A funny thing happened on the way to the scanner: humor detection correlates with gray matter volume

Maia Kipman, Mareen Weber, Zachary J. Schwab, Sophie R. DelDonno and William D. S. Killgore

The detection and appreciation of humor is a complex cognitive process that remains poorly understood. Although functional neuroimaging studies have begun to map the brain systems involved in humor appreciation, there are virtually no data on the structural correlates between gray matter volume and this capacity. Using voxel-based morphometry, the present study examined the association between gray matter volume and the ability to detect and appreciate humor. Fifty-nine healthy adults aged 18–45 years (30 men) underwent structural MRI and completed the University of Pennsylvania Humor Appreciation Test (HAT). After controlling for age and sex, gray matter volume of the left inferior frontal gyrus, left temporal pole, and left insula correlated positively with the appreciation of visual and verbal humor on the HAT, whereas the gray matter volume of the right inferior frontal gyrus correlated only with verbal humor appreciation scores. There were no negative correlations between gray matter volume and HAT performance. These data support a neurobiological basis for humor appreciation, particularly involving left-hemispheric cortical systems, and further suggest that individual differences in humor appreciation may be related to differences in regional gray matter volume. *NeuroReport* 23:1059–1064 © 2012 Wolters Kluwer Health | Lippincott Williams & Wilkins.

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Social, Cognitive and Affective Neuroscience Lab, McLean Hospital, Harvard Medical School, Belmont, Massachusetts, USA

Correspondence to William D. S. Killgore, PhD, Social, Cognitive and Affective Neuroscience Lab, McLean Hospital, Harvard Medical School, 115 Mill Street, Belmont, MA 02478, USA
Tel: +1 617 855 3166; fax: +1 617 855 2770;
e-mail: killgore@mclean.harvard.edu

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Introduction

The ability to detect and appreciate humor is an extraordinarily complex and sophisticated cognitive process [1]. Neuroevolutionary theories posit that humor developed as a false inference detection mechanism [2]. This perspective suggests that as humans evolved to think more creatively and solve increasingly complex problems in novel ways, it became advantageous to utilize mental shortcuts, or heuristics, in lieu of fully assimilating and comprehensively analyzing large amounts of data about the environment [3]. By definition, however, heuristics are crude approximations of reality and sometimes lead to incorrect solutions. To help avoid the pitfalls associated with false inferences, a system of error detection appears to have developed that rewards individuals for error checking. This system is hypothesized to be our sense of humor [3]. In this context, humor, or the experience of finding something is 'funny,' can be regarded as an affectively based cognition that involves deriving pleasure from the reconciliation of an apparent discrepancy or an unexpected insight into the cause of an anomaly. Laughter and smiling, from this perspective, can be thought of as methods for communicating false alarms in inference, indicating to conspecifics that there is no danger in the situation [2]. Thus, the primary components of humor include false inference detection, incongruity resolution, mirth production, reward, and social communication.

Although the neurobiological basis underlying humor appreciation remains largely unexplored, recent functional neuroimaging studies have begun to map the systems that contribute to this capacity. Functional MRI (fMRI) studies evaluating the funniness of jokes have found that activation of the anterior cingulate cortex (ACC) correlates with increased ratings of funniness [4,5], consistent with its role in error detection [6]. Greater ACC activation was also found for funny compared with unfunny stimuli irrespective of whether participants had to actually rate funniness [4,7,8]. In addition, salience-detection processes involving the amygdala alert the organism to potential danger, threat, or emotional consequences associated with an ambiguous situation or potential error [9]. Accordingly, several functional MRI studies have found greater amygdala activation in response to funny compared with unfunny stimuli [7,8,10,11].

Humor appreciation also appears to involve several higher order cognitive and social processing systems. For example, one study using event-related fMRI to separate detection, comprehension, and mirth of humor specifically found that the inferior frontal gyrus (IFG) was activated during the process of integrating new information from the environment to resolve or clarify discrepancies [10]. This finding is congruent with previous reports on both humans and primates that implicate the

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Fig. 1

Examples of the Pennsylvania Humor Appreciation Test (HAT) visual (left) and verbal (right) stimuli. These stimuli are from G. Mordillo and modified with the permission of his agent. Reprinted with permission from Ruben Gur, PhD. Copyright, Trustees of the University of Pennsylvania.

