Neural correlates of humor detection and appreciation

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Humor is a uniquely human quality whose neural substrates remain enigmatic. The present report combined dynamic, real-life content and event-related functional magnetic resonance imaging (fMRI) to dissociate humor detection ("getting the joke") from humor appreciation (the affective experience of mirth). During scanning, subjects viewed full-length episodes of the television sitcoms *Seinfeld* or *The Simpsons*. Brain activity time-locked to humor detection moments revealed increases in left inferior frontal and posterior temporal cortices, whereas brain activity time-locked to moments of humor appreciation revealed increases in bilateral regions of insular cortex and the amygdala. These findings provide evidence that humor depends critically upon extant neural systems important for resolving incongruities (humor detection) and for the expression of affect (humor appreciation).

The ability to comprehend and appreciate humor is a vital aspect of social functioning. Humor is a significant component of what makes us unique as human beings; we are perhaps alone among animals in engaging in behavior designed to encourage humorous responses. Without humor, much of the color and variety inherent in human social discourse would be lost (Brownell and Gardner, 1988). Indeed, the absence of a sense of humor can have distressing interpersonal consequences. Humor can be therapeutic, producing beneficial effects on the immune and central nervous system (Fry, 1992), and can provide coping mechanisms for life's tribulations (Lefcourt et al., 1997).

Conceptually, humor can be divided into cognitive and affective elements (Gardner et al., 1975). The cognitive element (humor detection) refers to "getting the joke"—these are moments where the perceiver attempts to comprehend disparities between punch lines and prior experience (Brownell et al., 1983). The affective element (humor appreciation) refers to "enjoying the joke"—moments where the perceiver experiences pure visceral, emotional responses dependent upon the hilarity of the experience. A fundamental question is whether anatomically distinct brain pathways subserve humor detection and humor appreciation. Specifically, humor detection might depend critically on brain pathways involved in understanding and resolving ambiguities between situational expectations and surprising outcomes, whereas humor appreciation might rely primarily upon engagement of limbic pathways involved in the processing and expression of affect.

Thus far, there is no clear consensus on the neural underpinnings subserving elements of humor. Work in the patient domain has suggested hemispheric differences such that the left hemisphere may be responsible for integrating information into a coherent manner to understand a joke, whereas the right hemisphere may be responsible for emotional processing associated with the surprise element of humor (Gardner et al., 1975). While this work has been successful in delineating at a gross level the brain systems responsible for the processing of humor, a fundamental question concerns the specific cortical regions that are involved in understanding and responding to humor. More recently, Goel and Dolan (2001) used functional magnetic resonance imaging (fMRI) to image subjects during the experience of one-line jokes and observed a functional dissociation between cognitive and affective elements of humor. Specifically, semantic comprehension of jokes was associated with increased activation in the left and right posterior middle temporal gyrus. By contrast, activity in ventromedial prefrontal cortex correlated with subjects' explicit ratings of how funny they found each joke.

Thus far, the relatively few neuropsychological (Bihrle et al., 1986; Brownell et al., 1983; Gardner et al., 1975; Shammi and Stuss, 1999) and neuroimaging (Coulson and Kutas, 2001; Goel and Dolan, 2001) investigations that have explored humor have principally relied on stylized cartoons or canned jokes as media. Further, such studies often require selection of an appropriate punch line from a list of choices or require appraisal of the quality of humor while it is experienced (e.g., "is this funny?"). However, the act of evaluating humor may itself affect the affective experience of the perceiver.

The present report attempts to extend previous findings to the domain of dynamic, humorous content (i.e., full-length episodes of television sitcoms). Importantly, to isolate cognitive and, to a greater extent, affective components of humor, it seems necessary to expose individuals to dynamic content without requiring overt task responses. To this end, neural correlates of humor detection and humor appreciation were examined in two event-related fMRI studies using full-length episodes of the television sitcoms *Seinfeld* and *The Simpsons*.

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Methods

Subjects

Informed consent was obtained from all participants. Twelve subjects (5 men, 7 women, aged 22–34) participated in Experiment 1 (*Seinfeld*); 13 subjects (6 men, 7 women, aged 22–46 years) participated in Experiment 2 (*The Simpsons*). Post-scan debriefing indicated that while each subject had regularly viewed and enjoyed episodes of *Seinfeld* and *The Simpsons* in the past, they had not previously viewed the particular episodes used in the study. No subjects were excluded for excessive head motion (defined as > 1 mm between successive volume acquisitions) in either study.

