Neural Correlates of Human Virtue Judgment

Hidehiko Takahashi[1,2], Motoichiro Kato[3], Masato Matsuura[2], Michihiko Koeda[4], Noriaki Yahata[5], Tetsuya Suhara[1] and Yoshiro Okubo[4]

[1]Department of Molecular Neuroimaging, National Institute of Radiological Sciences, 9-1, 4-chome, Anagawa, Inage-ku, Chiba 263-8555, Japan, [2]Department of Life Sciences and Bio-informatics, Graduate School of Health Sciences, Tokyo Medical and Dental University, 1-5-45 Yushima Bunkyo-ku Tokyo, Japan, [3]Department of Neuropsychiatry, Keio University School of Medicine, 35 Shinanomachi, Shinjuku-ku, Tokyo, Japan, [4]Department of Neuropsychiatry and [5]Department of Pharmacology, Nippon Medical School, 1-1-5, Sendagi, Bunkyo-ku, Tokyo, Japan

Neuroimaging studies have demonstrated that the brain regions implicated in moral cognition. However, those studies have focused exclusively on violation of social norms and negative moral emotions, and very little effort has been expended on the investigation of positive reactions to moral excellence. It remains unclear whether the brain regions implicated in moral cognition have specific roles in processing moral violation or, more generally, process human morality per se. Using functional magnetic resonance imaging, brain activations during evaluation of moral beauty and depravity were investigated. Praiseworthiness for moral beauty was associated with activation in the orbitofrontal cortex, whereas blameworthiness for moral depravity was related to the posterior superior temporal sulcus. Humans might have developed different neurocognitive systems for evaluating blameworthiness and praiseworthiness. The central process of moral beauty evaluation might be related to that of aesthetic evaluation. Our finding might contribute to a better understanding of human morality.

Keywords: blameworthiness, moral, orbitofrontal cortex, praiseworthiness, superior temporal sulcus, virtue

Introduction

The emerging field of cognitive neuroscience is providing new insights into the neural basis of moral cognition and behaviors. As David Hume (1978) and Adam Smith (1976) already noted in the 18th century, some contemporary philosophers have emphasized the importance of emotion and intuition in moral judgment, although moral reasoning could contribute to moral judgment (Haidt 2001; Greene and Haidt 2002). Supporting this view, recent neuroimaging studies and brain lesion studies have demonstrated that emotion-related brain regions such as the posterior superior temporal sulcus (pSTS), medial prefrontal cortex (MPFC), orbitofrontal cortex (OFC), and amygdala play important roles in moral judgment (Damasio 2000; Greene and Haidt 2002; Takahashi et al. 2004; Moll et al. 2005). Previous psychological as well as neuroimaging studies mainly focused on violation of social norms and negative moral emotions such as guilt or embarrassment (Greene and Haidt 2002; Haidt 2003a, 2003b; Takahashi et al. 2004; Moll et al. 2005; Mobbs et al. 2007). Morals are standards or principles of right or wrong behaviors and the goodness or badness of human character. It remains unclear whether the brain regions implicated in moral cognition are specialized in processing immorality, that is, negative deviance from social norms or,

more generally, processing deviance from social standards regardless of whether the stimuli positively or negatively deviate from them. There has been very little study on positive moral emotions or psychological responses to moral beauty, but with the advent of the positive psychology movement (Seligman and Csikszentmihalyi 2000), researchers have started to focus on positive moral emotions. Many people experience spontaneous pleasure when they can help others without any expectation of reward. Neuroimaging studies suggest that cooperative behaviors might be psychologically rewarding (Rilling et al. 2002; de Quervain et al. 2004; Moll et al. 2006). It is also human nature that we are easily and strongly moved by people who are cooperating with others. Haidt (2003a, 2003b) started to call an emotion elicited by others' act of virtue or moral beauty as "elevation." When people observe others' virtuous, commendable acts, they feel warm, pleasant, and "tingling" feelings and are motivated to help others and to become better people themselves. Hume (1978) wrote that "a generous and noble character never fails to charm and delight us" and Smith (1976) noted that "man desires, not only praise, but praiseworthiness." We also could have an aesthetic feeling in human virtuous acts and be often attracted by the beauty itself (Haidt 2003a). However, there are very few studies to have concentrated on this aspect of moral beauty. According to Haidt (2003a), we cannot have a full understanding of human morality until we can explain why and how people are so powerfully affected by the sight of a stranger helping another stranger.

