3 Brain Activation During Sight Gags and Language-Dependent Humor

3.1 Abstract

Humor is a hallmark of human discourse. People use it to relieve stress and to facilitate social bonding, as well as for pure enjoyment in the absence of any apparent adaptive value. Although recent studies have revealed that humor acts as an intrinsic reward, which explains why people actively seek to experience and create humor, few have addressed the cognitive aspects of humor. We used event-related fMRI to differentiate brain activity induced by the hedonic similarities and cognitive differences inherent in two kinds of humor: visual humor (sight gags) and language-based humor. Our findings indicate that the brain networks recruited during a humorous experience differ according to the type of humor being processed, with high-level visual areas activated during visual humor and classic language areas activated during language-dependent humor. Our results additionally highlight a common network activated by both types of humor that includes the amygdalar and midbrain regions, which presumably reflect the euphoric component of humor. Furthermore, we found that humor activates anterior cingulate cortex and fronto-insular cortex, two regions in the brain that are known to have phylogenetically recent neuronal circuitry. These results suggest that humor may have co-evolved with another cognitive specialization of the great apes and humans: the ability to navigate through a shifting and complex social space.

3.2 Introduction

The phenomenon of humor is universal among humans (Buss, 1988; Caron, 2002; Miller, 2000) and regarded by some as uniquely human (Bergson et al., 2003; Caron, 2002). Humor may have evolved to function as a coping mechanism. Freud (1960) posited that laughter served to discharge the accumulation of internal tension, an interpretation consistent with empirical observations of humor-induced stress reduction (Berk et al., 1989). In clinical contexts, “laughter therapy” is used to increase pain tolerance (Weisenberg et al., 1995) and immune function (Bennett et al., 2003; McClelland and Cheriff, 1997).

Humor also has a strongly social aspect, and in fact, measurements of extroversion in human subjects have been found to correlate with humor-elicited activity in reward regions as measured by functional magnetic resonance imaging (Mobbs et al., 2005). People are more likely to laugh when part of a crowd than in isolation (Devereux and Ginsburg, 2001; Fridlund, 1991; Smoski and Bachorowski, 2003), and a “sense of humor” in an individual may help raise that individual’s social status (Salovey et al., 2000), increase that individual’s social support network (Salovey et al., 2000), facilitate pair bonding in romantic relationships (Bippus, 2000; Ziv and Gadish, 1989), and attract compatible mates (Bressler and Balshine, 2005; Bressler et al., in press; Buss, 1988; Cann et al., 1997; Miller, 2000; Murstein, 1985). The role of humor in some of these social interactions has been proposed to differ according to gender (Bressler and Balshine, 2005; Bressler et al., in press; Nusbaum et al., 2006; Smoski and Bachorowski, 2003; Ziv and Gadish, 1989), and, intriguingly, a recent fMRI study suggests differences in brain activity in men and women during the perception of humor (Azim et al., 2005).

Presumably, the draw towards those who make us laugh is derived from the subjective pleasure that is inherent in a humorous experience. Recent imaging papers shed light on this aspect of humor by revealing that humor activates the ventral tegmentum and the ventral striatum (Mobbs et al., 2003), as well as regions associated with emotion, such as the amygdala and insular cortex (Moran et al., 2004). Thus, like the taste of fruit juice (Berns et al., 2001), the sight of an attractive face (Aharon et al., 2001; O'Doherty et al., 2003a), or the scent of vanilla (Gottfried et al., 2002), humor activates components of the system involved in reward processing. However, because humor differs from primary rewards in its cognitive complexity and abstract nature, we may also expect activity in “higher-order” reward regions that mediate association formation and learning. Such regions are thought to be located in frontal cortex, such as the site of ventromedial activation observed by Goel and Dolan (2001), as well as frontal pole, where damage results in a disturbance in the affective response to humorous cartoons and jokes despite retention of the ability to discriminate humorous from non-humorous stimuli (Shammi and Stuss, 1999).

The rewarding aspect of humor is only part of the humor phenomenon, however. In order to appreciate a joke, you must first “get” the joke. What exactly is this cognitive mechanism that precedes the mirthful aspect of humor? Some researchers posit that humor requires an element of incongruity or cognitive conflict (Coulson and Williams, 2005; Suls, 1972). Indeed, an ERP study by Coulson and Williams (2005) indicates that, compared to non-joke stimuli, jokes presented to the left hemisphere elicit larger amplitude N400s, a hallmark of cognitive conflict. Although the slow time resolution of fMRI somewhat hampers the disentanglement of the cognitive from the rewarding aspects of humor, Moran, et al.'s (2004) study used popular television sitcoms as humorous stimuli to gain some insight into this question. They used the onset of a laugh-track as a marker between humor comprehension and appreciation epochs. By observing activation two seconds prior to the onset of laughter, the authors found that brain activity during humor comprehension is distinct from that of humor appreciation, and is characterized by left lateralized activation in the left posterior temporal gyrus and left inferior frontal gyrus.

The affective dimension of humor appears to generalize across modalities; past studies have used both static and dynamic visual imagery (comics and film clips) to elicit humor, as well as auditory delivery of jokes. Some models (Suls, 1972) predict that the re-establishment of coherence – that is, the process of discarding prior assumptions and reinterpreting the joke in a new context -- is crucial to the comprehension of humor. If this is correct, then one should observe increased activation during the re-interpretation that is associated with the modality in which the humor is conceived. Goel and Dolan (2001) broached this question by observing activation associated with different types of auditory humor: semantic jokes and puns. They did indeed find differentiation between the two types of jokes. However, the anatomical sites of semantic and phonological processing are not always easily differentiated, which leaves this result open to interpretation.

In the present study, we used cartoons from “The Far Side” and “The New Yorker” to study brain activation specific to the type of humor portrayed. In cartoons containing language-independent “sight-gag” humor, the humorous element is often a visually improbable predicament, social scene, or action that violates a viewer’s initial expectations or assumptions. In cartoons containing language-based humor, the humor may be derived from incongruity between the picture and its descriptive caption, or from a verbal deviation from social norms. Although both types of funny cartoons contain similar levels of complexity, make similar demands on the low-level visual system, and elicit similar feelings of mirth, the cognitive aspect of “getting the joke” differs depending on the sort of incongruity (sight vs. semantic) that needs to be reconciled. This in turn should lead to distinctly different activation patterns associated with the different types of humor. Inversely, both types of humor should produce the same affective result. Thus, as in previous studies, we expect both language-based and sight-gag humor to increase activity in regions associated with reward and emotion, particularly the substantia nigra, nucleus accumbens, amygdala, and insular cortex.

The speculation that humor may be a uniquely human cognitive trait (Bergson et al., 2003; Caron, 2002) prompted our third hypothesis: Humor will activate both anterior cingulate cortex (ACC) and fronto-insula cortex (FI), the two regions in which an evolutionarily recent neuron type, the Von Economo cells (previously termed “spindle neurons”), are present (Allman et al., 2002; Allman et al., 2005). A review of the functional imaging literature reveals that the Von Economo cell regions, particularly FI, are active while reversal learning (O'Doherty et al., 2001), decision making under uncertain conditions (Critchley et al., 2001), and observing bizarre images of animal/object chimeras (Michelon et al., 2003). Like humor, these paradigms involve incongruity detection and reappraisal, and provided the impetus to formally test the hypothesis that humor activates the Von Economo regions ACC and FI.

3.3 Materials and methods

3.3.1 Subjects

Twenty right-handed healthy volunteers (median age 26 years, range 20-61 years, eight female) gave written consent to participate in this study. Four subjects were discarded from analysis for having three or fewer ratings of "very funny" across all trials. All subjects were fluent English speakers and had normal or corrected-to-normal vision. None had a history of psychiatric illness, and they took no regular medication. The study was approved by the Caltech Internal Review Board.

3.3.2 Stimuli

Stimuli consisted of 100 line drawing cartoons from "The Far Side" by Gary Larson (47 cartoons), or the New Yorker Magazine (various authors, 53 cartoons). 50 of these drawings had been altered slightly so that the humorous element was removed – these were intended to serve as controls for those cartoons found to be humorous. In a preliminary study, we gathered funniness ratings on a scale of 1-10 for each drawing, both with and without captions. From this pilot study, we selected 25 "language-dependent" cartoons, which had mean ratings that were more than one standard deviation away from their original mean rating in absence of a caption. 25 cartoons that were still within one standard deviation from their mean rating after the caption was removed were categorized as “sight-gag” stimuli, meaning that the humorous element was in the drawing itself, not the caption. Control groups of non-humorous cartoons were selected for each category, language-dependent and sight gag, so that the average number of words in the baseline (unfunny) group was not significantly different from the average number of words in the funny group. Thus, although each subject rated each cartoon separately, there were 50 canonically funny stimuli, as determined by the pilot study, and 50 canonically non-funny control stimuli. Of the 50 canonically funny stimuli, half were language-dependent and half were “sight-gag.”

