

Adaptation effects in facial expression recognition

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The effect of adaptation on facial expression recognition was investigated by measuring how identification performance of test stimuli falling along a particular expression continuum was affected after adapting to various prototype emotional faces or a control pattern. The results showed that for recognition of fear, happiness, and sadness, inhibition effects were observed on recognition of test expressions following 5 s adaptation to the same emotion, suggesting different neural populations tuned for the encoding of fearful, happy, and sad expressions. Facilitation of recognition of test stimuli differing in emotion to the adapting stimulus was also sometimes observed. The nature of these adaptation effects was investigated by introducing a size transformation or a delay between adapting and test stimuli and was found to survive these changes. The results of a further experiment argued against a criterion effect being the major source by demonstrating the importance of adapting time in generating the effects. Overall, the present study demonstrates the utility of adaptation effects for revealing functional characteristics of facial expression processing.

The ability to recognize facial expressions is thought to be part of our evolutionary heritage and to rely upon finely tuned neural mechanisms in the brain. Neurophysiological studies in macaques have found that facial expressions may elicit selective responses from single neurons in the superior temporal sulcus (Hasselmo, Rolls, & Baylis, 1989). Neuropsychological (Adolphs, Tranel, Damasio, & Damasio, 1994; Sprengelmeyer et al., 1996) and neuroimaging data (Breiter et al., 1996; Morris et al., 1996; Phillips et al., 1997) with humans have also suggested that recognition of some distinct facial expressions engages specific neural circuits. Although various brain regions have therefore been correlated with facial expression recognition, the nature of their contributions remains unresolved.

The act of seeing is so effortless that it is difficult to appreciate the sophisticated mechanisms underlying it. However, the structure of the visual system

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is sometimes exposed by illusory effects, which can serve as a powerful window into the neural architecture of vision. Adaptation effects or aftereffects are one of these phenomena, which are experienced after a period of prolonged constant stimulation. They have long been regarded as a way of probing the workings of visual processing by desensitizing the contribution of specific neural populations. Recent research has introduced the idea of using adaptation to investigate visual processing in high-order domains, revealing that the effects could occur at a level of visual representation where the coding of images was shape specific but nonretinotopic (Susuki & Cavanagh, 1998) and moreover, the effects could even be induced for subordinate-level encoding of shapes as complex as faces (Webster & Maclin, 1999). In the study of face identity recognition (Leopold, O'Toole, Vetter, & Blanz, 2001), high-level adaptation effects were also demonstrated to be a feasible tool to explore the neural mechanisms relevant for extraction of identity. Following a 5 s exposure to one face, the perceived identity of a second face was significantly biased, suggesting the presence of highly specific networks of neurons involved in differentiating face identity.

On the other hand, little evidence has been furnished to investigate the representation of facial affect with utilization of adaptation techniques. A behavioural test has found that viewing one facial expression shifted the intensity rating and category descriptor of an emotion seen in a subsequent expression (Russell & Fehr, 1987), which at least suggests that adaptation effects in facial expression recognition could be possible. Given the above research, it might be possible to adapt the neural populations tuned for encoding facial expressions and thereby generate expression-based aftereffects.

In Experiment 1, adaptation was therefore employed as an experimental tool to verify the presence of aftereffects in facial expression recognition. To establish the generality of the effects, the same phenomena were replicated using another sample of materials in Experiment 2. We then considered whether the contribution of these expression-specific neural populations could be further characterized from these effects. Subsequent experiments were implemented to investigate the spatial (Experiment 3) and temporal characteristics (Experiment 4) of the effects by manipulating the size and the time parameters of the stimuli. On the one hand, manipulating these variables allows us further to explore the nature of expression-specific aftereffects. On the other hand, because of the functional role of adaptation to temporarily isolate and diminish the visual processing relevant for expression representations, such manipulations may influence the potency of adaptation effects and in turn provide insight into the intrinsic properties of facial expression processing. Lastly, Experiment 5 was designed to investigate whether the adaptation effects observed can be interpreted as the results of criterion effects or desensitization of neural populations.

EXPERIMENT 1

The basic paradigm used in this study was as follows: An adapting stimulus was presented for a few seconds, and succeeded by a test expression after a delay. Then, participants had to make a judgement of the expression shown in the test stimulus. To examine the relationship between adaptation and facial expression recognition, participants' identification baseline for the test expressions was established from adaptation to a random-noise image. The effects of adaptation to different expressions were measured by comparing to this baseline condition.

Happiness, sadness and fearful expressions were selected for use in the experiment, to represent a range of basic emotions. The control image consisted of black dots randomly distributed in a rectangle having the same size as that of adapting and test stimuli; a copy is shown in Hsu (2003). Previous experimental work has also included a neutral face as one of the adapting stimuli. However, the results have shown that participants' identification performance did not differ following adaptation to either the neutral face or the random-noise image (Hsu, 2003). As a consequence, the random-noise image was selected as the control stimulus in this study.

The test expression stimuli adopted in the experiment were created by morphing a neutral face toward the prototype expressions of fear, happiness, or sadness in equal interpolated steps. Therefore, for fearful, happy, or sad test expression recognition, one might expect that a psychometric curve would be obtained, in which higher identification accuracy follows increasing level of morphing. This identification profile may then serve as a good candidate to be probed by expression adaptation, allowing a sensitive measure of whether a few seconds of exposure to an emotional face could alter identification performance.

Method

Participants. Thirteen females and three males contributed data used for analysis. A total of 19 participants were run, but three participants were excluded because of high missing data rates, as explained below. The participants were students and staff from the University of York. All had normal or corrected to normal vision.

Materials. Three continua of morphed facial expressions of the model JJ were taken from the FEEST (Young, Perrett, Calder, Sprengelmeyer, & Ekman, 2002), a facial expression image database: (1) Neutral to fearful expression, (2) neutral to happy expression, and (3) neutral to sad expression. In each continuum, the neutral facial expression was morphed 10%, 20%, 30%, 40%, 50%, and 60% of the physical distance to the other expression: Fear, happiness, or sadness. For a more detailed description of the morphing procedure see Young et al. (2002). These six morphed images in each neutral to prototype

continuum were used as test stimuli for participants to recognize in the experiment. In addition, three prototype expressions of JJ's face showing fear, happiness, or sadness from the same image set were used as adapting stimuli. As explained, a figure with a random-noise dot pattern was adopted as the adapting stimulus for the baseline control. The images were displayed in 256 grey scale on the centre of a computer monitor with 1024×768 spatial resolution and an eye-screen distance of 60cm. All images used were $7.6^\circ \times 10.8^\circ$ in size.

Procedure. Each trial began with an adapting stimulus displayed for 5000 ms. The adapting stimulus was either the prototype expression of fear, happiness, sadness, or the control (random-noise pattern) image. Then an interstimulus interval (ISI) of 100 ms was introduced. The ISI was immediately followed by a test stimulus presented for 50 ms, which was one of the morphed expressions from the three continua. A blank screen was presented at the offset of the test stimulus and participants had up to 2500 ms to respond.

Prior to the experiment, the participants were instructed to inspect the adapting stimulus (continuously but without a specific fixation point), and then to choose which one of three emotion categories (fear, happiness, and sadness) best described the test stimulus by pressing a labelled button as quickly as possible. The choices of the categories were recorded. The ordering of the response buttons was counterbalanced across the participants. No performance feedback was given during the whole experiment. To acquaint the participants with the procedure, the experiment began with 24 practice trials, selected at random. Following practice, 18 test stimuli ($3 \text{ continua} \times 6 \text{ morphs}$ in each continuum) with each of four adapting stimuli were presented in five separate blocks, resulting in a total of 360 trials for each participant. The order of the trials was randomized within each block and a short break was given between every block of trials.

Results

On some trials, participants did not respond within 2500 ms, resulting in missing data. These missing responses were counted as incorrect identifications. The missing data rate ranged from 0% to 4.2% except for three of the participants, whose missing data rates were greater than 5%. The data from these three participants were not analysed.

To provide background information concerning how participants classified the various test stimuli, the percentages of incorrect responses to each test emotion were computed under the control adaptation. The results showed that for fearful test morphs, the identity of errors was random; that is, participants did not consistently mistake fearful morphs for happiness or for sadness. Of all incorrect responses, 49.6% and 50.4% of fearful morphs were classified as "sadness" and "happiness" respectively. On the other hand, for 84% of

incorrect responses for happy morphs, participants responded to happy morphs as "sad" faces, whereas for 75% of incorrect responses for sad morphs, participants responded to sad test expressions as "happy" faces.

