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Research report

Enhanced neural activity in response to dynamic facial expressions of emotion: an fMRI study

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Abstract

Dynamic facial expressions of emotion constitute natural and powerful media of communication between individuals. However, little is known about the neural substrate underlying the processing of dynamic facial expressions of emotion. We depicted the brain areas by using fMRI with 22 right-handed healthy subjects. The facial expressions are dynamically morphed from neutral to fearful or happy expressions. Two types of control stimuli were presented: (i) static facial expressions, which provided sustained fearful or happy expressions, and (ii) dynamic mosaic images, which provided dynamic information with no facial features. Subjects passively viewed these stimuli. The left amygdala was highly activated in response to dynamic facial expressions relative to both control stimuli in the case of fearful expressions, but not in the case of happy expressions. The broad region of the occipital and temporal cortices, especially in the right hemisphere, which included the activation foci of the inferior occipital gyri, middle temporal gyri, and fusiform gyri, showed higher activation during viewing of the dynamic facial expressions than it did during the viewing of either control stimulus, common to both expressions. In the same manner, the right ventral premotor cortex was also activated. These results identify the neural substrate for enhanced emotional, perceptual/cognitive, and motor processing of dynamic facial expressions of emotion.

Theme: Neural basis of behavior
Topic: Cognition, motivation and emotion

Keywords: Dynamic facial expression; Amygdala; Inferior occipital gyrus; Middle temporal gyrus; Fusiform gyrus; Ventral premotor cortex

1. Introduction

Dynamic facial expressions of emotion are natural and powerful media of emotional communication between individuals. However, little is known about the neural substrate underlying the processing of dynamic facial expressions. Previous neuroimaging studies have used static facial images; however, these images do not necessarily reflect the liveliness and true form of dynamic facial expressions as they occur in daily life [20].

Existing psychological evidence indicates that emotional processing is facilitated when expressions are dynamic rather than static. Several studies have shown that the dynamic presentation of facial expressions improves recognition of the emotional content of the expressions [15,20,32]. In neuropsychological studies, dynamic presentation improved emotion recognition relative to static presentation in a brain damaged patients [10]. Another line of evidence indicates that the dynamic presentation of facial expressions affects not only emotional processing but also various types of perceptual and/or cognitive processing for faces. Several studies have reported that the differences between spontaneous and deliberate expressions were more evident in the case of dynamic expressions, as compared to static expressions [9,23,24]. Other studies have reported that the dynamic presentation of facial expressions facilitated age [5] and familiarity [33] recognition, as compared with static image presentations.

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Previous neuroimaging studies have demonstrated that static facial expressions of emotion activate the emotion-related brain regions, such as the amygdala, especially in the case of negative emotions such as fear [6,18,19,37,38,43,44,51,52]. Some areas in the visual cortices have also been shown to specifically relate to the analysis of observed facial images; these areas include the inferior occipital gyrus [28], the fusiform gyrus [30,45], and the middle temporal gyrus and superior temporal sulcus (STS) [30,45]. Based on the aforementioned psychological findings, we expected that these brain regions might be more activated by dynamic facial expressions than by the corresponding static expressions. This concept was also supported by recent functional imaging studies, which reported that the observation of another's eye and mouth movements, both of which are important social signals, induced higher activation of the STS [41,46,53] and fusiform gyrus [41].

One might also expect that additional brain structures may be involved in the processing of dynamic facial expressions. A recent fMRI study that examined the neural correlates of the perception of movement of others' facial parts reported the activation of the ventral premotor cortex [8] and intraparietal sulcus [41,46]. Though it remains uncertain whether these areas are also active when subjects observe facial movements that provide emotional information, previous psychological evidence indicating spontaneous facial mimicry while viewing others' facial expressions [25] suggests the involvement of these motor-related areas.

In the present study, we measured brain activity by fMRI when subjects were passively observing dynamic emotional facial expressions. We used a computer morphing technique to present the dynamic expressions. This method allowed us to strictly compare the dynamic and static presentation of facial expressions relative to other methods, such as comparison between videotaped films and frames cut from the films. In addition, because this method enabled us to implement motion on static images chosen from a stimulus set frequently used in previous studies [14], the results can be properly compared with previous findings. In particular, we were interested in the facial expressions of fear and happiness, as previous studies using static expressions have yielded a lot of information with respect to these expressions of emotion (e.g., Ref. [6]). For comparison with the dynamic expressions, two types of control condition were prepared. In the primary condition, subjects viewed fearful or happy expressions that were static; these expressions provided images of sustained emotional expression. In an additional condition, subjects observed dynamic mosaic images; these images provided dynamic information with no facial or emotional properties. This condition allowed us to test whether higher brain activity for dynamic facial expressions, as compared to static expressions, was due, simply, to the processing of dynamic visual information. Based on the aforementioned psychological and neuroscientific evidence, we predicted that, the observation of dynamic facial expressions would induce higher activation in the amygdala compared with both control conditions, specifically in the case of fearful expressions. In addition, we predicted that dynamic facial expressions of both emotions would elicit the higher activity in the face-related visual areas including the inferior occipital gyrus, middle temporal gyrus/STS, and fusiform gyrus, than both control stimuli would do. We also expected the activity of the premotor and parietal cortex in the same manner.

