Amygdala activity in response to forward versus backward dynamic facial expressions

Wataru Sato[1], Takanori Kochiyama[2], and Sakiko Yoshikawa[3]

Institutional affiliation

1 Department of Comparative Study of Cognitive Development (funded by Benesse Corporation), Primate Research Institute, Kyoto University, Inuyama, Aichi 484-8506, Japan.

2 Brain Activity Imaging Center, Advanced Telecommunications Research Institute International, 2-2-2 Hikaridai, Seika-cho, Soraku-gun, Kyoto 619-0288 Japan.

3 Kokoro Research Center, Kyoto University, Yoshida-honmachi, Sakyo-ku, Kyoto 606-8501, Japan.

Corresponding author

Wataru Sato, Department of Comparative Study of Cognitive Development (funded by Benesse Corporation), Primate Research Institute, Kyoto University, Inuyama, Aichi 484-8506, Japan.

E-mail: sato@pri.kyoto-u.ac.jp

ABSTRACT

Observations of dynamic facial expressions of emotion activate several brain regions, but the psychological functions of these regions remain unknown. To investigate this issue, we presented dynamic facial expressions of fear and happiness forwards or backwards, thus altering the emotional meaning of the facial expression while maintaining comparable visual properties. Thirteen subjects passively viewed the stimuli while being scanned using fMRI. After image acquisition, the subject's emotions while perceiving the stimuli were investigated using valence and intensity scales. The left amygdala showed higher activity in response to forward compared with backward presentations, for both fearful and happy expressions. Amygdala activity showed a positive relationship with the intensity of the emotion experienced. These results suggest that the amygdala is not involved in the visual but is involved in the emotional processing of dynamic facial expressions, including specifically the elicitation of subjective emotions.

Key words: amygdala, dynamic facial expression, emotional intensity, fMRI.

1. Introduction

Dynamic facial expressions of emotions are natural and powerful cues in our daily interactions. Psychological studies have indicated that dynamic facial expressions, as compared with static expressions, enhance a variety of psychological processes, including perception (Yoshikawa and Sato, 2008), identity recognition (e.g., Bruce and Valentine, 1988), facial mimicry (e.g., Sato and Yoshikawa, 2007b), emotion recognition (e.g., Harwood et al., 1999), and emotion elicitation (Sato and Yoshikawa, 2007a).

Some neuroimaging studies have depicted brain activity in response to dynamic facial expressions of emotion, comparing brain activity in response to dynamic emotional facial expressions with activity in response to static expressions (Kilts et al., 2003; LaBar et al., 2003; Sato et al., 2004a; Pelphrey et al., 2007). Although the details differ among the studies, the results generally indicated that several brain regions were more active when viewing dynamic facial expressions compared with static facial expressions; these regions included the posterior superior temporal sulcus (STS) and adjacent regions (Kilts et al., 2003; LaBar et al., 2003; Sato et al., 2004a; Pelphrey et al., 2007), the posterior fusiform gyrus (Kilts et al., 2003; LaBar et al., 2003; Sato et al., 2004a; Pelphrey et al., 2007), the inferior occipital gyrus (Sato et al., 2004a), the inferior frontal gyrus (LaBar et al., 2003; Sato et al., 2004a), and the amygdala (LaBar et al., 2003; Sato et al., 2004a; Pelphrey et al., 2007). As these regions are related to the processing of faces and facial expressions (Hoffman and Haxby, 2000; Rizzolatti et al., 2001), enhanced activity of this neural substrate is consistent with enhanced manifold psychological processes for dynamic facial expressions.

Nevertheless, the specific psychological functions of these brain regions remain unknown. The most prominent feature of dynamic facial expressions, as compared with static facial expressions, is dynamic visual information. Most brain regions activated by dynamic facial expressions have been shown to contain visual-responsive neurons (e.g., Ono and Nishijo, 1999). Thus, it is possible that the processing of visual motions may be the primary correlate in these regions. Alternatively, as dynamic facial expressions enhance various psychological processes such as emotion elicitation, some of these processes may be related to the activity in these regions.

To investigate the neural activity for dynamic biological stimuli while controlling for visual features, Brothers (1990) proposed the interesting strategy of presenting the stimuli backwards. Brothers insisted that if the stimuli were shown backwards, they would have the same visual features, but the meaning would be reduced. This would likely be the case for dynamic facial expressions, because dynamic facial expressions presented forwards and backwards would have comparable visual motions but quite different emotional meanings. The forward presentations would exhibit appearing emotional expressions, whereas the backward presentations would indicate disappearing emotional expressions. To investigate the neural activity related to emotional processing, and not visual processing, for dynamic facial expressions, we adopted the backward presentation strategy.

