

Putamen volume is negatively correlated with the ability to recognize fearful facial expressions

The final publication is available at Springer via <http://dx.doi.org/10.1007/s10548-017-0578-7>

Running title: Putamen structure and fear recognition

Author names and author affiliation:

Shota Uono¹, Wataru Sato¹, Takanori Kochiyama², Yasutaka Kubota³, Reiko Sawada^{1,4}, Sayaka Yoshimura¹, Toichi Motomi^{4,5}

¹ Department of Neurodevelopmental Psychiatry, Habilitation, and Rehabilitation, Graduate School of Medicine, Kyoto University, 53 Shogoin-Kawahara-cho, Sakyo-ku, Kyoto 606-8507, Japan.

² ATR Brain Activity Imaging Center, 2-2-2, Hikaridai, Seika-cho, Souraku-gun, Kyoto 619-0288, Japan

³ Health and Medical Services Center, Shiga University, 1-1-1, Baba, Hikone, Shiga 522-8522, Japan

⁴ The Organization for Promoting Neurodevelopmental Disorder Research, 40 Shogoin-Sannocho, Sakyo-ku, Kyoto 606-8392, Japan

⁵ Faculty of Human Health Sciences, Graduate School of Medicine, Kyoto University, 53 Shogoin-Kawahara-cho, Sakyo-ku, Kyoto 606-8507, Japan.

Corresponding author:

Shota Uono, Department of Neurodevelopmental Psychiatry, Habilitation, and Rehabilitation, Graduate School of Medicine, Kyoto University, 53 Shogoin-Kawahara-cho, Sakyo-ku, Kyoto 606-8507, Japan.

Tel: +81 75 751 3966; Fax: +81 75 751 3966; E-mail:

uonoshota1982@gmail.com

Abstract

Findings of previous functional magnetic resonance imaging (MRI) and neuropsychological studies have suggested that specific aspects of the basal ganglia, particularly the putamen, are involved in the recognition of emotional facial expressions. However, it remains unknown whether variations in putamen structure reflect individual differences in the ability to recognize facial expressions. Thus, the present study assessed the putamen volumes and shapes of 50 healthy Japanese adults using structural MRI scans and evaluated the ability of participants to recognize facial expressions associated with six basic emotions: anger, disgust, fear, happiness, sadness, and surprise. The volume of the bilateral putamen was negatively associated with the recognition of fearful faces, and the local shapes of both the anterior and posterior subregions of the bilateral putamen, which are thought to support cognitive/affective and motor processing, respectively, exhibited similar negative relationships with the recognition of fearful expressions. These results suggest that individual differences in putamen structure can predict the ability to recognize fearful facial expressions in others. Additionally, these findings indicate that cognitive/affective and motor processing underlie this process.

Keywords: Basal ganglia; Emotion recognition; Fearful face; Structural magnetic resonance imaging; Putamen

1. Introduction

The basal ganglia represent a group of deep brain structures that consists of the putamen, caudate, nucleus accumbens, and globus pallidus (Arsalidou et al. 2013). It is well-known that the basal ganglia serve as a point of communication between the frontal cortex and the thalamus during motor functioning (DeLong & Wichmann 2007), and that these deep structures, particularly the putamen and caudate, have somatotopic representations of faces and bodies (Gerardin et al. 2003). Degeneration within these regions is consistently associated with motor deficit diseases such as Huntington's disease and Parkinson's disease (Pitcher et al. 2012; Walker 2007), but recent research has shown that the basal ganglia also play important roles in cognitive and emotional functions (Arsalidou et al. 2013), including executive function (van den Heuvel et al. 2005) and mood changes (George et al. 1995).

We investigated the contribution of the basal ganglia to the recognition of other's facial expressions. The understanding of others' facial expressions is supported by the neurobiological orchestration of cognitive, emotional and motor processes, which may be mediated by the basal ganglia. For example, behavioral studies have demonstrated that the recognition of facial emotions is related to executive functions (Circelli et al. 2013), while other studies have revealed that aroused emotional states facilitate the understanding of mood congruent facial expressions in others (Lee et al. 2008; Richards et al. 2002). Furthermore, a growing body of evidence has demonstrated the contribution of motor function to emotion recognition. The occurrence and restriction of facial mimicry facilitate and suppress the recognition of others' facial expressions, respectively (Niedenthal 2007; Oberman et al. 2007). Similarly, a recent study revealed that the congruent facial muscle activities of an individual following observation of another's facial movements elicit emotional experiences and that the experienced emotion enhances emotion recognition (Sato, Fujimura, et al. 2013). Although the potential link between the psychological mechanisms underlying emotion recognition and basal ganglia function raises the possibility that the basal ganglia play a significant role in the neurocognitive processes involved in the understanding of others' facial expressions, no studies have investigated the relationship between individual basal ganglia structures and emotion

recognition.

Among the structures within the basal ganglia, the putamen represents a candidate for the neural correlate that underlies the recognition of emotion. A recent investigation of the regional specialization of basal ganglia structures associated with various psychological functions linked the putamen to social functions such as empathy (Pauli et al., 2016). A meta-analysis of functional magnetic resonance imaging (MRI) studies has demonstrated that the visual, limbic, temporo-parietal, and prefrontal brain regions, as well as the putamen, are activated during the observation of emotional facial expressions, happy facial expressions in particular (Fusar-Poli et al. 2009). For example, an early functional MRI study found that fearful and disgusted faces elicited a greater response in the putamen relative to neutral expressions (Phillips et al. 1998). Moreover, a task that required the inference of emotional and mental states in others based on observation of the eye region elicited an activation of the bilateral putamen in normal adults but not in adults with autism spectrum disorder (ASD) (Baron-Cohen et al. 1999). Although these findings suggest that the putamen is involved in the recognition of emotional facial expressions, the authors did not actively discuss the role of the putamen in emotion recognition.

Furthermore, a growing body of neuropsychological evidence has suggested that the putamen is involved in the recognition of facial emotions. For example, a lesion that included the putamen impaired a patient's recognition of emotional facial expressions specifically related to anger and disgust (Calder et al. 2000, 2004). Additionally, patients with Huntington's disease consistently show an inability to recognize anger, disgust and fear in facial expressions (Henley et al. 2012). Similarly, a meta-analysis found that patients with Parkinson's disease have marked impairments in the recognition of negative emotions (e.g., anger and fear) relative to positive emotions (e.g., happiness and surprise) (Gray & Tickle-Degnen 2010). Although the neural correlates underlying impaired emotion recognition in these patients remain unclear, a striking loss of volume in the putamen and caudate nucleus has been observed in patients with these disorders (Pitcher et al. 2012; Walker 2007).

On the other hand, the abovementioned evidence suggesting that the

putamen is involved in the recognition of others' facial expressions has some limitations. First, there has yet to be a functional MRI study investigating the relationship between the ability to recognize facial expressions and brain activation in the basal ganglia. Second, the inability of patients with brain damage and/or neurodegenerative diseases to identify facial expressions could also be explained by abnormalities outside the putamen, because this type of damage is not necessarily restricted to a specific brain area (e.g., Calder et al. 2000) and may indirectly influence the function of other brain regions. Finally, these neuropsychological studies have included relatively small numbers of patients. As a result, it remains unknown whether individual differences in putamen structure reflect changes in the ability to recognize facial expressions, particularly in healthy participants.

