

Sustained happiness? Lack of repetition suppression in right-ventral visual cortex for happy faces

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Emotional stimuli have been shown to preferentially engage initial attention but their sustained effects on neural processing remain largely unknown. The present study evaluated whether emotional faces engage sustained neural processing by examining the attenuation of neural repetition suppression to repeated emotional faces. Repetition suppression of neural function refers to the general reduction of neural activity when processing a repeated stimulus. Preferential processing of emotional face stimuli, however, should elicit sustained neural processing such that repetition suppression to repeated emotional faces is attenuated relative to faces with no emotional content. We measured the reduction of functional magnetic resonance imaging signals associated with immediate repetition of neutral, angry and happy faces. Whereas neutral faces elicited the greatest suppression in ventral visual cortex, followed by angry faces, repetition suppression was the most attenuated for happy faces. Indeed, happy faces showed almost no repetition suppression in part of the right-inferior occipital and fusiform gyri, which play an important role in face-identity processing. Our findings suggest that happy faces are associated with sustained visual encoding of face identity and thereby assist in the formation of more elaborate representations of the faces, congruent with findings in the behavioral literature.

Keywords: emotion; faces; repetition suppression; sustained processing; ventral visual cortex

INTRODUCTION

Preferential allocation of processing resources to emotional stimuli that signal potential reward or threat has obvious relevance to the survival of an individual. For example, prioritized detection of threatening emotional stimuli has been well studied such that they preferentially capture initial attention (Hansen and Hansen, 1988; Ohman *et al.*, 2001), regardless of task relevance (Vuilleumier *et al.*, 2001) or perceptual awareness (Morris *et al.*, 1998; Whalen *et al.*, 1998). This detection of threatening stimuli also occurs very rapidly probably through the ‘quick-and-dirty’ thalamo-amygdala pathway (LeDoux, 1996). The initial greater processing of emotional stimuli, relative to neutral stimuli, may also involve extended and sustained processing that help to preferentially encode details of the emotional stimuli. Indeed, memory studies showed that happy faces enhanced a conscious recollection of face identity rather than a feeling of familiarity, indicating the formation of fine representations

of faces (D’Argembeau *et al.*, 2003; D’Argembeau and van der Linden, 2007). In addition, Fox *et al.* (2001) demonstrated that participants had difficulty in disengaging attention from angry faces, especially in high-anxious individuals, implying an intrinsic effect of emotion to sustain processing of the emotional stimuli relative to neutral stimuli. However, such sustained processing of emotional stimuli has been rarely studied at the neural level. The present study addressed this issue by measuring repetition suppression of neural function for neutral and emotional faces with functional magnetic resonance imaging (fMRI).

Repetition suppression refers to the reduction of neural activity with repetition of stimuli, which has been replicated using a variety of stimuli and measurement techniques (Grill-Spector *et al.*, 2006). While multiple mechanisms may underlie this phenomenon, one likely function is to reduce demands on the brain from repeated stimuli of limited significance and to allocate more neural resources to novel stimuli of potential significance (Rolls, 2005). Importantly, when a task requires the detection of repetition of identical faces, the repetition of faces becomes task-relevant, resulting in neural responses being relatively maintained and an attenuation of repetition suppression (Henson *et al.*, 2002). Thus, given the intrinsic relevance of emotional faces for an individual’s behavior, emotional faces

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may also be associated with attenuated repetition suppression, when compared to neutral faces, due to sustained processing.