2. Materials and methods

2.1. Subjects

Twenty-two volunteers (12 women and 10 men; mean age, 26.5 years) participated in the experiment. All subjects were right-handed and had normal or corrected-to-normal visual acuity. All subjects gave informed consent to participate in the study, which was conducted in accordance with the institutional ethical provisions and the Declaration of Helsinki.

Half of the subjects ($n=11$) were assigned to observe images of the expression of fear, and the other half were assigned to images of the expression of happiness.

2.2. Stimuli

The raw materials were grayscale photographs of 10 individuals' faces chosen from a standard set [14] depicting fearful, happy, and neutral expressions. For most subjects, none of these faces were familiar.

For the dynamic expressions stimuli, computer animation clips of emotional facial expressions were made from these photos. First, between the neutral (0%) and emotional (100%) expressions, 24 intermediate images in 4% steps were created using computer morphing techniques [39] implemented on a computer running Linux. Fig. 1 shows an example of the stimulus sequence. Next, to create a moving clip, a total of 26 images (i.e., one neutral image, 24 intermediate images, and the final emotion's image) were presented in succession. Each image was presented for 40 ms, and the first and last images were additionally presented for 230 ms; thus each animation clips lasted for 1500 ms. This presentation speed has been found to sufficiently reflect natural changes in the dynamic facial expressions of fear and happiness [48].

For the primary control condition, the static emotional expressions that correspond to the final images in the dynamic expression condition were prepared. These faces were presented for 1500 ms.

For the other control condition, dynamic mosaic images were made from the same materials. All of the above face images were divided into an 18 × 12 grid and randomly reordered by a constant algorithm. This rearrangement made each face unrecognizable as a face. Then a set of 26 images, corresponding to the original dynamic expression images,

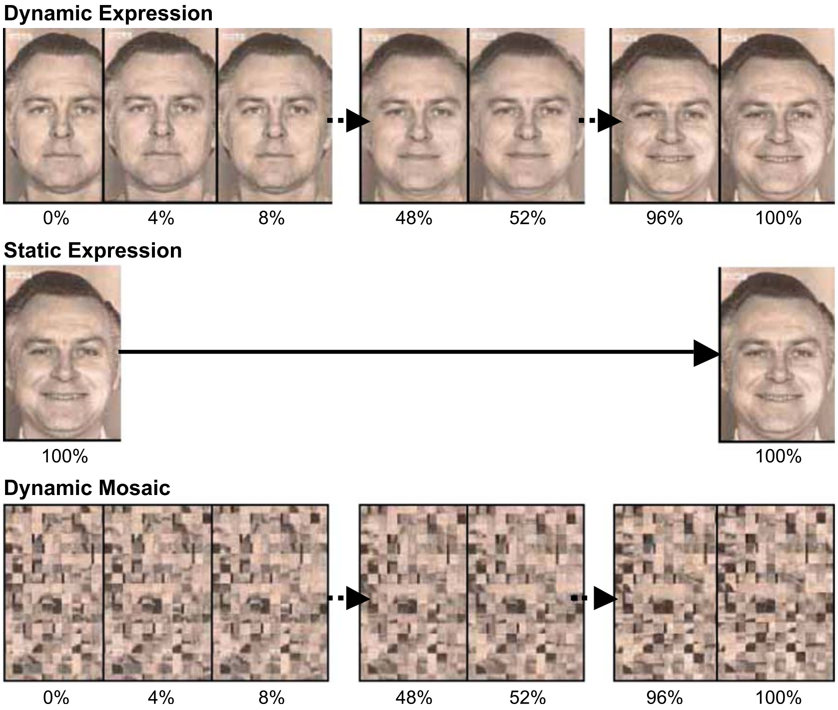

Fig. 1. Illustrations of stimulus presentations in the dynamic facial expression condition (upper), the static facial expression condition (middle), and the dynamic mosaic condition (lower).

was serially presented as a moving clip. The presentation speed was identical to that of the dynamic expression stimuli. These manipulations made the dynamic mosaic images almost equal to the corresponding original dynamic expression stimuli in terms of size, brightness, and dynamic information.

2.3. Presentation apparatus

The events were controlled by a program written in Visual C++ 5.0 (Microsoft, Seattle, WA, USA) implemented on a computer (Dimension 8000, Dell, Roundrock, TX, USA) running Windows (Microsoft, Seattle, WA, USA). The stimuli were projected from a liquid crystal projector (DLA-G11, Victor Company, Yokohama, Japan) to a mirror that was positioned in a scanner in front of the subject. In the present condition, the stimuli subtended a visual angle of about 15.0° vertical×10.0° horizontal.

2.4. Procedure

Each subject was run through an experimental session twice. Each session lasted 8 min and consisted of sixteen 30-s epochs with four 30-s rest periods interleaved (during which a fixation point was presented in the center of the screen). In each epoch, the 10 stimuli (each lasting 1500 ms) were presented twice. Each of the three stimulus conditions was presented in four different epochs within each scan. The order of the stimuli within each epoch and the order of epochs within each session were randomized at first and then fixed for all subjects.