The amygdala is a plausible neural substrate candidate for the emotional processing of dynamic facial expressions. Single unit recording studies in monkeys have shown that amygdala neurons discharged in response to significant aversive and rewarding stimuli (Ono and Nishijo, 1992). Lesion studies in monkeys have indicated that selective damage to the amygdala impaired the emotional responses to significant environmental stimuli (Aggleton and Young, 2000). In neuroimaging studies in humans, amygdala activity was associated with the intensity or arousal of emotions experienced in response to olfactory (Anderson et al., 2003) and gustatory stimuli (Small et al., 2003), for both negative and positive valences. A previous neuroimaging study also reported that amygdala activity was related to the intensity of negative emotion experienced while viewing static negative facial expressions (Sato et al., 2004b). Based on this evidence, we hypothesized that the amygdala is involved in the emotional processing of dynamic facial expressions of emotion, including the elicitation of subjective emotions while viewing the expressions.

In the present fMRI study, we examined the brain activity in subjects while they viewed forward and backward presentations of dynamic facial expressions (cf. Figure 1). We used a computer morphing technique to present dynamic expressions and prepared facial expressions of both negative (fearful) and positive (happy) emotional valences. To assess the emotion that the subjects experienced while viewing the facial expressions, we presented the same stimuli again after image acquisition and required the subjects to rate their subjective emotional experience, in terms of valence and intensity. Based on the aforementioned evidence regarding amygdala activity, we predicted that amygdala activity would be higher in response to forward compared with backward presentations for both valences, and that amygdala activity would correspond to the intensity of the experienced emotion. We also analyzed the activity of other brain regions that have been shown to relate to the processing of dynamic facial expressions, although we did not have specific hypotheses for these regions.

****
Figure 1
****

2. Results

2.1. Psychological rating

Mean ± *SE* valence ratings were –1.8 ± 0.3, -0.9 ± 0.1, 2.3 ± 0.2, and –1.0 ± 0.2 for forward fear, backward fear, forward happiness, and backward happiness, respectively (Supplementary Figure 1). The analysis of variance (ANOVA) for the valence ratings revealed significant main effects of presentation condition and emotion, and an interaction of presentation condition × emotion (Fs(1,12) = 62.37, 96.21, and 63.45; ps < 0.001). Follow-up analyses for the interaction revealed that the simple main effects of emotion were significant for fearful and happy expressions (Fs(1,24) = 8.88 and 117.50; ps < 0.005). For fearful expressions, more negative emotion was elicited for forward than backward presentations. For happy expressions, more positive emotion was induced for forward than backward presentations.

Mean ± *SE* intensity ratings were 5.3 ± 0.3, 3.5 ± 0.2, 5.4 ± 0.4, and 3.6 ± 0.3 for forward fear, backward fear, forward happiness, and backward happiness, respectively (Supplementary Figure 1). The ANOVA for the intensity ratings revealed that the main effect of the presentation condition was significant, indicating the experience of higher emotional intensity for forward than backward presentations ($F(1, 12) = 41.46$; $p < 0.001$). No significant main effect of emotion or interaction was found ($ps > .1$).

2.2. SPM analysis of brain activity

When brain activity in response to forward presentations was compared with that in response to backward presentations using the statistical parametric mapping (SPM) analysis, we found significant activation in the left amygdala (x-24, y-12, z-8, $T(12) = 4.55$; Figure 2). Significant activation was also observed in the left parahippocampal gyrus (x-32, y-40, z-2, $T(12) = 6.24$). Other significant areas of activation were not detected with our predefined thresholds. With a more liberal height threshold ($p < 0.005$, uncorrected), significant activations were also found in the right amygdala (x16, y-12, z-8, $T(12) = 3.88$). For the comparison of backward versus forward presentations, fear versus happiness, happiness versus fear, and an interaction between presentation condition and emotion, we found no significantly activated region.

****
Figure 2
****

2.3. Relationship between amygdala activity and psychological rating

In a regression analysis with left amygdala activity as the dependent variable and psychological ratings as the independent variables, the coefficient of the intensity was positive and significantly different from zero (standardized coefficient = 0.43; t (37) = 2.81, $p < 0.01$). The coefficient of the valence was not significantly different from zero (standardized coefficient = -0.14; t (37) = 1.05, $p > 0.1$).

2.4. ROI analysis of brain activity

We conducted region of interest (ROI) analyses of the activity in several other brain regions that have been shown to relate to the processing of dynamic facial expressions. The regions included the inferior occipital gyrus (Sato et al., 2004a), fusiform gyrus (Kilts et al., 2003; LaBar et al., 2003; Sato et al., 2004a; Pelphrey et al., 2007), STS (Kilts et al., 2003; LaBar et al., 2003; Sato et al., 2004a; Pelphrey et al., 2007), and inferior frontal gyrus (LaBar et al., 2003; Sato et al., 2004a) in the right hemisphere. The ANOVAs for the activity of these regions, with presentation condition and emotion as within-subject factors, showed no significant main effects or interactions (ps > 0.1), except that a main effect of emotion showed a trend toward significance for the inferior frontal gyrus ($F(1,12) = 3.50$, $p < 0.1$).