Thus, the present study examined the relationship between putamen volume and the ability to recognize emotional facial expressions in normal young adults. The volume of the putamen was calculated in both hemispheres for each participant using a structural MRI scan. For the facial expression recognition task, photographs of facial expressions depicting six basic emotions (anger, disgust, fear, happiness, sadness, and surprise) were presented to the participants; they were then asked to choose the label that best described the emotion expressed in each photograph. The correlational relationships between the volume of the bilateral putamen and the percent accuracy for each emotion condition (i.e. out of 100) were analyzed with a general linear model using the percent accuracy for emotion recognition as the effect of interest. The effects of hemisphere (left or right), sex (male or female), age, full-scale intelligence quotient (IQ), and total cerebral volume (TCV) were included as effects of no interest and were covaried out.

Based on previous findings, it was hypothesized that putamen volume would be associated with the ability to recognize emotional facial expressions. No hypotheses were made regarding the correlation between putamen volume and the ability to recognize specific facial expressions, because previous functional MRI and lesion studies have suggested that the putamen is involved in the processing of several emotion categories. Additionally, no specific hypotheses were made regarding the positive or negative direction of the correlations due to previous findings showing an

increased putamen volume in individuals with ASD (Sato et al. 2014) and psychopaths (Yang et al. 2015), who exhibit deficits in emotion recognition (Dawel et al. 2012; Uono et al. 2011, 2013), and decreased putamen volumes in patients with Huntington's disease (Walker 2007) and Parkinson's disease (Pitcher et al. 2012), who exhibit impairments in the ability to recognize emotion based on facial expressions (Gray & Tickle-Degnen 2010; Henley et al. 2012). For exploratory purposes, the present study also assessed the relationships between the ability to recognize facial expressions and the volumes of other basal ganglia structures, including the caudate, globus pallidus and nucleus accumbens, and other subcortical regions, including the hippocampus, amygdala and thalamus. Finally, as a complementary analysis, the present study investigated whether the ability to recognize emotion in facial expressions is associated with the local shapes of the putamen to determine which parts of the putamen (e.g., anterior and posterior) were associated with emotion recognition.

2. Material and Methods

2.1 Participants

The present study analyzed 50 healthy Japanese young adults (see Table 1.). All participants were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield 1971), and had normal or corrected-to-normal visual acuity. None of the participants had any neurological or psychiatric symptoms that were of clinical significance, as determined by a psychiatrist using the Japanese version of the Mini International Neuropsychiatric Interview (M.I.N.I.) (Otsubo et al. 2005). Trait anxiety and depression levels of the participants were assessed with the Japanese versions of the State-Trait Anxiety Inventory (STAI) (Hidano et al. 2000) and the Beck Depression Inventory-II (BDI-II) (Kojima & Furukawa 2003), respectively.

Following an explanation of the experimental procedures, all participants provided written informed consent. This study was part of a broad research project investigating mind-brain relationships and was approved by the local ethics committee of the Primate Research Institute at Kyoto University. All procedures were conducted in accordance with the guidelines of the Declaration of Helsinki.

2.2 Emotion recognition task

Using standardized photograph sets (Ekman & Friesen 1976; Matsumoto & Ekman 1988), a total of 48 photographs of facial expressions depicting six basic emotions (anger, disgust, fear, happiness, sadness, and surprise) were selected as the experimental stimuli. Half of these pictures were of Caucasian models and the other half were pictures of Japanese models. All experimental events were controlled by Presentation software (version 14.9, Neurobehavioral System), implemented on a Windows computer (HPZ200SFF, Hewlett-Packard Company), and the stimuli were individually presented on a 19-inch CRT monitor (HM903D-A, Iiyama) in random order in each block. Written labels identifying the six basic emotions were presented on both sides of each photograph.

The participants were asked to choose and orally answer which of the labels best described the emotion expressed in each photograph after being instructed to carefully consider all six alternatives prior to their response. No time limits were set and no feedback was provided regarding the responses. The participants viewed facial expressions associated with each of the six basic emotions eight times. The experiment consisted of four blocks (two Caucasian and two Japanese face blocks) of 12 trials. The position of the labels was counterbalanced across blocks, and the order of the blocks was counterbalanced across participants. It was confirmed that all participants understood the meanings of the labels as well as the instructions and, additionally, each participant performed two training trials to familiarize them with the procedure. After ensuring that the participants understood the task requirements, the experimental trials were initiated. Previous studies using this paradigm found differences in the ability to recognize facial expressions between normal and clinical populations (e.g., Okada et al. 2015; Sato et al. 2002; Uono et al. 2011, 2013).

2.3 MRI acquisition

The behavioral task and MRI acquisition procedure were conducted on separate days. Image scanning was performed on a 3-T scanning system (MAGNETOM Trio, A Tim System, Siemens) at the ATR Brain Activity Imaging Center using a 12-channel array coil. T1-weighted high-resolution anatomical images were obtained using a

magnetization-prepared rapid gradient-echo sequence (repetition time = 2250 ms, echo time = 3.06 ms, flip angle = 9°, inversion time = 1000 ms, field of view = 256 × 256 mm, matrix size = 256 × 256, voxel size = 1 × 1 × 1 mm).

2.4 Data analysis

2.4.1 Emotion recognition task

The percent accuracy (out of 100) for each emotion category and for all emotion categories combined were calculated. A repeated-measures analysis of variance was performed with emotion as an effect of interest and sex as an effect of no interest. The significance level (α) was set at 0.05. Although we had no specific predictions for the effect of sex, this factor was included in the model and assessed for descriptive purposes. Although some previous studies have shown a female advantage in emotional processing, others have failed to detect this (for a review, see Kret and de Gelder 2012). If the sphericity assumption was violated ($p < 0.05$), probability values were evaluated using the Greenhouse–Geisser adjustment of degrees of freedom. When a main effect for emotion was found, we used t -tests with Bonferroni correction for multiple comparisons ($\alpha = 0.003$) to assess differences in percent accuracy among emotion conditions.

We used one-sample t -tests with Bonferroni correction ($\alpha = 0.008$) to test whether the percent accuracy under each emotion condition was significantly greater than that by chance (16.7%).

2.4.2 Segmentation

Using MRI scans, volume and local shape analyses of the brain structures were performed with the Integrated Registration and Segmentation Tool (FIRST) in the FMRIB Software Library (FSL), ver. 5 (Patenaude 2007). FIRST is a semi-automated subcortical segmentation tool used for efficient modeling of the brain shape and appearance within a Bayesian framework (Patenaude, Smith, Kennedy, & Jenkinson 2011). This method has been validated (Patenaude et al. 2011) and applied to a wide range of volumetric analyses (e.g., Pardini et al. 2014).

All analyses were conducted using standard FIRST procedures. First, the images were registered to a common space based on the standard Montreal Neurological Institute (MNI)-152 template using the affine registration of the entire head and a subcortical mask to exclude voxels

outside of the subcortical regions. Then, the inversion transformation was applied to bring the images back into the original space. Finally, the brain structures were segmented based on a Bayesian shape and appearance model, which is part of the FSL package and was originally constructed from manually segmented images provided by the Centre for Morphometric Analysis (Boston, MA). One of the present researchers (T.K.) visually inspected the quality of the segmentation and validated the success of the automated segmentation procedure using FSL-provided script to generate summary images in a well-organized webpage format (`first_roi_slicesdir`).

2.4.3 Volume analysis

Volumes of the subcortical regions in both hemispheres, including those of the putamen, caudate, globus pallidus, nucleus accumbens, amygdala, hippocampus, and thalamus, were extracted for each participant. To control for TCV, modulated gray and white matter images were obtained using VBM8 software (<http://dbm.neuro.uni-jena.de/vbm/>), and the sum of gray and white matter volumes was calculated by integrating voxel intensities over the whole segmented image and then multiplying by voxel size.