Subjects were instructed to observe the images carefully while fixating on the center of the screen (i.e., where the fixation point was presented during rest periods). To avoid activations due to intentional evaluation of stimuli, working memory, or response selection, subjects were asked to view the stimuli passively, without making any response.

To confirm that the brain activations were not explained by eye movement artifacts, we preliminarily tested six subjects (different from those who took part in the imaging) while monitoring eye movements in the scanner. Dynamic fearful expressions, static fearful expressions, and dynamic mosaic images were presented, and horizontal eye movements were monitored with MR-Eyetracker (Cambridge Research Systems, Rochester, UK). This test showed that the numbers of horizontal eye movements exceeding 5° were very small under all conditions (mean ± s.d.: 0.3 ± 0.4, 0.1 ± 0.8, 0.6 ± 1.6 during each epoch of dynamic fearful expressions, static fearful expressions, and dynamic mosaics, respectively), and did not differ significantly across conditions ($p>0.1$, Friedman's one-way analysis of variance).

2.5. Image acquisition

Image scanning was performed on a 1.5-T scanning system (MAGNEX ECLIPSE 1.5T Power Drive 250, Shimadzu Marconi, Kyoto, Japan) using a standard radio frequency head coil for signal transmission and reception. A forehead pad was used to stabilize the head position. The functional images consisted of 52 consecutive slices parallel to the anterior–posterior commissure plane, covering the whole brain. The T2*-weighted gradient echo-planar imaging sequence was used with the following parameters: TR/TE = 6000/60 ms; FA = 90°; matrix size = 64 × 64; and voxel size = 3 × 3 × 3 mm. Before the acquisition of functional images, a T2-weighted anatomical image was obtained in the same plane as the functional images using a fast spin echo sequence (TR/TE = 9478/80 ms, FA = 90°; matrix size = 256 × 256; voxel size = 0.75 × 0.75 × 3 mm; number of echoes = 16). An additional high-resolution anatomical image was also obtained using a 3D RF-FAST sequence (TR/TE = 12/4.5 ms; FA = 20°; matrix size = 256 × 256; voxel dimension = 1 × 1 × 1 mm).

2.6. Image analysis

Image and statistical analyses were performed with the statistical parametric mapping package SPM99 (http://www.fil.ion.ucl.ac.uk/spm) implemented in MATLAB (Mathworks Inc., Sherborn, MA, USA). First, to correct for head movements, functional images of each run were realigned using the first scan as a reference. Data from all subjects showed small motion correction (< 2 mm). Then, T2-weighted anatomical images scanned in planes identical to the functional imaging slice were coregistered to the first scan in the functional images. Following this, the coregistered T2-weighted anatomical images were normalized to a standard T2 template image, as defined by the Montreal Neurological Institute (MNI), which involves linear and non-linear three-dimensional transformations [3,17]. The parameters estimated from this normalization process were then applied to each of the functional images. Finally, these spatially normalized functional images were resampled to a voxel size of 2 × 2 × 2 and smoothed with an isotopic Gaussian kernel (10 mm) to compensate for the anatomical variability between subjects. The high-resolution anatomical images were also normalized by the same procedure.

We searched for significantly activated voxels displaying interesting effects by using random effects analysis. First, we performed single-subject analysis [16,54]. The task-related neural activities for each condition were modeled with a box-car function convoluted with a canonical hemodynamic response function. We applied a band-pass filter composed of the discrete cosine basis function with a cut-off period of 240 s for high-pass filtering and a canonical hemodynamic response function for low-pass filtering. To correct the global fluctuation between scans, global scaling was conducted. The analyses were conducted for each emotion (fear, happiness). Preplanned comparisons were performed to test (1) dynamic expressions vs. static expres-

Table 1
Brain regions showing significant activation in response to dynamic facial expressions compared to static facial expressions (left) and dynamic mosaics (right) for fearful emotion

Brain region	BA	Dynamic vs. static facial expressions				Dynamic facial expressions vs. dynamic mosaics			
		Coordinates			*T*-value	Coordinates			*T*-value
		x	*y*	*z*		*x*	*y*	*z*	
R. inferior occipital gyrus	19	34	– 84	– 8	8.51	46	– 78	– 6	8.95
R. inferior occipital gyrus	19	42	– 74	– 4	6.73	38	– 72	– 2	6.19
R. middle occipital gyrus	19	44	– 82	4	6.79				
R. inferior temporal gyrus	37	46	– 62	– 6	8.00				
R. middle temporal gyrus	21	46	– 62	6	8.00	56	– 64	4	6.73
R. middle temporal gyrus	21	62	– 46	8	5.26	62	– 46	10	4.77
R. superior temporal gyrus	22	60	– 36	16	4.39	50	– 40	12	7.50
R. fusiform gyrus	37	44	– 60	– 12	8.88	46	– 66	– 16	5.85
R. fusiform gyrus						42	– 50	– 10	6.32
R. intra patietal sulcus	7	30	– 46	48	8.38				
R. intra patietal sulcus	40	40	– 32	40	5.07				
R. inferiror frontal gyrus	9	46	6	34	5.52	52	6	44	4.01
R. inferiror frontal gyrus	44	50	8	24	5.42	52	14	14	4.99
R. amygdala	–					18	– 12	– 14	5.09
L. inferior occipital gyrus	19	– 34	– 90	– 2	11.17	– 40	– 86	– 6	9.17
L. inferior occipital gyrus	37	– 40	– 68	– 8	7.95	– 42	– 72	0	3.30
L. middle occipital gyrus	19	– 34	– 90	2	5.76				
L. middle temporal gyrus	37	– 42	– 74	6	10.31	– 54	– 66	8	4.59
L. middle temporal gyrus	21					– 50	– 54	10	4.15
L. fusiform gyrus	37	– 38	– 62	– 16	5.34	– 38	– 62	– 8	4.26
L. amygdala	–	– 24	– 8	– 18	3.66	– 20	– 8	– 16	4.23
Brain stem	–					10	– 18	– 10	4.37
Brain stem	–					4	– 32	– 6	4.82