3.3.3 Task

The experiment consisted of an event-related design. Cartoons were presented in random order to subjects, with an interstimulus interval of 300, 600, or 900 ms. We used this short ISI in order to avoid disrupting the “flow” of the humorous stimuli, which we feared might generate a feeling of impatience or anticipation in the subject. Studies suggest that, as long as the ISI is not fixed, using short ISIs can maintain sufficient statistical power in fMRI studies (Elston et al., 1999; Seymour et al., 2004). Subjects were told to observe each cartoon and rate how funny they found it to be, any time after the “rating” cue appeared, four seconds after the stimulus onset. Ratings were done via button box, with one being “very funny,” four being “not funny at all,” and two and three indicating that it was somewhere in between (note that, due to the limitations of the button box, this rating scale is different from the 1-10 scale used in the pilot study).

3.3.4 Imaging procedure

The functional imaging was conducted by using a 3 Tesla Siemens Trio MRI scanner to acquire gradient echo T2* weighted echo-planar images (EPI) with blood oxygenation level (BOLD) contrast (TR = 2 s, TE=30 ms, flip angle = 90 degrees). Each functional volume consisted of 32 axial slices of 3.2 mm thickness and 3 mm in-plane resolution. Axial slices were acquired 20 degrees above the AC-PC line for each subject to minimize distortion and dropout in the orbitofrontal cortex area. A T-1 weighted structural image was also acquired for each subject using an MP Rage sequence (Siemens).

3.3.5 Imaging analysis

The images were analysed using SPM2 (Wellcome Department of Imaging Neuroscience, London, UK, http://www.fil.ion.ucl.ac.uk/spm/). In order to correct for subject motion, the images were realigned to the first volume. Slice timing correction was applied and images were spatially normalized to a standard MNI template. Spatial smoothing was applied using a Gaussian kernel with a full width at half maximum (FWHM) of 8 mm. Following pre-processing, statistical analysis was carried out using a general linear model, in which each interval (stimulus onset to response time) was convolved with a canonical hemodynamic response function. Analysis of the subjects' behavior indicated that reaction times for an intermediate score (three on the scale of one to four) were significantly longer ($p<0.05$), possibly because of the cognitive effort required to assign a score in this intermediate range. For this reason, only those cartoons which were rated with a one (least funny) or a four (most funny) by the subject were contrasted when exploring the main effect of humor, although all four scores were included as regressors. We additionally undertook a parametric analysis, in which linear increases in BOLD activation were correlated with the subjective rating of each image.

To look at modality-specific activation, we compared activation during the language-dependent funny cartoons and the visually funny cartoons (25 each), as determined in the pilot study, versus two matched unfunny cartoon control conditions (25 each). Control cartoons were selected for each group so that the average number of words in the cartoon did not differ significantly between funny and nonfunny control conditions. Head movements as determined by the motion correction preprocessing step were used as regressors of no interest. We performed a two way ANOVA, which allowed us to parse the main effects of cartoon humor (funny vs. not funny), the main effects of cartoon type (visual vs. verbal), and the interaction between the two factors. To identify directionality of the response [i.e., (language modulated humor) > (visually modulated humor) and vice versa], we subsequently performed t-tests. We additionally calculated the difference in betas [(βlanguage humor – βlanguage controls) – (βvisual humor – βvisual controls)], and vice versa, for each subject at the peak voxel for each of these contrasts in order to generate the population means. To determine the betas at these voxels, the peak voxel from each of the two second level t-tests was used as the center of a sphere with a radius of 10 mm. For each individual, we then found the peak voxel within this sphere and recorded the betas for all four regressors to determine population means.

Regions of activity were determined using a human brain atlas (Duvernoy, 1991). The SPM-based toolbox MarsBaR (Brett et al., 2002) was used to perform ROI analyses. We used canonical, MNI-atlas based regions of interest (ROIs) for corrections of the caudate, putamen, globus pallidus. Small volume correction for nucleus accumbens was accomplished by centering a sphere of 6.4 mm radius (based on reports that the mean volume of the structure is 1.1 cc in a group of normal human controls (Deshmukh et al., 2005)) at the coordinates (6, 2, -4) and (-6, 2, -4) as reported by Mobbs, et al. (2003). A ROI for ACC was delineated in order to approximate Brodmann's area 24. We drew a line connecting the genu and splenium on an average image created from the 16 normalized anatomical images. The extension of a perpendicular at the midpoint of this line across the cingulate cortex marked the posterior boundary of our anterior cingulate ROI. In the case of FI small volume correction, unnormalized anatomical scans for each individual were imported into MRIcro. The experimenter with extensive experience in locating region FI in human brain histology preparations (JMA) demarcated region FI on each anatomical scan. Normalizing and then averaging these images provided a region of interest used for small volume correction in MarsBaR.

3.4 Results

3.4.1 Behavior

Four subjects were discarded from analysis for having three or fewer ratings of "very funny" across all trials. Across the remaining 16 subjects, 19% of cartoons were scored as “very funny” and 40% scored as “not funny at all.” Of those cartoons rated “very funny,” about half were Far Side (mean 46.3%, s.d 10.9). There was no significant difference in ratings between Far Side and New Yorker cartoons (Far Side mean rating = 1.82, 0.28 s.d., New Yorker mean rating = 1.80, s.d. 0.21), nor was there a significant difference in the number of language and the number of visual cartoons selected as funny ($p = 0.90$; Figure 10a). Mean ratings for the canonically humorous cartoons (as determined in the pilot study) were significantly higher than the mean ratings for control cartoons ($p<0.01$, Figure 10b). Mean ratings for language-dependent and visual cartoons were not significantly different. Reaction times (mean 7.04 s, 2.95 s.d.) for cartoons rated “very funny” and “not funny at all” were not significantly different, though reaction times for an intermediate score of 3 on a 1-4 scale were significantly higher.