Direct comparisons of repetition suppression of emotional and neutral faces give mixed results. A number of fMRI studies reported repetition suppression for neutral faces in ventral visual cortex (Winston *et al.*, 2004; Rotshtein *et al.*, 2005) as well as in the amygdala (Glascher *et al.*, 2004). Rotshtein *et al.* (2001) showed that 'Thatcherized' faces that looked highly unusual or odd produced less repetition suppression (more sustained processing) in the middle fusiform compared to normal faces. But it was not clear whether their finding could be generalized to more natural emotional faces. Ishai *et al.* (2004) addressed this issue by comparing repetition suppression for fearful faces and for neutral faces. Surprisingly, they reported greater suppression for repeated fearful faces than for repeated neutral faces in both the fusiform and amygdala, which they argued resulted from greater initial attention to fearful faces (Vuilleumier *et al.*, 2001). This result in Ishai *et al.* (2004), however, may have been due to participants performing a match-to-target task. The task required different cognitive operations at the first viewing (encoding of a face) and at subsequent viewings (comparison with the encoded face), which were confounded with repetition and prevented a simple interpretation. In addition, previous studies of face emotion and repetition suppression did not examine emotionally positive faces. This is important because behavioral studies have demonstrated a memory advantage for happy faces, suggesting sustained preferential processing of emotionally positive material (D'Argembeau *et al.*, 2003; D'Argembeau and van der Linden, 2007).

In the present study, we studied repetition suppression for happy (positive), angry (negative) and neutral faces simultaneously in an effort to clarify the role of face emotion in engaging sustained neural processing. The experiment was based on a variant of the repeated-and-single-trials paradigm (Ollinger *et al.*, 2001), allowing us to estimate repetition suppression on an event-related basis. We focused on repetition suppression occurring in a short-time window because extensive repetition would habituate brain responses to any stimuli and thus be likely to obscure emotional modulation (Breiter *et al.*, 1996). Given the possible interference that could occur between directed cognitive operations and repetition suppression (Ishai *et al.*, 2004), we employed a passive-viewing task, which was shown to be an effective method in generating repetition suppression in our previous study (Goh *et al.*, 2004).

Our main interest was whether attenuation of repetition suppression would be observed for emotional faces compared to neutral faces. Less repetition suppression for emotional faces relative to neutral faces was expected in perceptual brain regions involved in face processing, reflecting the formation of more detailed face representations for emotional faces (Henson *et al.*, 2000). Such regions include

ventral visual cortex, consisting of the inferior occipital and fusiform gyri (Haxby *et al.*, 2000). The amygdala would also show attenuation of repetition suppression to emotional faces given its modulatory role in face perception and emotional processing (Vuilleumier, 2005). In addition, frontal regions have also been shown to play a role in processing face stimuli (Fairhall and Ishai, 2007). The frontal role in face processing may involve processes such as emotional empathy rather than facial detail (Nakamura *et al.*, 1999; Carr *et al.*, 2003; Winston *et al.*, 2003; Leslie *et al.*, 2004). Thus, it would be interesting to evaluate whether repetition suppression in frontal regions would similarly be modulated by emotion as in ventral visual cortex, or remain consistent across neutral, angry and happy stimuli as long as the same face emotions are repeated.

METHODS

Participants

Nineteen individuals (10 females, ages 19–29 with a mean age of 23.1) gave informed consent to participate in this study, which was approved by the University of Illinois at Urbana-Champaign Institutional Review Board. All the participants were right-handed, had normal or corrected-to-normal vision and reported no history of neurological or psychiatric illness.

Stimuli

Eighty-one digital images of faces were used as stimuli, comprised of neutral, angry and happy faces enacted by 27 posers. The stimuli were selected from four face databases developed by other research groups.¹ The stimuli were standardized using MATLAB 7 and Adobe Photoshop CS2 in the following manner: they were cropped into a square shape so that only central features of the face (eyes, eyebrows, nose and mouth) were present, and then converted into gray-scale, with size, mean luminance and contrast equated. The stimuli were used in the fMRI experiment, with each stimulus subtended at visual angles of about $10^\circ \times 10^\circ$.

