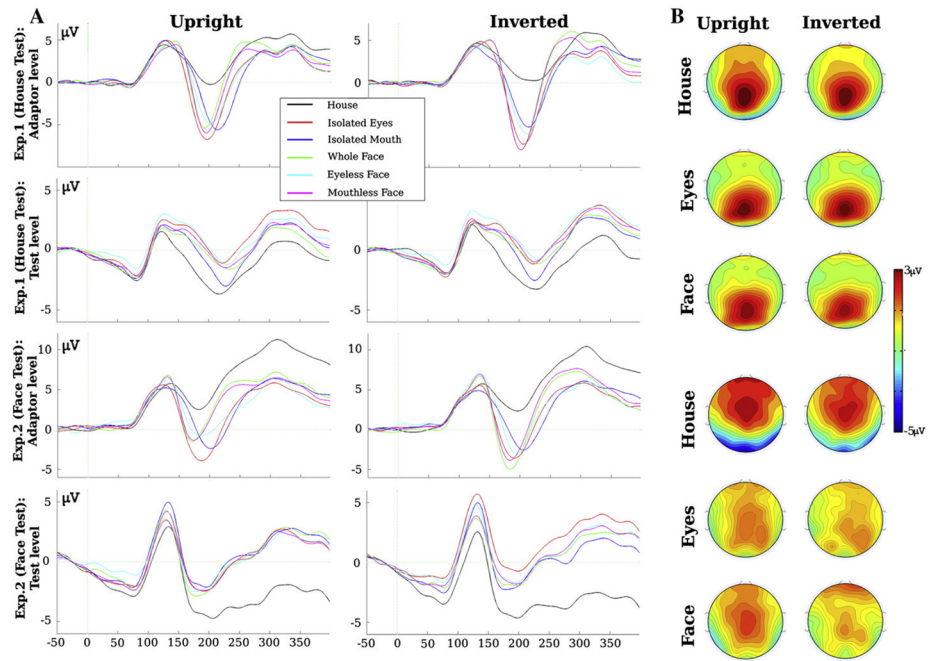
Fig. 2.
(A) Grand-averaged ERPs obtained in Experiment 1 (four top plots) with upright houses as test stimuli and Experiment 2 (four bottom plots) with upright faces as test stimuli, here presented at the right posterior electrode CB2, for upright (left plots) and inverted (right plots) categories respectively. The ERPs recorded to the adaptors showed the classic face-sensitive N170 component increase for inverted faces and isolated eyes compared to upright faces. The ERPs recorded to the test stimuli as a function of the preceding adaptor categories showed roughly similar patterns of responses across the two different test stimuli. (B) Topographic maps showing the scalp voltage distribution for the N170 peak recorded after test stimuli presentation for three key adaptor categories: houses, isolated eyes and faces.
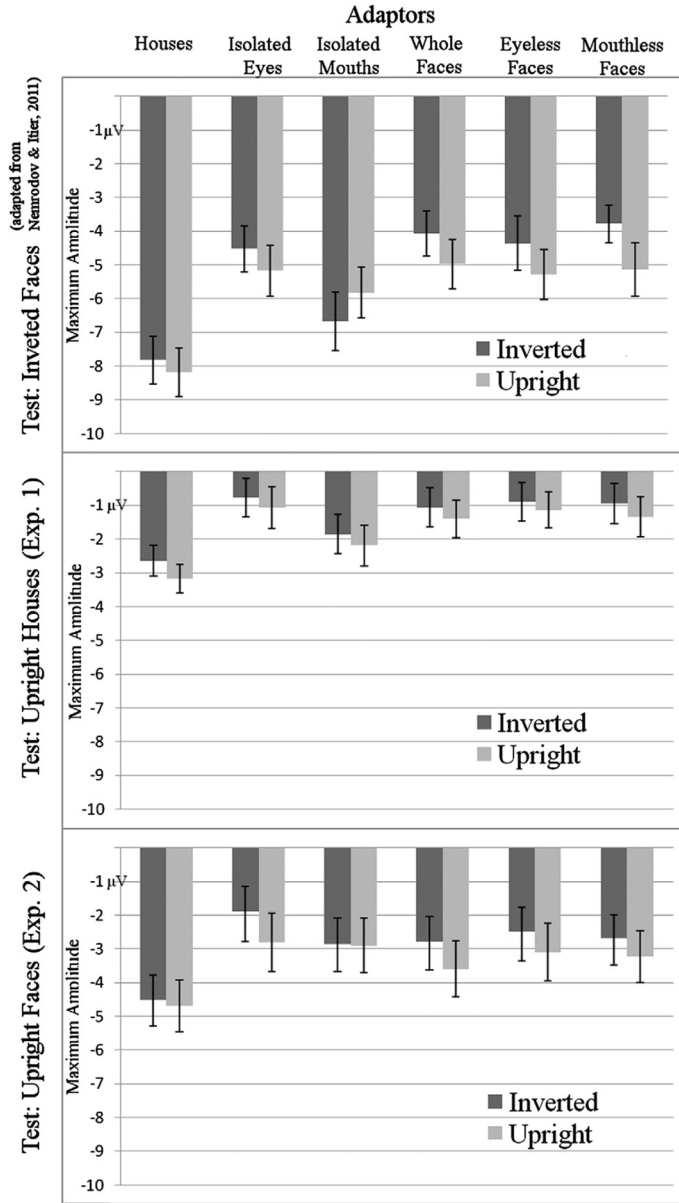
Fig. 3.