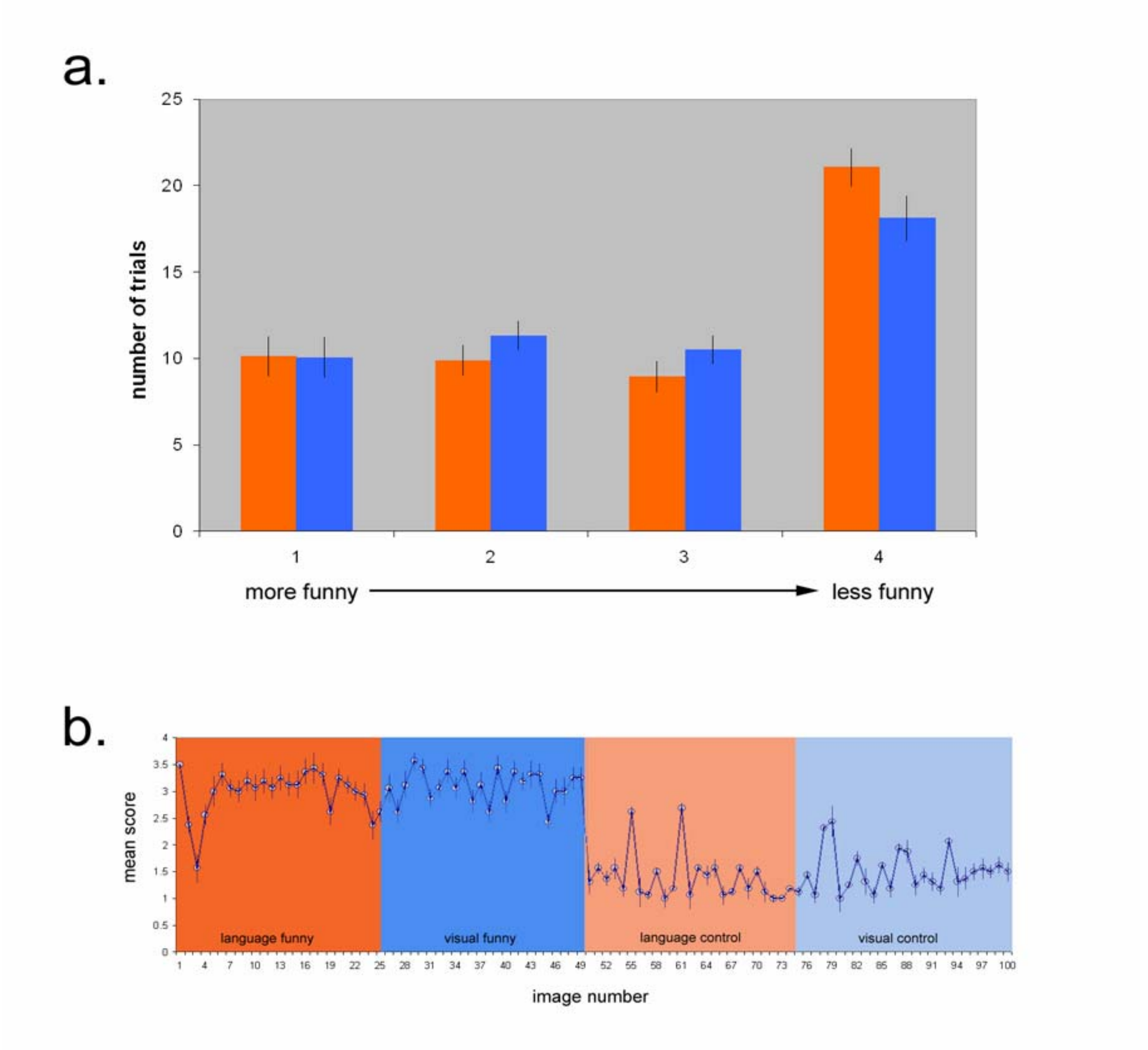

Figure 10 (a) Mean distribution of trial types across rating (1-4, with 4 being the most funny) and category (language based, red; visual, blue) for all 16 subjects. (b) Mean score (1-4, with 4 being the most funny) for each cartoon, computed across the 16 fMRI subjects. Cartoons 1-25 (red block) were canonically funny language cartoons, as determined in the pilot study, and cartoons 26-50 (blue block) were canonically funny visual cartoons. Cartoons 51-75 (pink block) were control language cartoons, while cartoons 76-100 (light blue block) were control visual cartoons. Note the relatively low mean scores of the control cartoons relative to funny cartoons.

3.4.2 Functional imaging

As predicted, comparison of the humor versus control states revealed activation in both of the Von Economo cell regions: bilateral fronto-insula (right, $p<0.03$; left, $p<0.01$;

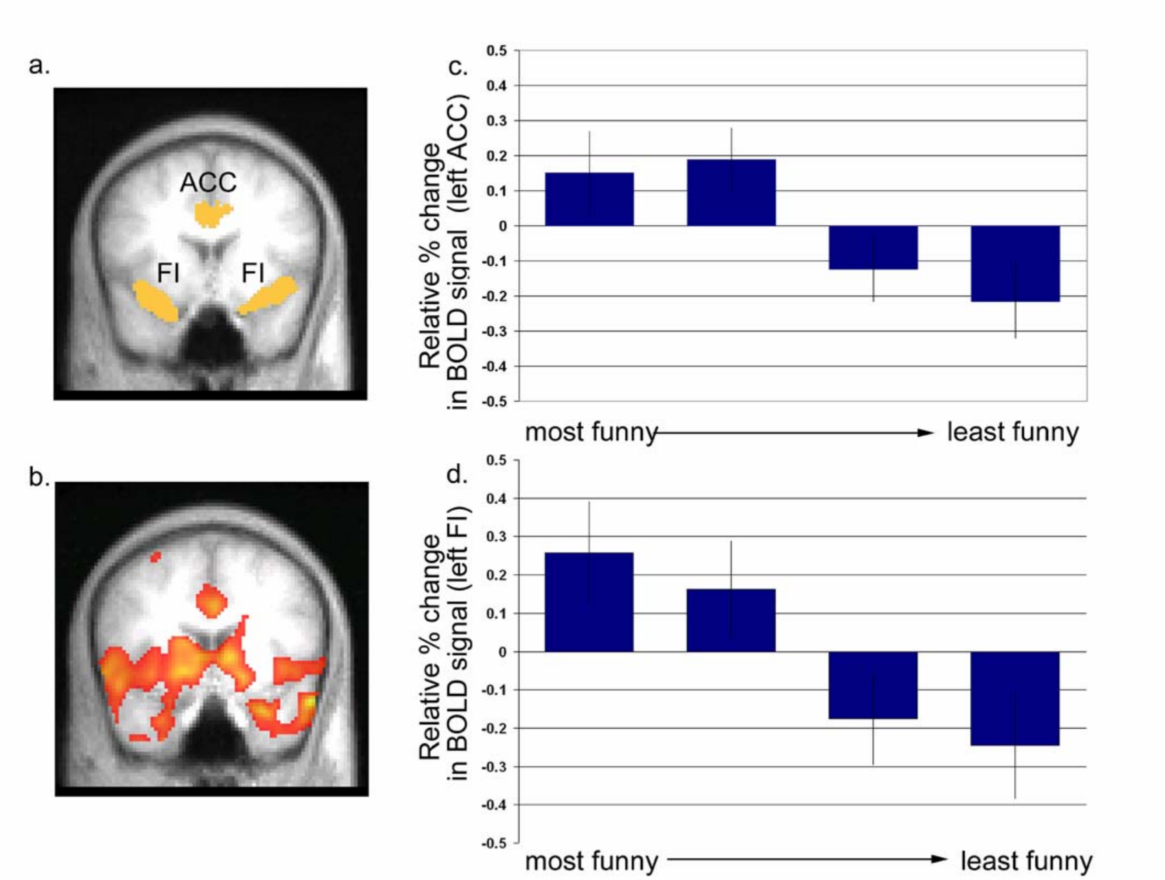

Figure 11 (a) Coronal view of anterior cingulate (ACC) and fronto-insula (FI) cortex ROIs (yellow) overlaid on an average of the subjects' anatomical images. (b) Coronal slice showing regions with significant ($p<0.001$, uncorrected) increases in activity with increasing ratings of funniness. (c) Relative percent change in ACC across all subjects. Error bars represent S.E.M. (d) Relative percent change in FI across all subjects. Error bars represent S.E.M.

corrected for corrected for multiple comparisons across a small volume of interest) and left anterior cingulate cortex ($p<0.03$ corrected for multiple comparisons across a small volume of interest) (Figures 11 and 12). Additional activation was similar to that reported earlier, namely an extended network involving the limbic system and reward areas: bilateral putamen, bilateral nucleus accumbens, and left insula all survived small volume correction ($p<0.05$).