The coordinates of activation foci in MNI system and their *T*-values are shown.

sions, and (2) dynamic expressions vs. dynamic mosaics. Contrast images were generated for each comparison and then entered into a one-sample *t*-test to create a random effect SPM $\{T\}$. For these analyses, voxels were identified as significantly activated if they reached the height threshold of $p < 0.001$ (uncorrected) with the extent threshold corrected for multiple comparisons of the entire brain volume ($p < 0.05$). For the analysis of the amygdala, which has been reported to have a small extent of activation (e.g., Ref. [43]), we used small volume correction. The regions were defined bilaterally by 6-mm radius spheres centered on the coordinates ($x \pm 20$, $y - 8$, $z - 16$ in the MNI space), which were derived from the stereotactic anatomical atlas [49] (cf., Ref. [44]).

3. Results

3.1. Brain activity for fearful expressions

3.1.1. Dynamic vs. static expressions

When the brain activity in response to dynamic fearful expressions was compared with that in response to static fearful expressions (Table 1; Fig. 2), we found significant

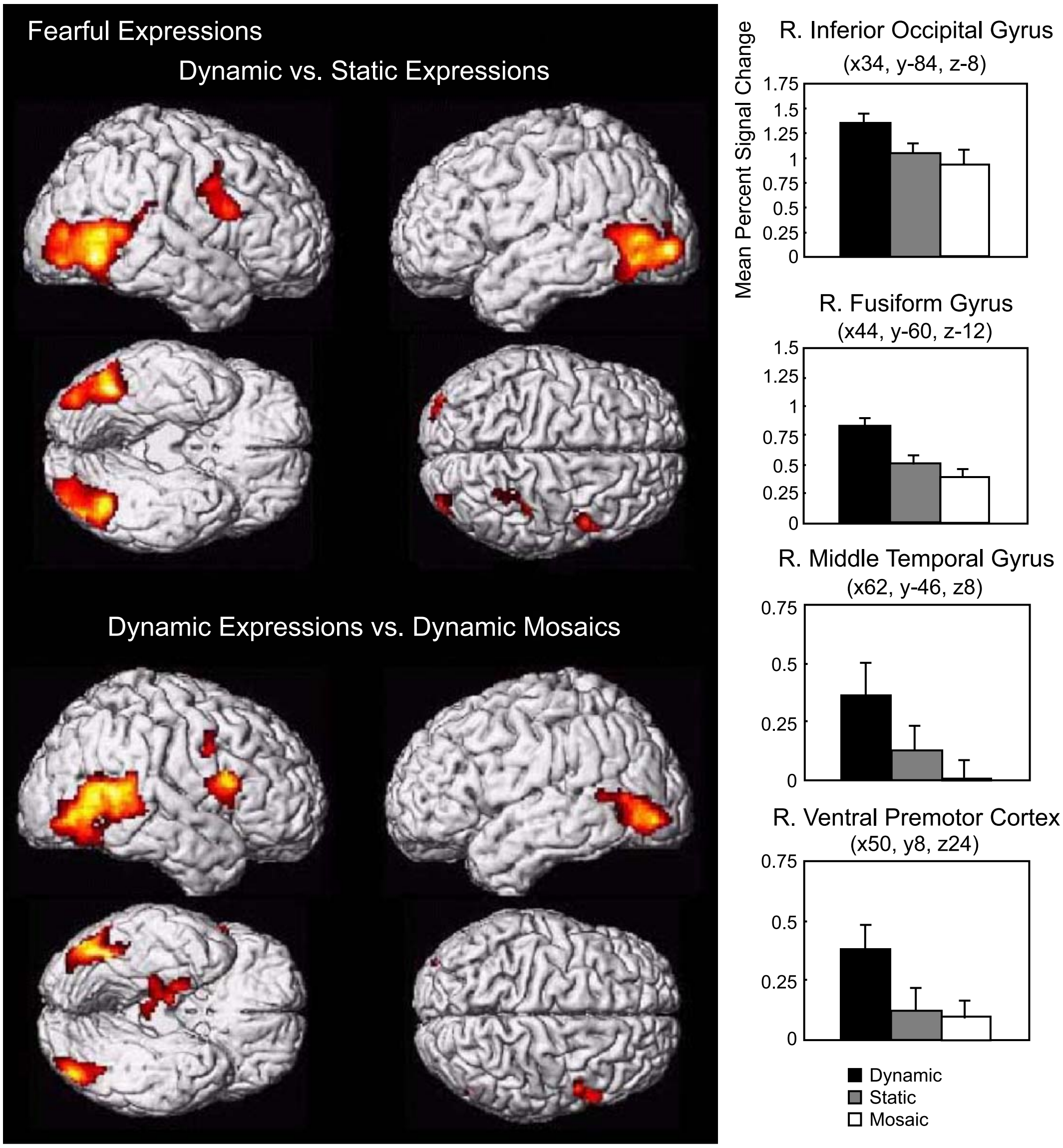

Fig. 2. Left: Statistical parametric maps showing brain regions activated in response to dynamic fearful expressions as compared to static fearful expressions (upper) and dynamic mosaics (lower). The areas of activation are rendered on spatially normalized brains. Right: Mean percent signal changes (with standard error) of the representative brain regions highly activated for dynamic fearful expressions. Data for dynamic fearful expressions (Dynamic), static fearful expressions (Static), and dynamic mosaics (Mosaic) are shown. The data were calculated by first sampling the spherical VOIs (6 mm radius) of these regions at the sites of peak activation in the comparison of dynamic vs. static expression and then subtracting the mean signal value of the rest condition (baseline) from those of the activation periods. Because of the time lag of hemodynamic responses, the first two image of each period was discarded.

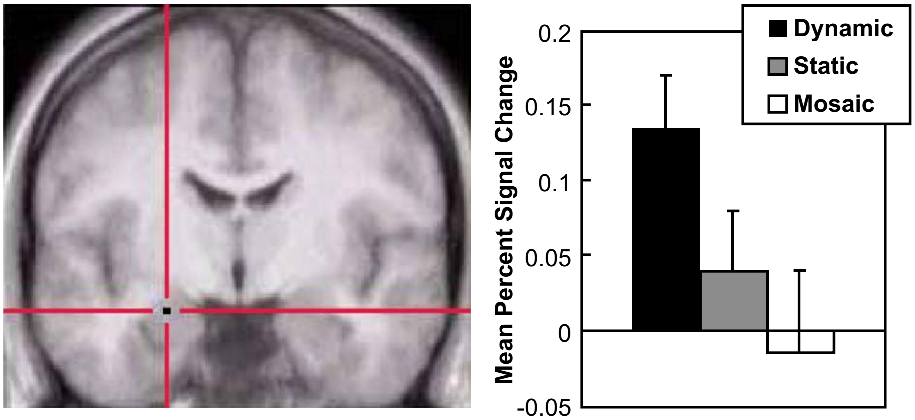