3. Discussion

The analysis of the psychological ratings revealed that the subjects experienced less intense emotions for the backward compared with the forward presentations, for both the fearful and happy facial expressions.

It must be noted that the forward and backward presentations contained quite comparable visual motions. The results indicate that although the backward presentations of dynamic facial expressions provided visual motions comparable to the forward presentations, they had reduced emotional significance.

The analysis of the brain activity demonstrated that the left amygdala was more active in response to forward compared with backward presentations, for both the fearful and happy facial expressions. Regression analysis showed that amygdala activity showed a positive relationship with the intensity of the experienced emotion. These results support our hypothesis that the activity in the amygdala is involved not in the visual but in the emotional processing of dynamic facial expressions, which specifically includes the elicitation of subjective emotions.

The activation of the amygdala for dynamic fearful facial expressions is consistent with previous studies (LaBar et al., 2003; Sato et al., 2004a; Pelphrey et al., 2007). Several other neuroimaging studies have reported amygdala activation in response to static fearful (e.g., Breiter et al., 1996) and happy (e.g., Wright et al., 2002; Killgore and Yurgelun-Todd, 2004; Fitzgerald et al., 2006) facial expressions.

Our results did not show a main effect of emotion, that is, higher activity for fearful than for happy facial expressions, in amygdala activity. Although this result is inconsistent with some previous studies reporting higher amygdala activity for static fearful than for static happy expressions (e.g., Morris et al., 1996), a recent meta-analysis of neuroimaging data revealed that the amygdala was *similarly* active in response to negative and positive facial expressions (Sergerie et al., 2008). Our data are consistent with this notion, indicating that the amygdala is active for forward-presented dynamic facial expressions, both fearful and happy.

Our finding that the amygdala was involved in emotional but not visual processing for dynamic emotional expressions is consistent with several previous studies. For example, electrophysiological studies in monkeys and cats indicated that the amygdala was involved in decoding significant aversive and rewarding stimuli, regardless of the physical features of the stimulus (Maeda et al., 1993; Ono and Nishijo, 1999). Lesion studies in monkeys have shown the importance of the amygdala in the triggering of emotional reactions to environmental stimuli (Aggleton and Young, 2000). Neuroimaging studies in humans showed that the activity of the amygdala elicited by olfactory and gustatory negative and positive stimuli was associated with the intensity or arousal of the experienced emotion and was not attributable to the basic sensory features of the stimulus (Anderson et al., 2003; Small et al., 2003). Our results extend this evidence, indicating that the amygdala is involved in emotional processing while viewing dynamic facial expressions of emotions.

Neuroanatomical studies of the primate amygdala support the idea that this structure is involved in emotional processing but not visual motion processing for dynamic facial expressions. Projections from the higher visual areas in the temporal cortex, such as the STS, provide input to the amygdala (Amaral et al., 1992). Some of these regions contain cell populations that respond selectively to dynamic biological stimuli (Perrett, 1999), and therefore the anatomical position of the amygdala is appropriate for receiving the processed visual information for dynamic facial expressions. For output, the amygdala projects to many brain regions, including the striatum, hypothalamus, and brainstem (Amaral et al., 1992). These regions are important in coordinating emotion-specific muscular, autonomic, and behavioral responses (LeDoux, 1996). Psychological studies have indicated that subjective, autonomic, and muscular emotional reactions while observing emotional expressions are intimately related (Johnsen et al., 1995; Lundqvist and Dimberg, 1995). The anatomical position of the amygdala would be appropriate for coordinating such widespread emotional reactions.

Our results showed greater activity in the left amygdala in response to forward compared to backward presentations of dynamic facial expressions. This left hemisphere dominance is in line with previous studies that found more activity in the left than in the right amygdala in response to emotional facial expressions (e.g., Breiter et al., 1996). Additionally, other researchers have provided evidence for the functional asymmetry of the amygdala, with greater involvement of the left versus right hemisphere in conscious versus unconscious (Morris et al., 1998) and slow versus rapid (Wright et al., 2001) processing of facial expressions. Our results extend the literature, indicating that the emotional processing of facial expressions tends to occur more in the left than in the right amygdala. However, it must be noted that we could measure activity in the right amygdala with a more liberal threshold. Hence, our results suggest that the hemispheric difference is not qualitative and emotion-elicitation activity in response to dynamic facial expressions is processed in the bilateral amygdala.