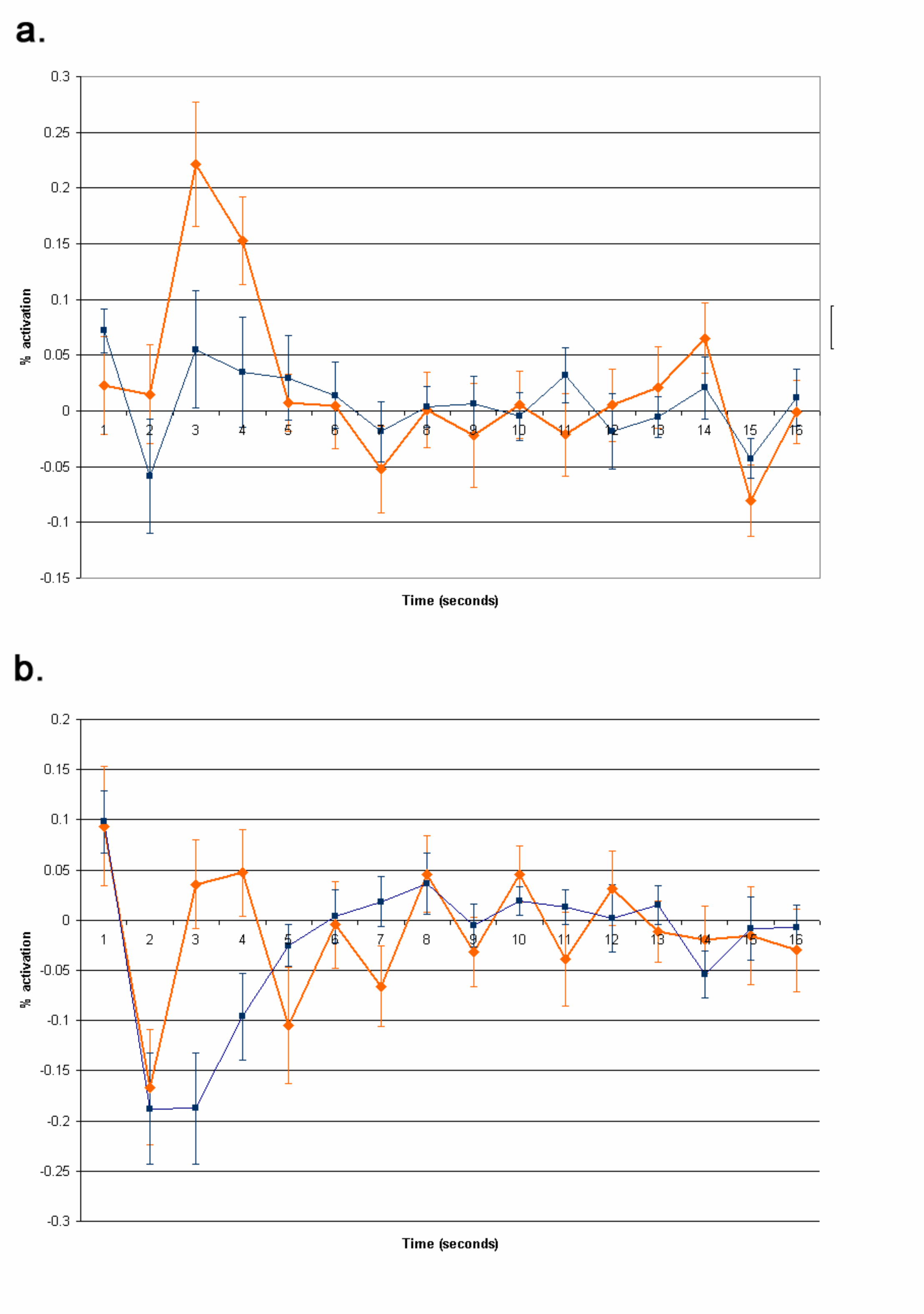

Figure 12 Timecourse of activation for (a) frontoinsula and (b) anterior cingulate cortex. Responses to those images rated as “most funny” are shown in red, and those rated “least funny” are shown in blue. Bars denote S.E.M.

The parametric analysis, which we undertook to explore which areas of activity covaried with the funniness ratings, yielded results similar to those of the funny vs. unfunny contrast described above. Regions of covariance included bilateral superior temporal sulcus, substantia nigra, and caudate; left putamen; left superior frontal gyrus, including dorsolateral prefrontal cortex; and left hippocampus and entorhinal cortex ($p<0.0005$; Table 3). Bilateral anterior cingulate cortex, fronto-insula, and insula proper all suvived small volume correction for the parametric model ($p<0.03$), as did caudate, putamen, nucleus accumbens, and amygdala (figure 13). Using a two-way t-test, we found sex differences in the parametric response similar to those found by Azim and others (2005), with women having greater activity in the middle frontal gyrus, inferior temporal lobe, posterior cingulate, and fusiform gyrus, among other places ($p<0.005$ uncorrected; figure 14). There were no regions with significantly greater activity in men compared to women.

Brain region	L/R	coordinates (x y z) of peak voxel	Z-score
superior temporal sulcus	L, R	-48 -60 20	5.56
middle temporal gyrus	R	56 12 -22	5.45
substantia nigra	R, L	6 -6 -12	5.36
superior parietal gyrus	L	-2 -56 46	5.09
hippocampus	L	-60 -14 -22	4.78
entorhinal area	L	-30 -4 -30	4.7
superior temporal gyrus	L, R	-58 14 -8	4.68
superior frontal gyrus, perigenual anterior cingulate gyrus*	L	-6 56 36	4.64
head of caudate	L, R	-6 -2 12	4.62
putamen	L	-18 6 -4	4.51
dorsal anterior cingulate gyrus*	R	2 10 32	4.45
temporal pole, anterior insula**	L	-42 28 -24	3.91

Table 3 Brain regions that display increasing activation with increasing scores of "funniness." (p<0.001). *includes anterior cingulate gyrus. **includes fronto-insula.

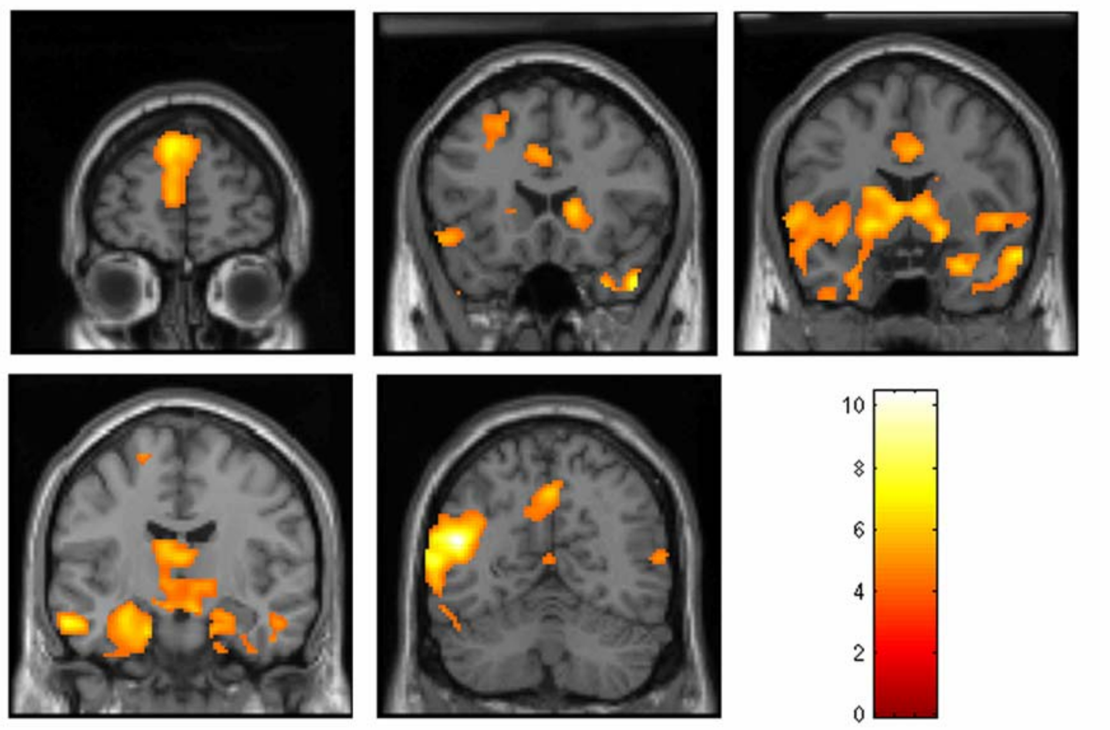

Figure 12 Coronal views of group contrast map for activity that correlates linearly with cartoon rating (increased activity with higher rating of funniness).

A two-way ANOVA revealed the differences in activity due to the main effects of humor, the main effects of humor type, and the interaction between these two factors (Figure 15). Interaction effects between the language-dependent and sight-gag humor categories revealed the functional dissociation between the two different types of humor (Figures 16 and 17, Table 4). Activity that was elicited by language-based humor compared to visual humor included the middle temporal gyrus, the inferior frontal gyrus, and the inferior temporal gyrus, regions functionally defined as Wenicke's area, Broca's area, and the basal temporal language area, respectively (Table 4a) (Benson, 1993; Friederici, 2002; Just et al., 1996). Application of a liberal probability threshold ($p<0.05$, uncorrected for multiple comparisons), suggested a more extended region of activity in the middle temporal gyrus that extended up the length of the temporal lobe (Figure 18).