Experimental procedure

The fMRI experiment was based on a variant of the repeated-and-single-trials paradigm (Figure 1; Ollinger *et al.*, 2001). In repeated trials, the same stimulus was presented twice consecutively and for 1.5 s each, separated by a 0.5-s fixation interval. In single trials, a single stimulus was presented once for 1.5 s. Between any two trials was a fixation interval of which duration randomly varied among 6.5, 8.5 and 10.5 s, with a mean of ~ 7.5 s. Each of the 81 faces was presented once in both repeated and single trials, resulting in a total of 162 trials with six trial-types

¹Pictures of Facial Affect, Paul Ekman Group, Oakland, CA, USA; The Karolinska Directed Emotional Faces, Department of Clinical Neuroscience, Karolinska Institutet, Stockholm, Sweden; NimStim Face Stimulus Set, The John D. and Catherine T. MacArthur Foundation Research Network on Early Experience and Brain Development; Facial Information Norm Database, Yamada Laboratory, Department of Psychology, Nihon University, Tokyo, Japan.

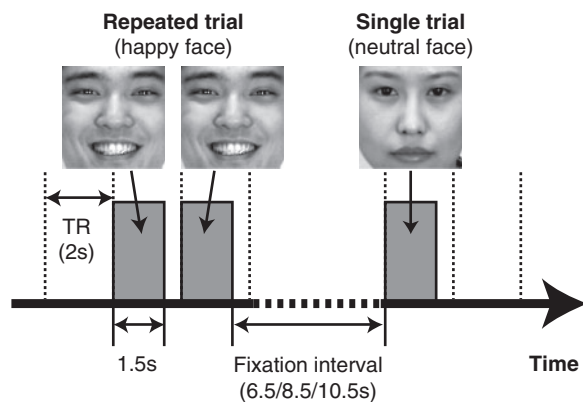


Fig. 1 A schematic time-course of the fMRI experiment.

[(repeated, single) \times (neutral, angry, happy)]. Participants were instructed to pay attention to the whole face when it appeared.

The fMRI experiment was divided into six runs that lasted for 308 s each. Each run was composed of 27 trials that were preceded and followed by a fixation interval that lasted for 24 and 18 s, respectively. The six trial-types were distributed almost equally across the six runs and were quasi-randomized within a run. In order to minimize long-lag repetition suppression across trials, the same stimulus was never presented in different trials within a run. Repeated and single trials that presented the same stimulus were separated by about 80 trials on average (32–158 trials).

After the fMRI experiment, participants performed a behavioral experiment outside the MRI scanner. They viewed all the 81 faces again, and were asked to rate the intensity of anger and happiness expressed by each face using a 4-point scale (3: 'very angry/happy', 2: 'moderately angry/happy', 1: 'a little angry/happy', 0: 'not angry/happy at all'). Ratings of the intensity of anger and happiness were made in different trials.

Imaging protocol

Imaging was performed with a 3-T Allegra scanner (Siemens, Erlangen, Germany). In the fMRI experiment, 154 functional images were acquired in each run using a gradient-echo spiral-in/spiral-out sequence, of which the first three images were discarded to allow for T1 equilibrium. Spiral-in/spiral-out images were reconstructed and combined following the weighted combination method described by Glover and Law (2001). The acquisition parameters were as follows: TR = 2000 ms, TE = 25 ms, flip angle = 80°, FOV = 240 mm, resolution = 3.75 \times 3.75 \times 3 mm (no gap). Each functional image contained 40 oblique axial slices approximately parallel to the AC-PC line, covering the whole brain. High-resolution coplanar T2 anatomical and 3D-MPRAGE anatomical images were also acquired for use in image co-registration and normalization.

fMRI data analyses

Image preprocessing and statistical analyses were conducted using SPM5 (Wellcome Department of Cognitive Neurology, Institute of Neurology, London, UK). Preprocessing of the functional images included slice-time correction, motion correction, co-registration with the anatomical images, spatial normalization to an MNI space (Montreal Neurological Institute, Montreal, Canada) and spatial smoothing with an 8-mm full-width at half-maximum Gaussian kernel.