Previous studies have reported the involvement of other regions, including the inferior occipital gyrus, fusiform gyrus, middle temporal gyrus, and inferior frontal gyrus, in the processing of dynamic facial expressions (Kilts et al., 2003; LaBar et al., 2003; Sato et al., 2004a; Pelphrey et al., 2007). The present results, showing no significant activation in these regions for the forward versus backward presentations, suggest that these regions are not specific to emotional processing of dynamic facial expressions. These regions may be involved in the processing of dynamic visual information contained in dynamic facial expressions of emotion. Alternatively, these regions may be involved in other non-emotional cognitive processing. For example, it has been proposed that the fusiform gyrus is involved in the processing of the identity of faces (Haxby et al., 2000) and that the inferior frontal gyrus is involved in the processing of communicative intention in dynamic faces (Rizzolatti et al., 2001).

Some limitations of this study should be acknowledged. First, it must be noted that although the present strategy of presenting facial expressions backwards is a reasonable method for strictly controlling the visual motions in dynamic facial expressions, this strategy cannot extinguish the emotional meaning in such stimuli. As the backward presentations contained the frames of the emotional facial expressions at first, they were not *non-emotional* stimuli but rather *low emotional* stimuli, relative to the high emotional forward presentations. Thus, the comparison between forward versus backward presentations was not truly a contrast between emotional versus non-emotional facial expressions, but was in fact a comparison of high versus low emotional facial expressions. Because of this, other brain regions related to emotional processing may not have shown activation for forward versus backward presentations. In future research, it would be helpful to find different strategies for contrasting emotional versus non-emotional dynamic facial expressions.

Second, although we asked the participants to rate their emotional experience, this procedure may not have revealed the participants' raw emotional feelings. It has been pointed out that the self-report of emotional experience could contain not only raw feelings, but also other reflective cognitions, such as conscious appraisals of the eliciting stimuli and emotional knowledge schemes (Nielsen and Kaszniak, 2007). However, a previous study reported that using a similar procedure, which asked participants to rate their emotional experience using dimensional measures while viewing facial expression stimuli, the subjective ratings systematically changed along with the simultaneously recorded physiological measures (Johnsen et al., 1995). These data suggest that subjective ratings could reflect holistic emotional responses while viewing facial stimuli. Another line of research revealed that, even when the emotional stimuli were presented subliminally, participants could rate their emotional experience using dimensional measures, as in the case of supraliminal presentations (Öhman and Soares, 1994). These findings suggest that subjective ratings could be made without conscious appraisal of the stimuli. Taken together, these data suggest that the present subjective rating data reflected, at least partially, raw emotional experience while viewing the facial expression stimuli.

In summary, our results revealed that the left amygdala showed higher activity in response to forward presentations compared with backward presentations of dynamic facial expressions of fear and happiness. A positive relation was found between amygdala activity and the intensity of the experienced emotion. These results indicate that the amygdala is not involved in the visual but is involved in the emotional processing of dynamic facial expressions of emotions, specifically including the elicitation of subjective emotions.

4. Experimental procedure

4.1. Subjects

Thirteen volunteers (8 females, 5 males; mean age ± SD, 24.9 ± 7.0 years) participated in the experiment. All subjects were right-handed, had normal or corrected-to-normal visual acuity, and gave informed consent to participate in the study. The study was conducted in accordance with institutional ethical provisions and the Declaration of Helsinki.

4.2. Experimental design

The experiment involved a within-subject two-factorial design, with presentation condition (forward/backward) and emotion (fear/happiness).

4.3. Stimuli

For both the forward and backward presentation conditions, the same grayscale photographs of 10 individuals with fearful, happy, and neutral expressions were chosen from a standard set (Ekman and Friesen, 1976). A computer morphing technique that had been used in a previous study (Sato et al., 2004a) was adopted to implement the dynamic presentations of facial images. Fig. 1 shows an example of the stimulus sequence. Twenty-four images intermediate between the neutral and emotional (fearful or happy) expressions were created in 4% steps, using computer-morphing software (Mukaida et al., 2000). For the forward presentation condition, clips that changed from neutral to emotional expressions, a total of 26 images (one neutral, 24 intermediate, and one fearful) were presented. Each image was presented for 40 ms, and the first and last images were each presented for an additional 230 ms; thus, the time for each animation clip was 1500 ms. This presentation speed has been shown to reflect sufficiently natural changes in dynamic facial expressions (Sato and Yoshikawa, 2004). For the backward presentation condition, clips that changed from emotional to neutral expressions at the same speed were presented.

4.4. Presentation apparatus

The events were controlled by a program written in Visual C++ 5.0 (Microsoft, 1997, WA, USA) and implemented on a computer running Microsoft Windows. The stimuli were projected from a liquid crystal projector (DLA-G150CL, Victor Co.) onto a half-transparent screen located behind the head coil. Subjects viewed the screen through a mirror over the head coil. In this position, the stimuli subtended a visual angle of about 15.0° vertical × 10.0° horizontal.

4.5. Procedure

Each subject completed two experimental sessions. Each session lasted 8 min and consisted of eight 30-s epochs with eight 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. The presentation conditions (forward and backward) were conducted alternately. Each session contained both emotions (fear and happiness). The order of the stimuli within each epoch was randomized at first and then fixed for all subjects. The order of the presentation condition and emotion were counterbalanced across subjects.