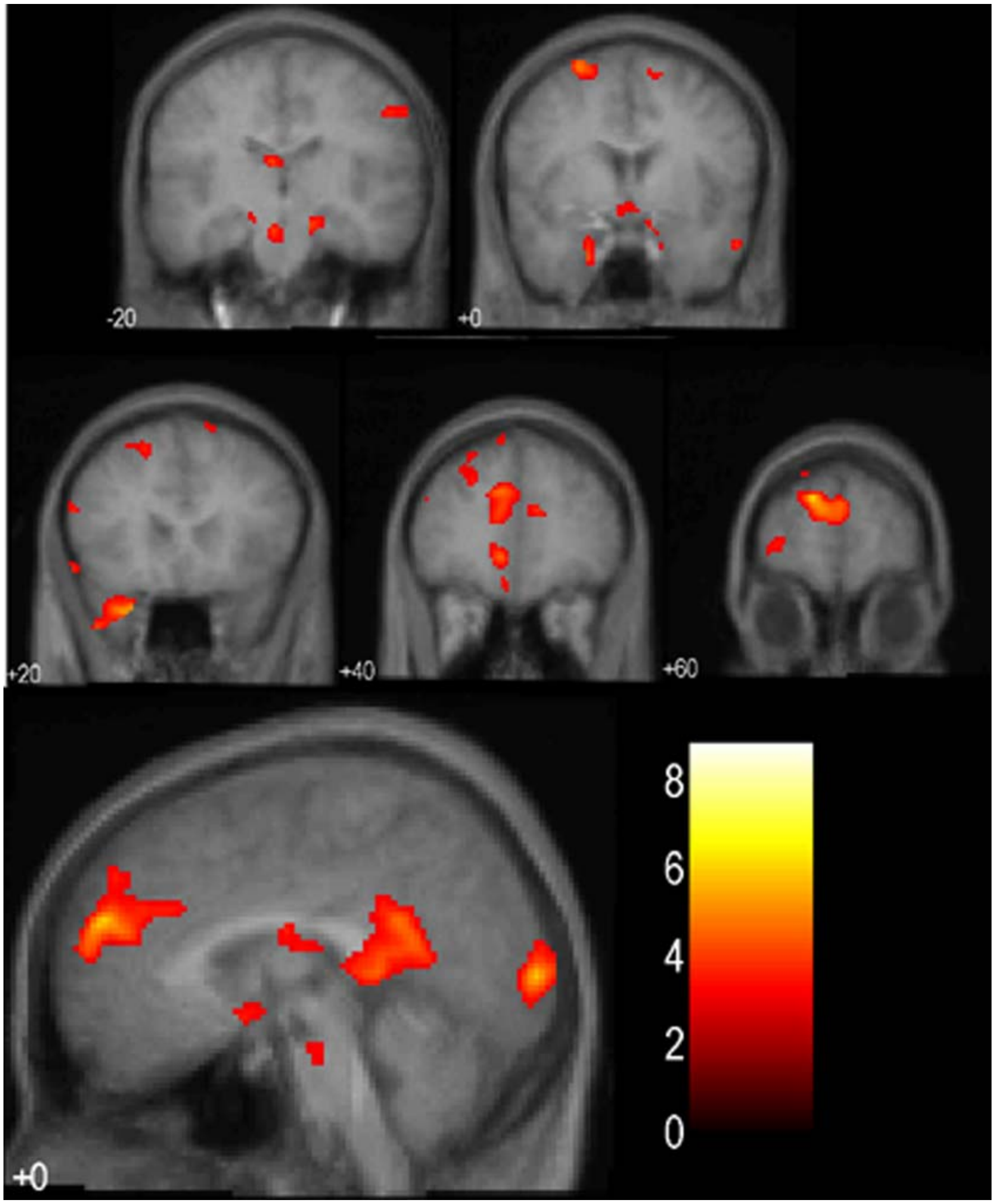

Figure 13 Statistical parametric analysis in which women had greater activity than men, overlaid on the average of the female structural scans ($p<0.005$, uncorrected). Similar to results reported by Azim and others (2005), regions included bilateral middle frontal gyrus and primary visual cortex, left medial orbitofrontal cortex (gyrus rectus and medial orbital gyrus), superior frontal gyrus, and inferior temporal cortex, and right posterior cingulate (ordered from most to least significant; not an exhaustive list). Right, but not left, nucleus accumbens was more active in women than men after ROI analysis as described in methods ($p<0.05$, corrected over small volume of interest). This differs from previously described results, which found the nucleus accumbens to be the site of greatest activation difference between sexes (Azim et al., 2005)

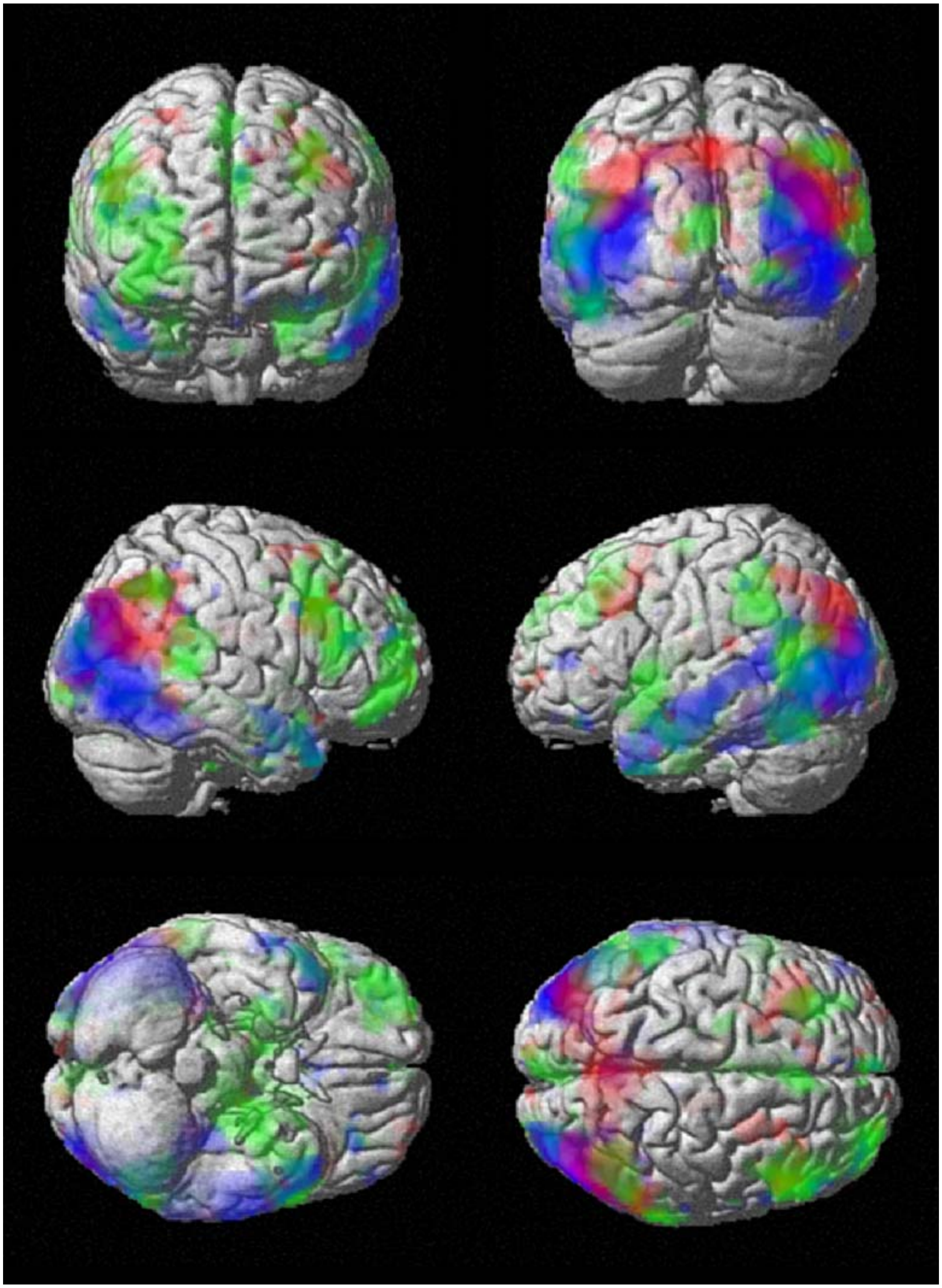

Figure 14 Surface projections of color-coded statistical parametric maps (SPMs) the results of a two-way ANOVA ($p<0.005$, uncorrected) overlaid onto canonical single-subject anatomic rendering. Green indicates the main effect of humor (humorous cartoon vs. control), blue indicates the main effect of cartoon type (language vs. visual), and red indications regions for which there is an interaction between these two effects. Violet indicates the regions that show variations in activity according to cartoon type (language vs. visual) as well as to the interaction. Trials were parsed into categories (funny or not funny, visual or language; 25 trials of each type) in a canonical fashion for all subjects.