IFG in the resolution of ambiguous information [12–14]. Furthermore, humor appreciation may also involve a social evaluation component, as several fMRI studies [11,15] have found activation in the temporal pole during the process of deciphering jokes that involve social scenarios or that require the ability to infer the thoughts or emotions of others. Finally, several studies have suggested that the insular cortex shows an increase in functional activation once a joke is comprehended, suggesting that the insula may play a role in the somatic–emotional sensations of mirth that contribute to humor appreciation [7,10,16]. These studies collectively illustrate a plausible humor-processing network involving the ACC, amygdala, IFG, temporal pole, and insula that contributes to the ability to detect and comprehend a joke or other humorous situation.

Although a number of studies have investigated the functional regions involved in humor appreciation, to our knowledge, no study has directly mapped this capacity to gray matter volume within the hypothesized neurocircuitry outlined above. Thus, whereas it is currently known that differences in the ability to detect and appreciate humor are reflected in functional brain activation, it remains to be shown whether the same applies for morphological differences. In the present study, we therefore set out to identify the morphological correlates between humor appreciation ability and gray matter volume using voxel-based morphometry (VBM) in healthy individuals. On the basis of the previously reviewed literature, we predicted that performance on a test of humor appreciation would be correlated positively with greater gray matter volume (GMV) in a network comprising the ACC, amygdala, insula, IFG, and temporal pole.

Methods

Participants

Fifty-nine right-handed, healthy, native English-speaking adults (mean age 30.6 ± 8.1 years, range 18–45; 30 men, 29 women) were recruited from the Boston metropolitan area through posted flyers and internet advertisements. By means of a detailed screening interview, all participants were determined to be free from any history of neurological, psychiatric, alcohol, or substance use disorders. Participants were compensated for their time. This research was approved by the McLean Hospital Institutional Review Board and was conducted in accordance with the 1964 Declaration of Helsinki. All participants provided written informed consent before participation.

Materials and procedure

Participants completed the computerized Pennsylvania Humor Appreciation Test (HAT) [17], which was administered outside of the MRI scanner. The HAT presents the participant with 40 pairs of stimuli (20 verbal, 20 visual) in a sequential pseudorandom order. The visual scenarios comprised 20 pairs of nearly identical nonverbal cartoons and the verbal scenarios comprised 20 pairs of nearly identical fictitious newspaper headlines (see Fig. 1 for an example). In each pair, one stimulus differed subtly from its counterpart by virtue of some contextual incongruity or alternative interpretation, making it humorous, whereas the other stimulus was not designed to be funny. By forced-choice button press, participants selected the funnier item of each pair or indicated that the two stimuli were equally funny. Time to respond was not restricted. Test performance was scored by summing the number of correct responses for the verbal and visual sections and for the total HAT. Higher HAT scores indicate greater capacity to detect and appreciate humor in the stimuli.

Magnetic resonance imaging parameters

Structural images were collected at 3.0 T using a Siemens Tim Trio scanner (Erlangen, Germany) equipped with a 12-channel head coil. Volumetric data were acquired with a T1-weighted 3D MPRAGE sequence (repetition time/echo time/flip angle = 2.1 s/2.25 ms/12°), 128 sagittal slices (256 × 256 matrix). The in-plane resolution was 1 × 1 mm with a slice thickness of 1.33 mm.

Voxel-based morphometry

Image analysis was carried out on SPM8 (Wellcome Department of Imaging Neuroscience Group, London, UK; *http://www.fil.ion.ucl.ac.uk/spm*) using the VBM8 toolbox (*http://dbm.neuro.uni-jena.de/vbm.html*). For preprocessing, the default settings in the VBM8 toolbox for modulated VBM were used (i.e. GMV was corrected for the total brain volume). For each participant, the T1-weighted structural images were first DARTEL-normalized to match the Montreal Neurological Institute (MNI) template. Using a fully automated algorithm, each image was segmented into gray matter, white matter, and cerebrospinal fluid. For spatial smoothing, an 8 mm full-width at half-maximum isotropic Gaussian kernel was applied to the normalized gray matter images.