For the evolution and persistence of cooperation, it is necessary for humans to detect cheaters and cooperators. Otherwise, selfish strategies will eliminate cooperative strategies (Axelrod and Hamilton 1981; Cosmides and Tooby 1992). Cosmides and Tooby (1992) argued that humans have evolved neurocognitive systems that specialize in detecting "cheating," violation of social contracts, and that produce a feeling that those who violate social norms should be blamed and punished. In fact, functional magnetic resonance imaging (fMRI) studies reported activation in brain regions such as pSTS and MPFC during detection of violation of social contracts (Canessa et al. 2005; Fiddick et al. 2005). On the other hand, it is also argued that humans have evolved a neurocognitive system that skillfully assesses the cooperativeness of others (Price 2006), and empirical evidence suggests that people will cooperate with those whom they have observed cooperating with others (Wedekind and Milinski 2000; Milinski et al. 2002). However, there is as yet no documented study regarding the investigation

of the neural correlates during the observance of praiseworthy, virtuous acts of others.

In this study, we investigated the brain activation associated with the judgment of moral beauty, virtue, comparing it with that of moral depravity, vice. We hypothesized that the judgment of moral beauty and depravity would show different brain activation patterns. Specifically, moral depravity would be linked to brain regions, such as pSTS and MPFC, and moral beauty would recruit the brain regions implicated in positive emotions, such as OFC.

Materials and Methods

Participants
Fifteen healthy volunteers (mean age 20.1 years, standard deviation [SD] = 0.8) participated in this study. All subjects were Japanese and right-handed. The participants were free of any criteria for neuropsychiatric disorders based on unstructured psychiatric screening interviews. None of the participants were taking alcohol at the time nor did they have a history of psychiatric disorder, significant physical illness, head injury, neurological disorder, or alcohol or drug dependence. All participants underwent an MRI to rule out cerebral anatomic abnormalities. After complete explanation of the study, written informed consent was obtained from all participants and the study was approved by the Institutional Ethics Committee.

Materials
Three types of short sentences were provided (neutral, moral beauty, and moral depravity). Each sentence was written in Japanese and in the 3rd person. Sentences of moral depravity were expressing moral violation, and those of moral beauty were expressing acts like charity, self-sacrifice, altruism, humanitarianism, and so on. Neutral sentences were expected to express no prominent emotional content. In order to validate our expected results, we conducted an initial survey. We prepared 30–35 sentences for each of 3 conditions (neutral, moral beauty, and moral depravity). Forty-two other healthy volunteers (21 males and 21 females, mean age 22.5 years, SD = 3.3) than the subjects participating in this fMRI study were screened. Using 7-point Likert scales, they read and rated each sentence in terms of morality/immorality (–3 = extremely immoral, 0 = neither moral nor immoral, and 3 = extremely moral) and praiseworthiness/blameworthiness (–3 = extremely blameworthy, 0 = neither praiseworthy nor blameworthy, and 3 = extremely praiseworthy). Based on the initial survey, we selected 18 sentences for each of the 3 conditions. These sentences are shown in Supplementary Table S1. The sentences were projected via a computer and a telephoto lens onto a screen mounted on a head coil. The subjects were instructed to read the sentences silently and were told to imagine the events described in the sentences. They were also told that they should rate the sentences according to how moral/immoral or praiseworthy/blameworthy the events were. After reading each sentence, the subjects were instructed to press a selection button with the right index finger, indicating that they had read and understood it. The experimental design consisted of 6 blocks for each of the 3 conditions (neutral, moral beauty, and moral depravity) interleaved with 20-s rest periods. We used a block design rather than an event-related design as it is difficult to obtain sufficient understandable stimuli, that is, depictions of moral beauty and depravity are difficult to parse rapidly (Luo et al. 2006). The order of presentation for the 3 conditions was randomized. During the rest condition, participants viewed a crosshair pattern projected to the center of the screen. In each 24-s block, 3 different sentences of the same condition were presented for 8 s each. Using 7-point Likert scales, the participants rated each sentence in terms of morality/immorality and praiseworthiness/blameworthiness after the scans.