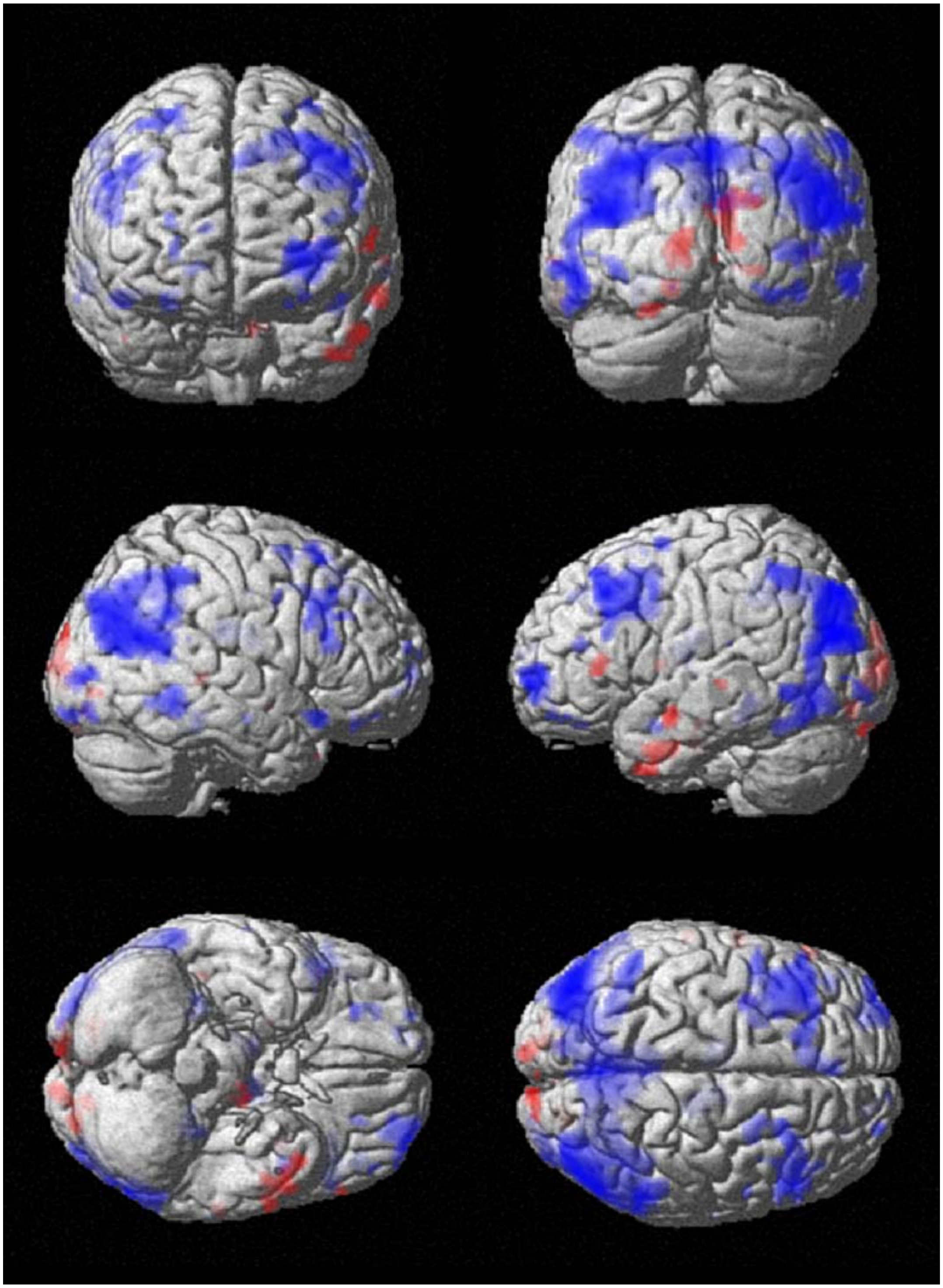

Figure 15 Surface projections of color coded statistical parametric maps (SPMs) showing the results of second-level t-tests ($p<0.005$, uncorrected) overlaid onto canonical single subject anatomic rendering. Blue indicates those regions where [(visual humor – visual control) > (language-based humor > language-based control)]; red indicates the opposite.

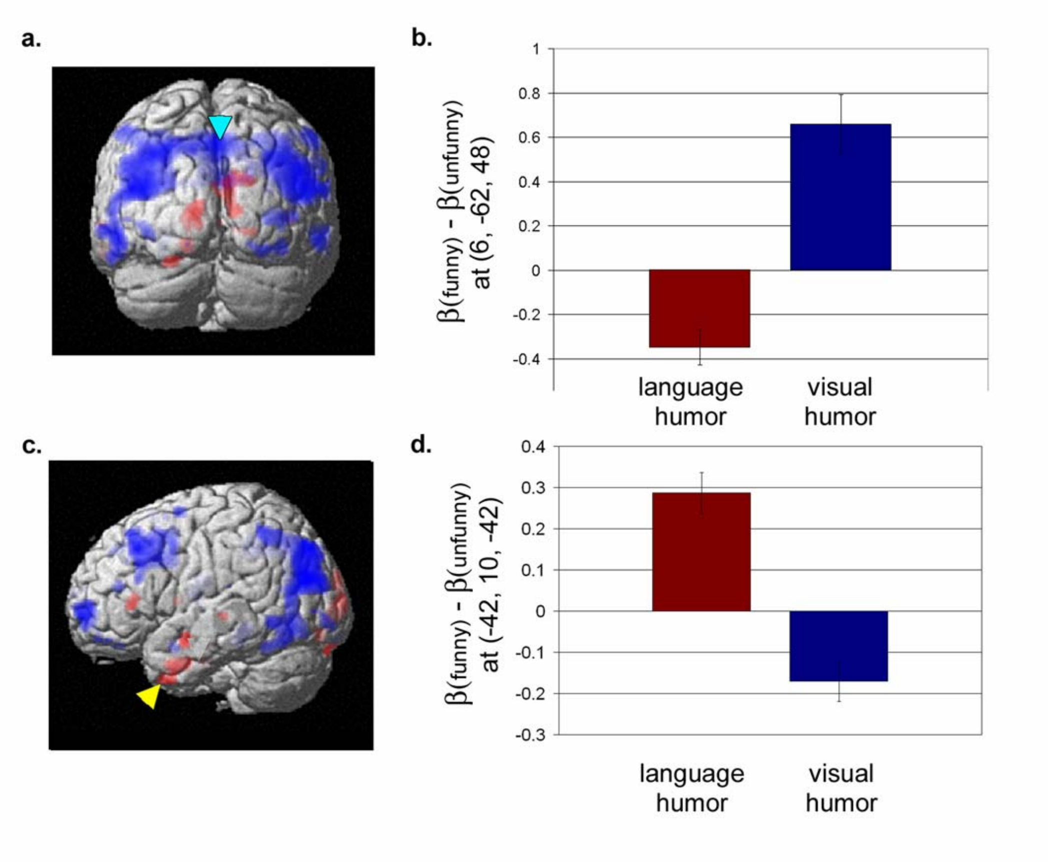

Figure 17 (a) Replication of surface projection from Figure 17, with peak voxel modulated by visual humor > language humor indicated by the cyan arrowhead. (b) Mean differences in betas across all subjects for the voxel indicated in a. Red bar, differences in betas for funny trials minus the betas for control trials for language-based cartoons; blue bar, differences in betas for funny trials minus betas for control trials for sight-gag cartoons. (c) Replication of surface projection from Figure 4, with peak voxel modulated by language humor > visual humor indicated by the yellow arrowhead. (d) Mean differences in betas across all subjects for the voxel indicated in c. Red bar, differences in betas for funny trials minus the betas for control trials for language-based cartoons; blue bar, differences in betas for funny trials minus betas for control trials for sight-gag cartoons. Note differences in y-axis scale between (b) and (d). Error bars represent S.E.M. in both graphs.

In contrast, the reverse comparison [(visually funny cartoons – visual controls) > (language based funny cartoons – language controls)], activated broad swaths of bilateral higher-order visual cortex, including the horizontal posterior segment of the superior temporal sulcus, the middle occipital gyrus, and the precuneus (Table 4b, Figures 16, and 17).