The main purpose of the experiment was to establish whether there was an overall difference in recognition of the test stimuli according to the type of adapting stimulus, and whether this involved facilitation or inhibition of recognition of each emotion relative to the baseline condition. Therefore, for each adapting condition, the number of correct identifications throughout the range of levels of fearful, happy, or sad test stimuli was first calculated, leading to an accuracy score out of a possible maximum of 30. After that, the score was converted into a proportion correct for recognition of fearful, happy or sad test stimuli following adaptation to fearful, happy, sad, or control stimuli for each participant. The results for all participants are plotted in Figure 1, which shows the impact of adaptation on overall identification performance of each test stimulus type. The obtained proportions were then transformed using the arcsine transformation before being analysed. This procedure improved conformity of data to the standard assumptions of an ANOVA (Howell, 1997). Moreover, all the values reported in ANOVA analyses were Geisser-Greenhouse adjusted whenever the sphericity assumption was violated.

For each test emotion, the data were entered into a one-way repeated measures ANOVA. The factor of interest was the adapting stimulus type, which had four levels (the prototype expressions of fear, happiness, sadness, and the control random-noise image). For fearful test stimuli, this ANOVA revealed a significant main effect of the nature of the adapting stimulus, $F(1.83, 27.47) = 18.09$, $MSE = 0.83$, $p < .001$, indicating an effect of adapting stimuli on identification performance. In order to explore whether performance following a specific adapting condition is significantly different from the baseline condition, a priori t -tests with a Bonferroni correction were carried out. The analyses showed that compared to the control condition, participants were less accurate at identifying fearful morphs under the fearful adapting condition ($p < .05$), whereas performance with the fearful morphs was improved under the happy adapting condition ($p < .01$) and the sad adapting condition ($p < .05$). For happy test stimuli, there was also a main effect of adapting stimulus, $F(3, 45) = 24.76$, $MSE = 1.38$, $p < .001$, with pairwise comparisons showing that adaptation to a happy emotional face impaired the identification of happy test stimuli ($p < .01$) but previous exposure to a sad face enhanced performance ($p < .01$). For sad test stimuli, an ANOVA revealed a similar significant main effect of the adapting stimulus type, $F(3, 45) = 20.21$, $MSE = 1.82$, $p < .001$, in which identification performance of sad test stimuli was significantly reduced under the sad adapting condition ($p < .01$) but was improved under happy adaptation ($p < .05$). In sum, the overall results demonstrated inhibition and facilitation effects on identification of each test emotion from different types of adapting stimuli. However,

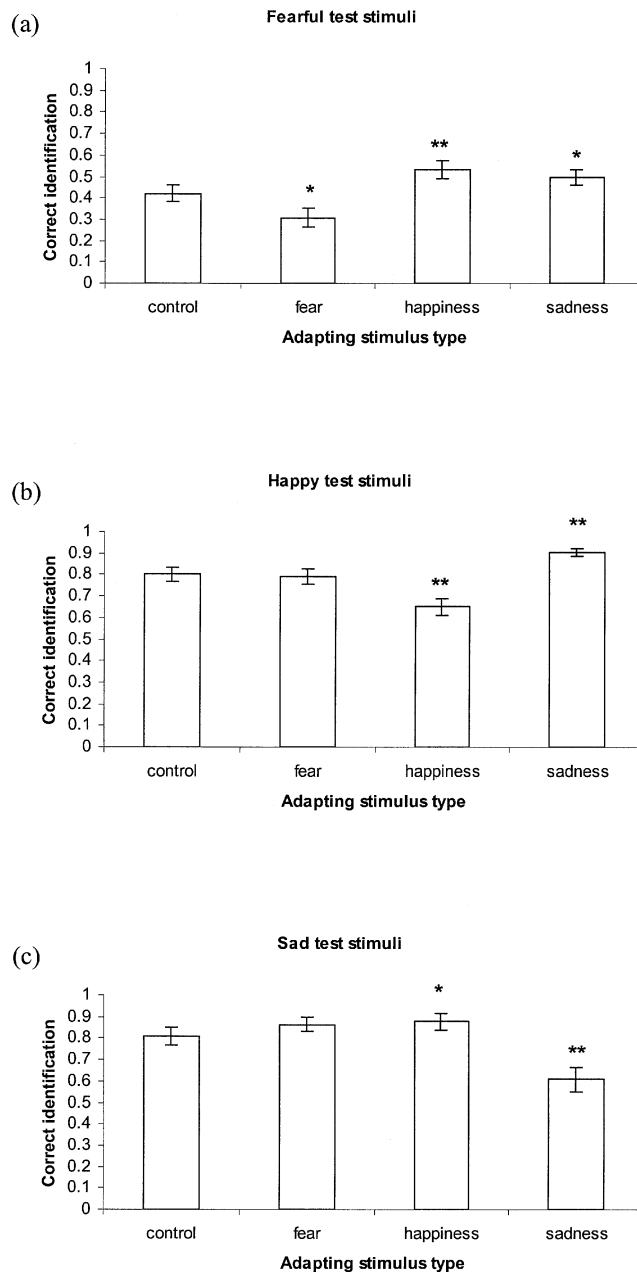


Figure 1. Identification performance of (a) fearful, (b) happy, and (c) sad test stimuli following different types of adapting stimuli. The y axis represents the proportion of trials in which participants made the correct judgements, i.e., “fear” in (a), “happiness” in (b), and “sadness” in (c). The asterisks indicate a significant difference between the control and adapting condition revealed by Bonferroni *t*-tests (* $p < .05$; ** $p < .01$). Error bars represent \pm SE.

we consider that it is also informative more closely to examine these effects by level of morphing of the test stimuli.

To better understand which range of test morphs actually contributed the difference, the number of correct identifications was computed at each level of test stimulus strength and again converted into a proportion for each participant. For each emotion continuum, the correct identification rates of individual morphed faces under the four adapting conditions for all participants are plotted in Figure 2. Figure 2 shows that increments of physical morphing correspond to increased sensitivity in recognition of test morphs, as was expected. Furthermore, baseline identification of happy and sad test morphs starts at higher identification rates in 10% morphing and reaches a monotonic plateau at a lower level of physical morphing than that of fearful morphs. These different psychometric profiles indicate that levels of morphs are not equivalent across these three test expressions.

After arcsine transformation, the data were submitted for a further analysis. As can be seen in Figure 2, for each test emotion, the psychometric curves are skewed after adapting to the various adapting stimuli. To explore whether the psychometric curve of a particular test emotion obtained under the control condition was altered according to the adapting stimulus type, three separate two-way repeated measures ANOVAs were performed for each test emotion continuum respectively, to examine the interaction of the nature of the adapting stimulus with expression strength of the test stimulus. The within-subject variables were adapting stimuli, which had four levels (the prototype expressions of fear, happiness, sadness, and the control image), and facial expression strength of the test stimulus, which had six levels (10, 20, 30, 40, 50, and 60% morphed images). All the values reported in ANOVA analyses were also Geisser-Greenhouse adjusted whenever the sphericity assumption was violated.

For the fearful expression test continuum, the analysis revealed a statistically significant interaction between the nature of the adapting stimulus and the expression strength of the fearful test stimulus, $F(6.04, 90.67) = 2.75$, $MSE = 0.74$, $p < .05$. For the happy expression test continuum, there was also a significant interaction between the adapting stimulus and the strength of the happy test stimulus, $F(6.49, 97.37) = 3.62$, $MSE = 0.97$, $p < .01$. For the sad expression test continuum, marginal significance was found for the adapting stimulus \times the strength of sad expression interaction, $F(6.43, 96.42) = 2.11$, $MSE = 0.50$, $p = .05$. Taken together, these significant interaction effects indicate that in each emotion category, differential identification profiles arose under different adapting conditions.