Image Acquisition
Images were acquired with a 1.5 Tesla Signa system (General Electric, Milwaukee, WI). Functional images of 203 volumes were acquired with T2*-weighted gradient echo planar imaging sequences sensitive to blood oxygenation level–dependent contrast. Each volume consisted of 40 transaxial contiguous slices with a slice thickness of 3 mm to cover almost the whole brain (flip angle, 90°; time echo [TE], 50 ms; time repetition [TR], 4 s; matrix, 64 × 64; and field of view, 24 × 24 cm). High-resolution, T1-weighted anatomic images were acquired for anatomic comparison (124 contiguous axial slices, 3-dimensional Spoiled-Grass sequence, slice thickness 1.5 mm; TE, 9 ms; TR, 22 ms; flip angle, 30°; matrix, 256 × 192; and field of view, 25 × 25 cm).

Analysis of Functional Imaging Data
Data analysis was performed with statistical parametric mapping software package (SPM02) (Wellcome Department of Cognitive Neurology, London, UK) running with MATLAB (Mathworks, Natick, MA). All volumes were realigned to the 1st volume of each session to correct for subject motion and were spatially normalized to the standard space defined by the Montreal Neurological Institute template. After normalization, all scans had a resolution of 2 × 2 × 2 mm^3. Functional images were spatially smoothed with a 3-dimensional isotropic Gaussian kernel (full width at half maximum of 8 mm). Low frequency noise was removed by applying a high-pass filter (cutoff period = 192 s) to the fMRI time series at each voxel. A temporal smoothing function was applied to the fMRI time series to enhance the temporal signal-to-noise ratio. Significant hemodynamic changes for each condition were examined using the general linear model with boxcar functions convolved with a hemodynamic response function. Statistical parametric maps for each contrast of the t-statistic were calculated on a voxel-by-voxel basis.

To assess the specific condition effect, we used the contrasts of the moral beauty minus neutral (MB – N) and moral depravity minus neutral (MD – N). A random effects model, which estimates the error variance for each condition across the subjects, was implemented for group analysis. This procedure provides a better generalization for the population from which data are obtained. The contrast images were obtained from single-subject analysis and entered into the group analysis. A 1-sample t-test was applied to determine group activation for each effect. We used SPM's small volume correction to correct for multiple testing in regions about which we had a priori hypothesis. These a priori volumes of interest (VOIs) included the pSTS, MPFC, and OFC. VOIs for pSTS (angular gyrus), MPFC (superior and medial frontal gyrus), and OFC (inferior frontal gyrus) were defined by standardized VOI templates implemented in brain atlas software (Maldjian et al. 2003). Significant activations surviving this correction at $P < 0.05$ are reported. We describe activations outside regions of interest surviving a threshold of $P < 0.001$, uncorrected, with an extent threshold of 10 contiguous voxels. To assess common activation in MB – N and MD conditions, we conducted a conjunction analysis of MB – N and MD – N contrasts at the 2nd level.

We conducted regression analysis to demonstrate a more direct link between regional brain activities with the subjective judgments of praiseworthiness and blameworthiness. Using the mean of the ratings of praiseworthiness and blameworthiness for each subject as the covariate, regression analysis with the contrasts (MB – N and MD – N) and the covariate was performed at the 2nd level. The masks of MB – N and MD – N contrasts from the 1-sample t-test ($P < 0.001$) were applied to confine the regions where significant activations were observed. Using the effect sizes, representing the percent signal change, of the contrasts (MB – N and MD – N) at the peak coordinates uncovered by regression analysis, we plotted the fMRI signal changes and ratings of praiseworthiness and blameworthiness.

Results

Initial Survey
As we predicted, neutral sentences were judged neither moral/praiseworthy nor immoral/blameworthy. The averages of the ratings of morality/immorality and praiseworthiness/blameworthiness for neutral sentences were 0.0 (SD = 0.1) and 0.0 (SD = 0.1), respectively. The average of ratings of morality and

praiseworthiness for 18 sentences of moral beauty were 2.3 (SD = 0.8) and 1.8 (SD = 0.9), respectively. The average of ratings of immorality and blameworthiness for 18 sentences of moral depravity were –2.4 (SD = 0.7) and –2.1 (SD = 0.8), respectively.