The correlational relationships between putamen volume and percent accuracy for facial emotion recognition within each emotion condition (anger, disgust, fear, sad, surprise, and the combined average) were analyzed using IBM SPSS statistics 22 software (IBM Corporation). A general linear model was performed using putamen volume as the dependent variable and emotion recognition (percent accuracy) as the effect of interest independent variable. Hemisphere, sex, age, full-scale IQ, and TCV, and their interactions with emotion recognition, were included as effects of no interest. Because an effect of sex and/or hemisphere on putamen volume has been reported previously (e.g., Ruigrok et al. 2014), although these findings are controversial (e.g., Sato et al. 2014), the effects of hemisphere and sex were assessed for descriptive purposes and reported when the effect of emotion recognition was significant. The effects of emotion recognition were assessed in both positive and negative directions using *F*-statistics. A *p* value < 0.008 (0.05/6) was considered to indicate statistical significance because the analysis included performance under each of six basic emotion conditions

(with the exclusion of happiness) and their averaged performance. Happy face recognition was excluded from the analysis because all but one participant recognized happy faces at the ceiling level (100%). For exploratory purposes, the same analysis was applied to the other subcortical structures (caudate, globus pallidus, nucleus accumbens, hippocampus, amygdala, and thalamus).

To complement the accuracy analysis, we investigated whether the significant relationship between putamen volume and fearful face recognition could be explained by a response bias toward reporting fear in general. We used the same general linear model described above except that the percentage of misinterpreting surprised faces as fearful faces (mean \pm *SD*: 4.75 \pm 9.41 %) was used as the independent variable, because the misinterpretation of other emotional (i.e., angry, disgusted, happy, and sad) faces as fearful faces at last count was low (mean \pm *SD*: 0.56 \pm 1.37%). *P*-values < 0.05 were considered to indicate statistical significance.

2.4.4 Local shape analysis

Putamen shape was analyzed by performing a surface morphometric analysis (Patenaude et al. 2011) implemented in the FSL software package. Because the FSL shape analysis is more sensitive to localized changes in the subcortical regions than is the volume analysis (Nemmi et al., 2015), it is suitable for investigating the neural substrates underlying a specific cognitive function in a small complex structure such as the putamen. Based on the results of the volume analyses, only the putamen and percent accuracy for the recognition of fearful faces were analyzed. Surface meshes were created on the left and right putamen using a deformable mesh model with each mesh comprised of a set of triangles; the apexes connecting the triangles were called as vertices. The number of vertices were held constant so that the corresponding vertices were comparable across participants. The vertex locations in each participant at corresponding anatomical points were projected onto the normal surface of the average shape of the present participants. The projections were scalar values that represented the vertex displacement from the average surface to each individual surface and served as the dependent variable in the multiple regression analyses. All meshes were reconstructed in the MNI space to normalize brain size. This process

allowed us to control for the effect of TCV.

To identify changes in the vertices that are associated with the ability to recognize fearful facial expressions, a vertex-wise multiple regression analysis was conducted using the percent accuracy for fearful face recognition as the effect of interest and sex, age and full-scale IQ as the effects of no interest. To assess the spatial extent of significant clusters, a shape analysis was performed separately in each hemisphere. The relationship between vertex change and percent accuracy for fearful face recognition was assessed using a non-parametric permutation-based inference (Winkler, Ridgway, Webster, Smith, & Nichols 2014). A total of 5,000 permutations of the data were generated to test against when building up the null distribution. A p value < 0.05 (cluster-level family-wise error (FWE) corrected) was considered to indicate statistical significance based on the threshold-free cluster enhancement method (Smith & Nichols 2009).

3. Results

3.1 Emotion recognition task

The percent accuracy in the emotion recognition task is shown in Table 2. The analysis revealed a significant main effect for emotion ($F_{(5, 240)} = 44.457, p < 0.001, \eta_p^2 = 0.481$). Follow-up t -tests with Bonferroni correction ($\alpha = 0.003$) revealed that the performance accuracy for happy faces was significantly higher than that for the other emotions ($t_{(49)} > 3.239, p < 0.002$). The performance accuracies for sad and surprised faces were significantly higher than those for angry, disgusted, and fearful faces ($t_{(49)} > 5.071, p < 0.001$). We found no significant differences in percent accuracy between sad and surprised faces ($t_{(49)} = 1.864, p = 0.068$) or among angry, disgusted, and fearful faces ($t_{(49)} < 1.603, p > 0.115$). We found a significant main effect for sex ($F_{(1, 48)} = 6.231, p = 0.016, \eta_p^2 = 0.115$), indicating that emotion recognition performance was better in females than in males. However, the effect of sex was not significant for every emotion ($t_{(48)} < 1.619, p > 0.112$). No significant interaction was found between emotion and sex ($F_{(5, 240)} = 0.557, p = 0.680, \eta_p^2 = 0.011$).

One-sample t -tests with Bonferroni correction ($\alpha = 0.008$) were performed to test for differences significantly greater than chance

(16.7%; 100/6). Performances were significantly greater than chance under all emotion conditions ($t_{(49)} > 13.543$, $p < 0.001$).

3.2 Volume analysis

In terms of the relationship between putamen volume and the accuracy of emotion recognition, an analysis of fearful expressions revealed a significant main effect of emotion recognition ($F_{(1, 44)} = 9.978$, $p = 0.003$, $\eta_p^2 = 0.185$). This indicates that the putamen volumes of the participants were negatively related with the recognition of fearful faces (Fig. 1). For exploratory descriptive purposes, we investigated the effects of sex and hemisphere. We found no significant main effect for sex ($F_{(1, 44)} = 1.254$, $p = 0.269$, $\eta_p^2 = 0.028$) or hemisphere ($F_{(1, 44)} = 0.666$, $p = 0.419$, $\eta_p^2 = 0.015$). Furthermore, the interactions of hemisphere with emotion recognition and sex did not reach statistical significance (hemisphere and fearful face recognition, $F_{(1, 44)} = 1.635$, $p = 0.208$, $\eta_p^2 = 0.036$; hemisphere and sex, $F_{(1, 44)} = 1.514$, $p = 0.225$, $\eta_p^2 = 0.033$).

When this analysis was conducted for the other emotion conditions, the main effects and interactions for the emotion recognition factor did not reach the threshold for significance ($F_{(1, 44)} < 5.685$, $p > 0.021$).

Likewise, analyses of the other subcortical structures did not reveal any main effects or interactions for emotion recognition in any of the emotion conditions at the threshold for significance; these results are provided for descriptive purposes in the Supplementary materials.

To demonstrate that the significant relationship between putamen volume and fearful face recognition was not due to a response bias toward reporting fear in general, we investigated whether the tendency to misinterpret surprised faces as fearful faces was correlated with putamen volume. We found no significant main effect of fear misinterpretation on putamen volume ($F_{(1, 44)} = 1.803$, $p = 0.186$, $\eta_p^2 = 0.039$), indicating that individuals with a small putamen accurately recognized fearful faces with no response bias.

3.3 Local shape analysis

Local shape analyses revealed significant negative associations between the percent accuracy for fearful face recognition and the anterior and posterior aspects of the left putamen and overall right putamen (all $p < 0.05$, cluster-level FWE corrected; Fig. 2).