Each participant's preprocessed functional images were submitted to a voxel-by-voxel general-linear-model analysis with finite-impulse-response (FIR) predictors. Six sets of FIR predictors were used to separately estimate activations for the first neutral, angry and happy faces and the second neutral, angry and happy faces in repeated trials. The activations for the first neutral, angry and happy faces in repeated trials were assumed to be equal to activations for neutral, angry and happy faces in single trials, respectively. Thus, we modeled the activations to the first faces in repeated trials and the faces in single trials together under the same set of FIR predictors, i.e. as the first face of each emotion condition. Ollinger *et al.* (2001) presented a theoretical and empirical validation showing that this paradigm correctly estimates activations for the first and second faces, and subsequent studies have demonstrated its successful application (Soon *et al.*, 2003; Kincade *et al.*, 2005).

Each set of FIR predictors consisted of 10 delta functions spanning from 2 to 20 s after stimulus onset. This yielded 10 contrast images for each of the six conditions [(first, second) \times (neutral, happy, angry)] per participant. The second to fifth contrast images (4–10 s after stimulus onset) from each condition were entered into a second-level random effect analysis, allowing for the latency of haemodynamic responses. To examine how each emotion condition would engage repetition suppression differently in face-responsive regions at the voxel-by-voxel level, we employed two functionally defined masks to restrict the number of voxels considered. In order to restrict analyses to face-responsive regions, we created a first mask that contained voxels significantly active for the first faces across all face emotions compared to fixation intervals.² Within this face-responsive regions mask, we performed contrasts to identify voxels showing repetition suppression for each of the emotion conditions. That is, we identified voxels within face-responsive regions that were significantly more active for the first than for the second faces for neutral, angry and happy conditions, separately. In this analysis (i.e. construction of the face-responsive regions mask and identification of voxels showing repetition suppression), the combined voxel intensity and cluster size thresholds of $P < 0.001$, uncorrected and $k > 20$ were used in

²Namely, when making the face-regions mask, we used the contrast of the first faces vs fixation rather than the contrast of the first 'and' second faces vs fixation. This was because, due to repetition suppression, the second faces might not activate face-responsive regions and thus because inclusion of the second faces might eliminate normally face-responsive regions.

order to reduce the risks of both Type I and II errors in a balanced manner (Forman *et al.*, 1995; Lieberman and Cunningham, 2009). Given that neural responses and repetition suppression to facial stimuli have been robustly observed (Haxby *et al.*, 2000; Grill-Spector *et al.*, 2006; Fairhall and Ishai, 2007), implying large effects, we chose this more stringent threshold.

Then, we defined a second mask as the union of those regions that showed significant repetition suppression for any of the three face emotions. Within this second mask of regions that showed repetition suppression to any face emotion, we performed pair-wise comparisons of differences in suppression between each of the emotion conditions, to identify voxels showing significantly greater suppression for one face emotion than for another face emotion. In addition, to evaluate if there were brain regions that showed a common pattern of repetition suppression across all three emotion conditions, we also identified voxels showing significant suppression irrespective of face emotion using a conjunction analysis within this second mask of regions showing suppression to any emotion. For both the pair-wise comparisons and the conjunction analysis, the threshold of $P < 0.005$, uncorrected, and $k > 10$ were used as suggested by Lieberman and Cunningham (2009). We chose this threshold for this second set of analysis because the effects of interest were expected to be small, given that pair-wise comparisons of repetition suppression are tests for 'differences of differences' which are associated with large error variances, and that the method of identifying functional regions by specifying conjunctions is conservative (Nichols *et al.*, 2005). Moreover, the use of less stringent thresholds is justifiable given that masking greatly reduced the search space compared to the whole brain (~2500 voxels; Gutchess *et al.*, 2006).

Finally, in order to illustrate the magnitude of repetition suppression as a function of emotion condition, we also conducted a regions-of-interest (ROIs) analysis. The ROIs were functionally defined as 1-cm spheres around the peak voxels that showed differences in repetition suppression in the pair-wise comparisons between emotion conditions as well as peak voxels that showed common repetition suppression to all emotion conditions in the conjunction analyses above. For each of the ROIs, the effect size of repetition suppression was computed as the standardized difference between activation (averaged parameter estimates within a peristimulus time of 4–10 s) for the first faces and activation for the second faces expressed in 'SD' units (Afraz *et al.*, 2006).