Self Rating

The self-rating results of the subjects participating in the fMRI study were comparable to the results obtained in the initial survey. The averages of the ratings of morality/immorality and praiseworthiness/blameworthiness for neutral sentences were 0.1 (SD = 0.2) and 0.0 (SD = 0.1), those of morality and praiseworthiness for sentences of moral beauty were 2.5 (SD = 0.3) and 2.1 (SD = 0.5), and those of immorality and blameworthiness for sentences of moral depravity were –2.4 (SD = 0.3) and –2.1 (SD = 0.4), respectively. Self-ratings of immorality were correlated with blameworthiness ($r = 0.58$, $P = 0.025$), and those of morality were correlated with praiseworthiness ($r = 0.68$, $P = 0.005$).

fMRI Result

The MB-N condition produced activations in the left OFC, left dorsal lateral prefrontal cortex (DLPFC), left supplementary motor area (SMA), left temporal pole, and visual cortex, (Table 1 and Fig. 1A). The MD – N condition produced activations in the left pSTS and MPFC (Table 1 and Fig. 1B). The activations in a priori regions (pSTS, MPFC, and OFC) survived a threshold of $P < 0.05$ corrected for multiple comparisons across a small VOI. A conjunction analysis of MB – N and MD – N contrast revealed no significant activations.

Regression analysis revealed positive linear correlations between self-rating of praiseworthiness and the degree of activation in the left OFC ($x = -38$, $y = 28$, and $z = -20$) in MB – N contrast (Figs 2A and 3A). There were correlations between self-rating of blameworthiness and the degree of activation in the left pSTS ($x = -54$, $y = -66$, and $z = 28$) in MD – N contrast (Figs 2B and 3B). Theses correlations in a priori regions (pSTSC and OFC) survived a threshold of $P < 0.05$ corrected for multiple comparisons across a small VOI.

Discussion

This study has demonstrated that the brain activations during evaluation of positive deviance from the moral standard, moral beauty, showed different patterns from those of negative deviance, moral depravity. In line with previous reports, moral depravity conditions relative to neutral condition produced greater activity in the left pSTS and MPFC, the components of neural substrates that have been suggested to be involved in human moral cognition (Takahashi et al. 2004; Moll et al. 2005). A novel finding in this study was that moral beauty conditions relative to neutral condition produced greater activity in the left frontal regions, such as OFC, DLPFC, and SMA. This means that the regions suggested to play important roles in moral cognition are more specialized in processing moral violation and do not cover human morality per se.

Although self-ratings of immorality were correlated with blameworthiness and those of morality were correlated with praiseworthiness, empirical evidence suggests that blameworthiness for immoral acts and praiseworthiness for commendable or cooperative acts were not symmetrical. In other words, blameworthiness for impulsive immoral acts without deliberate

Table 1

Brain activations in moral beauty condition and moral depravity condition relative to neutral condition

Brain region	L/R	Coordinates			Z-score
		x	y	z	
Moral beauty-neutral					
Visual cortex	L/R	14	−90	−8	4.59
OFC*	L	−40	32	−20	3.39
Temporal pole	L	−50	18	−24	3.51
SMA	L	−48	0	48	3.52
DLPFC	L	−52	26	14	3.30
Moral depravity-neutral					
MPFC*	L/R	6	58	14	4.35
pSTS*	L	−54	−64	30	3.40

Note: Coordinates and Z-score refer to the peak of each brain region. L, left; R, right. All values, $P < 0.001$, uncorrected. *$P < 0.05$, corrected for multiple comparisons across a small VOI.
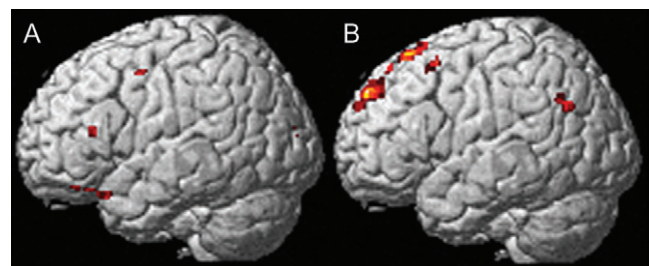