Statistical analysis

In SPM8, the normalized smoothed gray matter images were entered into three separate random-effects multiple regression analyses to predict GMV from the overall HAT sum score as well as from the HAT headline and HAT cartoon subscale scores, respectively. On the basis of previous fMRI findings specifying the functional neurocircuitry involved in humor appreciation [8,18], we solely carried out a region-of-interest (ROI) analysis of the bilateral insula, amygdala, IFG, ACC, and temporal pole regions. The ROI anatomical mask was created using the Automated Anatomical Labeling Atlas [19] as part of the Wake Forest University PickAtlas Utility for SPM [20]. Thus, the insula included gray matter internal to its circular sulcus. Similarly, the precentral sulcus defined caudal limits of the IFG, whereas dorsal and rostral region borders were defined by the inferior frontal sulcus. The corpus callosum and the paracingulate sulcus represented the caudal and rostral borders to the ACC. Finally, the temporal pole was limited by the anterior part of the superior temporal gyrus and thus included portions of both the superior and the middle temporal gyri anterior to the anterior commissure. For a more comprehensive description of the ROI borders, the reader is referred to the published atlas [19]. Each ROI analysis was thresholded at P less than 0.001, uncorrected, with an empirically defined cluster extent threshold defined as the number of voxels expected per cluster in each analysis (i.e. 90) derived from the SPM8 output. Age and sex were controlled as nuisance covariates in each regression model.

Results

The mean HAT total score was 29.23 (SD = 7.24), the mean HAT visual score was 14.48 (SD = 3.81), and the mean HAT verbal score was 14.76 (SD = 4.14). Higher HAT scores indicate greater capacity to detect and appreciate humor in the stimuli. The HAT total score correlated positively with GMV in two clusters. The first cluster encompassed the left insula and IFG pars opercularis and pars triangularis (1128 voxels, $T = 4.89$, MNI coordinates: $x = -38$, $y = 11$, $z = -3$; Fig. 2a), whereas the second included the left inferior orbitofrontal gyrus and the left superior temporal pole (414 voxels, $T = 3.95$, MNI coordinates: $x = -46$, $y = 21$, $z = -12$; Fig. 2b). The HAT visual score correlated positively with GMV in a cluster comprising the left superior temporal pole, the left IFG pars opercularis, and the left insula (424 voxels, $T = 4.78$, MNI coordinates: $x = -32$, $y = 15$, $z = -23$; Fig. 2c). The HAT verbal score correlated positively with GMV of three clusters, including (i) the left insula and left IFG pars triangularis and pars opercularis (1039 voxels, $T = 4.71$, MNI coordinates: $x = -36$, $y = 12$, $z = -2$; Fig. 2d); (ii) the left orbital IFG and left superior temporal pole (178 voxels, $T = 3.99$, MNI coordinates: $x = -46$, $y = 30$, $z = -11$; Fig. 2e); and (iii) the orbital portion of the right IFG (118 voxels, $T = 3.61$, MNI coordinates: $x = 50$, $y = 26$, $z = -12$; Fig. 2f). There were no significant negative correlations within any of the ROIs.

Discussion

The ability to detect and appreciate humor, as reflected in HAT performance, was associated with GMV in three brain regions that have also been implicated in humor processing using fMRI [8,11]. These regions included the left IFG, an area known to engage in the resolution of incongruity in general [12–14] and of humorous stimuli in particular [5,8,11,15,21–23], the left temporal pole, a structure important for social and emotional problem solving [24], and the left insula, which has been implicated in the feeling of mirth during humor [7,10,16]. For all three brain regions, greater humor detection ability was associated with greater GMV. These structural volumetric findings comport with previous fMRI research showing greater activation in these areas in response to funny versus unfunny stimuli [8,10]. Furthermore, our data suggest that individual differences in humor appreciation may be at least partially related to trait-like differences in morphology between individuals. Importantly, GMV of these structures was predicted similarly by the HAT visual as well as the HAT verbal score, suggesting that these structure–function relationships exist independent of humor presentation modality. Interestingly, however, the HAT verbal score also uniquely predicted GMV of the right IFG, raising the possibility