Materials

The *Seinfeld* episode "The Tape"(1991) and *The Simpsons* episode "Bart the General" (1990) were digitally recorded and edited using the program iMovie (Apple, Cupertino, CA) to remove commercials. The resulting videos were 21:42 (*Seinfeld*) and 22:22 (*The Simpsons*) in length. Videos were projected onto a screen positioned at the head end of the bore. Subjects viewed the screen through a mirror and listened to the audio portion of the episode through MR compatible headphones.

To create a virtual laugh track for *The Simpsons*, the episode was separately shown to 82 college participants in an auditorium. Their laughter was digitally recorded and used to identify portions of the episode that were considered to be "funnier" on average than the rest of the episode.

In both experiments, humorous moments were defined as those containing laughter. Three independent coders recorded the onsets and offsets of laughter moments in each episode. Only those moments agreed upon by all three coders were included as humor appreciation moments in the analysis, leading to 127 separate humorous events for Experiment 1 and 60 for Experiment 2.

Functional imaging

Anatomical and functional whole-brain imaging was performed on a 1.5 T GE Signa Scanner. Anatomical images were acquired using a high-resolution 3-D spoiled gradient recovery sequence (SPGR; 124 sagittal slices, TE = 6 ms, TR = 25 ms, flip angle = 25°, $1 \times 1 \times 1.2$ mm voxels). Functional images were collected using a gradient spin-echo, echo-planar sequence sensitive to blood-oxygen level-dependent contrast (T2*) (20 slices per whole-brain volume, 3.75-mm in-plane resolution, 5.5-mm thickness, 1-mm skip, TR = 2000 ms, T2* evolution time = 35 ms, flip angle = 90°).

Data analysis

fMRI data were analyzed using the general linear model for event-related designs in SPM99 (Wellcome Department of Cognitive Neurology, London, UK) (Friston et al., 1995). First, functional data were time-corrected to correct for differences in acquisition time between slices for each whole-brain volume, realigned to correct for head movement, and co-registered with each participant's anatomical data. Functional data were then transformed into a standard anatomical space (3-mm isotropic voxels) based on the ICBM 152 brain template (Montreal Neuro-logical Institute) which approximates Talairach and Tournoux atlas space (Talairach and Tournoux, 1988). Normalized data were then spatially smoothed (6-mm full-width-at-half-maximum [FWHM]) using a Gausian kernel.

Because *Seinfeld* was filmed before a live studio audience, we took advantage of the laugh track that was embedded in the episode to identify moments that were, on average, "funnier" than the rest of the episode. While there is certainly some individual variability for what one finds to be humorous, the laugh track reflects those portions of the episode that the majority of the audience found to be humorous. As such, laugh track moments can be considered to have a greater percentage of humorous content than the remainder of the episode.

Two analyses followed from this reasoning: To identify neural correlates of humor detection, we contrasted brain activity for events time-locked to each moment preceding laughter with brain activity for the remainder of the episode. To identify neural correlates of humor appreciation, we contrasted brain activity for events time-locked to the laugh track with the remainder of the episode (Fig. 1). In this way, the remainder of the episode served as a control condition.

Specifically, humor detection moments were defined as transient events by specifying each 2-s trial that immediately preceded laughter on the laugh track. Humor appreciation moments were defined using variable-length durations and were time-locked to the laugh track.

To uniquely estimate neural correlates for humor detection and humor appreciation, two separate models were used. Both event types could not be uniquely estimated within a single general linear model because each humor detection moment was immediately followed by a subsequent humor appreciation moment. For each subject, general linear models incorporating a single task effect (humor detection, model I; humor appreciation, model II) modeled with a canonical set of three functions (the hemodynamic response function, its temporal derivative, and its dispersion derivative) and covariates of no interest (a session mean, a linear trend, and six movement parameters derived from realignment corrections) were used to compute parameter estimates and t-contrast images (containing weighted parameter estimates) at each voxel. Individual contrast images were then submitted to a second-level, random effect analysis to create mean t-images (thresholded at $P < 0.0005$, uncorrected). An automated peak-search algorithm identified the location of peak activations. The same analysis was applied to both experiments.