4. Discussion

The present study explored the relationship between the volume of putamen and other subcortical structures and the ability to recognize faces expressing the six basic emotions. We found a significant negative relationship between putamen volume and percent accuracy for fearful face recognition without an interaction effect of hemisphere after controlling for the effects of TCV, age, sex, and full-scale IQ. Our findings could not be fully explained by a response bias toward reporting fear, because the misinterpretation of surprised faces as fearful faces was not associated with putamen volume. Several lines of evidence have provided partial support for the involvement of the putamen in the processing of emotional facial expressions. A meta-analysis of functional MRI studies identified activation in the putamen during observation of emotional facial expressions (i.e., anger/disgust/fear/happiness/neutral/sadness > baseline) (Fusar-Poli et al. 2009). An early functional MRI study found that compared with neutral expressions, facial expressions of fear and disgust differentially activated the putamen (Phillips et al. 1998). A recent study demonstrated that fearful and surprised faces elicited activation in the putamen (Zhao et al. 2017). Another study found that task instructions modulated the putamen response to fearful faces (Lange et al. 2003). Additionally, neuroanatomical studies have determined that individuals with high-functioning ASD (Sato et al. 2014) and psychopaths (Yang et al. 2015), who both exhibit impairments in the recognition of negative facial emotions, fearful faces in particular (Dawel et al. 2012; Uono et al. 2013), have enlarged putamen structures. Together with previous findings, the present study suggested that an increased bilateral putamen volume is related to difficulties recognizing fearful faces.

Local shape analyses revealed that deformities within the anterior and posterior aspects of the bilateral putamen are also negatively correlated with the percent accuracy for fearful face recognition. Given that changes in the boundaries of structures (in a vertex-based manner) are indicative of local volume changes, the results of this analysis also suggest that increased local volumes of both the anterior and posterior putamen were correlated with difficulties recognizing fearful faces. A recent meta-analysis of functional MRI studies found that the more

anterior aspect of the putamen is involved in cognitive (executive function/working memory) and affective (reward/emotion) processing, while the more posterior aspect of the putamen contributes to motor function (body/eye movements) (Arsalidou et al. 2013). Consistent with these findings, anatomical studies have indicated that the anterior and posterior putamen are associated with cognitive/affective processing and motor function, respectively, because the former receives inputs from the dorsolateral and medial prefrontal cortex while the latter receives inputs from the motor cortex (Draganski et al. 2008; Grahn et al. 2008). These anatomical connections might allow the putamen to an important role during emotion recognition in terms of orchestrating cognitive, affective and motor functions.

Although the specific cognitive, emotional and/or motor functions of the putamen during the recognition of fearful expressions remain to be fully characterized, neurological evidence has provided insight into its motor functions. The putamen has somatotopic representations of facial structures (Gerardin et al. 2003), and damage to or the enlargement of this region can induce various types of focal dystonia, such as blepharospasm; an apraxia of eyelid opening that is caused by spasms of the orbicularis oculi muscles (Black et al. 1998; Etgen et al. 2006; Verghese et al. 1999), which are involved in expression of fear (Ekman & Friesen 1978). Furthermore, functional imaging studies have observed activation in the putamen and motor cortex associated with spasms and during a blinking task in patients with blepharospasm (Baker et al. 2003; Schmidt et al. 2003). These findings suggest that an increased putamen volume might interfere with the smooth response of facial muscles around the eyes, even in healthy adults. It has been proposed that automatic and intentional facial mimicry modulate the recognition of others' facial expressions (Niedenthal 2007; Oberman et al. 2007; Sato, Fujimura, et al. 2013), and that information from the eye region plays a critical role when discriminating fearful faces from other facial expressions (Adolphs et al. 2005). Taken together, the previous and present findings suggest that an increased putamen volume may restrict automatic facial mimicry, particularly in the eye region, and induce difficulties when recognizing fearful faces. Structural MRI studies have demonstrated that high-functioning individuals with ASD exhibit increased volumes in the

putamen (Sato et al. 2014), while behavioral studies have shown that this population has impaired facial mimicry (Yoshimura et al. 2015) and difficulties in recognizing negative facial emotions, fearful faces in particular (Uono et al. 2013). Based on such findings, there may be a link between increased putamen volume and impaired recognition and expression of emotional faces. However, to directly confirm this link, further studies are necessary to investigate the relationships among the function and structure of the putamen, facial mimicry and emotion recognition in healthy participants and patients with restricted putamen damage.

Given that the putamen is involved in emotion processing, it is possible to argue that there was a significant relationship between putamen volume and emotion recognition in the present study, because the stable emotional characteristics of the participants, namely their levels of anxiety and depression, as well as their brain volumes, may have influenced their ability to recognize emotion. Previous studies have demonstrated that high trait anxiety enhances the recognition of fearful faces (Richards et al. 2002; Surcinelli et al. 2006), while a meta-analysis found that clinical depression impaired recognition of all basic emotions except sadness (Dalili et al. 2015). However, a meta-analysis of voxel-based studies did not find changes in putamen volume, even in patients with anxiety disorders (Shang et al. 2014) or major depression (Bora et al. 2012). Our analysis, which controlled for the effects of trait anxiety and depression revealed a significant effect on the ability to recognize fearful faces (see Supplementary material). Based on this evidence, the stable emotional characteristics of the participants cannot explain the positive correlation between an increased volume in the bilateral putamen and difficulties recognizing fearful faces. It is possible that the cognitive/affective subregion of the putamen may contribute to the recognition of emotions via changes in the transient emotional state (e.g., emotional changes induced by facial mimicry). Further study is needed to determine whether additional variables moderate the relationship between putamen volume and emotion recognition.

The present study did not find a significant relationship between the volumes of the other subcortical regions and the ability to recognize emotion in facial expressions. In contrast, previous studies have observed

correlations between impaired recognition of specific emotions and structural and/or functional abnormalities in various subcortical regions, including fear and the amygdala (Adolphs et al. 2005), and disgust and the basal ganglia (Calder et al. 2000). Additionally, it was recently shown that the volume of the amygdala is correlated with the accurate recognition of fearful, but not other emotional, faces, although this particular study utilized a different experimental paradigm and different segmentation methods, and did not control for age, sex or IQ of the participants (Zhao et al. 2013). There may be some explanations regarding the discrepancies among the present study and previous lesion and functional imaging studies. First, the present study measured individual differences in subcortical volume in healthy adults, and the volume loss that was induced by neurological disease may have had a more striking effect on the ability to recognize emotions compared to volume changes across development. Second, the task in the present study required the participants to carefully consider all six alternatives prior to responding and no time limits were set. A task requiring a rapid response under time pressure might have altered the relationship between amygdala volume and the ability to recognize fearful faces (Zhao et al. 2013), because the amygdala is involved in the rapid and unconscious processing of emotional stimuli (Sato, Kochiyama, et al. 2013).