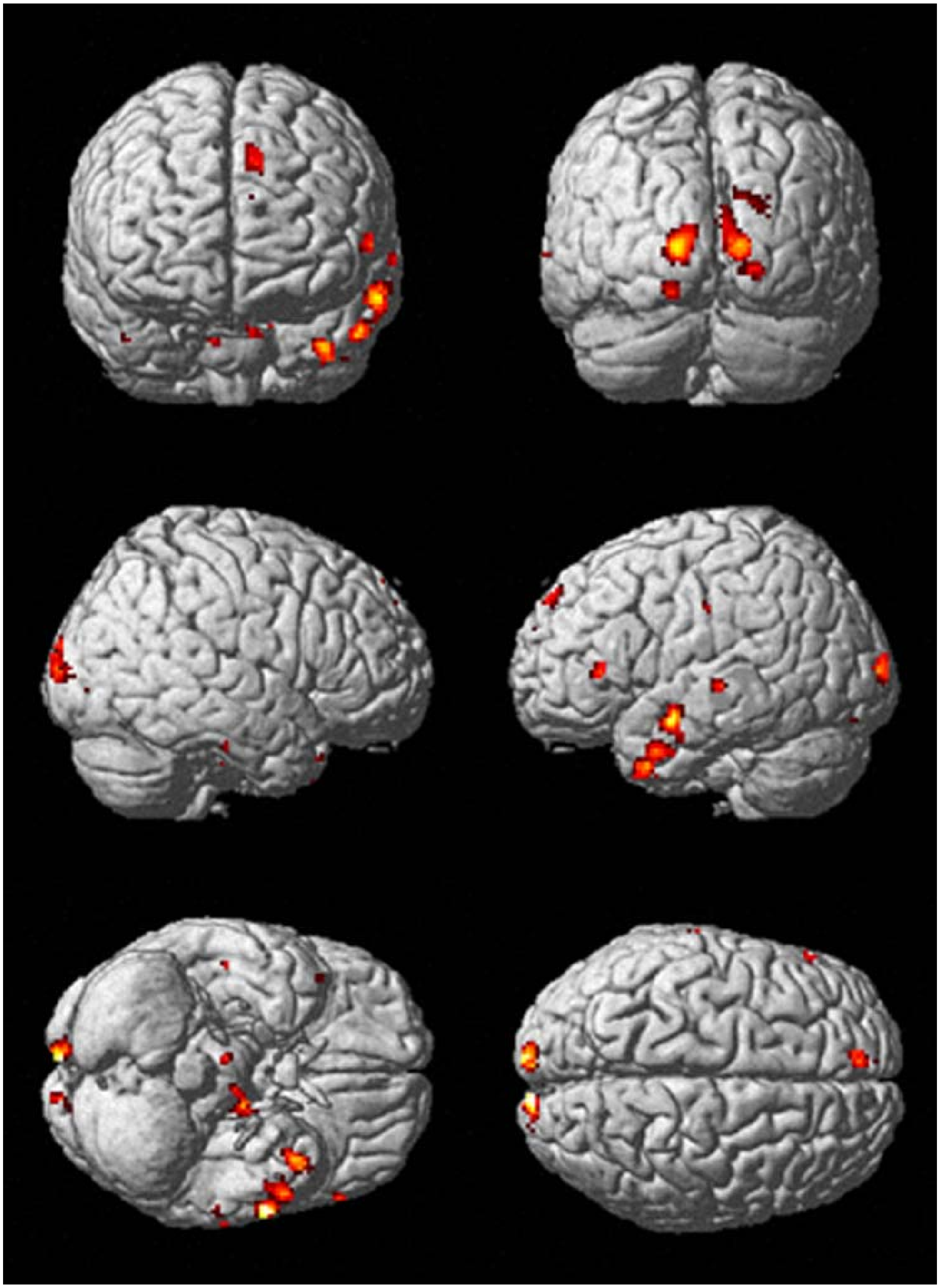

Figure 18 Surface rendering of brain regions for which language humor is greater than visual humor ($p<0.05$, uncorrected).

Table 4 a

Brain region	L/R	coordinates (x y z) of peak voxel	Z-score
inferior temporal gyrus	L	-42 10 -42	3.75
middle temporal gyrus	L	-52 4 -32	3.31
inferior temporal sulcus	L	-50 -4 -30	3.18
superior occipital gyrus	R	4 -98 20	3.53
superior occipital gyrus	R	12 -98 28	3.10
cuneus	L, R	14 -98 8	3.00
transverse occipital sulcus	L	-14 -94 -2	2.78
fourth occipital gyrus	L	-14 -86 -14	3.27
inferior frontal gyrus, pars triangularis	L	-58 32 6	3.18
superior temporal sulcus	L, R	-64 -26 0	3.10
inferior occipital gyrus	L, R	-24 -92 -22	3.07
subiculum	L	-14 -16 -20	3.03
parahippocampal gyrus	L	-10 -14 -28	2.86
short insular gyrus	L	-32 2 8	2.82

Table 4 b.

Brain region	L/R	coordinates (x y z) of peak voxel	Z-score
precuneus	R	6 -62 48	5.03
superior temporal sulcus, horizontal posterior segment	L, R	-38 -76 20	4.94
middle frontal gyrus	L, R	-36 26 44	4.70
inferior temporal gyrus	R	60 -48 -10	4.60
inferior frontal gyrus	L, R	-30 62 0	4.60
anterior orbital gyrus	L	-28 52 -16	3.38
superior temporal gyrus	R	48 20 -18	4.41
fronto-insula	R	38 18 -14	2.72
superior frontal sulcus	R	26 18 62	3.42
middle occipital gyrus	L	-38 -90 -4	3.87
anterior orbital gyrus	R	26 38 -20	3.70
middle frontal gyrus	R	42 24 38	3.50
inferior occipital gyrus	R	38 -86 -14	3.43
fourth occipital gyrus	R	32 -94 -14	3.39
thalamus	L	-8 -12 16	3.39
fusiform gyrus	L, R	-26 -40 -8	3.38
posterior cingulate gyrus	R	6 -48 24	3.21
lateral occipital sulcus	R	38 -90 2	3.20
lateral orbital gyrus	L	-46 46 -18	3.11

Table 4 Atlas coordinates (in MNI space) and z-scores of peak activation during the cartoon task for the interaction between the “sight gag” and “language-dependent” categories. Table 2(a) lists regions for which [language-dependent humor (funny – unfunny) > sight-gag humor (funny – unfunny)], i.e., regions of activation for which language-based humor is significantly greater than sight-gag humor. Table 2(b) lists regions for which [Sight-gag humor (funny – unfunny) > language-dependent humor (funny – unfunny)], i.e., regions more strongly activated by sight-gag humor than by language-based humor (all comparisons p<0.005, uncorrected, cluster>10 voxels).

Brain region	L/R	coordinates (x y z) of peak voxel	Z-score
midbrain	L	-10 -24 -12	4.61
amygdala	L/R	-28 -4 -30	4.13
hippocampus	L	-22 -24 -12	3.93
fusiform gyrus	L	-48 -56 -20	3.78
superior temporal sulcus	L/R	66 -40 10	3.54
middle temporal gyrus	L	-60 -54 2	3.39
hypothalamus	R	8 -4 -8	3.31
subiculum	R	14 -28 -6	3.19
nucleus accumbens	L	-12 4 6	2.88
inferior temporal gyrus	R	32 -6 -40	2.87
entorhinal area	R	28 0 -34	2.85
inferior frontal gyrus	L	-60 12 2	2.83

Table 5 Atlas coordinates (in MNI space) and z-scores of peak activation from a conjunction analysis of both visual humor and language based humor [(language funny – language unfunny) and (visual funny – visual unfunny)].

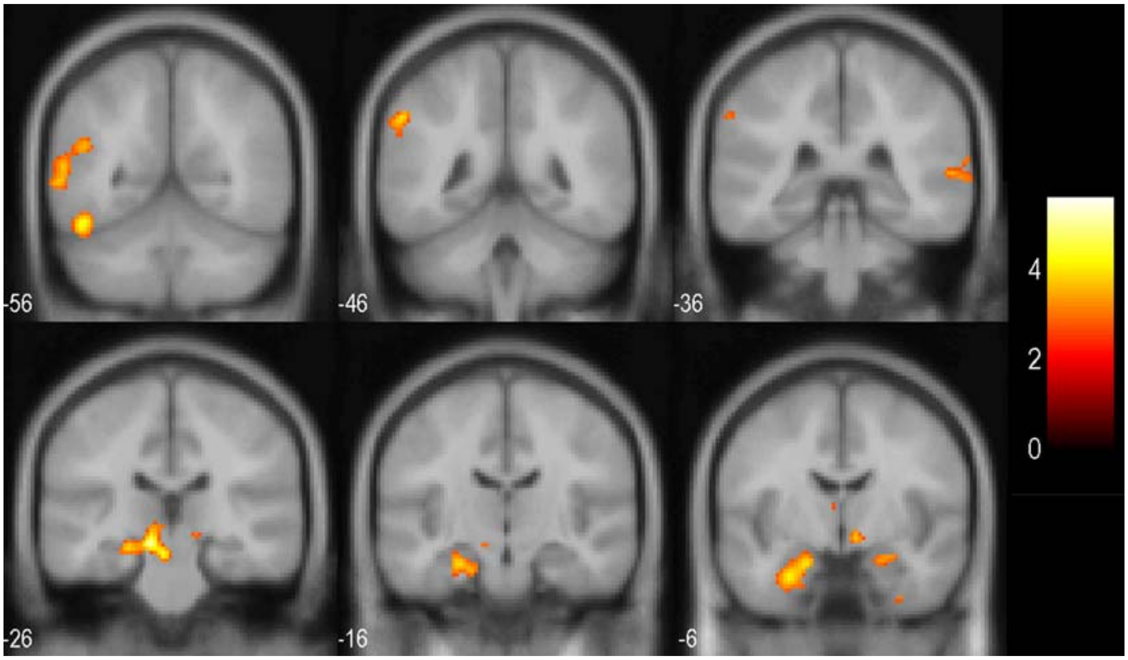

Figure 19 Coronal view of activity elicited in both language-dependent (funny – control) and visual (funny – control) humor ($p<0.005$, uncorrected, for both).