Top panel: mean N170 amplitudes in response to inverted face tests for each adaptor category, averaged across CB1 and CB2 sites (adapted from Nemrodov and Itier, 2011). Middle and bottom panels: mean N170 amplitudes in response to house (Experiment 1) and upright face (Experiment 2) test stimuli, for each adaptor category, averaged across CB1/2 and P7/8 sites. Bars represent standard errors. Similar adaptation effects are seen across conditions in all three experiments despite the use of a different test stimulus.
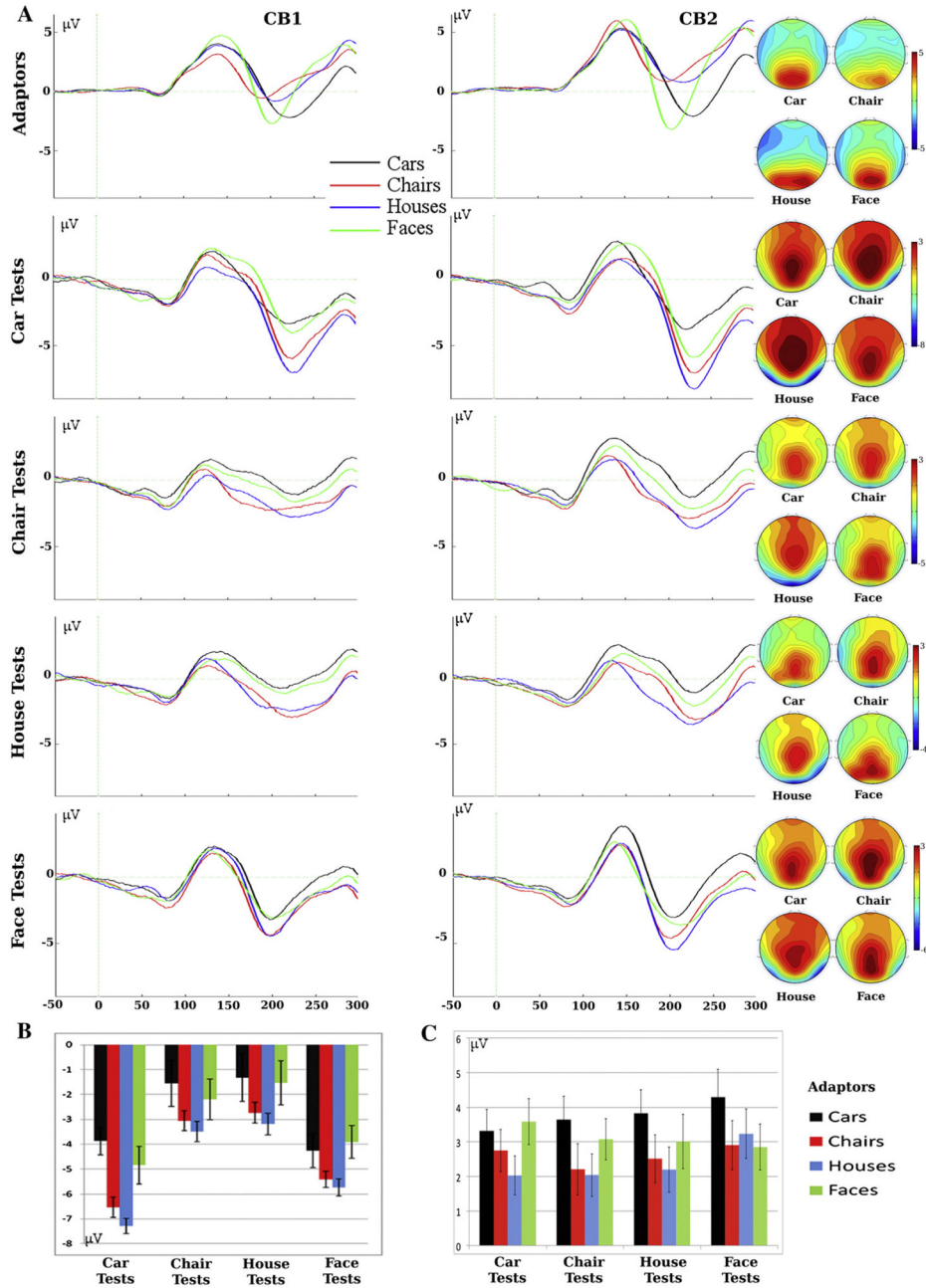
Fig. 4.
Results of Experiment 3. (A) ERPs obtained at the posterior electrodes CB1 (left) and CB2 (right) in response to adaptors and to test stimuli separated by adaptor categories, with topographic maps showing voltage distribution at the N170 peaks. (B) Mean N170 amplitudes for each test stimulus according to each adaptor category. Bars represent standard errors. No interaction between adaptor and test categories was found and the same pattern of results can be clearly seen regardless of the test category. (C) Mean P1 amplitudes for each test stimulus according to each adaptor category. Bars represent standard errors.