Fig. 3. Left: A statistical parametric map showing left amygdala activity for dynamic fearful expressions, as compared to static fearful expressions. The activation is overlayed on the coronal sections of the anatomical MRI of the mean brain of subjects involved in this study. Right: Mean percent signal changes (with standard error) of amygdala activity. Data for dynamic fearful expressions (Dynamic), static fearful expressions (Static), and dynamic mosaics (Mosaic) are shown. The data were calculated by the method depicted in the legend of Fig. 2.

activation in the left amygdala (Fig. 3). Additionally, broad ranges of bilateral posterior regions were also significantly activated, including the activation foci of the inferior occipital gyri, middle occipital gyri, inferior temporal gyri, middle temporal gyri, superior temporal gyri and fusiform gyri. This posterior activation was evident in the right hemisphere relative to the left hemisphere. Furthermore, significant activation of the ventral premotor cortex and intraparietal sulcus was observed in the right hemisphere.

3.1.2. Dynamic expressions vs. dynamic mosaics

When the brain activity in response to dynamic fearful expressions was compared with that in response to dynamic mosaic images made from fearful expressions (Fig. 2), almost all brain areas that were detected in the above comparison were detected. Significant amygdala activity was detected in both hemispheres. Bilateral activities in the occipital and temporal gyri were also detected, although the activations in this comparison were relatively small, especially in the posterior dorsal portions; the activation foci were not detected in the middle occipital gyri. As with the above comparison, the visual area activation was dominant in the right hemisphere. Significant activity of the right ventral premotor cortex was also shown. Unlike the above comparison, significant activation of the intraparietal sulcus was not detected.

3.2. Brain activity for happy expressions

3.2.1. Dynamic vs. static expressions

For the happy expression, the results showed almost the same pattern of results as for the fearful expression. When brain activity in response to the dynamic happy expressions was compared with that in response to the static happy

Table 2
Brain regions showing significant activation in response to dynamic facial expressions compared to static facial expressions (left) and dynamic mosaics (right) for happy emotion