RESULTS

Behavioral experiment

Results confirmed the validity of the stimuli as follows. Angry faces attained the largest mean intensity rating of anger (2.28 ± 0.33), which was significantly larger than for neutral (0.77 ± 0.25 , $t = 21.52$, $P < 0.001$) and happy faces

(0.04 ± 0.06 , $t = 31.25$, $P < 0.001$). Happy faces attained the largest mean intensity rating for happiness (2.48 ± 0.22), which was significantly larger than neutral (0.40 ± 0.23 , $t = 33.97$, $P < 0.001$) and angry faces (0.03 ± 0.05 , $t = 49.43$, $P < 0.001$).

fMRI experiment

The contrast of the first faces *vs* fixation intervals that defined the face-responsive regions, revealed a distributed neural system for face processing (Haxby *et al.*, 2000; Fairhall and Ishai, 2007), including ventral visual cortex, the amygdala and the inferior frontal gyrus (Figure 2). The patterns of repetition suppression for each face emotion within these face-responsive regions were then examined separately for each emotion (Figure 3). Repetition suppression in ventral visual cortex was the most extensive for neutral faces, followed by angry faces, but was not significant for happy faces. In contrast, in the left-inferior frontal gyrus (slice $y = 21$ in Figure 3), repetition suppression was commonly observed across all three emotion conditions. Repetition suppression in the amygdala did not reach significance for any face emotion, probably due to the low signal-to-noise ratio in this region (LaBar *et al.*, 2001; Zald, 2003). Table 1 provides more detail about repetition suppression for each face emotion.

Within the union of these regions showing significant repetition suppression for any of the three emotion conditions ('Methods' section), suppression was compared pair-wise between each of the face emotions. The comparisons revealed that the right-inferior occipital and fusiform gyri showed significantly greater suppression for repeated neutral faces than for repeated happy faces (inferior occipital: peak MNI coordinate = $[30 \ -93 \ -12]$, $t = 3.39$, $P < 0.001$; fusiform: $[36 \ -57 \ -21]$, $t = 2.98$, $P = 0.002$). The difference in repetition suppression between neutral and angry faces did not reach significance in any region. Furthermore, no regions showed significantly greater repetition suppression for emotional faces than for neutral faces. In contrast to the right-ventral visual regions that showed differences in repetition suppression due to face emotion, a conjunction analysis revealed that the left-inferior frontal gyrus (peak MNI coordinate = $[-51 \ 21 \ -6]$, $t = 3.17$, $P = 0.001$) and the right-precentral gyrus ($[51 \ -3 \ 42]$, $t = 3.15$, $P = 0.001$) commonly showed repetition suppression across emotion conditions.

The effect sizes of repetition suppression in the ROIs that showed differences as well as commonalities in suppression between emotion conditions ('Methods' section) are shown in Figure 4A. In the right-ventral visual regions, neutral faces showed the largest repetition suppression, and, most interestingly, happy faces showed almost no repetition suppression. The lack of repetition suppression for happy faces cannot be attributed to a floor effect because activation for the second neutral faces was well below activation for the second happy faces (Figure 4B). While angry faces appeared

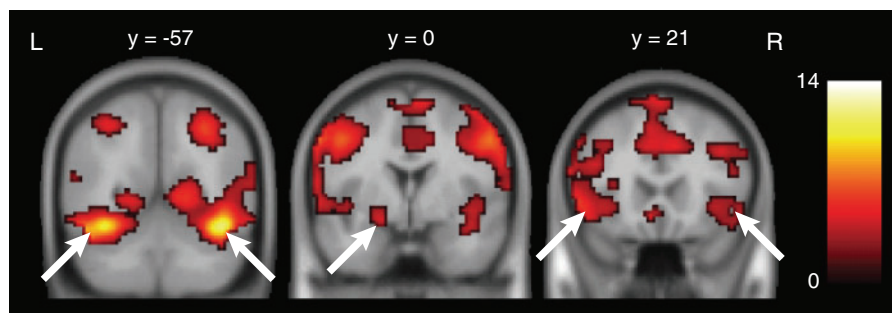


Fig. 2 Face-responsive regions. Shown from left to right are coronal sections illustrating activation in ventral visual cortex (indicated by the arrows at $y = -57$ in an MNI space), the amygdala ($y = 0$) and the inferior frontal gyrus ($y = 21$).