Head motion was quantified for each subject across the entire scanning session by computing vector distances (derived from the x, y, and z translational realignment corrections) between sequential functional volumes. Vector distances for each time point for each subject were then assigned to "laughter" or "non-laughter" groups (defined from the laugh track) and submitted to a paired t test.

To assess the reliability of results across the two data sets, activations identified in the *Seinfeld* data set were formally tested for replication in *The Simpsons* data set. The rationale for the replication approach is based on the assumption that reproducibility of activations across data sets is the strongest indication that activations generalize and are not attributable to spurious artifact (e.g., motion). Regions of interests were defined based on peak activations identified in the *Seinfeld* data set (all significant voxels [$P < 0.0005$] within 8 mm of the peak location were included in each region) and tested for replication in *The Simpsons* data set.
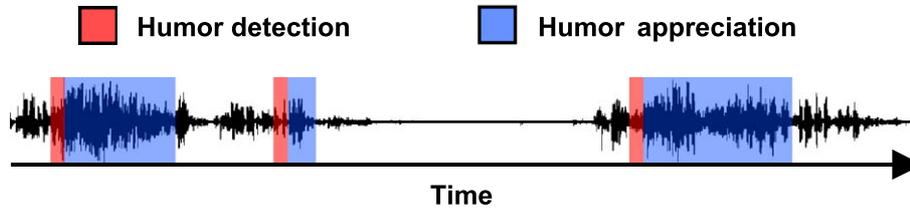
Fig. 1. Moments of humor detection and humor appreciation were defined based on *Seinfeld's* embedded laugh track. Moments of humor detection (red) and humor appreciation (blue) are shown superimposed on a representative portion of the audio waveform from the episode. Humor detection moments were modeled as transient events directly preceding the onsets of laughter. Humor appreciation events were time-locked directly to the laugh track and were modeled with varying durations to reflect the rise and fall of a moment of laughter. To create a virtual laugh track for *The Simpsons*, the episode was separately shown to 82 college students in an auditorium. Their laughter was digitally recorded and used to identify portions of the episode that were considered "funnier" on average than the rest of the episode.

For each subject in *The Simpsons* data set, parameter estimates for each region were computed and submitted to a one-sample *t* test (with a hypothesized mean of zero). A Bonferroni-corrected alpha of 0.05 was set as the statistical threshold necessary for replication. For activations that replicated, a peak-search algorithm was used to identify coordinate locations in *The Simpsons* data set.

The statistical approach used here can be considered a conservative approach, as a single design matrix (time-locked to the laugh track) was used to capture most of the would-be-humorous events (but not all—owing to individual variability in humor appreciation across subjects) from one subject to the next. Activations found to survive this stringent analysis can be considered highly reliable, particularly when such activations replicate across both data sets.

Results

Experiment 1

In the first experiment, 12 normal right-handed subjects were scanned while passively viewing an entire episode of *Seinfeld* without any specific task requirement. During moments of humor detection, significant activation was noted in left posterior middle temporal gyrus (Brodmann's Area [BA] 21, −48, −38, −3), and left inferior frontal gyrus (BA 47, −48, 26, −14). Humor appreciation was associated with increased activation in bilateral regions of insular cortex (left −36, 11, −3; right 36, 5, −10), and the amygdala (left −21, −1, −17; right 21, −2, −16) (Fig. 2, top panel). Using a less stringent statistical threshold ($P < 0.001$, uncorrected), additional activations were noted bilaterally in anterior temporal cortex (BA 20; −45, −5, −35, and 35 −5, −35), left inferior temporal gyrus (BA 20; −33, −3, −20), right posterior middle temporal gyrus (BA 21; 47, −26, −6), and right cerebellum (24, −69, −34) during humor detection, and in left (−18, −21, 7) and right (6, −11, 6) thalamus, left hippocampus (−33, −32, −7), left lateral parietal cortex (BA 40; −23, −38, 57), right inferior frontal cortex (BA 44; 53, 12, 2), and fusiform gyrus (BA 37; 39, −47, −14) during humor appreciation.