Brain region	BA	Dynamic vs. static facial expressions				Dynamic facial expressions vs. dynamic mosaics			
		Coordinates			*T*-value	Coordinates			*T*-value
		x	*y*	*z*		*x*	*y*	*z*	
R. inferior occipital gyrus	19	34	– 84	– 10	15.50	46	– 76	– 4	7.92
R. middle occipital gyrus	19	32	– 88	6	8.69				
R. inferior temporal gyrus	37	48	– 64	– 8	11.89	42	– 68	– 14	4.61
R. middle temporal gyrus	21	62	– 46	2	4.87	60	– 48	2	5.27
R. fusiform gyrus	37	42	– 58	– 16	7.98	42	– 60	– 18	6.45
R. fusiform gyrus	37					38	– 46	– 18	4.74
R. intra patietal sulcus	7	30	– 46	48	9.34				
R. intra patietal sulcus	40	42	– 36	52	4.07				
R. Inferiror frontal gyrus	44	54	8	20	5.27	56	14	14	4.44
R. amygdala	–					20	– 8	– 14	4.83
L. inferior occipital gyrus	19	– 34	– 90	– 2	14.40	– 40	– 86	– 61	6.01
L. middle occipital gyrus	37	– 42	– 72	4	10.52				
L. superior occipital gyrus	19	– 24	– 86	14	5.53				
L. inferior temporal gyrus	37	– 42	– 68	– 8	9.03				

The coordinates of activation foci in MNI system and their *T*-values are shown.

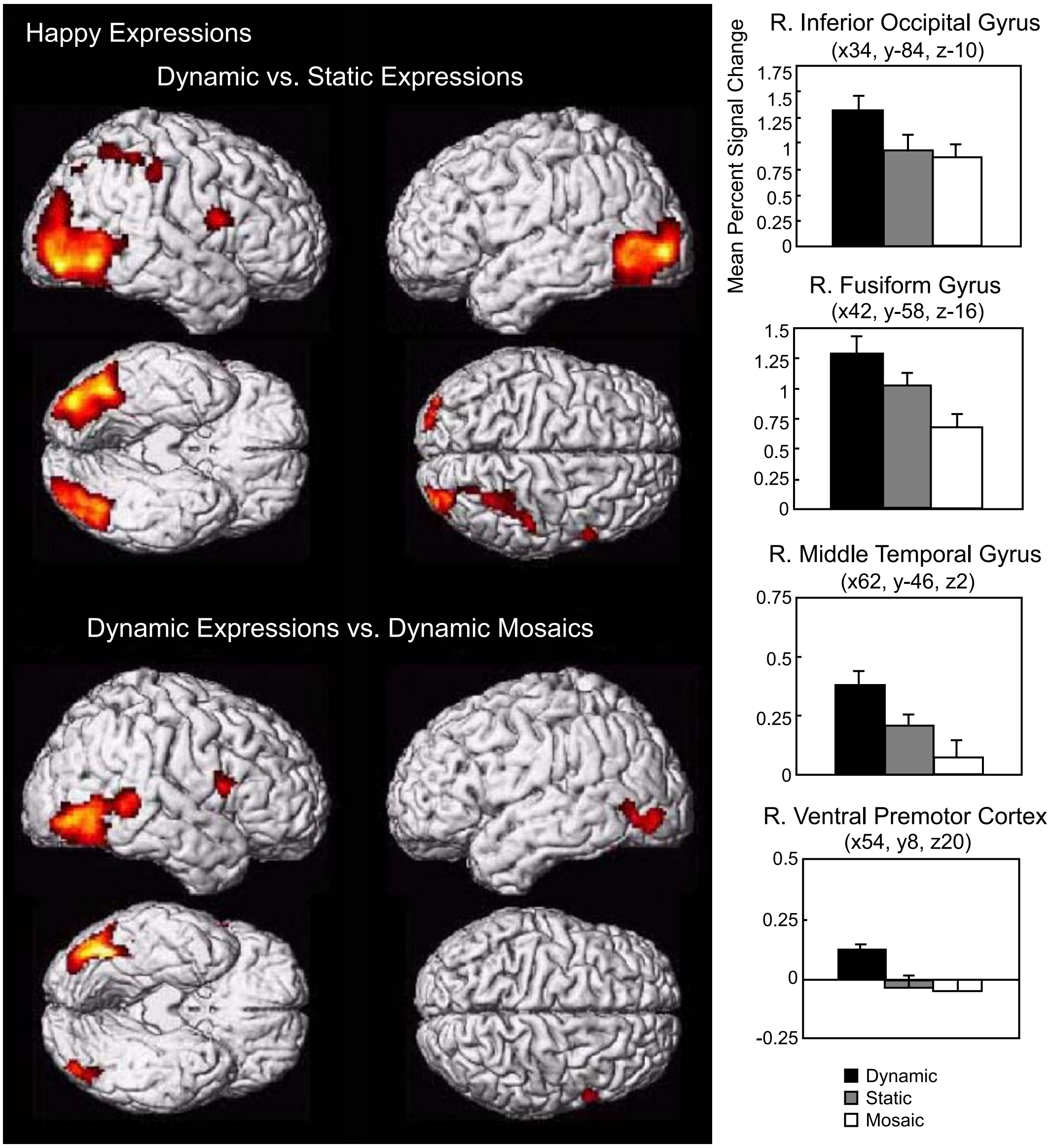

Fig. 4. Left: Statistical parametric maps showing brain regions activated for dynamic happy expressions, as compared to static happy expressions (upper) and dynamic mosaics (lower). The areas of activation are rendered on spatially normalized brains. Right: Mean percent signal changes (with standard error) of the representative brain regions highly activated for dynamic happy expressions. Data for dynamic happy expressions (Dynamic), static happy expressions (Static), and dynamic mosaics (Mosaic) are shown. The data were calculated by the method depicted in the legend of Fig. 2.

expressions (Table 2; Fig. 4), broad ranges of bilateral posterior regions, which included the activation foci of the inferior occipital gyri, middle occipital gyri, inferior temporal gyri, middle temporal gyri, and fusiform gyri, were detected significantly. These active fields were dominant in the right hemisphere. Significant activities of the ventral premotor cortex and intraparietal sulcus in the right hemisphere were also observed. A marked difference from the results for fearful expression was that the amygdala did not show significant activation in this comparison.