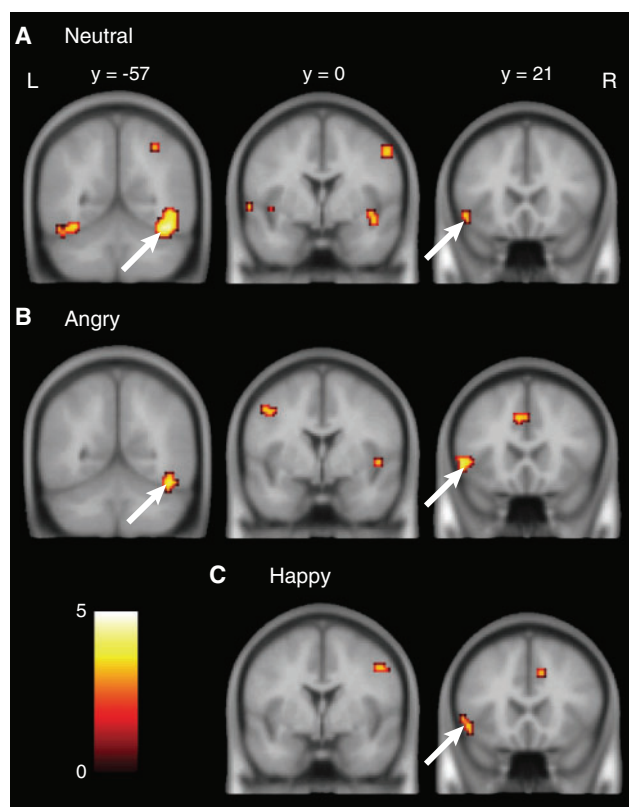


Fig. 3 Repetition suppression for (A) neutral, (B) angry and (C) happy faces in the face-responsive regions. Suppression was observed for repeated neutral and angry faces but not for happy faces in the right-fusiform gyrus (indicated by the arrow at $y = -57$) and for all faces in the left-inferior frontal gyrus ($y = 21$). Suppression in the amygdala was not significant for any face ($y = 0$).

to have intermediate responses relative to happy and neutral faces, these relative differences were not significant. Consistent with the conjunction analysis, on the other hand, the frontal regions showed equivalent repetition suppression across emotion conditions.

DISCUSSION

The present study examined whether emotional faces would attenuate repetition suppression compared to neutral faces

Table 1 Peak voxels showing repetition suppression for each face emotion in the face-responsive regions

Brain region	L/R	MNI co-ordinate	<i>t</i>
Neutral faces			
Inferior occipital gyrus	R	[36 -90 -12]	4.99
Fusiform gyrus	R	[42 -60 -15]	4.88
Superior parietal gyrus	R	[27 -66 51]	3.79
Precentral gyrus	R	[54 -3 45]	3.88
Insula	L	[-42 3 -3]	3.32
	R	[42 -3 -12]	3.68
Temporal pole	L	[-54 12 -6]	4.67
	R	[51 18 -15]	3.28
Angry faces			
Calcarine cortex	R	[12 -87 -3]	3.85
Cuneus	R	[9 -93 27]	4.05
Fusiform gyrus	R	[42 -57 -18]	3.79
Cingulate gyrus	L	[-6 24 36]	3.57
	R	[9 9 39]	3.56
Precentral gyrus	L	[-45 -3 42]	3.51
Insula	R	[45 6 -3]	3.72
Inferior frontal gyrus	L	[-54 21 0]	4.09
Happy faces			
Middle temporal gyrus	L	[-57 -27 -12]	3.70
	R	[63 -39 -6]	4.00
Cingulate gyrus	R	[12 18 39]	3.31
Precentral gyrus	R	[48 -3 42]	3.50
Inferior frontal gyrus	L	[-48 27 -9]	3.87