Importantly, brain activations observed during humor appreciation could not be attributed to head motion, as quantitative measurements of head motion did not differ between moments of humor appreciation and the remainder of the episode (paired *t* test, $t = 1.24$, $df = 11$, $P > 0.2$).
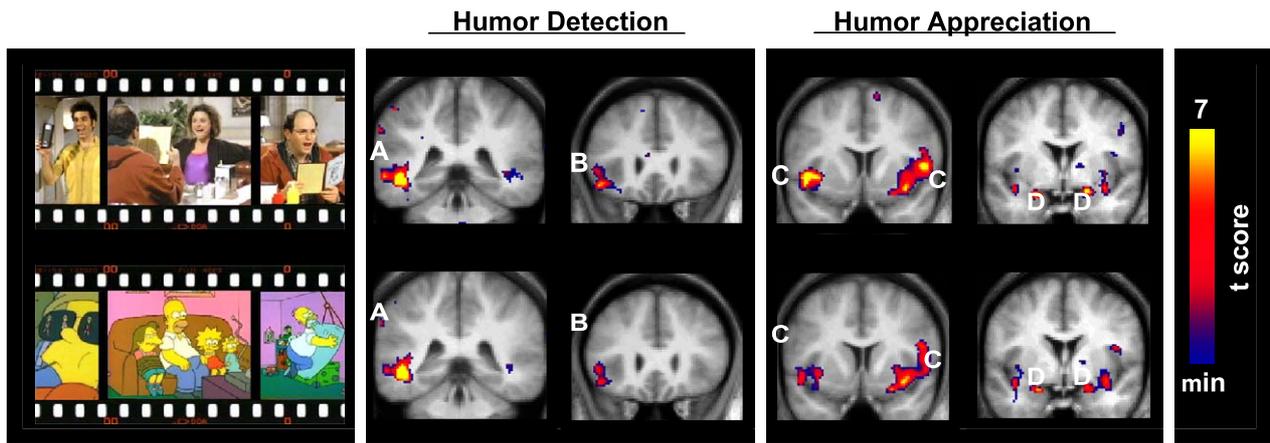

Fig. 2. Whole-brain statistical activation maps averaged across subjects viewing *Seinfeld* (top panel) and *The Simpsons* (bottom panel) reveal a functional dissociation between humor detection and humor appreciation. Images are coronal sections with the left side of the image corresponding to the left hemisphere. In both studies, humor detection led to greater activation in the left posterior middle temporal gyrus (A: *Seinfeld*: −48, −38, −3 and *The Simpsons*: −48, −38, −3; BA 21) and the left inferior frontal gyrus (B: *Seinfeld*: −48, 26, −14 and *The Simpsons*: −45, 26, −11; BA 47). By contrast, humor appreciation yielded greater activation bilaterally in insular cortex (C: *Seinfeld*: left −36, 11, −3; right 36, 5, −10 and *The Simpsons*: left −33, 14, −6; right 39, 5, −8) and the amygdala (D: *Seinfeld*: left −21, −1, −17; right 21, −2, −16 and *The Simpsons*: left −21, −1, −17; right 21, −1, −16).

Experiment 2

In Experiment 1, subjects heard laughter during each humor appreciation moment. To ensure that activations observed during humor appreciation were not simply related to hearing laughter, we repeated our experimental procedure using a sitcom that did not include a laugh track. In the second experiment, 13 normal right-handed subjects were imaged while passively viewing a full-length episode of *The Simpsons*. To identify portions of the episode that could be linked to humor detection and appreciation, we screened the episode before a live audience and recorded their reactions to create a virtual laugh track (see Fig. 1). This permitted the same analyses to be applied in the absence of hearing laughter. More-over, the same approach could be used to examine whether different genres of comedy (e.g., animated cartoons) would yield similar patterns of brain activity.

A formal replication analysis was conducted to determine the reliability of activations across the two data sets. Results obtained using *The Simpsons* revealed near identical patterns of activation to those observed during *Seinfeld*. Consistent with results observed in the first experiment, humor detection was associated with increased activation in the left posterior middle temporal gyrus (BA 21, −48, −38, −3) and left inferior frontal gyrus (BA 47, −45, 26, −11), whereas humor appreciation produced increased activation bilater-ally in the insula (left −33, 14, −6; right; 39, 5, −8) and the amygdala (left −21, −1, −17; right 21, −1, −16) (Fig. 2, bottom panel).