Analysis of the conjunction of the two humor types [(language humor – language controls) ∩ (visual humor – visual controls), all thresholded at $p<0.005$, cluster size > 20] revealed activity in several hedonic regions, including the midbrain and amygdala (Table 5, Figure 19).

3.5 Discussion

The results reported here demonstrate the disparate mechanisms underlying the euphoric and cognitive aspects of humor. Specifically, we show that language-dependent cartoons elicit activity in classical language areas in the left temporal lobe, while sight-gag cartoons elicit activity in higher-order visual areas. We additionally demonstrate that both types of humor result in increased activity in reward and emotion related areas, including the nucleus accumbens and the amygdala.

The two stage model of humor consists of an initial recognition of incongruity (surprise), and the subsequent reinterpretation of the incongruent situation into a coherent whole (framework shifting) (Suls, 1972). This suggests that the details relevant to the humor require additional processing, possibly engaging feedback loops between lower level sensory areas and regions in frontal cortex associated with attention and executive function. Consistent with this model, our data show that cognitive processing during the experience of humor is domain specific, with increased activation in the modules most relevant to the element from which the humor is derived.

Sight-gag humor is dependent on visual incongruities between several elements in the cartoon. Functionally, our results show that the processing of sight-gag humor shows increased activation in higher-order visual regions bilaterally when compared to language-dependent humor, consisting of a large expanse of extrastriate regions beyond V2 (Tootell et al., 1996). Interestingly, areas V1 and V2 are not more active during the funny cartoons than they are during the non-funny cartoons, suggesting that the activation elicited by visual humor is a result of top-down modulation, rather than an increase in sensory stimulation per se. The strongest sites of activation were the precuneus and dorsolateral prefrontal cortex (BA 9/46), anatomically known as middle frontal gyrus. These two regions are associated with visual imagery (Ishai et al., 2000), contextual associations (Linden et al., 2003; Lundstrom et al., 2005; Rorie and Newsome, 2005), and conscious awareness of visual stimuli (Kjaer et al., 2001). Evidence also exists that the precuneus is active during paradigms that require varied perspective-taking (Jackson et al., In press; Ruby and Decety, 2001) or the recruitment of theory of mind (Gallagher et al., 2000), cognitive mechanisms that are similar to the re-interpretation step that precedes “getting” a joke.

Interaction between frontal regions and stimulus-specific regions in the temporal lobe are thought to underlie recognition for faces (Haxby et al., 1994; Kanwisher et al., 1997) and objects (Riesenhuber and Poggio, 2002). Our results are consistent with this, as frontal regions and higher visual areas act reciprocally to place the cartoons’ visual elements into a sensible context. This requires various inferences about spatial and conceptual relationships between objects, based on information-sparse line drawings. This cognitive effort results in the relative activation of both the parietal “where” stream as well as the temporal “what” stream of visual processing, both of which act in concert with frontal regions that integrate this processing and hold relevant information in working memory (Ungerleider and Haxby, 1994).

Activation that is present during language-dependent humor as opposed to sight-gag humor is located in left-lateralized temporal and frontal corticies. Left-hemispheric damage has long been associated with language deficits in regions associated with language processing, and the regions activated by language-dependent humor correspond strongly to classical language areas, including Broca’s area, anatomically described at inferior frontal gyrus; Wernicke’s area, including middle temporal gyrus and superior temporal sulcus; and the basal temporal language areas located in inferior temporal gyrus (Benson, 1993; Friederici, 2002; Just et al., 1996). Surprisingly, language-dependent humor also elicited activation increases in the region of the occipital lobe corresponding to the primary visual areas. This could arise either from increased visual input during language humor, for example from a relatively large search pattern that includes both the caption and the picture, or from a relative suppression in primary visual activity during visual humor.

Although it is clear that a dissociation exists between the mechanisms that underlie different forms of humor, our results also emphasize the common features that characterize various types of humor. Our study replicates the results of past studies (Mobbs et al., 2003) that found heightened activity in a network of subcortical regions, including the nucleus accumbens and substantia nigra, thought to underlie the hedonic aspect of humor. For most regions, this was true not only for an investigation of the main effect of humor, but also for a parametric analysis (observing correlations of activity in these regions with varying levels of reported amusement) and for a conjunction analysis between the two different types of humor (visual and language-based). This further strengthens the evidence that humor acts similarly to primary rewards via the mesolimbic dopaminergic system. We also observed amygdala activity in both the parametric and main effects analyses, which corroborates past results (Mobbs et al., 2003; Moran et al., 2004). Recent evidence supports a role for amygdala in the processing of rewards as well as aversive events (for review, see Baxter and Murray, 2002), and animal lesion studies show that an intact amygdala is necessary to link an object to a current (as opposed to consistent) reward value. Amygdala activity may thus relate to the "re-interpretation" step in the Suls model and the associated update of the cartoon's value. Another interpretation of the amygdalar activity relates to the observation that patients with bilateral amygdala lesions fail to show normal changes in skin-conductive response (SCR) in a gambling task (Bechara et al., 1999). Changes in somatic markers such as

SCR may be concomitant with, or a crucial feature of, humor, a phenomenon that could explain the observed activity in both the amygdala and the hypothalamus

Regions of the brain highlighted in the conjunction analysis of language-based and sight-gag humor may reflect cognitive demands common to processing both types of humorous cartoons in addition to the hedonic component of humor. For example, our conjunction analysis revealed activity in the superior temporal sulcus and middle temporal lobe, regions associated with face-perception (Desimone, 1991) and with the processing of social informational cues such as the assessment of gaze and head direction (O'Doherty et al., 2003b). Inferior temporal gyrus is known to be associated with the semantic retrieval processes that occur when viewing line drawings (Mazard et al., 2005), and the hippocampus is also postulated to have a role in semantic processing under conditions of lexico-semantic ambiguity (Hoenig and Scheef, 2005). In all of these cases, it is likely that we are seeing heightened processing of relevant stimuli in the funny cartoons in comparison with the non-humorous control cartoons, analogous to the increased activity we report in domain-specific areas during the processing of language-dependent or sight-gag cartoons.

We also report in this study that humorous cartoons activate the two regions in the human brain known to have Von Economo cells (von Economo and Koskinas, 1929), a specialization in neuronal morphology that has evolved in the last 15 million years (Allman et al., 2002; Allman et al., 2005; Nimchinsky et al., 1999). Furthermore, we show that the BOLD response in these two regions, anterior cingulate cortex (ACC) and fronto-insula cortex (FI), is correlated with the subjective rating of funniness (see Figure 13). Humor involves both uncertainty (during the initial appraisal of the humorous situation) and sociality (via laughter or other social signals), both of which have been shown to elicit activity in ACC and FI (Bartels and Zeki, 2004; Critchley et al., 2001; O'Doherty et al., 2003a; Shin et al., 2000; Singer et al., 2004a; Singer et al., 2004b). We propose that the ability to appreciate humor is related to the ability to make rapid, intuitive assessments, a skill that would be particularly adaptive during the complex social interactions typical of the hominoids, and that the von Economo cells are a phylogenetic specialization in the circuitry that underlies such fast and intuitive decisions. It is the convergence of this fast intuition with a slower, deliberative assessment that creates the cognitive mismatch upon which humor is based. A listener “gets” a joke the moment that the initial intuitive interpretation is updated, thus providing the input required to “re-calibrate” ACC and FI. We propose that a similar mechanism enables fluent social interaction. This is consistent with a recent study using a placebo paradigm, which suggests that the ACC and orbitofrontal cortex modulate expectation in a top-down manner (Petrovic et al., 2005). Another interpretation involves the regions’ roles in mediating the autonomic changes that are likely to be induced by humor (Critchley, 2002; Critchley et al., 2001). Again, this is consistent with the activity we observed in the amygdala and hypothalamus, both of which have descending projections to autonomic output nuclei. Critchley suggests that these two regions play a primary role in mediating autonomic changes. These various explanations are not mutually exclusive, since the changes in expectation that occur during humor are likely to be associated with fluctuations in anticipatory arousal states. This could be the physiological correlate of the “release of tension” humor mechanism proposed by Freud (Freud, 1960).

3.6 Acknowledgements

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