Figure 1. Images showing brain activations in response to (A) MB − N condition and (B) MD − N condition. (A) Significant activation in OFC is shown. (B) Significant activations in MPFC and pSTS are shown.
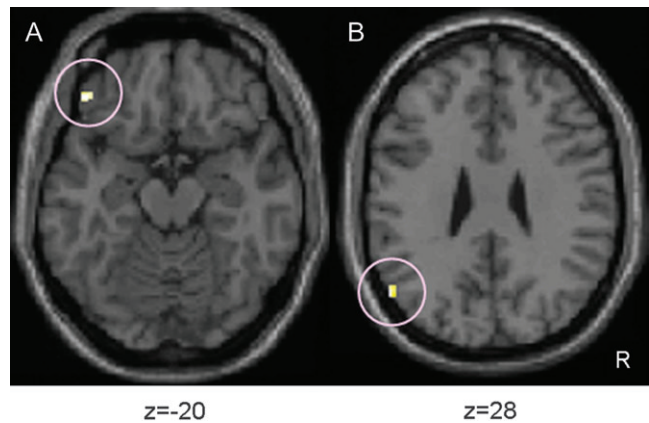

z=-20   z=28

Figure 2. Correlations between self-ratings of (A) praiseworthiness (B) blameworthiness and brain activations. (A) Correlation between self-rating of praiseworthiness and degree of activation in left OFC in MB − N contrast. (B) Correlations between self-rating of blameworthiness and degree of activation in pSTS in MD − N contrast. Within the images, R indicates right. Numbers at bottom indicate coordinates of Montreal Neurological Institute brain.

intention was discounted compared with deliberate immoral acts, whereas praiseworthiness for commendable acts was not discounted regardless of whether the positive acts were impulsive or deliberate (Pizarro et al. 2003). This is also common in legal culpability. This means that people tend to link blameworthiness to intention and the process of wrong-doing, whereas they tend to link praiseworthiness to outcomes of positive acts regardless of deliberate intention or not.
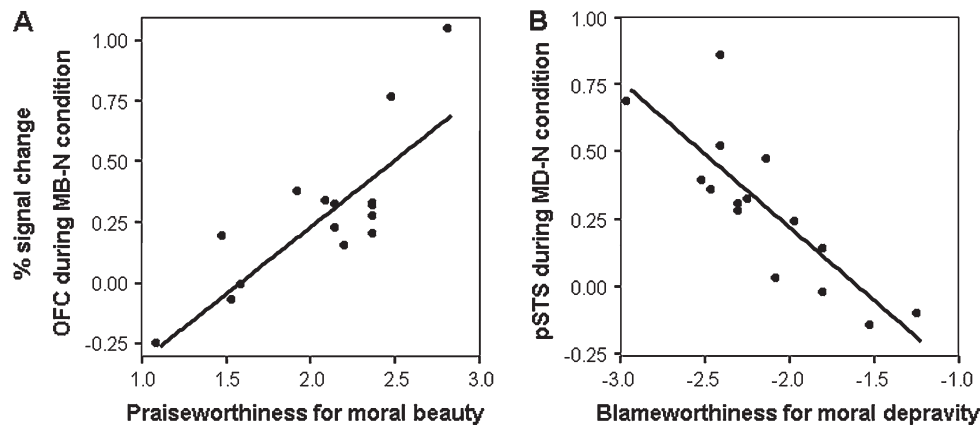
Figure 3. Regression lines of correlations between (*A*) praiseworthiness (*B*) blameworthiness and degree of brain activation. (*A*) There were correlations (*r* = 0.82, degrees of freedom [df] = 13, *P* < 0.001) between self-rating of praiseworthiness and degree of activation in OFC. (*B*) There were positive linear correlations (*r* = −0.83, df = 13, *P* < 0.001) between self-rating of blameworthiness and degree of activation in pSTS.