3.2.2. Dynamic expressions vs. dynamic mosaics

As was the case for fearful expressions, almost all brain areas detected in the above comparison showed activation when brain activity in response to dynamic happy expressions was compared with that in response to dynamic mosaic images (Fig. 4). Bilateral activities in the posterior regions were significant. As with fearful expressions, posterior dorsal activations in this comparison were restricted, and the activation foci in the middle occipital gyri were not detected. The activations in this comparison were highly lateralized to the right hemisphere; the cluster in the right hemisphere included the activation foci in the inferior occipital gyri, middle temporal gyri, and fusiform gyri, and the cluster in the left hemisphere showed the foci only in the inferior occipital gyrus. The right ventral premotor cortex was also activated, although the active field was small and the extent of activation only reached uncorrected marginal significance ($p = 0.055$). As with fearful expressions, significant activation of the intraparietal sulcus was not detected.

4. Discussion

The results revealed that distributed brain areas were highly activated by the observation of dynamic facial expressions of emotion. The left amygdala was highly activated in response to dynamic facial expressions relative to both control stimuli in the case of fear, but not in the case of happiness. The broad region of occipital and temporal cortices, especially in the right hemisphere, showed higher activation while viewing the dynamic facial expressions than while viewing either of the control stimuli, and this pattern was common to both happy and fearful expressions. In the same manner, the right ventral premotor cortex was also activated.

Such enhanced neural activity for dynamic facial expressions relative to static expressions is consistent with the proposal that static materials do not capture the liveliness and true form of the facial expressions that typically occur in day-to-day interactions [20]. Motion may endow the facial expressions with emotional messages that appear more realistic.

4.1. Amygdala

The amygdala was more activated during observation of dynamic emotional facial expressions than it was during observation of either of the control stimuli in the case of fear, but not in the case of happiness. These results are consistent with previous imaging studies, which reported that the amygdala is more active for emotional expressions, particularly with regard to fear [6,18,19,37,38,44,51,52].

One of these imaging studies [38] showed that this amygdala activity increased when the fearful expression was enhanced. Neuropsychological evidence indicated that damage to the amygdala impairs recognition of fearful expressions [1]. Previous psychological studies have indicated that dynamic presentations of facial expressions of emotion enhance emotion recognition, as compared to static presentations [10,15,20,27,32]. In concert, the higher amygdala activity for dynamic fearful expressions may be responsible for the enhanced emotional processing of dynamic facial expressions.

4.2. Visual areas

The occipital and temporal cortical clusters were activated for the dynamic facial expressions, including strong activation foci in the middle temporal gyrus and its adjacent areas including STS. The middle temporal gyrus/STS region was shown to activate during the processing of static expressions of emotions [31,40]. Single-unit recording studies in monkeys have also shown that some STS cells strongly respond to the viewing of certain facial expressions [21]. As the monkey neuroanatomical studies have indicated that the STS is reciprocally connected with the amygdala [2], the higher activation of this region may be related to the facilitation of emotional processing for dynamic facial expressions.

At the same time, previous functional imaging studies have reported higher responses of the bilateral STS and their adjacent areas for movements of facial features [41,46,53]. Single-unit recording studies in monkeys have also shown that STS cells respond strongly while a monkey is viewing movements of facial features [21,42]. Together with these data, the present result suggests the possibility that this region processes the dynamic properties on faces.

The other visual region related to face processing, the inferior occipital gyrus and fusiform gyrus, also showed higher activity in the case of dynamic expressions than for either control stimulus. The activation of the fusiform gyrus in response to movements of facial features is consistent with a previous fMRI study [41]. Haxby et al. [22] recently proposed a neuro-cognitive model for face processing, in which the inferior occipital gyrus conducts the basic perception of facial features, and fusiform gyrus processes the identity of the person. It may be that higher activity in these visual areas is related to enhanced perceptual and/or cognitive processing for dynamic characteristics of faces that relate to age [5] and familiarity identity [33].

Our results also showed that not only these face-specific areas, but also a broad range of visual-related areas in the occipital and temporal cortex were more activated for dynamic facial expressions than they were for either static facial expressions or dynamic mosaics. A previous fMRI study showed that observation of motions made by facial features strongly activated the human MT/MST regions, as compared to the effect of mosaic movements [46]. The movements of human faces may have some impact on brain regions that are not specific to face processing. Alternatively, as previous imaging studies (e.g., Ref. [34]) showed broad extrastriate activation during the observation of positive or negative stimuli, the overall activation of the visual areas may be attributable to the strong emotional signal conveyed in dynamic facial expressions.