A series of Bonferroni *t*-tests were used to further compare the means between each adapting and the control condition at each level of morphing of the test stimuli. As Figure 2 shows, these analyses showed that adaptation to a happy or a sad face caused the subsequently presented corresponding expression to be recognized less readily (for 10%, 30% happy and 10%, 40% sad morphs,

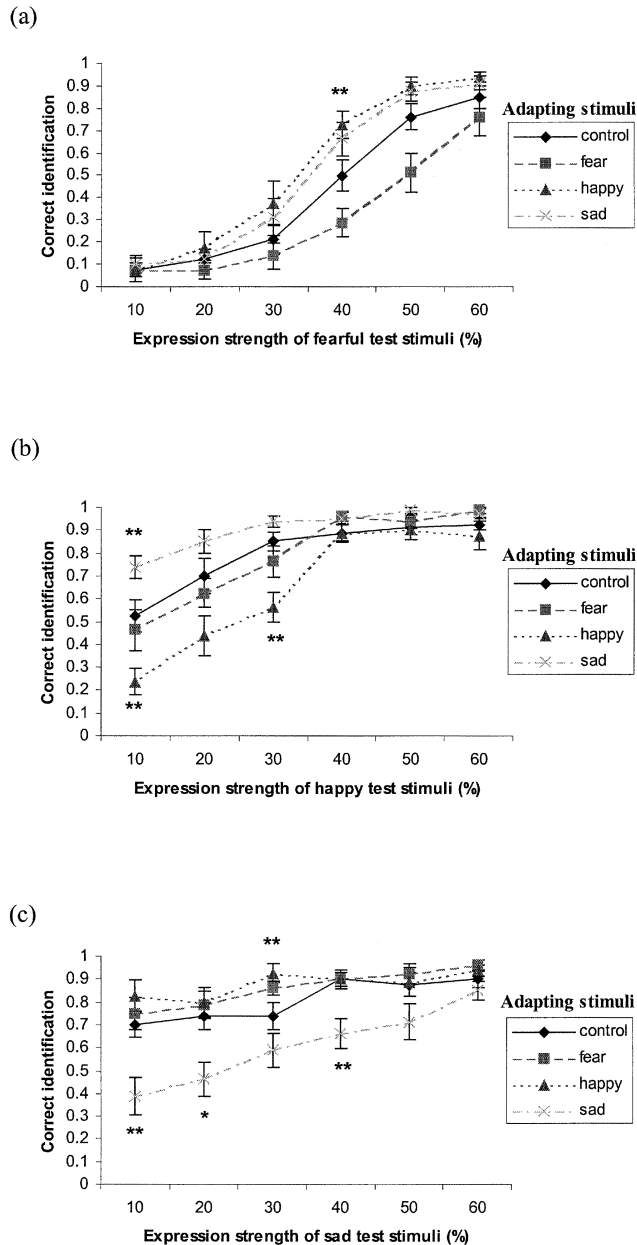


Figure 2. Sensitivity to different levels of strength of (a) morphed fearful, (b) morphed happy, and (c) morphed sad expressions with previous exposure to various adapting stimuli. The y axis represents the proportion of trials in which participants made the correct judgements, i.e., “fear” in (a), “happiness” in (b), and “sadness” in (c). For each test stimulus, the asterisks indicate a significant difference between the control and adapting condition revealed by Bonferroni *t*-tests (* $p < .05$; ** $p < .01$). Error bars represent \pm SE.

$p < .01$; for 20% sad morph, $p < .05$). Participants' identification of the 40% fearful test stimulus was also impaired following adaptation to the prototype fearful expression, as the difference between the control and the fearful adaptation was marginally significant ($p = .07$). In general, these results are in keeping with the inhibition effects reported from the previous overall analyses, showing that exposure to a prototype facial emotion could impair the subsequent recognition of morphed expressions from the same emotion category. Furthermore, some facilitation effects were also found using the Bonferroni t -tests. Adaptation to the prototype expression of happiness could aid subsequent recognition of 40% fearful and 30% sad morphs ($p < .01$), whereas recognition of 10% happy morphs was enhanced with previous exposure to the prototype expression of sadness ($p < .01$).

Discussion

The present results demonstrated that adaptation to a prototype facial expression had a significant impact on categorization of a following morphed test expression. Interestingly, the inhibition effects were circumscribed in that they mainly involved prior adaptation to the same type of facial emotion. That is, when preceded by a few seconds of exposure to an emotional face, a test expression from the same emotion category was recognized less accurately. Adaptation effects are widely thought to reflect the result of the fatigue of specific neural populations tuned for particular visual functions. As a consequence, the presence of such behaviour in expression aftereffects suggests the existence of distinct neural populations in which fearful, happy, and sad expressions are optimally tuned.

Facilitation effects were also found in the current experiment. For instance, exposure to a prototype sad expression facilitated the subsequent recognition of a happy expression and vice versa. However, as is evident from the response curves, participants exhibited high sensitivity on identifying morphed happy and sad expressions and the performances reached ceiling when the expression to be identified was at strength 40% or higher. Such ceiling performance might therefore mask some facilitation effects. Since evidence of facilitation was patchier than evidence of inhibition, the discussion in the following experiments will mainly focus on the inhibition effects, whereas the implications of all facilitation phenomena will be grouped and discussed in the General Discussion.

EXPERIMENT 2

Having established the presence of an adaptation effect in facial expression recognition, it was considered important to demonstrate that the results could be generalized across stimulus material; that is, that the effect was not confined to the particular model used. In Experiment 2, we therefore employed another

sample of the same three types of expression continua from a different model, MO, to test whether the effects still remained.

Method

The forced-choice procedure and time parameters from Experiment 1 were used, except that morphed test faces and adapting expressions of model MO were substituted for JJ. These face stimuli again were taken from the FEEST database (Young et al., 2002).

Participants. Data from 13 females and 3 males were used for analysis. A total of 18 participants were run. Two participants were excluded because of high missing data rates as explained below. None of them had taken part in Experiment 1.

Results

In Experiment 2, the missing data rate for the participants ranged from 0% to 2.5% except for two of them, whose missing data rates exceeded 5%. The data from these two participants were therefore not submitted for further analysis. As before, an arcsine transformation was carried on all data before analysis and the analyses were identical to those performed in Experiment 1.

For fearful test stimuli, a one-way ANOVA revealed a significant main effect of the nature of the adapting stimulus, $F(1.91, 28.65) = 35.70$, $MSE = 1.54$, $p < .001$. The follow-up Bonferroni t -tests showed that compared to the control condition, participants were less accurate at identifying fearful morphs under the fearful adapting condition ($p < .01$) but that performance across all the fearful morphs was improved under the happy ($p < .01$) and the sad adapting condition ($p < .01$). For happy test stimuli, there was also a main effect of adapting stimulus, $F(3, 45) = 42.73$, $MSE = 1.27$, $p < .001$, with pairwise comparisons showing that adaptation to a happy emotional face impaired the identification of happy test stimuli ($p < .01$) but performance was improved with previous exposure to a sad ($p < .01$) and a fearful face ($p < .05$). For sad test stimuli, an ANOVA revealed a similar significant main effect of the adapting stimulus type, $F(3, 45) = 7.12$, $MSE = 0.40$, $p < .01$, in which identification performance of sad test stimuli was significantly reduced under the sad adapting condition ($p < .05$). All these results are shown in detail in Figure 3.

We then further analysed the data at different levels of test stimulus strength (Figure 4). For the fearful expression test continuum, a two-way repeated measures ANOVA revealed a statistically significant interaction between the nature of the adapting stimulus and the expression strength of the fearful test stimulus, $F(7.23, 108.42) = 4.63$, $MSE = 1.41$, $p < .001$. For the happy expression test continuum, there was also a significant interaction between the adapting stimulus and the strength of the happy test stimulus, $F(6.22, 93.35) =$

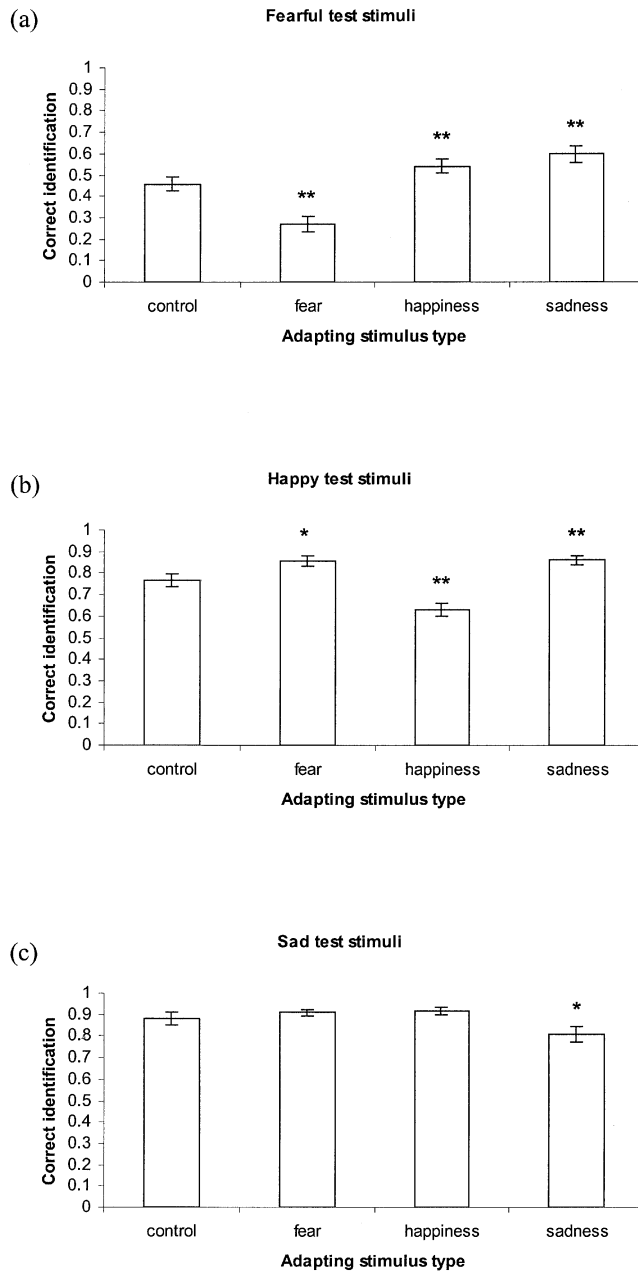


Figure 3. Identification performance of (a) fearful, (b) happy, and (c) sad test stimuli of model MO following different types of adapting stimuli. The y axis represents the proportion of trials in which participants made the correct judgements, i.e., “fear” in (a), “happiness” in (b), and “sadness” in (c). The asterisks indicate a significant difference between the control and adapting condition revealed by Bonferroni *t*-tests (* $p < .05$; ** $p < .01$). Error bars represent \pm SE.