Moral depravity produced activation in the pSTS and MPFC, and the degree of pSTS activation was correlated with blameworthiness. Originally, STS was known to be activated by biological motions such as movement of eyes, mouth, hands, and body (Allison et al. 2000), and it has been suggested to have a more general function in social cognition such as detecting behavioral information that signals the intention of others (Gallagher and Frith 2003) and behavior of agents (Frith U and Frith CD 2003). MPFC appears to be responsible for inferring the cause of others' behavior, attribution. Previous studies have shown activation in the MPFC during judgments made on the basis of attributional information (Amodio and Frith 2006). It is suggested that, for the evolution and persistence of cooperation, humans have evolved neurocognitive systems that specialize in the detection of cheating and that motivate people to blame and punish those who violate social norms (Cosmides and Tooby 1992). Supporting this view, recent fMRI studies reported activation in brain regions such as the pSTS and MPFC during detection of the violation of social contracts (Canessa et al. 2005; Fiddick et al. 2005). Considering the functions of pSTS and MPFC, these regions might process intention of wrongdoings and, consequently, blameworthiness might be associated with the activation in pSTS.

The lack of activation in the pSTS and MPFC in response to moral beauty supports psychological studies in which people do not put a premium on the deliberate intention of commendable acts. Instead, correlation between the subjective ratings of praiseworthiness and the degrees of activation in the left OFC suggests that they regard positive outcome itself rather than intention of the act to be a main factor for praiseworthiness because the OFC is known to be involved in processing reward (Rolls 2006) and positive stimuli such as pictures (Northoff et al. 2000), taste (Small et al. 2003), and music (Blood and Zatorre 2001). It is also reported that the OFC was associated with maternal love (Bartels and Zeki 2004; Nitschke et al. 2004). The association between OFC activation and self-rating of praiseworthiness could be regarded as corresponding to Smith's phrase "The love of praiseworthiness" (Smith 1976).

Previous functional imaging studies have investigated the neural correlates processing facial beauty (Aharon et al. 2001; O'Doherty et al. 2003) or aesthetic beauty such as shapes or arts (Kawabata and Zeki 2004; Vartanian and Goel 2004; Jacobsen et al. 2006), and activation of reward-related subcortical and limbic areas including the OFC was reported. The connection between aesthetic judgment and moral feeling has long been emphasized in aesthetic theory (Kant 1952). Our finding could be interpreted in the context of aesthetic theory, that is, the neurocognitive system processing moral beauty might be related to that of aesthetic beauty.

We observed activation in other prefrontal areas in the left hemisphere, such as DLPFC and SMA, although activation in these unpredicted areas needs to be interpreted with caution. It is still unclear whether there is a hemispheric specialization in the processing of moral cognition, but it is suggested that frontal regions in the left hemisphere are associated with approach behavior, whereas frontal areas in the right hemisphere are associated with avoidance (Davidson 1992). Previous studies reported activation in the motor area in response to positive stimuli such as paintings, music, money, humor, and concepts (Blood and Zatorre 2001; Elliott et al. 2003; Mobbs et al. 2003; Kawabata and Zeki 2004; Cunningham et al. 2005). Although the exact role of the motor area in such tasks is not well known, it is suggested that the positive stimuli might mobilize the motor system to take some action toward them.

Although domain-specific emotional response is suggested to play a central role in moral judgments, domain-neutral reasoning could play certain roles as well (Haidt 2001; Greene and Haidt 2002). In a predictable situation, context-independent knowledge of event is processed automatically and routinely. This domain-specific process is suggested to be mediated in the medial and ventral prefrontal cortex. On the other hand, in a less predictable situation, context-dependent knowledge of event is processed with the operation of domain-neutral reasoning, which is suggested to be mediated in the DLPFC (Greene and Haidt 2002; Moll et al. 2005). It is also widely argued that emotions evolved to promote quick and automatic reaction in life-threatening situations (Fredrickson 1998). Although these models have been well fitted for negative emotions, quick and decisive actions are not typically required in a situation that gives rise to positive emotions. Instead, a wider range of thoughts or actions is required in situations where positive emotions occur (Fredrickson 1998). The DLPFC was reported to be recruited during evaluation of natural or

artistic aesthetic stimuli (Cela-Conde et al. 2004). Although the exact role of the DLPFC in aesthetic evaluation remains unclear, our results suggested that context-dependent knowledge contributes to the evaluation of moral beauty.