It should be noted that the present study has several limitations. First, the recognition of emotion involves several stages of processing including perceptual processing, motor and affective responses, and the interpretation of emotional meanings (e.g., Sato et al. 2013). Although the present study speculated on the involvement of the putamen in facial mimicry, further studies are necessary to specify the particular functional role of the putamen via the use of a task that focuses on the specific components of emotion recognition. Second, all but one participants showed a clear ceiling effect for the recognition of happy faces. The percent accuracy scores for the sad and surprised faces were significantly higher than those for the other negative facial emotions (anger, disgust, and fear). The high mean percent accuracy for these conditions (> 85%) may be explained by the fact that several participants had 100% accuracy, which may have confounded the volume analysis. Furthermore, differences in difficulty across the emotion categories may have affected

the participant's labeling strategy, such that when they found it difficult to identify an emotional expression, participants may have selected a complex emotion category (e.g., fear). Although we did not find a response bias toward reporting fear, a behavioral task in which the difficulty level is consistent across all emotion categories should be applied to avoid these potential confounding factors in future studies. The use of subtle emotional expressions created by a computer morphing technique (e.g., Uono et al., 2014) may help achieve a consistent level of difficulty across emotion categories. Furthermore, the presentation of dynamic facial expressions that reliably recruit multiple brain regions and elicit several psychological processes (Arsalidou et al., 2011; Sato et al., 2017) would prevent a floor effect.

5. Conclusion

The present study found that individual differences in putamen volume predicted the ability of healthy adults to recognize fearful facial expressions after controlling for age, sex, full-scale IQ, and emotional traits. However, it could not predict the ability to recognize other emotional facial expressions. These findings indicate that an increased volume in the bilateral putamen may be correlated with difficulties recognizing fearful faces, and that the anterior and posterior regions of the putamen, which support cognitive/affective and motor processing, respectively, are involved. This evidence provides insights into the role of the putamen during emotion recognition. Because neurological findings have shown that an increased putamen volume is associated with spasms of the orbicularis oculi muscles, it is possible to speculate that this increase may restrict automatic facial mimicry, particularly in the eye region, and induce specific difficulties when recognizing fearful faces. The relationships among the brain, facial muscles, and the recognition of emotion offer promising avenues for future research in social cognition.

Acknowledgments

We thank the ATR Brain Activity Imaging Center for their support in acquiring the data, Kazusa Minemoto, Akemi Inoue, and Emi Yokoyama for their technical support, and our anonymous reviewers for their helpful advice. Our study was supported by the JSPS Funding Program for Next Generation World-Leading Researchers (LZ008). The funding sources had no involvement in the study design; in the collection, analysis and interpretation of the data; in the writing of the report; or in the decision to submit the article for publication. The authors declare no competing interests.

References

- Adolphs R, Gosselin F, Buchanan TW, Tranel D, Schyns P, Damasio AR (2005) A mechanism for impaired fear recognition after amygdala damage. *Nature* 433:68–72. doi:10.1038/nature03086
- Arsalidou M, Duerden EG, Taylor MJ (2013) The centre of the brain: Topographical model of motor, cognitive, affective, and somatosensory functions of the basal ganglia. *Hum Brain Map* 34:3031–3054. doi:10.1002/hbm.22124
- Arsalidou M, Morris D, Taylor MJ (2011) Converging evidence for the advantage of dynamic facial expressions. *Brain Topogr* 24:149–63. doi:10.1007/s10548-011-0171-4.
- Baker RS, Anderson AH, Morecraft RJ, Smith CD (2003) A functional magnetic resonance imaging study in patients with benign essential blepharospasm. *J Neuro-Ophthalmol* 23:11–15.
- Baron-Cohen S, Ring HA, Wheelwright S, Bullmore E, Brammer MJ, Simmons A, Williams SCR (1999) Social intelligence in the normal and autistic brain: An fMRI study. *Eur J Neurosci* 11:1891–1898.
- Black KJ, Ongür D, Perlmutter JS (1998) Putamen volume in idiopathic focal dystonia. *Neurology* 51:819–824.
- Bora E, Fornito A, Pantelis C, Yucel M (2012) Gray matter abnormalities in Major Depressive Disorder: A meta-analysis of voxel based morphometry studies. *J Affect Disord* 138:9–18. doi:10.1016/j.jad.2011.03.049
- Calder AJ, Keane J, Lawrence AD, Manes F (2004) Impaired recognition of anger following damage to the ventral striatum. *Brain* 127:1958–1969.
- Calder AJ, Keane J, Manes F, Antoun N, Young AW (2000) Impaired recognition and experience of disgust following brain injury. *Nat Neurosci* 3:1077–1078.
- Circelli K, Clark US, Cronin-Golomb A (2013) Visual scanning patterns and executive function in relation to facial emotion recognition in aging. *Neuropsychol Dev Cogn B Aging Neuropsychol Cogn* 20:148–173. doi:10.1080/13825585.2012.675427
- Dawel A, O'Kearney R, McKone E, Palermo R (2012) Not just fear and sadness: Meta-analytic evidence of pervasive emotion recognition deficits for facial and vocal expressions in psychopathy. *Neurosci Biobehav Rev* 36, 2288–2304. doi:10.1016/j.neubiorev.2012.08.006
- Dalili MN, Penton-Volak IS, Harmer CJ, Munafò MR (2015) Meta-analysis of emotion recognition deficits in major depressive disorder. *Psychol Med* 45: 1135–1144. doi: 10.1017/S0033291714002591

- DeLong MR, Wichmann T (2007) Circuits and circuit disorders of the basal ganglia. *Neurol Rev* 64:200–224.
- Draganski B, Kherif F, Klöppel S, Cook PA, Alexander DC, Parker GJ, Deichmann R, Ashburner J, Frackowiak RSJ (2008) Evidence for segregated and integrative connectivity patterns in the human basal ganglia. *J Neurosci* 28:7143–7152. doi:10.1523/JNEUROSCI.1486-08.2008
- Ekman P, Friesen, WV (1976) *Pictures of facial affect*. Palo Alto, CA: Consulting Psychologists Press.
- Ekman P, Friesen WV (1978) *Facial action coding system: A technique for the measurement of facial movement*. Palo Alto: Consulting Psychologists Press.
- Etgen T, Muhlau M, Gaser C, Sander D (2006) Bilateral grey-matter increase in the putamen in primary blepharospasm. *J Neurol Neurosurg Psychiatry* 77:1017–1020.
- Fusar-Poli P, Placentino A, Carletti F, Landi P, Allen P, Surguladze S, Benedetti F, Abbamonte M, Gasparotti R, Barale F, Perez J, McGuire P, Politi P (2009) Functional atlas of emotional faces processing: A voxel-based meta-analysis of 105 functional magnetic resonance imaging studies. *J Psychiatry Neurosci* 34:418–432.
- George M, Ketter TA, Parekh PI, Horwitz B, Herscovitch P, Post RM (1995) Brain activity during transient sadness and happiness in healthy women. *Am J Psychiatry* 152:341–351.
- Gerardin E, Lehericy S, Pochon JB, Tézenas du Montcel S, Mangin JF, Poupon F, Agid Y, Le Bihan D, Marsault C (2003) Foot, hand, face and eye representation in the human striatum. *Cereb Cortex* 13:162–169.
- Grahn JA, Parkinson JA, Owen AM (2008) The cognitive functions of the caudate nucleus. *Prog Neurobiol* 86:141–155. doi:10.1016/j.pneurobio.2008.09.004
- Gray HM, Tickle-Degnen L (2010) A meta-analysis of performance on emotion recognition tasks in Parkinson's disease. *Neuropsychology* 24:176–191. doi:10.1037/a0018104
- Henley SM, Novak MJ, Frost C, King J, Tabriz SJ, Warren JD (2012) Emotion recognition in Huntington's disease: A systematic review. *Neurosci Biobehav Rev* 36:237–253. doi:10.1016/j.neubiorev.2011.06.002
- Hidano N, Fukuhara M, Iwawaki M, Soga S, Spielberger CD (2000) *Manual for the State-Trait Anxiety Inventory-Form JYZ*. Tokyo: Jitsumu-Kyoiku-Shuppan.
- Kojima M, Furukawa T (2003) *The Japanese version of Beck Depression Inventory-II (BDI-II)*. Tokyo: Nihon-Bunka-Kagaku-Sha.