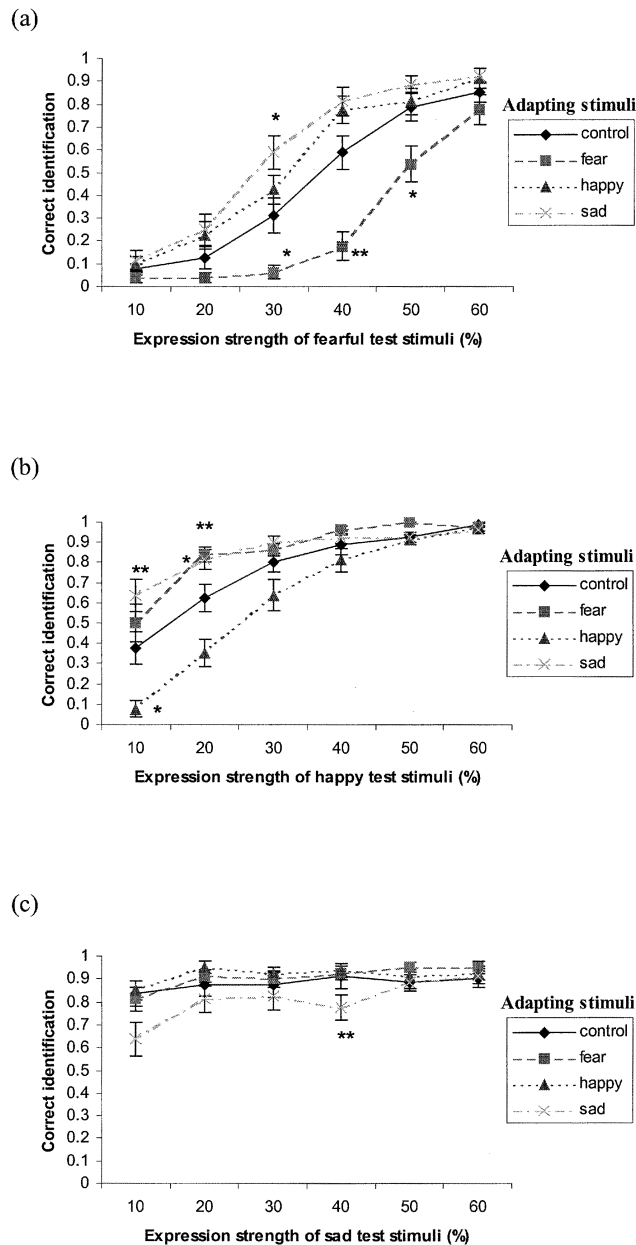


Figure 4. Sensitivity to different levels of strength of (a) morphed fearful, (b) morphed happy, and (c) morphed sad expressions with previous exposure to various adapting stimuli, using model MO's face. The y axis represents the proportion of responses in which participants made the correct judgements, i.e., "fear" in (a), "happiness" in (b), and "sadness" in (c). For each test stimulus, the asterisks indicate a significant difference between the control and adapting condition revealed by Bonferroni *t*-tests (* $p < .05$; ** $p < .01$). Error bars represent \pm SE.

5.84, $MSE = 1.59$, $p < .001$. For the sad expression test continuum, the interaction between the nature of adapting stimulus and the expression strength of the sad test stimulus did not show any difference, $F(15, 225) = 1.08$, $MSE = 0.29$, $p = .38$. Because there is an effect of diluting the overall F in the situation where several group means are equal to each other but different from some other mean (Howell, 1997), the nonsignificant interaction effect in sad test expression recognition is likely due to evident ceiling performance in recognition of MO's sad morphs at strength greater than 10%.

Next, a series of Bonferroni t -tests were performed at individual levels of test conditions, as was done for Experiment 1. These pairwise comparisons showed that previous exposure to a prototype expression impaired subsequent recognition of corresponding test stimuli (see Figure 4 for details). On the other hand, identification performance for happy test stimuli was enhanced with previous adaptation to the prototype expression of sadness and fear. In addition, adaptation to a sad face also facilitated subsequent recognition of fearful morphs.

Discussion

The overall analyses revealed a similar pattern of an adaptation effect in facial affect recognition. As was found in Experiment 1, exposure to an emotional face for a few seconds could impair subsequent perception of a morphed facial expression from the same emotion category. Thus, the consistency in producing altered identification performances of the test stimuli prepared from another model (MO) demonstrates that the observed inhibition effect is a general phenomenon and not unique to the interactions among a particular set of stimuli.

EXPERIMENT 3

From the primary visual cortex along the ventral visual stream to the inferotemporal cortex, there is good evidence to suggest that cells show an increase in receptive field size and that the coding of the cells becomes more robust over the types of transformation encountered in object vision, such as scaling or translation (for a review, see Riesenhuber & Poggio, 2002). An important characteristic of aftereffects for orientation (Blakemore & Campbell, 1969) and spatial frequency (Blakemore, Nachmias, & Sutton, 1970) is that they are sensitive to translation transformation. That is, test stimuli have to be presented at the site of adaptation in order to obtain the effect. This is consistent with the observation that cells responding to the perception of orientation (Hubel & Weisel, 1968) and spatial frequency (de Valois, Albrecht, & Thorell, 1982) are located in the primary visual cortex, where the cells have retinotopic receptive fields.

On the other hand, complex object recognition engages higher visual areas beyond the primary visual cortex and is to a large extent invariant to stimulus transformations. Findings from single-cell recordings in the monkey, for

instance, have shown that face-selective neurons are broadly tuned for face size (Rolls & Baylis, 1986). If the adaptation effects demonstrated in the present study manifest a neural interaction in the higher visual areas, adaptation should still generate significant effects on the subsequent perception of facial affect even when the size of the test stimulus is changed with respect to the adapting stimulus. Furthermore, if the impact of adaptation on recognition of test expressions is robust over a size transformation, this would provide evidence that expression aftereffects might arise at a level of visual representations where the coding is object-form specific (in this case, facial expressions) and are not simply a combination of low-level aftereffects for orientation and spatial frequency.

Method

Participants. Twelve females and three males participated in the experiment. The participants were students from the University of York. Only one of the participants had taken part in a previous experiment in this series.

Materials. Other than the size change between adapting and test stimuli, the stimuli used in this experiment were the prototype expressions of JJ and their respective morphs from Experiment 1. At the viewing distance of 60 cm, the images used as test stimuli were always $7.6^\circ \times 10.8^\circ$ in size, the same size used in previous experiments. On the other hand, the size of adapting stimuli was $15.0^\circ \times 20.8^\circ$.

Procedure. The same general procedure described for Experiment 1 was used in the present experiment.

