Humor Modulates the Mesolimbic Reward Centers

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Summary

Humor plays an essential role in many facets of human
life including psychological, social, and somatic func-
tioning. Recently, neuroimaging has been applied to
this critical human attribute, shedding light on the af-
fective, cognitive, and motor networks involved in hu-
mor processing. To date, however, researchers have
failed to demonstrate the subcortical correlates of the
most fundamental feature of humor—reward. In an
effort to elucidate the neurobiological substrate that
subserves the reward components of humor, we un-
dertook a high-field (3 Tesla) event-related functional
MRI study. Here we demonstrate that humor modu-
lates activity in several cortical regions, and we pres-
ent new evidence that humor engages a network of
subcortical regions including the nucleus accumbens,
a key component of the mesolimbic dopaminergic re-
ward system. Further, the degree of humor intensity
was positively correlated with BOLD signal intensity
in these regions. Together, these findings offer new
insight into the neural basis of salutary aspects of
humor.

Introduction

Without humor, life would undeniably be less exhilarat-
ing. Indeed, the ability to comprehend and find a joke
funny plays a defining role in the human condition, es-
sentially helping us to communicate ideas, attract part-
ners, boost mood, and even cope in times of trauma
and stress (Dixon, 1980; Gavrilovic et al., 2003; Martin,
2001; Neuhoff and Schaefer, 2002; Nezlek and Derks,
2001). These beneficial manifestations are compli-
mented at the physiological level where humor (i.e., the
perception that something is funny; McGhee, 1971) is
thought to have numerous salutary effects, including
acting as a natural stress antagonist and possibly en-
hancing the cardiovascular, immune, and endocrine
systems (Bennett et al., 2003; Berk et al., 1989; Fred-
rickson and Levenson, 1998; Fry, 1992; Lefcourt et al.,
1990). It is therefore apparent that developing a sophisti-
cated understanding of the discrete neural systems that

modulate humor appreciation is of both social and clini-
cal relevance.

Recent advances in functional neuroimaging have en-
abled researchers a clear avenue from which to explore
this critical human attribute. Figuring prominently in the
semantic and linguistic aspects of humor comprehen-
sion are the temporo-occipital junction, middle/inferior
temporal cortex, and inferior frontal gyrus (IFG), includ-
ing Broca's area (Goel and Dolan, 2001; Ozawa et al.,
2000). Moreover, stimuli that provoke laughter (i.e., the
motor response to humor) have been shown to modulate
activity in the supplementary motor area (SMA) proper,
a somatotopically mapped region involved in multiple
motor operations (e.g., Toyokura et al., 2002), including
motor components of expressive laughter (Iwase et al.,
2002; Osaka et al., 2003). One preliminary fMRI study of
joke-induced humor implicated the right medial ventral
prefrontal cortex (MVPFC) in the amusing, or rewarding,
feeling that accompanies a joke, although this has yet
to be replicated (Goel and Dolan, 2001). Despite this
sequence of discoveries, investigations have failed to
conclusively demonstrate the subcortical correlates of
the most fundamental feature of humor—reward.

Important clues about the neurological systems in-
volved in regulating reward have come from a recent
flurry of fMRI studies using a myriad of primary and
secondary rewarding tasks, including monetary reward
paradigms, the perception of aesthetically attractive
faces, and objects signifying wealth/dominance (Aharon
et al., 2001; Breiter et al., 2001; Erk et al., 2002; Knutson
et al., 2001). These studies have convergently docu-
mented increased hemodynamic signal in the mesolim-
bic dopaminergic reward system, a system known to
play a pivotal role in drug reward and motivational be-
haviors (for review, see Schultz, 2002). This system en-
compasses a variety of distinct, but interconnected,
dopamine-enriched structures, including the ventral stri-
atum/nucleus accumbens (NAcc), the ventral tegmental
area (VTA), and the amygdala. Although our understand-
ing of the anatomical organization and function of the
mesolimbic dopaminergic reward system is relatively
advanced, our understanding of this system's role in
humor, a powerful endogenous reward, remains remark-
ably poor.