- Kret ME, de Gelder B (2012) A review on sex differences in processing emotional signals. *Neuropsychologia* 50:1211–1221. doi: 10.1016/j.neuropsychologia.2011.12.022
- Lange K, Williams LM, Young AW, Bullmore ET, Williams SCR, Gray JA, Phillips ML (2003) Task instructions modulate neural responses to fearful facial expression. *Biol Psychiatry* 53:226–232.
- Lee TM, Ng EH, Tang SW, Chan CC (2008) Effects of sad mood on facial emotion recognition in Chinese people. *Psychiatry Res* 159:37–43. doi:10.1016/j.psychres.2007.04.022
- Matsumoto D, Ekman P (1988) Japanese and Caucasian facial expressions of emotion. San Francisco, CA: Intercultural and Emotion Research Laboratory, Department of Psychology, San Francisco State University.
- Nemmi F, Sabatini U, Rascol O, Peran P (2015) Parkinson's disease and local atrophy in subcortical nuclei: insight from shape analysis. *Neurobiol Aging* 36:424–433. doi: 10.1016/j.neurobiolaging.2014.07.010
- Niedenthal PM (2007) Embodying emotion. *Science* 316:1002–1005.
- Oberman LM, Winkielman P, Ramachandran VS (2007) Face to face: Blocking facial mimicry can selectively impair recognition of emotional expressions. *Soc Neurosci* 2:167–178. doi:10.1080/17470910701391943
- Okada T, Kubota Y, Sato W, Murai T, Pellion F, Gorog F (2015) Common impairments of emotional facial expression recognition in schizophrenia across French and Japanese cultures. *Front Psychol* 6:1018. doi: 10.3389/fpsyg.2015.01018
- Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9:97–113.
- Otsubo T, Miyaoka H, Kamijima K (2005) M.I.N.I. Mini International Neuropsychiatric Interview. Tokyo: Seiwa Shoten.
- Pardini DA, Raine A, Erickson K, Loeber R (2014) Lower amygdala volume in men is associated with childhood aggression, early psychopathic traits, and future violence. *Biol Psychiatry* 75:73–80. doi: 10.1016/j.biopsych.2013.04.003
- Patenaude B (2007) Bayesian statistical models of shape and appearance for subcortical brain segmentation. University of Oxford.
- Patenaude B, Smith SM, Kennedy DN, Jenkinson M (2011) A Bayesian model of shape and appearance for subcortical brain segmentation. *Neuroimage* 56:907–922. doi:10.1016/j.neuroimage.2011.02.046
- Pauli WM, O'Reilly RC, Yarkoni T, Wager TD (2016) Regional specialization within the human striatum for diverse psychological functions. *Proc Natl Acad Sci U S A*

- A 113: 1907–1912. doi: 10.1073/pnas.1507610113
- Phillips ML, Young AW, Scott SK, Calder AJ, Andrew C, Giampietro V, Williams SC, Bullmore ET, Brammer M, Gray JA (1998) Neural Responses to facial and vocal expressions of fear and disgust. *Proc R Soc Lond B* 265:1809–1817.
- Pitcher TL, Melzer TR, Macaskill MR, Graham CF, Livingston L, Keenan RJ, Watts R, Dalrymple-Alford JC, Anderson TJ (2012) Reduced striatal volumes in Parkinson's disease: A magnetic resonance imaging study. *Transl Neurodegener* 1:17. doi:10.1186/2047-9158-1-17.
- Richards A, French CC, Calder AJ, Webb B, Fox R, Young AW (2002) Anxiety-related bias in the classification of emotionally ambiguous facial expressions. *Emotion* 2:273–287.
- Ruigrok AN, Salimi-Khorshidi G, Lai MC, Baron-Cohen S, Lombardo MV, Tait RJ, Suckling J (2014) A meta-analysis of sex differences in human brain structure. *Neurosci Biobehav Rev* 39:34–50. doi: 10.1016/j.neubiorev.2013.12.004
- Sato W, Fujimura T, Kochiyama T, Suzuki N (2013) Relationships among facial mimicry, emotional experience, and emotion recognition. *PLoS One* 8:e57889. doi:10.1371/journal.pone.0057889
- Sato W, Kochiyama T, Uono S, Matsuda K, Usui K, Inoue Y, Toichi M (2013) Rapid and multiple-stage activation of the human amygdala for processing facial signals. *Commun Integr Biol* 6:e24562. doi:10.4161/cib.24562
- Sato W, Kochiyama T, Uono S, Yoshikawa S, Toichi M (2017) Direction of amygdala-neocortex interaction during dynamic facial expression processing. *Cereb Cortex* 27:1878–1890. doi: 10.1093/cercor/bhw036
- Sato W, Kubota Y, Kochiyama T, Uono S, Yoshimura S, Sawada R, Sakihama M, Toichi M (2014) Increased putamen volume in adults with autism spectrum disorder. *Front Hum Neurosci* 8:957. doi:10.3389/fnhum.2014.00957
- Sato W, Kubota Y, Okada T, Murai T, Yoshikawa S, Sungoku A (2002) Seeing happy emotion in fearful and angry faces: qualitative analysis of facial expression recognition in a bilateral amygdala-damaged patient. *Cortex* 38:727–742.
- Schmidt KE, Linen DEJ, Goebel R, Zanella FE, Lanfermann H, Zubcov A (2003) Striatal activation during blepharospasm revealed by fMRI. *Neurology* 60:1738–1743.
- Shang J, Fu Y, Ren Z, Zhang T, Du M, Gong Q, Lui S, Zhang W (2014) The common traits of the ACC and PFC in anxiety disorders in the DSM-5: Meta-analysis of voxel-based morphometry studies. *PLoS One* 9:e93432 . doi:10.1371/journal.pone.0093432