The activation of the visual cortices during the observation of dynamic facial expressions was more evident in the right than the left hemisphere. Consistent with this result, right hemispheric dominance in various types of visual processing for facial expressions has been reported in the psychological literature (e.g., Ref. [26]). Our results extend these findings, suggesting that this right hemispheric dominance may be enhanced when the expressions are dynamically presented and, hence, may be more evident in daily communication with dynamic facial expressions than in experimental investigations with static facial stimuli.

4.3. Ventral premotor cortex and intraparietal sulcus

Activation was observed in the right ventral premotor cortex during observation of dynamic facial expressions. These results are in agreement with recent findings of fMRI studies reporting that the observation of another person's mouth actions without emotional content more highly activated the ventral premotor cortex [8], bilaterally, but especially in the right cortex. The present data confirm the earlier findings and extend these findings to the observation of dynamic facial motion with emotional messages.

According to many researchers' interpretations of the evidence (e.g., Ref. [47]), the activities of these motor-related areas might reflect a ''mirror'' function, when subjects observe others' actions. Consistent with this proposal, behavioral studies have shown that the observation of others' facial expressions induces spontaneous facial mimicry in adults [25], and even in newborn infants [36]. Consistent with our data, recent facial electromyography studies have shown that this facial mimicry is elicited automatically [12] and is dominantly processed in the right hemisphere [11].

The activation of the right ventral premotor cortex for dynamic facial expressions was more evident in the case of fear than in the case of happiness. It may be that the higher amygdala activity that is specific to dynamic fearful expressions modulates the activity of this region. Monkey anatomical studies have indicated that the amygdala contains direct projections to the premotor cortex [4].

The right intraparietal sulcus was also activated for dynamic facial expressions, as compared with static facial expressions. The activation of the right intraparietal sulcus is in agreement with a previous fMRI study, which reported that the observation of motion of facial parts activated this region, especially in the right hemisphere [41,46]. As the ventral premotor cortex and intraparietal sulcus have rich bidirectional connectivity [35], such a frontal–parietal network may be involved in the processing of dynamic facial expressions.

However, the intraparietal sulcus did not show significant activation for dynamic facial expressions, as compared with dynamic mosaics. This is in line with recent neuroimaging findings, which have reported the activation of the intraparietal sulcus in response to simple visual motion [7]. In concert with this evidence, our results suggest the possibility that the intraparietal sulcus activity for dynamic facial expressions may not be specific to facial expressions with motion but may be related to motion per se.

4.4. Limitations and future directions

Some limitations of this study should be acknowledged.

First, since we tested angry and happy facial expressions of emotion in two different groups of subjects, the brain activity with these two emotions could not be compared directly. We used two groups because our primary purpose in this study was to investigate the effect of presentation condition, using as simple a design as possible. The direct comparison of brain activities for each emotional category using a within-subject design will be an important issue for future research.

Second, it is possible that our within-subject approach for the presentation condition incorporates some historical effects in the brain activity in response to dynamic or static facial expressions. A recent single-unit recording study in monkeys [29] revealed that the responses of some STS cells in response to static faces could incorporate the effect of the sight immediately preceding the dynamic faces. Future studies may be necessary to confirm the brain activity found in our study, dissociating the historical effect of preceding conditions.

Finally, the contrast between dynamic emotional and dynamic neutral expressions remains untested. One of the reasons why we did not include a dynamic neutral expression condition was that it was difficult to prepare the appropriate stimuli for this condition. One possibility is to use the face of a person speaking with a neutral expression, such as the face of a reporter reading a news report. However, we decided that this was not an appropriate stimulus for two reasons. First, while emotional facial expressions contain complex motions involving multiple facial parts [13], the movement in the faces of people speaking is mostly in the lower area of the face, such as the mouth and chin. Second, there is evidence that even a facial motion that is not included in facial expressions of prototypical emotions can sometimes be recognized as conveying an emotional message [50]. It is extremely difficult to make dynamic face stimuli that neutralize all emotional meaning and have dynamic properties comparable with those of dynamic emotional expressions. The presentation of inverted emotional faces is one possibility, because inversion makes the perception of emotion from facial expression very difficult, while the dynamic properties of the stimuli remain unchanged. Future research using this contrast would provide further evidence regarding the brain mechanism involved in the perception of dynamic facial expressions of emotion.

4.5. Summary

We measured brain activity by fMRI when subjects were passively observing dynamic emotional facial expressions. The facial expressions were dynamically morphed from neutral faces to fearful or happy faces. Static expressions and dynamic mosaic images were prepared to compare with the dynamic expressions. For fearful expressions, the left amygdala, right dominant occipital and temporal clusters, including the activation foci of the inferior occipital gyri, middle temporal gyri, and fusiform gyri, and right ventral premotor cortex showed higher activation during viewing of the dynamic facial expressions than during viewing of either of the control stimuli. For happy expressions, the results were almost the same, except for a lack of amygdala activity. These results contribute to the understanding of the neural substrate for enhanced emotional, perceptual/cognitive, and motor processing of dynamic facial expressions of emotion.

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