Additional activations that were found to replicate across data sets included left anterior temporal cortex (BA 21; −48, −3, −33), right posterior middle temporal gyrus (BA 21; 48, −22, −4), and right cerebellum (33, −71, −34) during humor detection and left (−18, −20, 7) and right (6, −11, 6) thalamus, left lateral parietal cortex (BA 40; −23, −38, 57), left hippocampus (−24, −27, −15), and right inferior frontal cortex (BA 44; 53, 9, 8) during humor appreciation (all *P*'s < 0.001).

Again, the amount of head motion during *The Simpsons* did not differ between moments of humor appreciation and the remainder of the episode (paired *t* test, *t* = 0.48, *df* = 12, *P* > 0.6).

Discussion

The current study introduces the use of natural, dynamic content to the neuroscientific investigation of social behavior. Here we used full-length television sitcoms to dissociate cognitive and affective elements of humor. While the dynamic content used here is complex by cognitive neuroscience standards, the simplicity of analysis is clear; predefined behavioral reactions to temporally evolving events can be used to investigate the neural responses in independent cohorts. This approach represents an exciting meth-odological advance in the emerging field of social neuroscience and is likely to be amenable and attractive to a broad range of research interests that may benefit from the use of materials as complex and realistic as those encountered in everyday life, including investigations of person construal, perspective taking, and theory of mind.

Humor detection is critically dependent upon resolving incon-gruities between punch lines and expectations shaped by the storyline (Suls, 1972). Consistent with this notion, the posterior temporal and inferior frontal regions engaged during humor detection have previously been implicated in language tasks that

encourage retrieval and appraisal of relevant semantic knowledge (Binder et al., 1997; Petersen et al., 1988; Price et al., 1999; Raichle et al., 1994; Thompson-Schill et al., 1997). Indeed, recent studies indicate further specialization within left inferior frontal cortex for reconciling ambiguous semantic content with stored knowledge (Gold and Buckner, 2002; Thompson-Schill et al., 1997). In the context of humor detection, posterior temporal lobe regions may bring stored expectations online; inferior frontal regions may then resolve ambiguities between these expectations and punch lines. Similar dissociations are noted for one-line jokes when incongruous punch lines are compared with predictable completions (Coulson and Kutas, 2001; Goel and Dolan, 2001).

Behavioral models of humor have suggested a further segre-gation of humor detection into *surprise* and *coherence* elements. Surprise occurs when an event is incongruous with expectations primed by prior events. Individuals must then reestablish coher-ence to "get the joke". This two-stage model of humor detection is difficult to test using neuroimaging techniques such as fMRI because there is no clear behavioral transition marker (e.g., laughter) to delineate the two putative processes. As the present results are consistent with previous neuroimaging work on ambi-guity resolution, the most parsimonious interpretation is that activations observed here during humor detection in posterior temporal and inferior frontal regions subserve the cognitive operations engaged during the coherence stage of humor detec-tion. Indeed, previous work by Coulson and Kutas (2001) was not able to distinguish between surprise and coherence on the milli-second scale of evolving event-related potentials, although their results did suggest a dissociation between surprise and coherence in that there was a sustained negativity over anterior left lateral sites, "which may reflect the frame-shifting needed to reestablish coherence".

By contrast, humor appreciation demands an "after-the-fact" visceral, emotional response. In line with this idea, insular cortex has been implicated in a wide range of visceral responses, but its functions are usually considered aversive, including pain percep-tion (Ostrowsky et al., 2002), the perception of disgust (Phillips et al., 1997), and even vomiting (Fiol et al., 1988). Our findings extend current understanding of insular function by demonstrating activation of these structures during highly pleasurable experien-ces. While novel, this finding fits nicely with earlier research on insula function (Fiol et al., 1988; Ostrowsky et al., 2002; Phillips et al., 1997), as many emotions, regardless of valence, share func-tionally indistinguishable autonomic signatures (e.g., increased heart rate, respiration rate, and sweating). An alternative, less appealing account for the insula activity observed here during humor appreciation is that insula activity is reflecting an "intention to remain still". While we formally tested for and found no differences in subject motion between humor appreciation moments and the rest of the episode, the possibility remains that there were qualitative differences in the effort required to keep still. This potential confound is difficult to test, as there is no reliable way to measure such differences in effort. Intuitively, one might expect that more effort is needed to "try to remain still" during those moments where one might ordinarily laugh. Interestingly, however, overt laughter is greatly diminished when individuals experience humor in isolation (Devereux and Ginsburg, 2001; Fridlund, 1991; Young and Frye, 1966), suggesting that the effort to remain still (i.e., suppress laughter) during humor appreciation might depend strongly on whether one would normally laugh out loud when alone.