- Smith SM, Nichols TE (2009) Threshold-free cluster enhancement: Addressing problems of smoothing, threshold dependence and localisation in cluster inference. *Neuroimage* 44:8398. doi:10.1016/j.neuroimage.2008.03.061
- Surcinelli P, Codispoti M, Montebanocci O, Rossi N, Baldaro B (2006) Facial emotion recognition in trait anxiety. *J Anxiety Disord* 20:110–117.
- Uono S, Sato W, Toichi M (2011) The specific impairment of fearful expression recognition and its atypical development in pervasive developmental disorder. *Soc Neurosci* 6:452–463. doi:10.1080/17470919.2011.605593
- Uono S, Sato W, Toichi M (2013) Common and unique impairments in facial-expression recognition in pervasive developmental disorder-not otherwise specified and Asperger's disorder. *Res Autism Spectr Disord* 7:361–368. doi:10.1016/j.rasd.2012.10.007
- Uono S, Sato W, Toichi M (2014) Reduced representational momentum for subtle dynamic facial expressions in individuals with autism spectrum disorders. *Res Autism Spectr Disord* 8:1090–1099. doi.org/10.1016/j.rasd.2014.05.018
- van den Heuvel OA, Veltman DJ, Groenewegen HJ, Cath DC, van Balkom AJ, van Hartkamp J, Barkhof F, van Dyck R (2005) Frontal-striatal dysfunction during planning in obsessive-compulsive disorder. *Arch Gen Psychiatry* 62:301–309.
- Vergheze J, Milling C, Rosenbaum DM (1999) Ptosis, blepharospasm, and apraxia of eyelid opening secondary to putaminal hemorrhage. *Neurology* 53:652.
- Walker FO (2007) Huntington's disease. *Lancet* 369:218–228.
- Winkler AM, Ridgway GR, Webster MA, Smith SM, Nichols TE (2014) Permutation inference for the general linear model. *Neuroimage* 92:381–397. doi:10.1016/j.neuroimage.2014.01.060
- Yang Y, Narr KL, Baker LA, Joshi SH, Jahanshad N, Raine A, Thompson PM (2015) Frontal and striatal alterations associated with psychopathic traits in adolescents. *Psychiatry Res* 231:333–340. doi:10.1016/j.psychresns.2015.01.017.
- Yoshimura S, Sato W, Uono S, Toichi M (2015) Impaired overt facial mimicry in response to dynamic facial expressions in high-functioning autism spectrum disorders. *J Autism Dev Disord* 45:1318–1328. doi:10.1007/s10803-014-2291-7
- Zhao K, Yan WJ, Chen YH, Zuo XN, Fu X (2013) Amygdala volume predicts inter-individual differences in fearful face recognition. *PLoS One* 8:e74096. doi:10.1371/journal.pone.0074096
- Zhao K, Zhao J, Zhang M, Cui Q, Fu X (2017) Neural Responses to Rapid Facial Expressions of Fear and Surprise. *Front. Psychol.* 8:761. doi:10.3389/fpsyg.2017.00761

Tables

Table 1.

Participant characteristics

Sex (male:female)	26:24
	Mean (SD)
Age (y)	22.4 (4.4)
Verbal IQ	121.5 (9.3)
Performance IQ	116.7 (10.4)
Full IQ	121.4 (8.6)
STAI (trait anxiety)	46.4 (8.6)
BDI-II	9.4 (6.8)

IQ: intelligence quotient; STAI: State and Trait Anxiety

inventory; BDI: Beck depression inventory

Table 2.

Emotion recognition performance for each condition

Emotion category	Anger	Disgust	Fear	Happiness	Sadness	Surprise	ALL
Mean	57.8	63.8	64.0	99.8	86.0	92.0	77.2
SD	20.0	22.1	24.7	1.8	15.1	16.7	7.1

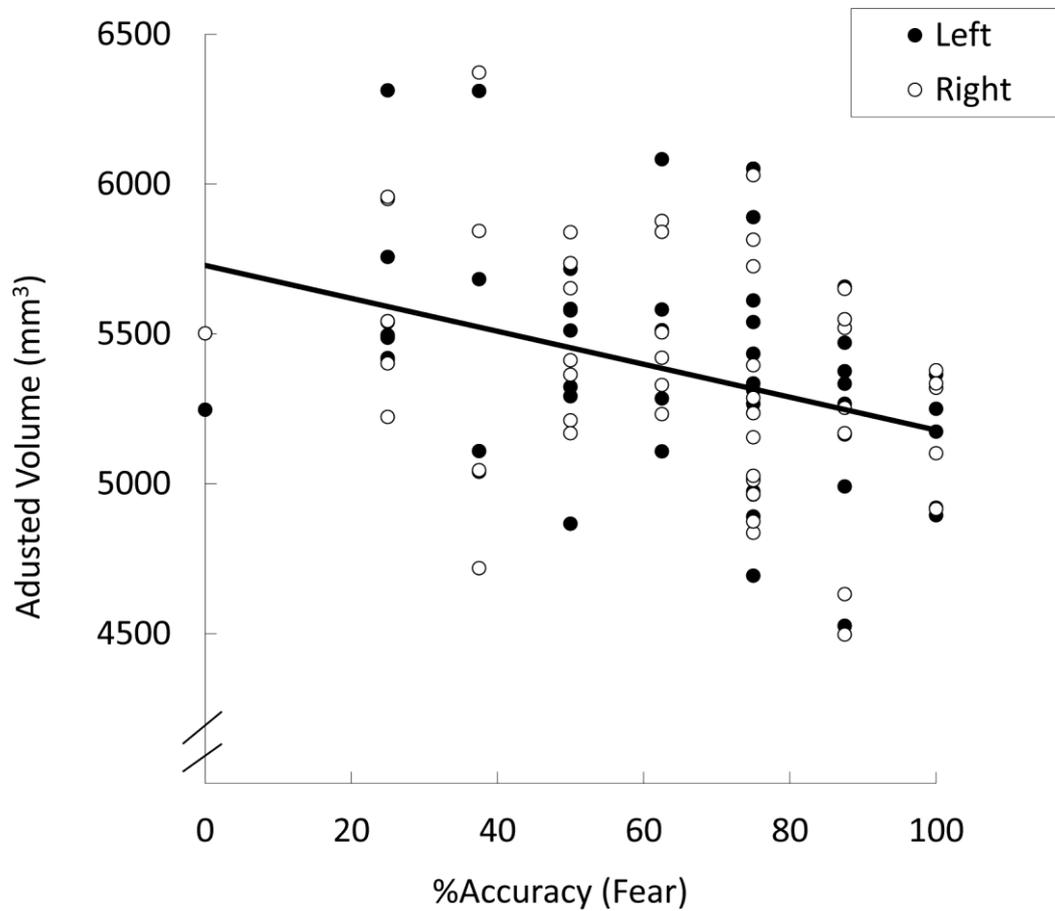


Figure 1. Relationship between the accurate recognition of fearful faces and adjusted putamen volume in the left and right hemispheres. The effects of sex, age, full-scale intelligence quotient, and total cerebral volume were covaried out.