The 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, the subjects were asked to view the stimuli passively, without making any response.

After MR image acquisition, the stimuli for each presentation condition were randomly presented to the subjects, and they were asked, “How did you feel emotionally when you viewed the stimuli?” The subjects were to rate their emotions in terms of emotional valence (-4, negative; +4, positive) and intensity (1, low intensity; 9, high intensity) in response to each stimulus. The order of stimulus presentations was counterbalanced across subjects.

4.6. Image acquisition

Image scanning was performed on a 1.5-T scanning system (Magnex Eclipse 1.5 T Power Drive 250, Shimadzu Marconi), using a standard radio frequency head coil for signal transmission and reception. A forehead pad was used to stabilize the head position. Functional images consisted of 28 consecutive slices made parallel to the anterior–posterior commissure plane, covering the whole brain. A T2*-weighted gradient echo-planar imaging sequence was used with the following parameters: TR/TE = 3000/60 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 T1-weighted anatomical image was 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).

4.7. Behavioral data analysis

Each rating (valence, arousal) was analyzed separately in a two-way ANOVA with presentation condition and emotion as within-subject factors. For significant interactions, follow-up simple effect analyses were conducted. When interactions were significant, main effects were not subjected to interpretation. The results of all tests were deemed statistically significant at $p < 0.05$.

4.8. Image analysis

Image and statistical analyses were performed with the statistical parametric mapping package SPM5 (http://www.fil.ion.ucl.ac.uk/spm) implemented in MATLAB7 (Mathworks, Inc.). First, to correct for head movements, the functional images of each run were realigned using the first scan as a reference. Data from all subjects showed small motion corrections (<1 mm). Then, T2-weighted anatomical images scanned in planes identical to the functional imaging slices 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); this involved linear and non-linear three-dimensional transformations (Friston *et al.*, 1995a; Ashburner and Friston, 1999). 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 among subjects. The high-resolution anatomical images were also normalized by the same procedure.

We used random effects analyses to search for significantly activated voxels that displayed interesting effects. First, we performed a single-subject analysis (Friston et al., 1995b; Worsley and Friston, 1995). The task-related neural activity for each condition was modeled with a boxcar function, convoluted with a canonical hemodynamic response function. We used a high-pass filter composed of a discrete cosine basis function, with a cut-off period of 128, to eliminate the artifactual low-frequency trend. Serial autocorrelation, assuming a first-order autoregressive model, was estimated from the pooled active voxels with a restricted maximum likelihood (ReML) procedure and was used to whiten the data and the design matrix (Friston et al., 2002). Planned contrast was thereafter performed for the main effect of presentation condition, forward versus backward, based on our a priori hypothesis. The reverse contrast of the main effect of presentation condition (backward versus forward), main effect of emotion, and the interaction were also tested as exploratory analyses. Contrast images were used to create a random effects statistical parametric map, SPM$\{T\}$. For these analyses, significantly activated voxels were identified as those reaching the extent threshold of $p < 0.05$, corrected for multiple comparisons, with a height threshold of $p < 0.001$ (uncorrected). For the analysis of the amygdala, our region of interest, we used small volume correction (SVC). The regions were defined using the WFU PickAtlas (Maldjian et al., 2003). Other areas were corrected for the entire brain volume.

For the regression analysis and ROI analysis, the mean percentage signal change in the brain regions for each condition in each subject was calculated. For the regression analysis of the amygdala activity, based on the results of the main effect in the SPM analysis, the activity of the left amygdala was analyzed. The center coordinate was at the site of peak activation in the main effect contrast. For the ROI analysis, the center coordinates in the MNI space were derived from the results of a previous study (Sato et al., 2004) as follows: the inferior occipital gyrus (x34, y-84, z-8), fusiform gyrus (x44, y-60, z-12), STS (x62, y-46, z8), and inferior frontal gyrus (x50, y8, z24). First, the high-pass filtered raw data were extracted from the 6-mm radius spherical volume of interest (VOI). The time series data were summarized by the first eigenvariate of all suprathreshold signals within the VOI. Then, the percentage signal change was calculated as follows: [(mean signal in the specified period − mean signal in a rest condition)/(mean signal in a rest condition)] × 100. The first images for each period were discarded, because of the time lag in the hemodynamic responses. The data were averaged per subject and condition.

A multiple regression analysis was conducted, with the percentage signal change of the amygdala activity as the dependent variable and the psychological ratings (experienced valence and intensity) as independent variables. To represent the within-subject experimental design, a series of dummy variables to represent the subject effect (12 vectors identifying the subjects) were added as independent variables (cf. Knight, 1984). The coefficients of the psychological ratings were evaluated using one-tailed *t*-tests. To plot the relationship between amygdala activity and emotion ratings, we calculated the adjusted percentage signal change by removing the effect of nuisance covariates (i.e., subject effects).