Emotionally arousing events, both pleasant and aversive, are typically well remembered relative to neutral events. The amygdala, which has strong reciprocal connections to insular cortex, has been shown to play a critical role in emotional memory processes (Hamann, 2001). Not surprisingly, humorous material is known to be more memorable than nonhumorous material (Schmidt, 1994); this phenomenon is even evident in discussions around the proverbial "water cooler" the morning after a new episode of a popular sitcom has aired. The amygdala projects directly to the hippocampal memory system and co-activates with these structures during memory formation for emotional experiences (Hamann et al., 1999). Thus, amygdala participation during humor appreciation may reflect the neural substrate behind this memorial advantage. Other work has demonstrated that the amygdala responds to surprised faces and may play a role in the detection of ambiguity in response to facial expressions (Adams et al., 2003; Kim et al., in press; Whalen, 1998). To the extent that amygdala activity functioned in a similar capacity in the present work, one might expect such activity to be present during humor detection. Here, however, the amygdala activations occurred following the conclusion of humor detection events and mirrored the rise and fall of heard (and unheard) laughter. Our speculation is that the mirth experience can only occur when a joke has been fully assimilated. In this regard, registration of surprise and its resolution would necessarily need to conclude before one could enjoy a joke. Thus, it is difficult to explain the amygdala activations observed in the present studies in terms of registration of surprise or ambiguity, or in terms of other cognitive processes that might occur during humor detection moments and extend beyond modeled boundaries into moments of humor appreciation. Even allowing for such possibilities, these activations would not be expected to mirror the temporal evolution of the laugh track.

Previous patient and neuroimaging work has implicated regions of ventromedial prefrontal cortex in humor appreciation that were not observed in the present report (Bihrle et al., 1986; Brownell et al., 1983; Gardner et al., 1975; Goel and Dolan, 2001; Shammi and Stuss, 1999). Interestingly, each of these studies required ongoing, explicit appraisal of humorous material. Indeed, ventromedial prefrontal cortex has been implicated in "appraising the reward value of ongoing behavior" (Dolan, 1999). By exposing individuals to dynamic, realistic comedy and eliminating the need for metacognition (i.e., thinking about one's own responses), the present study may have bypassed involvement of ventromedial prefrontal cortex and more directly wedded the affective experience of humor to its specific neural underpinnings.

While dynamic comedy of the kind used here adds an element of realism to the neuroanatomical study of social behavior, this naturalistic approach also adds additional layers of complexity to the kinds of interpretations that can be drawn. Subtle differences between moments of humor and the other portions of the episodes are not amenable to experimental manipulation. For example, sitcom actors may insert dramatic pauses following joke deliveries. Such pauses may permit other systematic differences to occur between the conditions of interest. Actors may move less, exhibit unique facial expressions, or refrain from speech during these moments. While actors can take cues from the live audience, and indeed, provide cues to the live audience, this option is not available during animation comedy. Moreover, some of the humor contained in *The Simpsons* is entirely independent of the animation of the characters (e.g., writing on a wall or chalkboard). Because we observed comparable activations during humor appreciation in both studies, it would be difficult to explain this pattern of results in terms of "bottom-up" processing differences across humorous and nonhumorous moments unless such effects were consistent across these two disparate genres of comedy.

Our results specify a cascade of neural events required to understand and appreciate humor. Moreover, the neural signatures of humor detection and appreciation are functionally separable within the brain and are consistent across different genres of comedy. The direct replication of results during *The Simpsons*, even in the absence of a laugh track, highlights the broad nature of these effects. Elements of humor exploit existing functional anatomic architectures: Brain regions dedicated to resolving contextual ambiguities are likewise engaged during humor detection. Similarly, the mirth experience depends upon brain regions necessary for emotional and visceral sensation.

In short, humor may have evolved from our separate abilities to understand language and respond emotionally. Curiously, the neural circuitry that permits mirth appears to be available to many animal species. What appears to be lacking in other species is the functional architecture necessary to resolve incongruities, and, as demonstrated by our results, comprehend humor. This critical dependence on circuitry involved in the semantic processing of language is perhaps what makes humor such a unique human characteristic.

Acknowledgments

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