In the experiment reported here, we used event-
related fMRI (efMRI) to seek hemodynamic increases in
regions associated with cartoons considered to be
funny. While in the scanner, each subject was presented
with 42 cartoons previously rated, by a separate group
of matched subjects, as being funny and 42 nonfunny
cartoons (i.e., cartoons with funny cues omitted). Sub-
jects were explicitly asked to respond with a press of a
button if they found the cartoon funny (Figure 1A) or not
(Figure 1B). Our rationale for the present efMRI design
was 3-fold: (1) the unpredictable nature of random efMRI
designs allowed us to look at pure reward, rather than
anticipatory rewards (cf. Braver and Brown, 2003); (2)
because of the subjective quality of humor appreciation,
we parsed out activation on a subject-by-subject and
cartoon-by-cartoon basis, thus allowing us to take into

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A **B**

2003 Dan Piraro, reprinted with permission. Cartoons drawn by Dan Piraro, written by Dan Piraro and Daniel J. Levitin. Bizarro cartoons can be found at: www.kingfeatures.com/features/comics/bizarro/about.htm
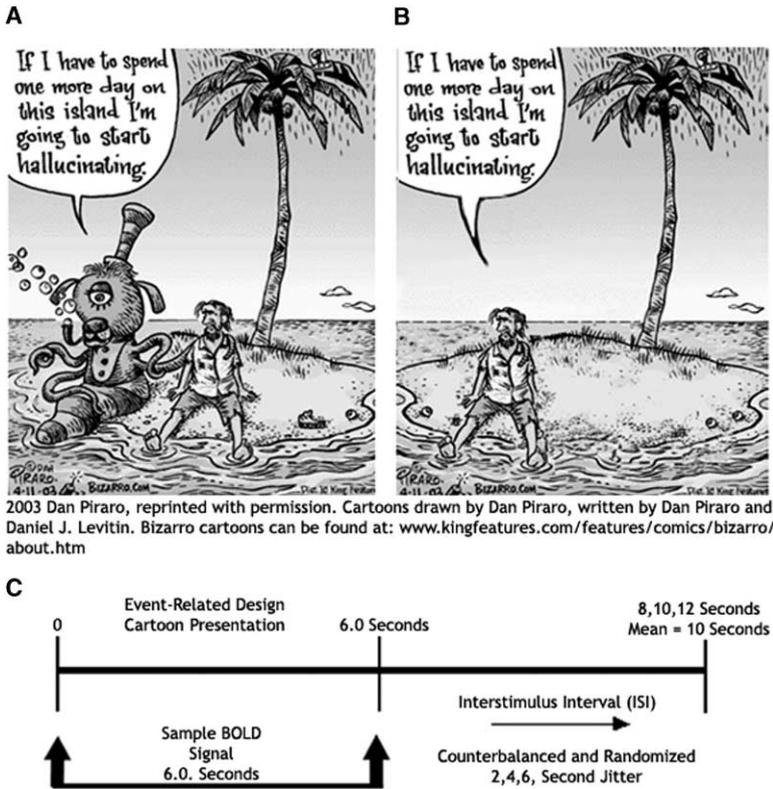
C

Figure 1. Example of a Funny Cartoon and the Same Cartoon with Funny Cues Omitted

(A) Funny cartoon. (B) Nonfunny cartoon. Stimuli were presented in an event-related fMRI paradigm, with each cartoon being presented in random order for 6000 ms. A jittered interstimulus interval (ISI) was used, varying randomly between 2000, 4000, and 6000 ms and counterbalanced, a priori, across funny and nonfunny events. Analysis was limited to the blood-oxygenation level-dependent (BOLD) signal acquired during stimulus presentation (Figure 1C). Data were collected in one 15 min and 4 s session consisting of 84 events using a TR of 2000 ms (see Experimental Procedures for more details).

consideration individualistic differences in humor; and (3) ultimately, this design allowed us, using postscan ratings by each volunteer, to parametrically examine the association between humor intensity (and presumably the degree of reward) and blood-oxygen level-dependent (BOLD) signal magnitude.