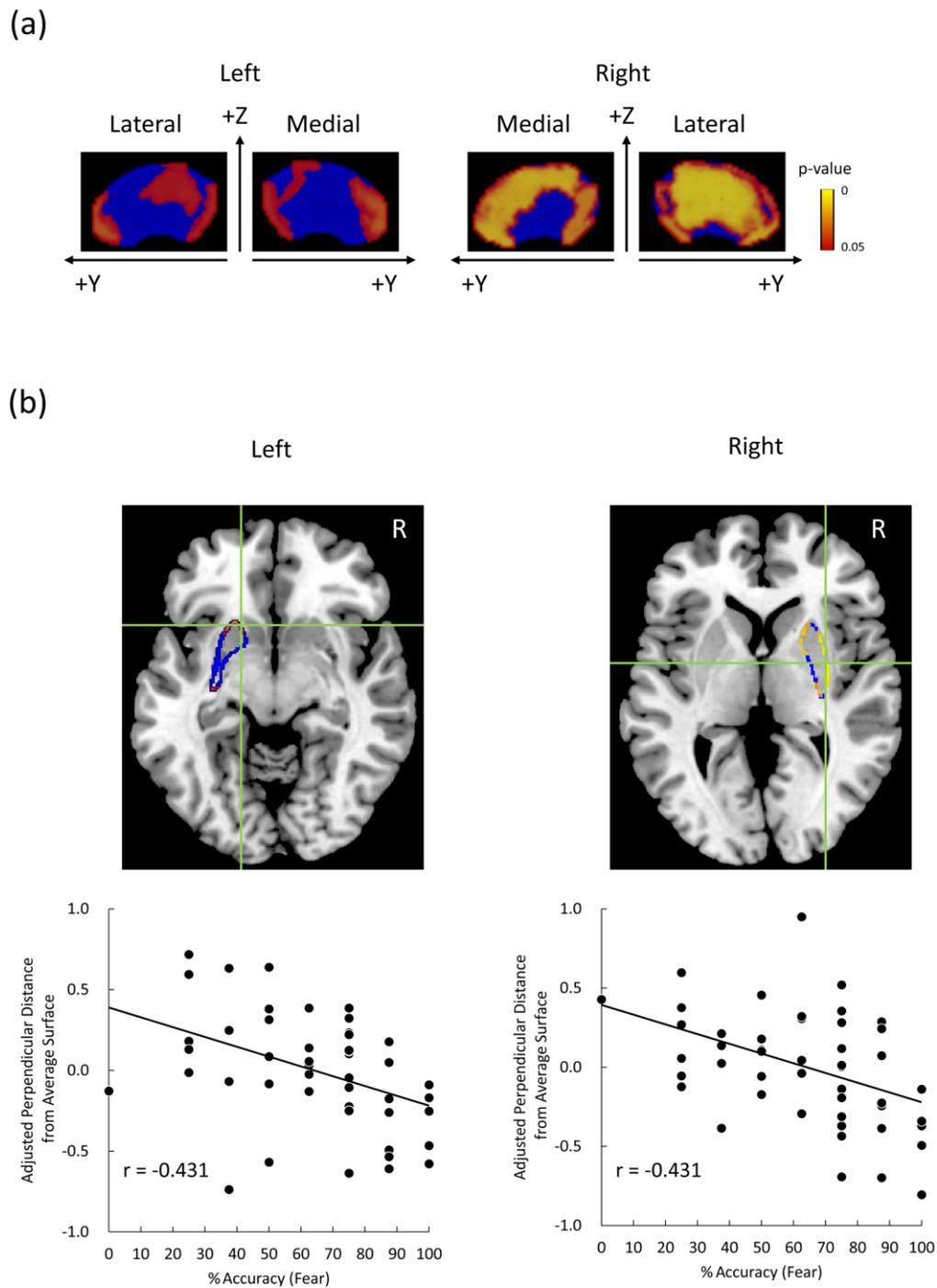


Figure 2. Local shape analyses showing significant negative associations with percent accuracy for fearful face recognition in the left and right

putamen. The effects of sex, age, and full-scale IQ were covaried out. (a) Surface maps showing significant clusters. The lateral and medial surfaces (z - y planes) are shown. Yellow-red color indicates the p -value after cluster-level family-wise error (FWE) corrections for multiple comparisons. (b) Axial sections in the MNI space showing the mean normalized putamen shape (blue), localization of statistically significant correlations with vertex displacements, and percent accuracy for fearful face recognition. The green lines indicate peaks at the anterior ($x = -17$, $y = 17$, $z = -8$) and posterior ($x = 32$, $y = -2$, $z = 3$) putamen in the left and right hemispheres, respectively. R, right. Scatter plots with regression lines indicate the perpendicular distance from the average surface as a function of the percent accuracy of fearful face recognition at the left and right putamen foci, respectively.

Supplementary Materials

1. *Exploratory analysis at a liberal threshold*

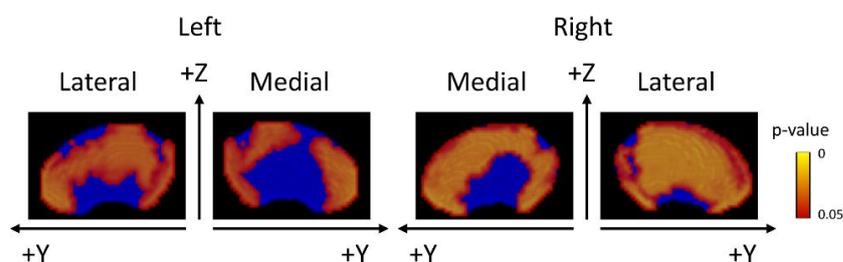
The analyses in the present study were also conducted using a more liberal threshold ($p < 0.05$) for exploratory purposes. Of the basal ganglia structures, there was a main effect of emotion recognition only in the nucleus accumbens for fearful ($F_{(1, 44)} = 5.091, p = 0.029, \eta_p^2 = 0.104$) and sad ($F_{(1, 44)} = 4.875, p = 0.033, \eta_p^2 = 0.100$) expressions. These findings indicate that the nucleus accumbens volume was positively and negatively correlated with the recognition of sad and fearful faces, respectively. In terms of the volumes of the putamen, caudate and globus pallidum, although there was an interaction between hemisphere and emotion recognition (putamen-surprise: $F_{(1, 44)} = 5.685, p = 0.021, \eta_p^2 = 0.114$; caudate-surprise: $F_{(1, 44)} = 6.245, p = 0.016, \eta_p^2 = 0.124$; globus pallidus-anger: $F_{(1, 44)} = 5.681, p = 0.022, \eta_p^2 = 0.114$), the main effect of emotion recognition did not reach even the liberal threshold for either hemisphere ($F_{(1, 44)} < 1.887, p > 0.176$). Additionally, there were no significant effects of emotion recognition in the other subcortical regions including the thalamus, amygdala and hippocampus ($F_{(1, 44)} < 3.847, p > 0.056$).

2. *Effects of stable emotional characteristics of the participants on the relationship between putamen volume and fearful face recognition*

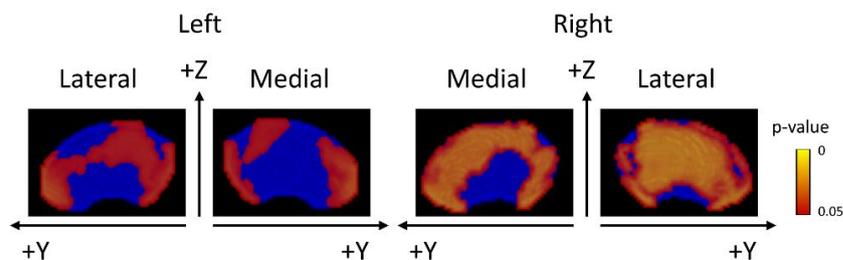
To exclude the possibility that the stable emotional characteristics of the participants may have influenced the relationship between the ability to recognize emotion and putamen volume, additional analyses were conducted using a repeated-measures general linear model. Percent accuracy for fearful face recognition was used as an independent variable (effect of interest). Hemisphere (left or right), sex (male or female), age, full-scale IQ, TCV, and trait anxiety or depression were included as covariates (effect of no interest). The levels of trait anxiety and depression were measured with the Japanese version of the STAI and the BDI-II, respectively. The effects of recognition of fearful faces remained significant when the level of trait anxiety ($F_{(1, 43)} = 10.375, p = 0.002, \eta_p^2 = 0.194$) or depression ($F_{(1, 43)} = 11.393, p = 0.002, \eta_p^2 = 0.209$) were included as additional factors. The stable emotional characteristics of the participants could not explain the negative correlation between the

increased volume of the bilateral putamen and the percent accuracy for fearful face recognition. For the local shape analysis, multiple regression analyses were conducted using the percent accuracy for fearful face recognition as the independent variable and sex, age, full-scale IQ, and trait anxiety or depression as covariates (effects of no interest). There were significantly spread clusters that exhibited negative associations with the percent accuracy for fearful face recognition in the bilateral putamen after controlling for trait anxiety or depression (all $p < 0.05$, cluster-level FWE corrected; Supplementary Fig. 1).

Adjusted by Gender & Age & FIQ & BDI



Adjusted by Gender & Age & FIQ & STAI



Supplementary Figure 1.