Fig. 2

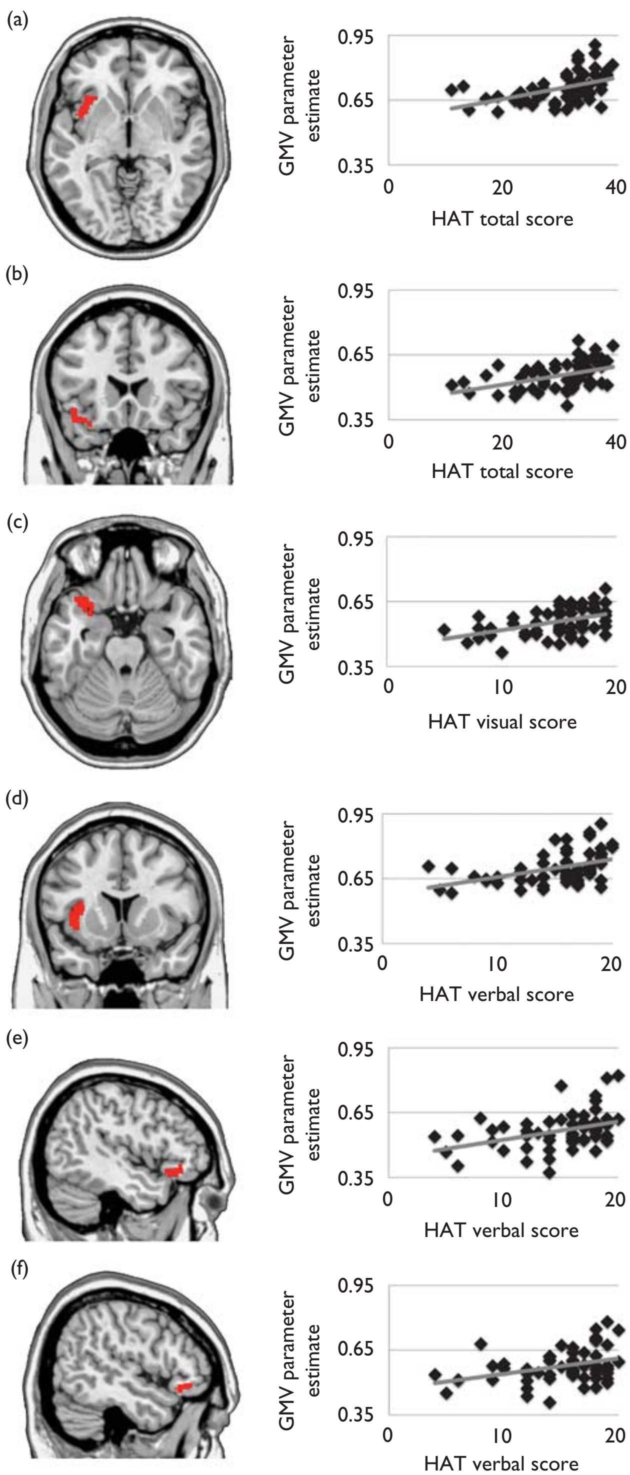

Fig. 2

Brain regions with significant positive correlations between gray matter volume and Humor Appreciation Test (HAT) scores superimposed on single-subject T1-weighted structural images and corresponding scatterplots. (a) Axial view of the left insula and inferior frontal gyrus regions that correlate positively with the HAT total score. (b) Coronal view of the left inferior orbitofrontal gyrus and left temporal pole regions that correlate positively with the HAT total score. (c) Axial view of the left superior temporal pole, left inferior frontal gyrus, and left insular regions that correlate positively with the HAT visual score. (d) Coronal view of the left insula and left inferior frontal gyrus regions that correlate positively with the HAT verbal score. (e) Sagittal view of the left inferior frontal gyrus and left superior temporal pole regions that correlate positively with the HAT verbal score. (f) Sagittal view of the right inferior frontal gyrus regions that correlate positively with the HAT verbal score. GMV, gray matter volume.

that this region may also play an important role in some of the unique processes involved in detecting or appreciating the humor of verbal stimuli with multiple meanings (i.e. double entendre).