In accordance with previous neuroimaging studies of humor, laughter, and reward, we hypothesized that funny cartoons, in comparison to nonfunny cartoons, would elicit increased activation in several language and semantic regions, including the left anterior and posterior temporal regions and IFG, including Broca's area. We also predicted that motor aspects of humor would be expressed in the SMA (i.e., laughter and smiling). Ultimately, we hypothesized, several structures within the mesolimbic dopaminergic reward system, including the NAcc, would become active as subjects interpreted cartoons they subjectively considered funny.

Results

Behavioral Results

Examination of response latencies showed a robust, albeit nonsignificant, trend [$t(15) = -1.8$, p < .093] for subjects to respond faster to nonfunny cartoons (mean ± standard deviation: 3645.1 ± 691.1) than to funny cartoons (3859.1 ± 438.4). Of the funny cartoons, subjects rated an average of 61.5% ± 6.9% as subjectively funny. These findings parallel those of a prior efMRI study of humor appreciation (Goel and Dolan, 2001).

fMRI Results

We used a random-effects model to identify residual activation patterns for subjectively (i.e., subject-by-sub-

ject and cartoon-by-cartoon basis) preferred funny cartoons to those considered not funny (see Figures 1A and 1B). The primary voxel-based analysis revealed a network of cortical and subcortical regions involved in humor appreciation (Figure 2). Significantly higher BOLD signal was identified in three cortical areas. One cluster was centered in the left temporo-occipital junction extending into the fusiform gyrus (Brodmann area [BA] 37). A second cluster was observed in Broca's area of the left lateral IFG (BA 44/45). This cluster also extended ventrally to include a subcluster in the temporal pole (BA 38). The third cortical cluster was observed in the SMA proper (BA 6) contiguously extending to the pre-SMA and dorsal anterior cingulate (dACC; BA 32). A significant activation cluster was also found encapsulating the anterior thalamus, ventral striatum/NAcc, ventral tegmental area (VTA), hypothalamus, and amygdala. These results are summarized in Table 1.

A post hoc covariate analysis examining the association between humor intensity (i.e., degree of funniness as rated by each experimental subject) and BOLD signal magnitude revealed a striking concordance with whole-brain activation. This analysis showed humor intensity to be associated with increased activation in several regions also detected in our primary analysis including the left temporo-occipital junction, IFG, temporal pole, SMA proper, and the mesolimbic dopaminergic reward system (see Figure 3 and Experimental Procedures for more details).

Time-Series Analysis: Nucleus Accumbens

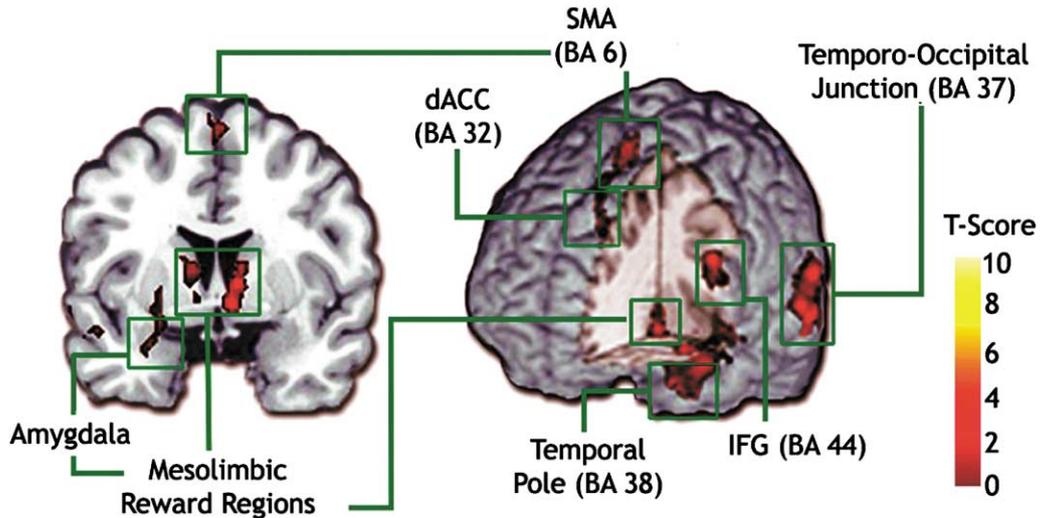To further probe the hemodynamic response of the NAcc to humor, we raised the height threshold and isolated