Note: the statistical threshold was $P < 0.001$ (uncorrected) with >20 contiguous voxels.

due to sustained processing. Our results indicate that this is the case for emotionally positive faces, or happy faces. First, significant repetition suppression was observed in extensive regions of ventral visual cortex for neutral faces but not for happy faces. Second, direct comparison revealed that part of the right inferior occipital and fusiform gyri showed significantly less repetition suppression for happy faces than for neutral faces. Third, in those right-ventral visual regions, happy faces showed almost no repetition suppression. On the other hand, attenuation of suppression was not as evident, or intermediate, for angry faces.

The lack of repetition suppression for happy faces in the right-inferior occipital and fusiform regions is of great

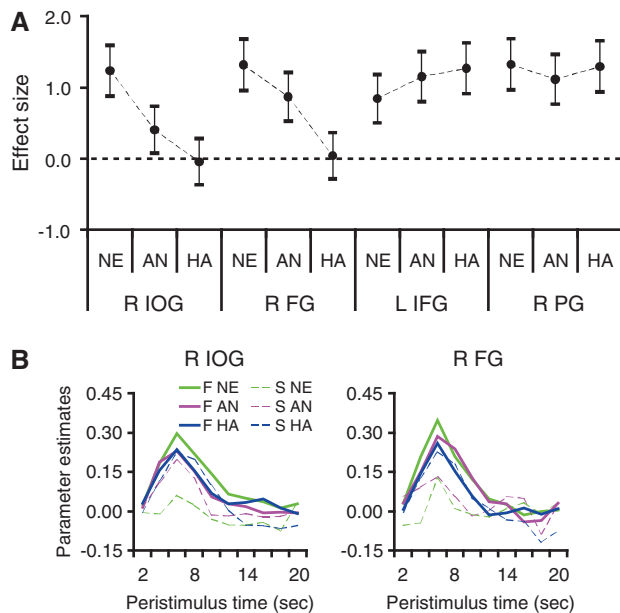


Fig. 4 (A) Effect size of repetition suppression. Namely, the standardized difference between activation (averaged parameter estimates within a peristimulus time of 4–10 s) for the first faces and activation for the second faces expressed in 'SD' units (Afraz *et al.*, 2006). Error bars represent standard errors. R IOG, right-inferior occipital gyrus (MNI coordinate = [30 -93 -12]); R FG, right fusiform gyrus ([36 -57 -21]); L IFG, left-inferior frontal gyrus ([-51 21 -6]); R PG, right-precentral gyrus ([51 -3 42]). (B) Activation time-courses in the right inferior occipital and fusiform gyri as a function of repetition (F, first faces; S, second faces) and face emotion (NE, neutral faces; AN, angry faces; HA, happy faces).

interest. These ventral visual regions constitute the so-called 'core system' for visual analysis of faces (Haxby *et al.*, 2000), and are shown to play an important role in face-identity processing (Winston *et al.*, 2004; Rotshtein *et al.*, 2005). The lack of repetition suppression in these regions suggests prolonged visual encoding of face identity, which is likely to reflect the formation of new representations of unfamiliar faces (Henson *et al.*, 2000). Consistently, D'Argembeau and colleagues showed that happy faces enhanced recollective memory for face identity (D'Argembeau *et al.*, 2003; D'Argembeau and van der Linden, 2007). Although classical models of face recognition have emphasized independent neural pathways for the processing of face identity and face emotion (Bruce and Young, 1986; Haxby *et al.*, 2000), increasing evidence challenges this dichotomy (Calder and Young, 2005; Tsuchiya *et al.*, 2008). Our results also imply the interaction between the two processes such that the identity of a face may be sustainably processed when the face expresses happy emotion.