Consistent with some previous fMRI research [7,8,10, 11,15,23], our data show a predominant left lateralization of most of the structure–function associations involved in humor appreciation, particularly for the insula and the temporal pole regions. This pattern is intriguing and raises the possibility that the neurocircuitry of humor appreciation may rely largely on language systems [21] and possibly also emotion-processing streams [25], even when the modality of presentation involves nonverbal cartoon images. A previous event-related fMRI study showed left IFG activation during the humor detection phase and bilateral insula activation during the experience of mirth, or the appreciation phase, of watching humorous video clips [10]. Because the present study only examined detection/appreciation performance as a variable of interest, it is impossible to distinguish between the detection and mirth experience phases of the task, and both are likely to be necessary components for successful humor appreciation.

The neuroevolutionary inference error detection theory suggests that a major component of humor appreciation is the ability to notice incongruities, errors, or discrepancies, and orient the organism toward their resolution [2]. Functional neuroimaging has suggested that the ACC and amygdala are predominantly involved in these error detection and alerting responses [8,10]. Contrary to this theory, however, we did not find the volume of either of these structures to be related to HAT performance. Of course, larger structural volume does not necessarily imply better function, and humor appreciation may be too subtle a capacity to be related to volumetric differences in these structures. Alternatively, it is possible that the simple forced-choice nature of the task itself was too gross a metric to draw heavily upon error detection or too artificial a situation to require vigilance to potential environmental threat, thus minimizing the role of these factors. This null finding might have been further influenced by the rather conservatively set cluster extent threshold (i.e. $k \geq 90$), meaning that small structures such as critical affect-related subnuclei of the amygdala were less likely to survive the analysis. Future research might benefit from more sensitive and ecologically valid paradigms within a more naturalistic setting, such as watching humorous television episodes or stand-up comedy routines, to map the relationship between humor detection and GMV.

For the present study, we focused specifically on only a limited number of brain regions. The HAT specifically assesses humor detection ability as opposed to the participant's experience of reward. Therefore, for the purposes of the present study, we did not place ROIs in dopaminergic structures such as the nucleus accumbens and ventral striatum, even though functional activation in these areas has been demonstrated in the humor literature [7,8,11,16,22]. Future work might include scaled funniness ratings in addition to forced-choice funniness decisions to explore these relationships more comprehensively. Although potentially relevant, we also did not record behavioral aspects of humor reactions, such as the amount of participant laughter or smiling in response to the material presented in the HAT. Therefore, in the present study, we did not place ROIs in motor response regions such as the supplementary motor area or the cerebellum, which are believed to contribute to the physical communication of humor [8,10,21]. Incorporating psychophysiological measures of humor expression in response to HAT stimuli and exploring other reward-related brain regions might help answer the question of whether GMV within these networks might be related to the extent to which an individual communicates an affective humor response, irrespective of the stimuli's subjective funniness.

Several caveats should be kept in mind when evaluating these findings. First, because this is the first study to use VBM to predict GMV from a humor detection task, our data should be considered as preliminary and in need of independent replication. Second, it is important to consider the limitations of the specific task used. Notably, because of its artificial nature, the HAT is somewhat removed from naturalistic and more spontaneous settings in which humor and its appreciation typically occur. However, the HAT task was used for this initial investigation because it allows for a very controlled assessment to isolate and examine humor detection and appreciation. In addition, no data were collected examining the extent of amusement or pleasure produced by the stimuli. This may be a key element in the process of humor appreciation and should be investigated further. Of additional interest may be sex differences in humor appreciation, which were not investigated in the current study. Finally, future research should focus on structural and functional connectivity among areas of the humor detection network to determine whether the strength of connectivity is related to humor detection ability or to the subjective experience of reward or amusement to humorous material.

Conclusion

The ability to detect and appreciate humor, irrespective of whether assessed in the verbal or the visual modality, was associated with greater GMV in several brain regions involved in higher order cognitive processing, social inference, and somatic–emotional processing. Our data are concordant with a number of functional neuroimaging studies and suggest that the capacity of humor appreciation is related to distinct morphological differences in the brain structures comprising this complex system.

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Conflicts of interest

There are no conflicts of interest.

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