Results

All participants produced satisfactory response rates, with missing data rates ranging from 0% to 4.4%. The details of data processing and analyses are the same as described before. A one-way repeated measures ANOVA was first carried out to examine identification performance of each test emotion according to the adapting stimulus type. The ANOVA revealed a significant main effect of the nature of the adapting stimulus for fearful test stimuli, $F(2.25, 33.74) = 14.42$, $MSE = 0.37$, $p < .001$. As is shown in Figure 5, Bonferroni *t*-tests showed that compared to the control condition, participants were less accurate at identifying fearful morphs under the fearful adapting condition ($p < .01$), whereas performance with fearful morphs was improved under the happy adapting condition ($p < .05$). There was also a main effect for happy test stimuli, $F(1.97, 29.56) = 14.90$, $MSE = 0.63$, $p < .001$, with pairwise comparisons showing that adaptation to a happy emotional face impaired the identification of happy test stimuli ($p < .05$) but previous exposure to a sad face

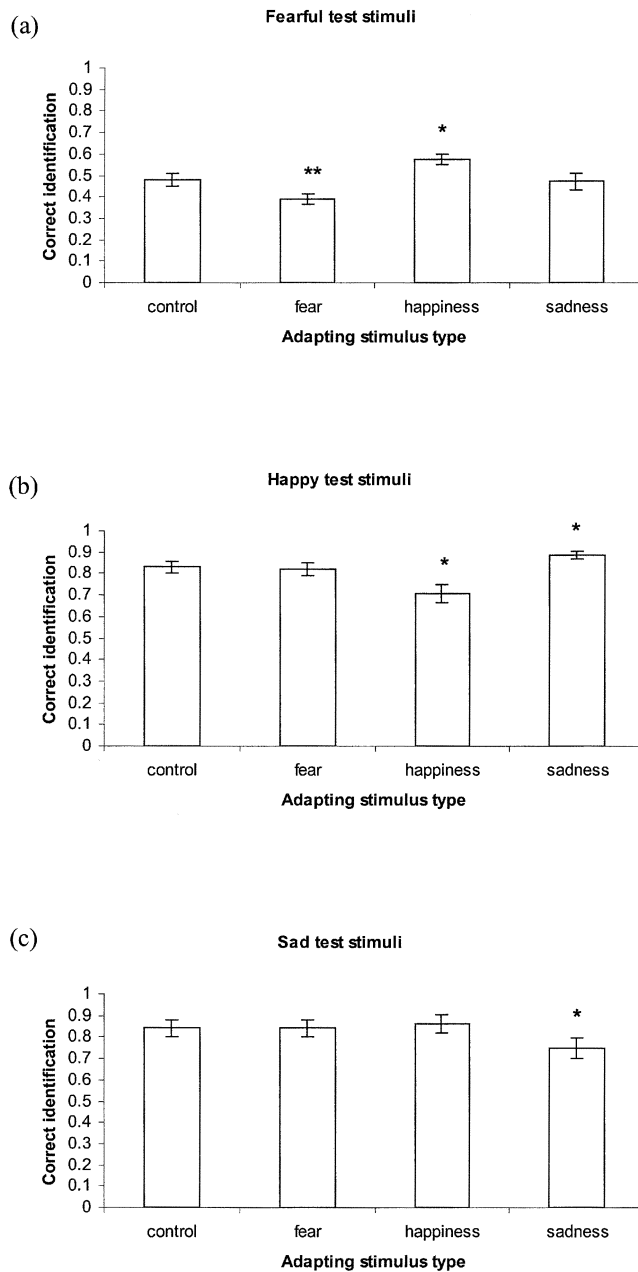


Figure 5. Identification performance of (a) fearful, (b) happy, and (c) sad test stimuli of size $7.6^\circ \times 10.8^\circ$ following different types of adapting stimuli of size $15.0^\circ \times 20.8^\circ$. The y axis represents the proportion of trials in which participants made the correct judgements, i.e., “fear” in (a), “happiness” in (b), and “sadness” in (c). The asterisks indicate a significant difference between the control and adapting condition revealed by Bonferroni *t*-tests (* $p < .05$; ** $p < .01$). Error bars represent \pm SE.

improved performance ($p < .05$). For sad test stimuli, a similar significant main effect of adapting stimulus type was found, $F(3, 45) = 7.65$, $MSE = 0.37$, $p < .001$, in which identification performance of sad test stimuli was significantly reduced under the sad adapting condition ($p < .05$).

How identification performance at each level of morphing of test stimuli was affected by the adapting stimulus type is shown in Figure 6. For the fearful expression test continuum, a two-way repeated measures ANOVA revealed a statistically significant interaction between the nature of the adapting stimulus and the expression strength of the fearful test stimulus, $F(7.1, 106.48) = 3.00$, $MSE = 0.63$, $p < .01$. For the happy expression test continuum, there was also a significant interaction between the adapting stimulus and the strength of the happy test stimulus, $F(6.47, 96.98) = 3.82$, $MSE = 0.85$, $p < .01$. For the sad expression test continuum, the interaction between nature of adapting stimulus and the expression strength of the sad test stimulus approached significance, $F(15, 225) = 1.60$, $MSE = 0.37$, $p = .08$.

As is illustrated in Figure 6, the follow-up Bonferroni t -tests showed that by comparing the means between the adapting and the control condition for each test morph, previous adaptation to prototype expressions of fear and happiness caused a subsequently presented corresponding expression to be recognized less readily. Facilitation effects were also found between sad adaptation and happy test stimuli.

Discussion

Replicating the main findings of Experiment 1, participants were less accurate at identifying fearful, happy, and sad morphs after adapting to the corresponding prototype expression of fear, happiness, and sadness. Such effects that can transfer across different sizes of adapting and test faces show evidence of nonretinotopic representations. On this ground, expression aftereffects might be rooted in complex shape representations in higher visual areas. Furthermore, the present results also provide evidence that the adaptation effects demonstrated in the present study may primarily derive from adaptation to expression per se, but are unlikely to derive simply from adaptation to low-level features such as orientation and spatial frequency.

EXPERIMENT 4

The potency of motion aftereffects (Sekuler & Pantle, 1967) and figural aftereffects (Hammer, 1949) has been known to be able to persist for a period of nonstimulation. The phenomenon is known as the storage effect. Previous evidence has shown that adaptation to an individual face continued to influence the face identity perception of the following test face even after a delay of 1000 ms between adaptation and testing (Leopold et al., 2001). The survival of this face identity aftereffect across a blank interval suggests that a related storage

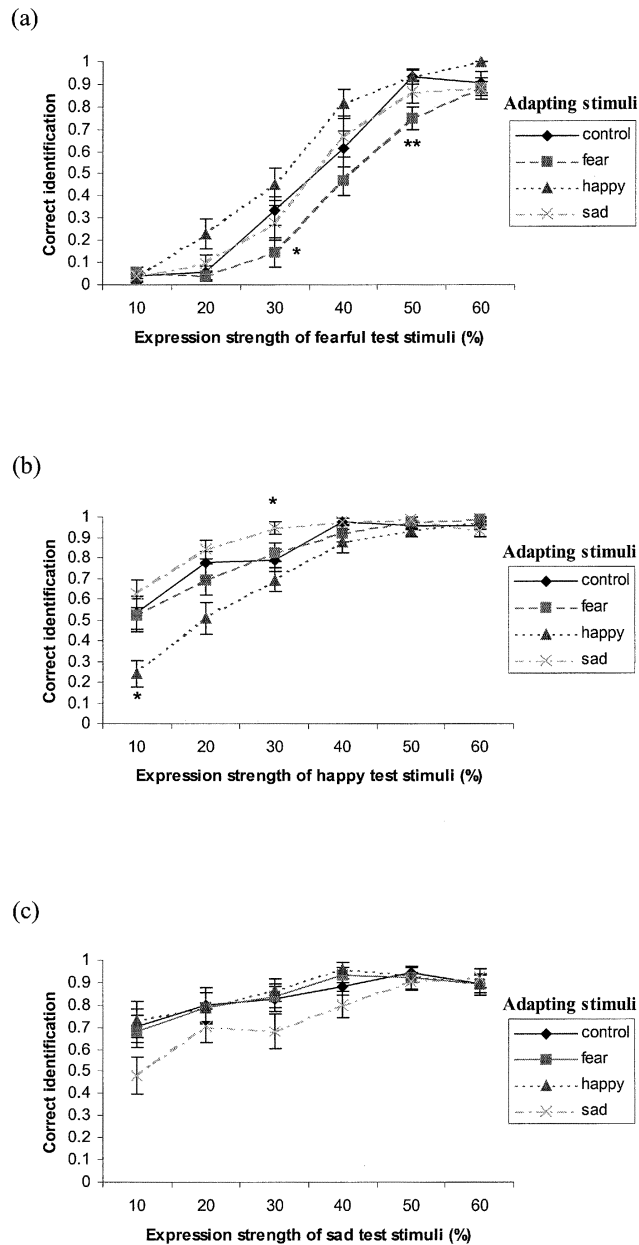


Figure 6. Sensitivity to different levels of strength of (a) morphed fearful, (b) morphed happy, and (c) morphed sad expressions of size $7.6^\circ \times 10.8^\circ$ after previous exposure to various adapting stimuli of size $15.0^\circ \times 20.8^\circ$. The y axis represents the proportion of trials in which participants made the correct judgements, i.e., “fear” in (a), “happiness” in (b), and “sadness” in (c). For each test stimulus, the asterisks indicate a significant difference between the control and adapting condition revealed by Bonferroni *t*-tests (* $p < .05$; ** $p < .01$). Error bars represent \pm SE.

phenomenon can occur even using high-order natural image stimuli such as faces. In the same vein, a longer interval between adapting and test stimuli was introduced in Experiment 4 to examine whether adaptation effects in facial expression recognition would survive a 1 s delay.