Acknowledgments

This study was supported by Special Coordination Funds for promoting

Science and Technology by the Science and Technology Agency of the Japanese Government.

References

Aggleton, J.P., Young, A.W., 2000. The enigma of the amygdala: On its contribution to human emotion. In Cognitive Neuroscience of Emotion. R.D. Lane, L. Nadel, eds. Oxford University Press, New York, pp. 106-128.

Amaral, D.G., Price, J.L., Pitkanen, A., Carmichael, S.T., 1992. Anatomical organization of the primate amygdaloid complex. In The Amygdala: Neurobiological Aspects of Emotion, Memory, and Mental Dysfunction. J.P. Aggleton, ed. Wiley-Liss, New York, pp. 1-66.

Anderson, A.K., Christoff, K., Stappen, I., Panitz, D., Ghahremani, D.G., Glover, G., Gabrieli, J.D., Sobel, N., 2003. Dissociated neural representations of intensity and valence in human olfaction. Nat. Neurosci. 6, 196-202.

Ashburner, J., Friston, K., 1999. Nonlinear spatial normalization using basis functions. Hum. Brain Mapp. 7, 254-266.

Breiter, H.C., Etcoff, N.L., Whalen, P.J., Kennedy, W.A., Rauch, S.L., Buckner, R.L., Strauss, M.M., Hyman, S.E., Rosen, B.R., 1996. Response and habituation of the human amygdala during visual processing of facial expression. Neuron 17, 875-887.

Brothers, L., 1990. The social brain: A project for integrating primate behavior and neurophysiology in a new domain. Concepts.

Neurosci. 1, 27-51.

Bruce, V., Valentine, T., 1988. When a nod's as good as a wink: The role of dynamic information in facial recognition. In Practical Aspects of Memory: Current Research and Issues, Vol. 1. M.M. Gruneberg, P.E. Morris, R.N. Sykes, eds. John Wiley & Sons, New York, pp. 169-174.

Ekman, P., Friesen, W.V., 1976. Pictures of Facial Affect. Consulting Psychologist, Palo Alto.

Fitzgerald, D.A., Angstadt, M., Jelsone, L.M., Nathan, P.J., Phan, K.L., 2006. Beyond threat: Amygdala reactivity across multiple expressions of facial affect. Neuroimage 30, 1441-1448.

Friston, K.J., Ashburner, J., Poline, J.B., Frith, C.D., Heather, J.D., Frackowiak, R.S.J., 1995a. Spatial registration and normalization of images. Hum. Brain Mapp. 2, 165-189.

Friston, K.J., Holmes, A.P., Poline, J.B., Grasby, P.J., Williams, S.C., Frackowiak, R.S., Turner, R., 1995b. Analysis of fMRI time-series revisited. Neuroimage 2, 45-53.

Friston, K.J., Glaser, D.E., Henson, R.N., Kiebel, S., Phillips, C., and Ashburner, J., 2002. Classical and Bayesian inference in neuroimaging: Applications. Neuroimage 16, 484-512.

Harwood, N.K., Hall, L.J., Shinkfield, A.J., 1999. Recognition of facial emotional expressions from moving and static displays by individuals with mental retardation. Am. J. Ment. Retard. 104, 270-278.

Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2000. The distributed human neural system for face perception. Trends Cog. Sci. 4, 223-233.

Hoffman, E.A., Haxby, J.V., 2000. Distinct representations of eye gaze and identity in the distributed human neural system for face perception. Nat. Neurosci. 3, 80-84.

Johnsen, B.H., Thayer, J.F., Hugdahl, K., 1995. Affective judgment of the Ekman faces: A dimensional approach. J. Psychophysiol. 9, 193-202.

Killgore, W.D., Yurgelun-Todd, D.A., 2004. Activation of the amygdala and anterior cingulate during nonconscious processing of sad versus happy faces. Neuroimage 21, 1215-1223.

Kilts, C. D., Egan, G., Gideon, D. A., Ely, T. D., Hoffman, J. M., 2003. Dissociable neural pathways are involved in the recognition of emotion in static and dynamic facial expressions. Neuroimage 18, 156-168.

Knight, G.P., 1984, A survery of some important techniques and issues in multiple regression. In New Methods in Reading Comprehension Research. D.E. Kieras, M.A. Just, eds. Lawrence Erlbaum Associates, Hillsdale, pp. 13-29.

LaBar, K.S., Crupain, M.J., Voyvodic, J.T., McCarthy, G., 2003. Dynamic perception of facial affect and identity in the human brain. Cereb. Cortex 13, 1023-1033.

LeDoux, J.E., 1996. The Emotional Brain: The Mysterious Underpinnings of Emotional Life. Simon & Schuster, New

York.

Lundqvist, L.O., Dimberg U., 1995. Facial expressions are contagious. J. Psychophysiol. 9, 203-211.