Sustained neural processing of emotionally positive stimuli is also indicated by Delgado *et al.* (2000). Using a gambling task, they demonstrated that reward feedback led to prolonged activation in the ventral striatum and the medial temporal region including the amygdala. In the present study, repetition suppression did not reach significance level in the amygdala probably due to its low signal-to-noise

ratio (LaBar *et al.*, 2001; Zald, 2003). However, given the modulatory role of the amygdala in face processing (Vuilleumier, 2005), it is likely that sustained amygdala activation to emotionally positive stimuli maintains the activation in ventral visual cortex, resulting in attenuation of repetition suppression. Although repetition suppression has been theorized as reflecting local neural changes (Grill-Spector *et al.*, 2006), such global modulation of repetition suppression would merit further investigation given interaction among distant brain regions during face processing (Vuilleumier, 2005; Fairhall and Ishai, 2007).

As for angry faces, we did not obtain clear evidence for attenuation of repetition suppression as seen for happy faces. While speculative, this might reflect individual variability in sustained processing of emotionally negative stimuli. Fox *et al.* (2001) reported that attentional dwelling on angry faces was most reliably observed in high-anxious participants. It would thus be interesting to examine the relationship between repetition suppression for angry faces and trait anxiety.

The present study seems incompatible with Ishai *et al.* (2004), where they found greater repetition suppression for fearful faces than for neutral faces. Both angry and fearful faces are emotionally negative stimuli. The two faces, however, provide different types of threat information (Adams *et al.*, 2003). Whereas an angry face constitutes a direct threat to the observer, a fearful face conveys that a threat is somewhere in the environment. It may thus be adaptive that fearful faces engage repetition suppression as in Ishai *et al.* (2004) in order to allocate more neural resources to peripheral stimuli, as indicated by a recent behavioral study (Becker, 2009). Another difference between the two studies is the task imposed. Whereas we employed a passive viewing task, Ishai *et al.* (2004) used a match-to-target task: each trial began with presentation of a target face, followed by serial presentation of 13 faces, during which participants had to respond to the target face. This procedure resulted in distinct cognitive operations between the first presentation (encoding of the target) and the second to later presentations (comparison with the target), which introduced another factor confounding with repetition and hampered a simple interpretation. In fact, Ishai *et al.* (2004) observed repetition suppression only at the second and third repetitions; the first repetition was associated with even increased activation in some brain regions including the fusiform gyrus. Their findings are in contrast to a number of reports that repetition suppression occurred even at the first repetition (Soon *et al.*, 2003; Rotshtein *et al.*, 2005).

In contrast to the smaller repetition suppression for emotional faces in ventral visual cortex, equivalent suppression regardless of face emotion was observed in part of the left-inferior frontal gyrus and the right-precentral gyrus, which have been shown to play an important role in recognizing face emotion through emotional empathy (Nakamura *et al.*, 1999; Carr *et al.*, 2003; Leslie *et al.*, 2004).

Theoretically, detecting changes in facial expression is critical in emotion recognition but not in identity recognition (Bruce and Young, 1986; Haxby *et al.*, 2000). As such, the frontal regions may be more sensitive to detecting whether there are changes in emotional expression in the face stimuli rather than engaging sustained identity processing upon encountering emotional content. Thus, when there is no change in facial expressions across faces, as in our repeated trials, the frontal regions may respond minimally, resulting in repetition suppression for all face emotion conditions. Alternatively, previous studies have shown that frontal activation to face stimuli is the most evident when explicitly judging face emotion (Nakamura *et al.*, 1999; Winston *et al.*, 2003). Then, the possibility is that emotional modulation of repetition suppression would be observed also in frontal regions when an appropriate cognitive task is imposed instead of passive viewing, which remains to be tested in the future research. Nevertheless, our results demonstrate an interesting dissociation between the way frontal and ventral visual regions respond to face repetition within a passive viewing design.

In conclusion, the present study suggests that emotionally positive stimuli maintain sustained neural processing. More specifically, we found that happy faces engaged part of right-ventral visual cortex in a sustained manner evidenced by the lack of repetition suppression. This may be a neural signature of sustained processing of face identity from happy faces, as indicated in the behavioral literature. Future studies would be beneficial to establish a direct link between the neural and behavioral manifestations of such sustained happiness.

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