In conclusion, evaluation of moral excellence and moral violation might be processed differently in the human brain. However, any generalization of our findings needs to be approached with caution as the social background of the participants, such as culture, generation, religion, and education, could affect the results. Still, our results suggest that humans might have developed different neurocognitive systems for evaluating blameworthiness (cheaters) and praiseworthiness (cooperators). Our finding might contribute to a better understanding of the neural basis of human morality.

Supplementary Matrial

Supplementary table S1 can be found at: http://www.cercor.oxfordjournals.org/.

Notes

Conflict of Interest: None declared.

Address correspondence to Hidehiko Takahashi, MD, PhD, Department of Molecular Neuroimaging, National Institute of Radiological Sciences 9-1, 4-chome, Anagawa, Inage-ku, Chiba, Japan 263-8555. Email: hidehiko@nirs.go.jp.

References

Aharon I, Etcoff N, Ariely D, Chabris CF, O'Connor E, Breiter HC. 2001. Beautiful faces have variable reward value: fMRI and behavioral evidence. Neuron. 32:537–551.

Allison T, Puce A, McCarthy G. 2000. Social perception from visual cues: role of the STS region. Trends Cogn Sci. 4:267–278.

Amodio DM, Frith CD. 2006. Meeting of minds: the medial frontal cortex and social cognition. Nat Rev Neurosci. 7:268–277.

Axelrod R, Hamilton WD. 1981. The evolution of cooperation. Science. 211:1390–1396.

Bartels A, Zeki S. 2004. The neural correlates of maternal and romantic love. Neuroimage. 21:1155–1166.

Blood AJ, Zatorre RJ. 2001. Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. Proc Natl Acad Sci U S A. 98:11818–11823.

Canessa N, Gorini A, Cappa SF, Piattelli-Palmarini M, Danna M, Fazio F, Perani D. 2005. The effect of social content on deductive reasoning: an fMRI study. Hum Brain Mapp. 26:30–43.

Cela-Conde CJ, Marty G, Maestu F, Ortiz T, Munar E, Fernandez A, Roca M, Rossello J, Quesney F. 2004. Activation of the prefrontal cortex in the human visual aesthetic perception. Proc Natl Acad Sci U S A. 101:6321–6325.

Cosmides L, Tooby J. 1992. Cognitive adaptations for social exchange. In: Barkow J, Cosmides L, Tooby J, editors. The adapted mind: evolutionary psychology and the generation of culture. New York: Oxford University Press. p. 163–228.

Cunningham WA, Raye CL, Johnson MK. 2005. Neural correlates of evaluation associated with promotion and prevention regulatory focus. Cogn Affect Behav Neurosci. 5:202–211.

Damasio A. 2000. The feelings of what happens. New York: Basic Books.

Davidson RJ. 1992. Emotion and affective style: hemispheric Substrates. Psychol Sci. 3:39–43.

de Quervain DJ, Fischbacher U, Treyer V, Schellhammer M, Schnyder U, Buck A, Fehr E. 2004. The neural basis of altruistic punishment. Science. 305:1254–1258.

Elliott R, Newman JL, Longe OA, Deakin JF. 2003. Differential response patterns in the striatum and orbitofrontal cortex to financial reward in humans: a parametric functional magnetic resonance imaging study. J Neurosci. 23:303–307.

Fiddick L, Spampinato MV, Grafman J. 2005. Social contracts and precautions activate different neurological systems: an fMRI investigation of deontic reasoning. Neuroimage. 28:778–786.

Fredrickson BL. 1998. What good are positive emotions? Rev Gen Psychol. 2:300–319.

Frith U, Frith CD. 2003. Development and neurophysiology of mentalizing. Philos Trans R Soc Lond B Biol Sci. 358:459–473.

Gallagher HL, Frith CD. 2003. Functional imaging of 'theory of mind'. Trends Cogn Sci. 7:77–83.

Greene J, Haidt J. 2002. How (and where) does moral judgment work? Trends Cogn Sci. 6:517–523.

Haidt J. 2001. The emotional dog and its rational tail: a social intuitionist approach to moral judgment. Psychol Rev. 108:814–834.

Haidt J. 2003a. Elevation and the positive psychology of morality. In: Keyes CLM, Haidt J, editors. Flourishing: positive psychology and the life well-lived. Washington DC: American Psychological Association. p. 275–289.