Method

Experiment 4 was a replication of Experiment 1 with the same stimuli and paradigm. The key difference was that the time lag between the adapting and test stimulus was 1000 ms (instead of 100 ms) in this experiment.

Participants. Eight females and ten males contributed data used in Experiment 4. A total of 19 participants were run, but one participant was excluded because of an unacceptable missing data rate, as explained below. The participants were students and staff from the University of York. None of them had taken part in previous experiments.

Results

The missing data rate for the participants ranged from 0% to 3.1% in Experiment 4. One participant's data were dropped due to a high missing data rate, greater than 5%. The details of data processing and analyses are identical to those performed earlier.

The identification performance of each test emotion under different adapting conditions is shown in Figure 7. A one-way repeated measures ANOVA was performed to establish whether recognition of a particular test emotion was affected by the adapting stimulus type. This ANOVA revealed a significant main effect of the nature of the adapting stimulus for fearful test stimuli, $F(3, 51) = 21.00$, $MSE = 0.49$, $p < .001$. Bonferroni t -tests showed that compared to the control condition, participants were less accurate at identifying fearful morphs under the fearful adapting condition ($p < .01$) whereas performance with fearful morphs was improved under the happy adapting condition ($p < .01$). For happy test stimuli, there was also a main effect of adapting stimulus, $F(3, 51) = 7.38$, $MSE = 0.67$, $p < .001$, with pairwise comparisons showing that adaptation to a happy emotional face impaired the identification of happy test stimuli ($p < .01$). For sad test stimuli, the ANOVA revealed a similar significant main effect of the adapting stimulus type, $F(3, 51) = 9.83$, $MSE = 0.40$, $p < .001$, in which identification performance of sad test stimuli was significantly reduced under the sad adapting condition ($p < .05$).

Figure 8 illustrates participants' identification performances across each level of test morphing after adaptation to various adapting stimuli. For the fearful expression test continuum, the interaction between the nature of the adapting stimulus and the expression strength of the fearful test morph approached statistical significance in a two-way repeated measures ANOVA analysis,

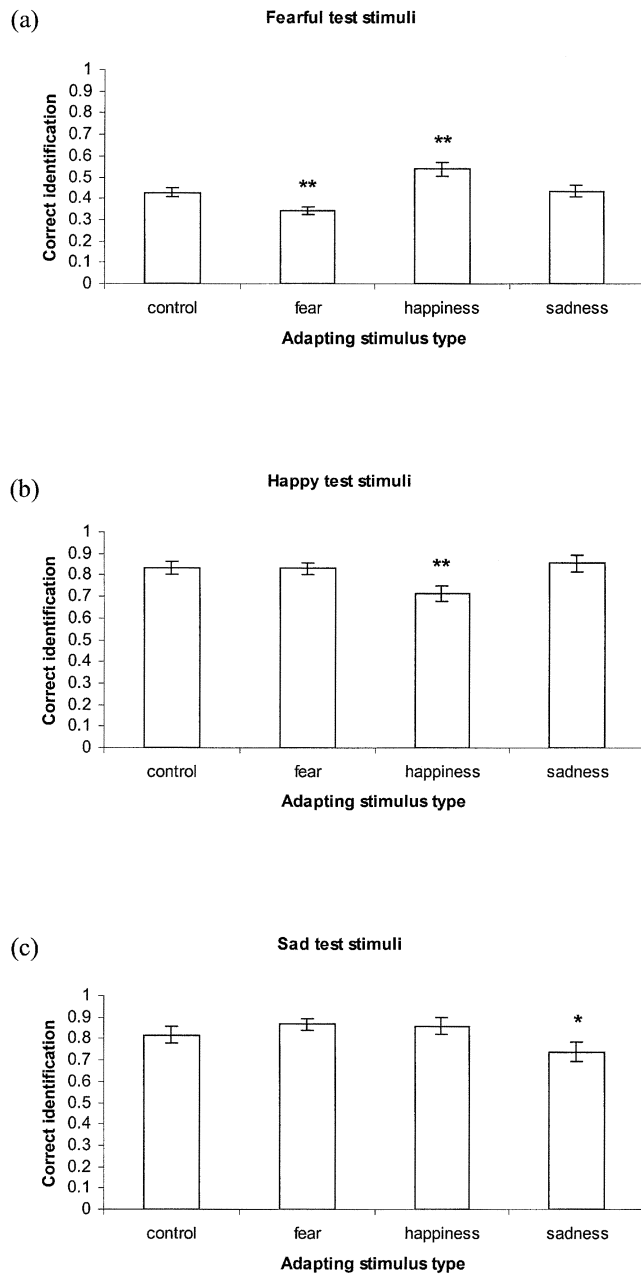


Figure 7. Following an ISI of 1000 ms, identification performance of (a) fearful, (b) happy, and (c) sad test stimuli with different types of adapting stimuli. The y axis represents the proportion of trials in which participants made the correct judgements, i.e., “fear” in (a), “happiness” in (b), and “sadness” in (c). The asterisks indicate a significant difference between the control and adapting condition revealed by Bonferroni *t*-tests (* $p < .05$; ** $p < .01$). Error bars represent \pm SE.

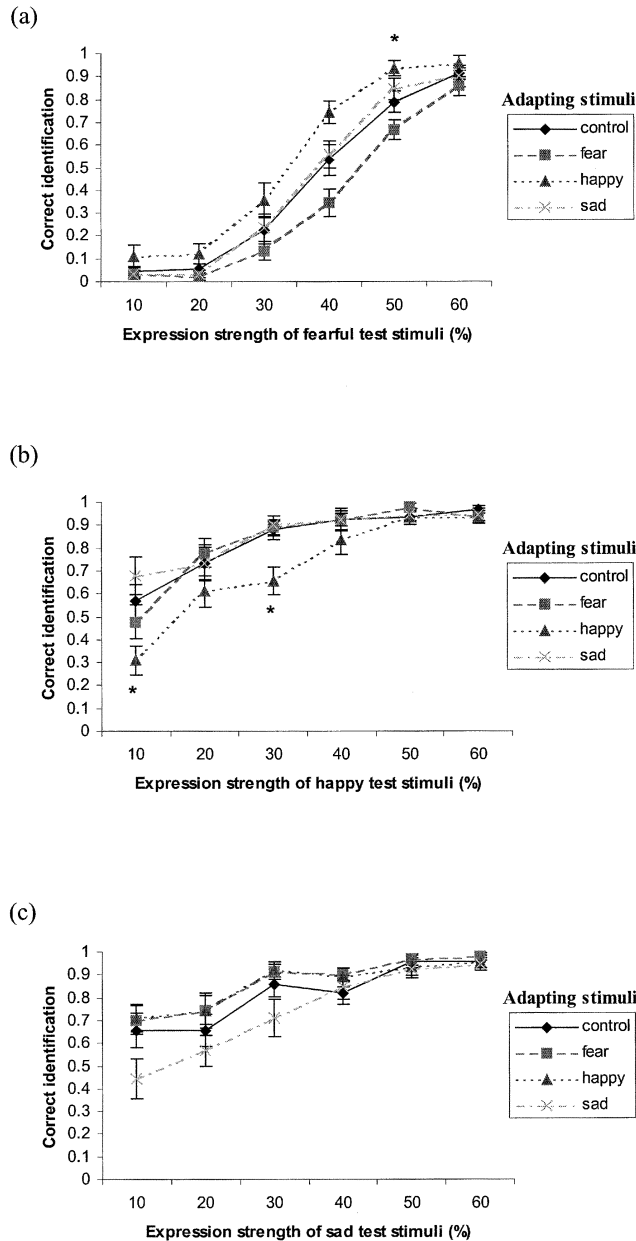


Figure 8. Following an ISI of 1000 ms, sensitivity to different levels of strength of (a) morphed fearful, (b) morphed happy, and (c) morphed sad expressions as a function of various adapting stimuli. The y axis represents the proportion of trials in which participants made the correct judgements, i.e. “fear” in (a), “happiness” in (b), and “sadness” in (c). For each test stimulus, the asterisks indicate a significant difference between the control and adapting condition revealed by Bonferroni *t*-tests ($*p < .05$). Error bars represent \pm SE.

$F(6.81, 115.71) = 1.69$, $MSE = 0.36$, $p = .12$. For the happy expression test continuum, an ANOVA showed a significant interaction between the adapting condition and the expression strength of the happy test morph, $F(8.36, 142.15) = 2.69$, $MSE = 0.62$, $p < .01$. For the sad expression test continuum, the interaction between the nature of adapting stimulus and the expression strength of the sad test morph was of marginal statistical significance, $F(7.13, 121.15) = 1.90$, $MSE = 0.37$, $p = .07$.