Maeda, H., Morimoto, H., Yanagimoto, K., 1993. Response characteristics of amygdaloid neurons provoked by emotionally significant environmental stimuli in cats, with special reference to response durations. Can. J. Physiol. Pharmacol. 71, 374-378.

Maldjian, J.A., Laurienti, P.J., Kraft, R.A., Burdette, J.H., 2003. An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. Neuroimage 19, 1233-1239.

Morris, J.S., Frith, C.D., Perrett, D.I., Rowland, D., 1996. A differential neural response in the human amygdala to fearful and happy facial expressions. Nature 383, 812-815.

Morris, J.S., Öhman, A., Dolan, R.J. 1998. Conscious and unconscious emotional learning in the human amygdala. Nature 393, 467-470.

Mukaida, S., Kamachi, M., Kato, T., Oda, M., Yoshikawa, S., Akamatsu, S., 2000. Foolproof Utilities for Facial Image Manipulation (unpublished computer software). ATR, Kyoto.

Nielsen, L., Kaszniak, A.W. 2007. Conceptual, theoretical, and methodological issues in inferring subjective emotion experience: Recommendations for researchers. In Handbook of Emotion Elicitation And Assessment. J.A. Coan and J.J.B.

Allen eds. Oxford University Press, Oxford, pp. 361-375.

Öhman, A., Soares, J.J.F. 1994. "Unconscious anxiety": Phobic responses to masked stimuli. J. Abnorm. Psychol. 103, 231-240.

Ono, T., Nishijo H., 1992. Neurophysiological basis of the Kluver-Bucy syndrome: responses on monkey amygdaloid neurons to biologically significant objects. In The Amygdala: Neurobiological Aspects of Emotion, Memory, and Mental Dysfunction. J.P. Aggleton, ed. Wiley-Liss, New York, pp. 167-190.

Ono, T., Nishijo H., 1999. Neurophysiological basis of emotion in primates: Neuronal responses in the monkey amygdala and anterior cingulate cortex. In The New Cognitive Neurosciences, 2nd ed. S.M. Gazzaniga, MIT Press, Cambridge, pp. 1099-1114.

Pelphrey, K.A., Morris, J.P., McCarthy, G., Labar, K.S., 2007. Perception of dynamic changes in facial affect and identity in autism. Soc. Cogn. Affect. Neurosci. 2, 140-149.

Perrett, D.I., 1999. A cellular basis for reding minds from faces and actions. In The Design of Animal Communication. M.D. Hauser, M. Konishi, eds. MIT Press, Cambridge, pp. 159-185.

Rizzolatti, G., Fogassi, L., Gallese, V., 2001. Neurophysiological mechanisms underlying the understanding and imitation of action. Nat. Rev. Neurosci. 2, 661-670.

Sato, W., Kochiyama, T., Yoshikawa, S., Naito, E., Matsumura, M., 2004a. Enhanced neural activity in response to dynamic facial expressions of emotion: an fMRI study. Cogn. Brain Res. 20, 81-91.

Sato, W., Yoshikawa, S., 2004. The dynamic aspects of emotional facial expressions. Cogn. Emo. 18, 701-710.

Sato, W., Yoshikawa, S., Kochiyama, T., Matsumura, M., 2004b The amygdala processes the emotional significance of facial expressions: An fMRI investigation using the interaction between expression and face direction. Neuroimage 22, 1006-1013.

Sato, W., Yoshikawa, S., 2007a. Enhanced experience of emotional arousal in response to dynamic facial expressions. J. Nonverbal Behav. 31, 119-135.

Sato, W., Yoshikawa, S., 2007b. Spontaneous facial mimicry in response to dynamic facial expressions. Cognition 104, 1-18.

Sergerie, K., Chochol, C., Armony, J.L., 2008 The role of the amygdala in emotional processing: A quantitative meta-analysis of functional neuroimaging studies. Neurosci. Biobehav. Rev. 32, 811-830.

Small, D.M., Gregory, M.D., Mak, Y.E., Gitelman, D., Mesulam, M.M., Parrish, T., 2003. Dissociation of neural representation of intensity and affective valuation in human gustation. Neuron 39, 701-711.

Worsley, K.J., Friston, K.J., 1995. Analysis of fMRI time-series revisited--again. Neuroimage 2, 173-181.

Wright, C.I., Fischer, H., Whalen, P.J., McInerney, S.C., Shin, L.M., Rauch, S.L. 2001. Differential prefrontal cortex and amygdala habituation to repeatedly presented emotional stimuli. Neuroreport 12, 379-383.

Wright, C.I., Martis, B., Shin, L.M., Fischer, H., Rauch, S.L., 2002. Enhanced amygdala responses to emotional versus neutral schematic facial expressions. Neuroreport 13, 785-790.