Haidt J. 2003b. The moral emotions. In: Davidson RJ, Scherer KR, Goldsmith HH, editors. Handbook of affective sciences. New York: Oxford University Press. p. 852–870.

Hume D. 1978/1739-40. A treatise of human nature. Oxford: Oxford University Press.

Jacobsen T, Schubotz RI, Hofel L, Cramon DY. 2006. Brain correlates of aesthetic judgment of beauty. Neuroimage. 29:276–285.

Kant I. 1952/1790. The critique of judgement. Oxford: Oxford University Press.

Kawabata H, Zeki S. 2004. Neural correlates of beauty. J Neurophysiol. 91:1699–1705.

Luo Q, Nakic M, Wheatley T, Richell R, Martin A, Blair RJ. 2006. The neural basis of implicit moral attitude—an IAT study using event-related fMRI. Neuroimage. 30:1449–1457.

Maldjian JA, Laurienti PJ, Kraft RA, Burdette JH. 2003. An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fmri data sets. Neuroimage. 19:1233–1239.

Milinski M, Semmann D, Krambeck HJ. 2002. Reputation helps solve the 'tragedy of the commons'. Nature. 415:424–426.

Mobbs D, Greicius MD, Abdel-Azim E, Menon V, Reiss AL. 2003. Humor modulates the mesolimbic reward centers. Neuron. 40:1041–1048.

Mobbs D, Lau HC, Jones OD, Frith CD. 2007. Law, responsibility, and the brain. PLoS Biol. 5:e103.

Moll J, Krueger F, Zahn R, Pardini M, de Oliveira-Souza R, Grafman J. 2006. Human fronto-mesolimbic networks guide decisions about charitable donation. Proc Natl Acad Sci U S A. 103:15623–15628.

Moll J, Zahn R, de Oliveira-Souza R, Krueger F, Grafman J. 2005. Opinion: the neural basis of human moral cognition. Nat Rev Neurosci. 6:799–809.

Nitschke JB, Nelson EE, Rusch BD, Fox AS, Oakes TR, Davidson RJ. 2004. Orbitofrontal cortex tracks positive mood in mothers viewing pictures of their newborn infants. Neuroimage. 21:583–592.

Northoff G, Richter A, Gessner M, Schlagenhauf F, Fell J, Baumgart F, Kaulisch T, Kotter R, Stephan KE, Leschinger A, et al. 2000. Functional dissociation between medial and lateral prefrontal cortical spatiotemporal activation in negative and positive emotions: a combined fMRI/MEG study. Cereb Cortex. 10:93–107.

O'Doherty J, Winston J, Critchley H, Perrett D, Burt DM, Dolan RJ. 2003. Beauty in a smile: the role of medial orbitofrontal cortex in facial attractiveness. Neuropsychologia. 41:147–155.

Pizarro D, Uhlmann E, Salovey P. 2003. Asymmetry in judgments of moral blame and praise: the role of perceived metadesires. Psychol Sci. 14:267–272.

Price ME. 2006. Monitoring, reputation and "greenbeard" reciprocity in a Shuar work team. J Organ Behav. 27:201–219.

Rilling J, Gutman D, Zeh T, Pagnoni G, Berns G, Kilts C. 2002. A neural basis for social cooperation. Neuron. 35:395-405.

Rolls ET. 2006. Brain mechanisms underlying flavour and appetite. Philos Trans R Soc Lond B Biol Sci. 361:1123-1136.

Seligman M, Csikszentmihalyi M. 2000. Positive Psychology: an introduction. Am Psychol. 55:5-14.

Small DM, Gregory MD, Mak YE, Gitelman D, Mesulam MM, Parrish T. 2003. Dissociation of neural representation of intensity and affective valuation in human gustation. Neuron. 39:701-711.

Smith A. 1976/1759. The theory of moral sentiments. Oxford: Oxford University Press.

Takahashi H, Yahata N, Koeda M, Matsuda T, Asai K, Okubo Y. 2004. Brain activation associated with evaluative processes of guilt and embarrassment: an fMRI study. Neuroimage. 23:967-974.

Vartanian O, Goel V. 2004. Neuroanatomical correlates of aesthetic preference for paintings. Neuroreport. 15:893-897.

Wedekind C, Milinski M. 2000. Cooperation through image scoring in humans. Science. 288:850-852.