Further pairwise comparisons at each level of test morphing revealed that prior adaptation to a happy face could induce impaired performance in recognition of happy morphs (see Figure 8). For 10% sad morphs, the difference between the control and the happy adaptation was also marginally significant ($p = .06$), indicating the presence of inhibition effects on sad expression recognition. In addition, identification performance on fearful morphs also increased after adapting to a happy face.

Discussion

In general, the overall data are in keeping with previous findings that prior exposure to a prototype expression for a few seconds caused a corresponding morphed expression to be recognized less accurately. Thus, the fact that stimulation continued to influence participants' sensitivity to test stimuli across a temporal gap suggests a storage effect in expression-based aftereffects.

EXPERIMENT 5

Although the aim of the current research is to determine how adaptation to an emotional face affects the recognition of a following expression, results of Experiments 1–4 may not only reflect a temporary fatigue of neural populations tuned for facial emotion recognition but might also involve a temporary change in the participant's criterion for what counts as a good example of an expression. This criterion effect is possible if the responses given to the test stimuli by participants are based on the measurement of physical or psychological distance between the adapting stimuli and test stimuli but do not depend on the sole basis of the test stimuli as instructed, as might be expected from approaches such as adaptation-level theory (Helson, 1964). More specifically, on each trial, after being exposed to an adapting stimulus, the internal criterion used for a subsequent evaluation might be shifted and a new reference point formed. Such a notion has been demonstrated in research on binary categorization of simple one-dimensional stimuli such as pitch and geometric figures (Stewart, Brown, & Chater, 2002). Participants showed a tendency to respond with the same category label on trial n as on the previous trial ($n - 1$) if there was a small within-category shift between the two stimuli, and to respond with a different label if the shift was large. These results suggest that the classification of a stimulus is related to the contrast produced when the stimulus is placed in temporal

proximity with another element. By analogy to this idea, a criterion shift might be the reason causing the observed inhibition effects in the present experiments since our paradigm involved adapting to a high-strength (prototype) expression and then testing with a less good (morphed) example of an emotion. It might be thought that participants would be less likely to assign the same category descriptor to a low strength expression after viewing a corresponding prototype expression (high strength) that could be counted as a good example of this emotion category by the participants. On this account, the inhibition effects could be construed as due to a criterion change rather than to neural fatigue.

Accordingly, one might expect that if the inhibition phenomena observed previously can be solely ascribed to a criterion change, the duration of adaptation times should be irrelevant to inducing the effects as long as information about the adapting stimulus is available for participants to create an internal criterion. On the contrary, as is shown from the previous literature (Hammer, 1949), the robustness of aftereffects involving in some form of neural fatigue (Barlow & Hill, 1963) depends heavily on the induction times, with short adaptation times failing to produce the effects.

If previous results are due to adaptation of neural populations tuned for facial expression recognition, then, the potency of expression aftereffects should be attenuated after a shorter period of stimulation. Hence, a short adaptation time was introduced in Experiment 5 in order to probe the contribution of neural fatigue and criterion effects to expression aftereffects. Moreover, the ISI was kept at 1000 ms in Experiment 5. This long ISI was used for the following reasons. On one hand, this long ISI allowed sufficient time for any new criterion to be formed based on an internal evaluation of the adapting stimulus. On the other hand, as was described in Experiment 4, a 5 s exposure to an emotional face continued to influence subsequent identification performance of test stimuli even after a delay of 1000 ms between adaptation and testing. By comparison to the results from Experiment 4 using the same ISI but a different induction time, the relative impact of neural fatigue and criterion change on the observed effects could thus be evaluated. On a neural fatigue account, the 500 ms adapting time and 1000 ms ISI used in Experiment 5 would severely reduce any inhibition effect, whereas on a criterion change account it would have little effect.

Method

The same procedure as Experiment 4 was repeated in Experiment 5, but the duration of the adapting stimulus was shortened to 500 ms.

Participants. Fourteen females and four males took part in Experiment 5. A total of 19 participants were run, but one participant was excluded because of a high missing data rate. The participants were students and staff from the University of York. None of them had taken part in previous experiments.

Results

The missing data rate for the participants ranged from 0% to 4.2%. One participant was eliminated for failing to produce a satisfactory response rate (the missing data rate exceeded 5%). The overall identification performance for each test emotion following different types of adapting stimuli is shown in Figure 9, whereas performance at each individual level of test stimulus strength is shown in Figure 10.

Firstly, a one-way repeated measures ANOVA showed that for fearful test stimuli, there was no significant main effect of the nature of adapting stimulus. For happy test stimuli, there was a main effect of the adapting stimulus type, $F(3, 51) = 5.19$, $MSE = 0.26$, $p < .01$, but pairwise comparisons did not show any reliable difference between the adapting conditions and the control condition. For sad test stimuli, although a significant main effect was also shown, $F(3, 51) = 4.02$, $MSE = 0.23$, $p < .05$, no pairwise comparison between the adapting conditions and the control condition reached significance.

A subsequent two-way repeated measures ANOVA was carried out to examine the effects by level of morphing of the test stimuli. All adapting stimulus \times expression strength of test stimulus interactions did not reach statistical significance. The follow-up Bonferroni *t*-tests at each level of test condition also confirmed that participants' identification performances of all three types of morphed expressions were unaffected by adaptation.

Discussion

In contrast to the results for 5000 ms adaptation and 1000 ms ISI from Experiment 4, the adaptation effects were entirely abolished with the 500 ms adaptation and 1000 ms ISI used in Experiment 5. These findings are similar to previous observations of figural aftereffects (Hammer, 1949), suggesting the importance of the induction time in generating robust adaptation effects. More importantly, this adapting-time-dependent behaviour further implies the dominant contribution of some form of neural fatigue in expression aftereffects and is incompatible with the view that a criterion change is the major source of the observed effects.

GENERAL DISCUSSION

Our results have demonstrated the presence of adaptation effects in facial expression recognition. After adapting to an emotional face for 5 s, participants' identification performance of a following test expression was significantly impaired when the adapting and test stimuli were taken from the same emotion category. In addition to this main finding, the experiments have also identified a number of specific details about the particular nature of the adaptation effects. We organize the discussion of these findings around two fundamental issues: The source of expression adaptation, and implications of expression adaptation.

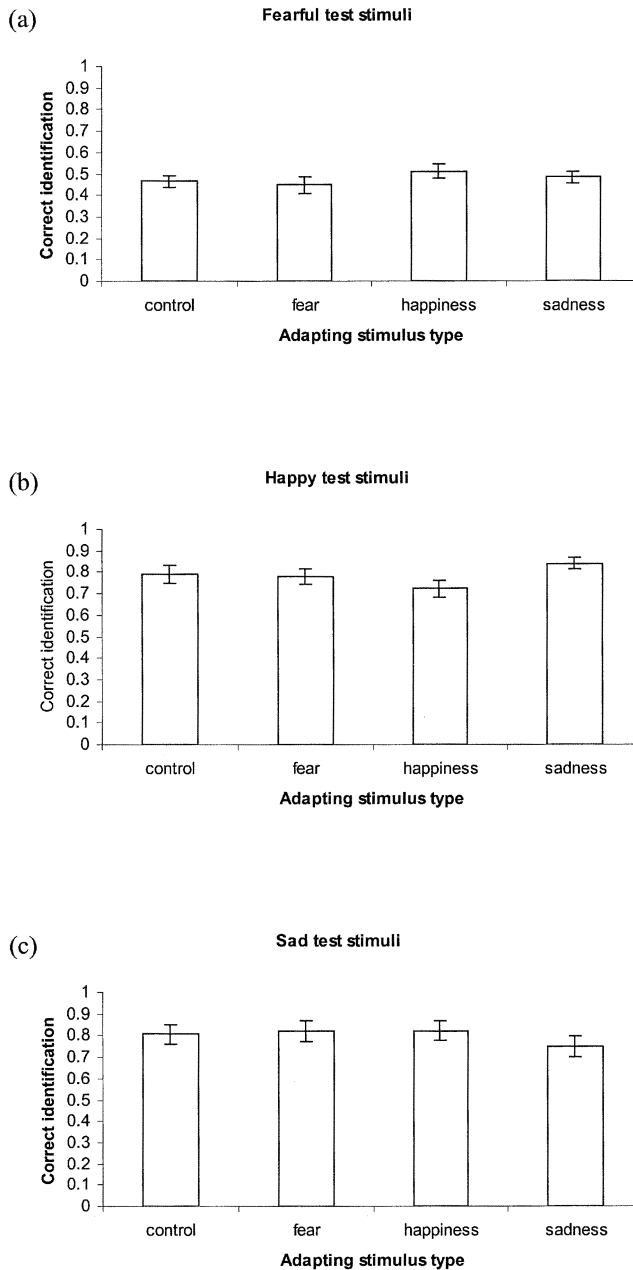


Figure 9. Following adaptation of 500 ms and an ISI of 1000 ms, identification performance for (a) fearful, (b) happy, and (c) sad test stimuli with different types of adapting stimuli. The y axis represents the proportion of trials in which participants made the correct judgements, i.e. “fear” in (a), “happiness” in (b), and “sadness” in (c). Error bars represent \pm SE.