Yoshikawa, S., Sato, W., 2008. Dynamic facial expressions of emotion induce representational momentum. Cogn. Affect. Behav. Neurosci. 8, 25-31.

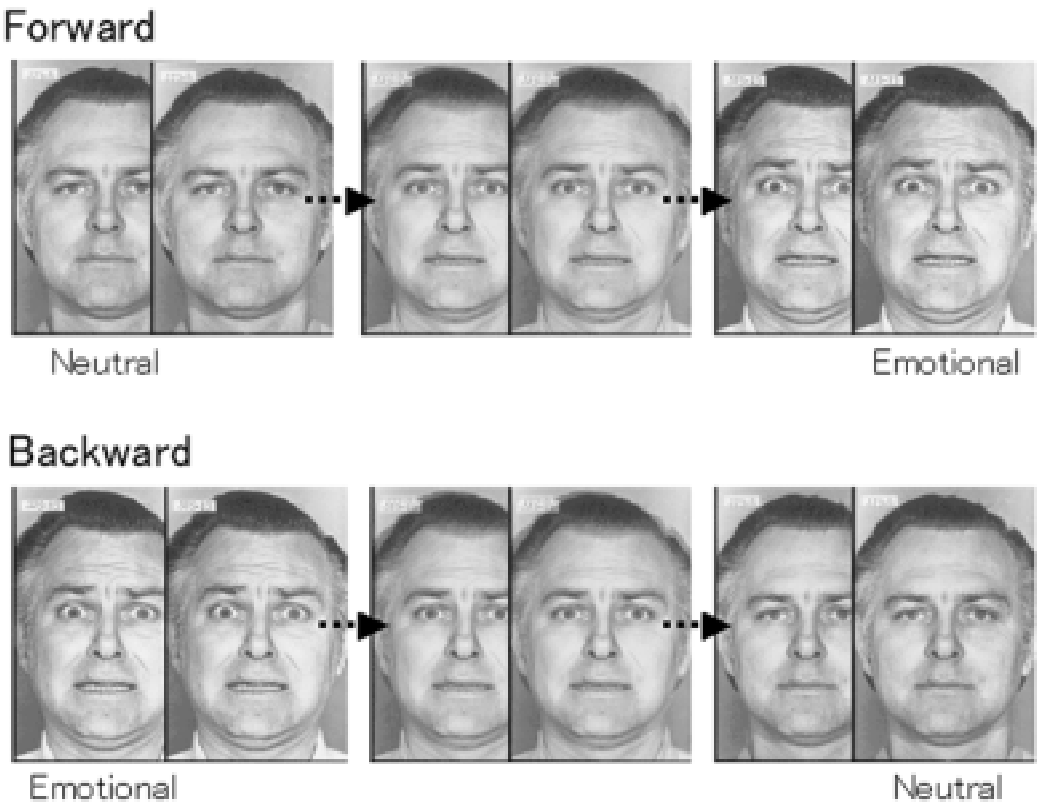

Figure 1. Illustrations of stimulus presentations, forward (upper) and backward (lower). Note that the frames were the same for the two conditions.

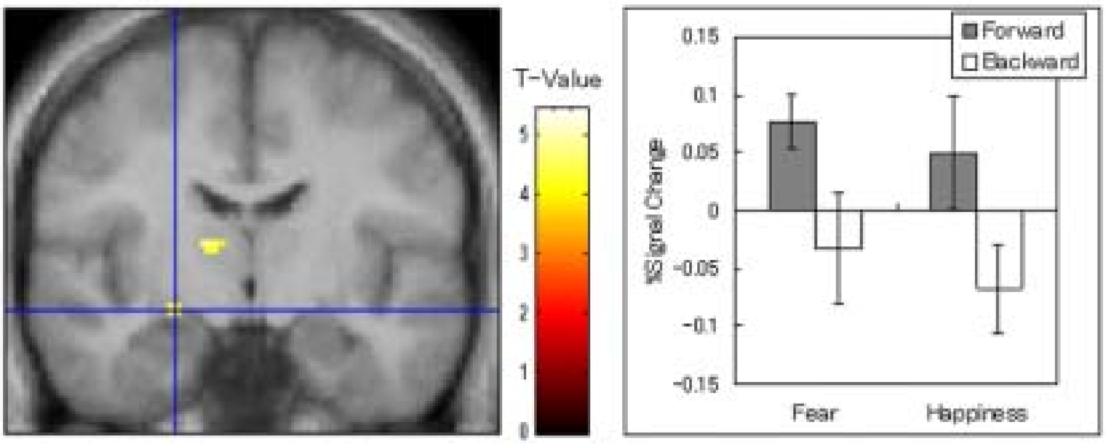

Figure 2. Left. A statistical parametric map of the left amygdala showing higher activity for forward compared with backward presentations. The activation is overlayed on the anatomical MRI of the mean brain of the subjects involved in the study. Right. Mean percentage signal changes (with standard error) of amygdala activity.