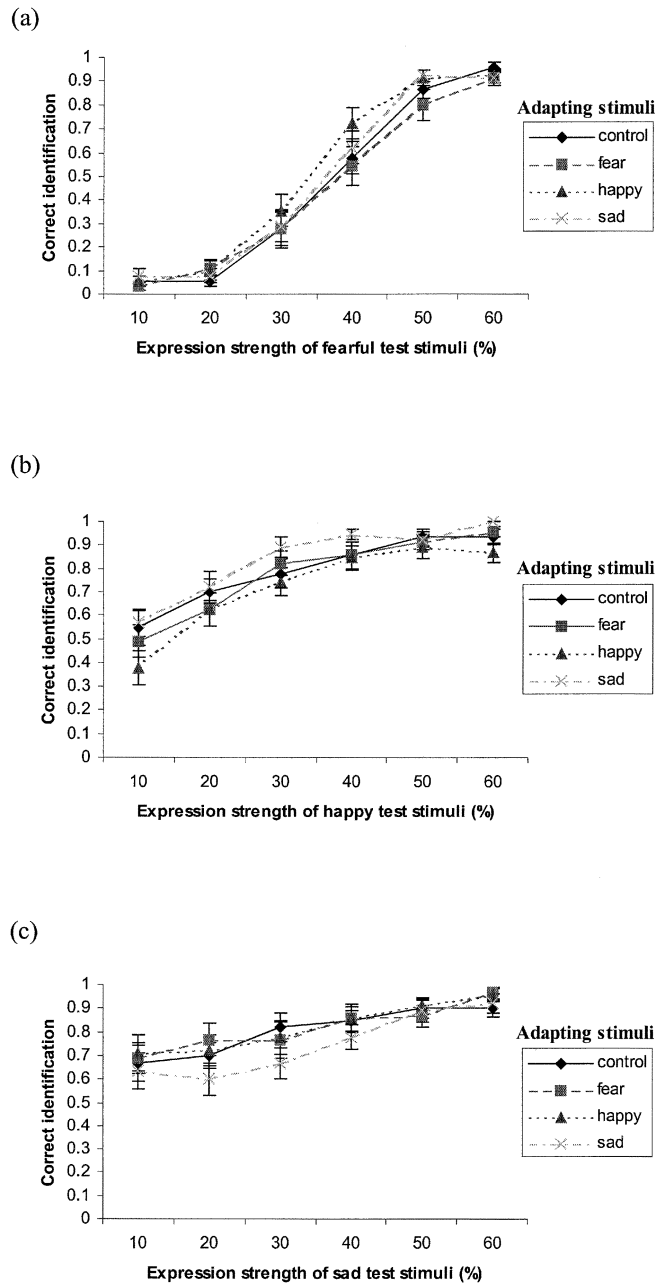


Figure 10. Following adaptation of 500 ms and an ISI of 1000 ms, sensitivity to (a) morphed fearful, (b) morphed happy, and (c) morphed sad expressions as a function of various adapting stimuli. The y axis represents the proportion of trials in which participants made the correct judgements, i.e. “fear” in (a), “happiness” in (b), and “sadness” in (c). Error bars represent \pm SE.

The source of adaptation effects in facial expression recognition

The claim that our results, especially concerning inhibition effects, were due to some form of neural fatigue rather than a criterion shift follows from the demonstration that the potency of adaptation effects was determined by the duration of the adapting time. Prolonged (5 s) as opposed to shorter (500 ms) exposure of the adapting stimulus could continue to influence the judgement of a test expression even with a condition of relatively long (1000 ms) ISI. This phenomenon cannot be explained as a product of a criterion shift exclusively.

Some form of desensitization based on neural fatigue therefore seems the most likely basis for the adaptation effects observed. However, this did not involve fatigue of low-level receptors coding orientation or spatial frequency, since equivalent adaptation effects were found even when adapting and test stimuli were of different sizes. These nonretinotopic adaptation effects are best construed as involving desensitization of higher-order representations.

Implications of adaptation effects in facial expression recognition

Adaptation has been considered to be able to temporarily isolate and diminish the function of a specific neural population. Thus, the result that previous adaptation to the prototype facial expression of fear as opposed to happiness or sadness decreased sensitivity to morphed fearful faces demonstrates the presence of a distinct neural population optimally tuned to the representation of a fearful expression but not a happy or sad expression. Likewise, the circumscribed inhibition effects in happy and sad expression recognition might lend weight to the view that different neural populations are tuned to mediate recognition of sad and happy expressions respectively.

Nevertheless, several sources of facilitation effects between different types of facial emotions were also found in our study. For instance, recognition of fearful morphs was improved after adapting to a happy face. Mutual enhancements were also observed between happy and sad expression identification. These facilitation effects suggest that the representations tuned for recognition of different expressions are not isolated, but implemented in a manner that creates a partial cross-talk among them. This contention is consistent with previous work demonstrating relative judgements in the perception of emotion in facial expressions (Russell & Fehr, 1987), but stands in contrast with the view that facial expressions are perceived as belonging to qualitatively discrete categories (Ekman, 1982).

In Russell's view, facial expressions can be represented as points in an emotion space with two-dimensional attributes of positive or negative arousal

and valence and neutral at the centre (Russell, 1980). Recognition of a facial expression is not fixed solely by its location in the emotion space, but rather depends on how it compares with other expressions. When an expression of happiness is preceded by a sad emotional face, for example, previous viewing of the sad face increases the relative valence and arousal value of the happy face and this has the effect of causing the happy expression to be recognized more readily.

However, Russell's two-dimensional account of facial expression recognition is not free from difficulties. It runs into problems accounting for the effects of computer morphing between facial expressions, which lead to clear categorical perceptual properties (Calder, Young, Perrett, Etcoff, & Rowland, 1996; Etcoff & Magee, 1992; Young, Rowland, Calder, Etcoff, Seth, & Perrett, 1997), and it also does not account fully for the effects of computer caricatures (Calder, Rowland, Young, Nimmo-Smith, Keane, & Perrett, 2000). Moreover, in the present study, it is not clear from Russell's view why the influence of relative judgements is so heavily dependent on adapting time.

Categorical perception findings have resulted in category-based accounts of facial expression perception becoming dominant in the literature (Ekman, 1982). In contrast, our findings of facilitation as well as inhibition in adaptation to facial expressions show that emotion categories are not perceived entirely independently from each other. This point will need to be incorporated into future models, whether they are fundamentally category or dimension based. A promising approach is to use techniques like principal component analysis (PCA) to explore the statistical structure of facial expressions (Calder, Burton, Miller, Young, & Akamatsu, 2001). Application of PCA to the facial expressions in the Ekman and Friesen (1976) set (from which the faces used in the present study were derived) has shown that a PCA-based system can support facial expression recognition and that the essential features of dimension-based models are reflected in the statistical structure of the Ekman and Friesen facial expressions (Calder et al., 2001). Potentially, this gives a clear insight into what populations of neurons that have been fatigued following adaptation to a facial expression might be coding.

Concluding remarks

Adaptation has been increasingly used to study more cognitive aspects of vision (Leopold et al., 2001; Webster & Maclin, 1999). In this study, we broadened the relevance of adaptation to the facial expression domain and demonstrated reliable adaptation effects involving inhibition of recognition of the adapted expression and facilitation of recognition of some other expressions, relative to a neutral baseline condition. The facilitation effects show that there is some form of cross-talk between emotions in facial expression recognition even though expressions can show category-like properties. The inhibition effects are of

particular interest because the paradigm is not unlike a typical priming experiment, in which the prime is followed by a target stimulus type after an ISI. Instead of a prime, we have used an adapting stimulus presented for a relatively long time. Priming experiments generally demonstrate the pervasive psychological phenomenon that something that was recently recognized will be recognized easily when it is encountered again. The finding of an inhibition effect of prolonged adaptation is thus the exact reverse of the usual priming phenomenon, and as such will need to be properly incorporated into theoretical models. Capitalizing on adaptation, a time-honoured tool of psychophysics, thus allows a new source of insight into the mechanisms of facial expression recognition.

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