Figure 2. Functional Topographical Map of Funny Minus Nonfunny Cartoons

Activation clusters were superimposed on Talairach normalized brain using MRIcro (http://www.psychology.nottingham.ac.uk/staff/cr1/mricro.html). Significant clusters of activation were determined using the joint expected probability distribution (Poline et al., 1997) with height (p < 0.01) and extent threshold (p < 0.05) corrected at the whole-brain level. Results revealed activation in the left temporo-occipital junction (Brodmann area [BA] 37), inferior frontal gyrus (IFG; BA 44/45) extending ventrally to include a subcluster in the temporal pole (BA 38), and supplementary motor area (SMA proper; BA 6/32) extending to the pre-SMA and dorsal anterior cingulate (dACC). A subcortical cluster also was observed encompassing the ventral striatum/NAcc, anterior thalamus, ventral tegmental area (VTA), hypothalamus, and amygdala (see Results and Experimental Procedures for more details).

the caudal aspect of this structure as a 10 voxel subcluster (at p < 0.0001; peak stereotaxic coordinate at: 6, 2, −4) within the larger subcortical cluster. Using this 10 voxel region of interest (ROI), we extracted the average time courses for funny and nonfunny cartoons across all 16 subjects (Figure 4). This analysis emphasizes the prominent increase in BOLD signal in the NAcc during funny cartoons, compared to negligible BOLD signal decreases in response to those that were not funny.

Discussion

The results reported here provide the first evidence that humor engages a network of subcortical structures, including the VTA, NAcc, and amygdala—key components of the mesolimbic dopaminergic reward system. With respect to cortical components of humor appreciation, our results are in good agreement with previous studies. We found that funny cartoons when contrasted with nonfunny cartoons activated the temporo-occipital junction, IFG/temporal pole, and SMA/dACC, all in the left hemisphere. This distinct pattern of left-lateralization has been observed in monetary and video-game reward tasks, in addition to event-related potential (ERP) and clinicopathological studies of humor appreciation, signifying that this hemisphere plays a distinct role in the processing of reward and positive emotional stimuli (Breiter et al., 2001; Coulson and Kutas, 2001; Gardner et al., 1975; Koepp et al., 1998).

Activation of the temporo-occipital junction (BA 37), a division of the ventral-stream of visual cortical processing (Ungerleider and Haxby, 1994), has previously been implicated in the semantic processing of jokes needing holistic coherence (Goel and Dolan, 2001), detection of incongruity (Iwase et al., 2002), and the identification of emotionally important visual cues (Geday et al., 2003). Intriguingly, this activation cluster encompassed the left fusiform gyrus, a region which, when electrically

Table 1. Brain Areas in Which Stimuli-Related BOLD Signal Was Significant for Funny Cartoons over and above Nonfunny Cartoons

Regions	Right/Left	Brodmann's Area	p Value	Cluster Size (Voxel)	z Score	Talairach Coordinates (x, y, z)
Temporo-occipital junction[a]	L	37	<0.001	587	5.63	(−44, −60, 12)
IFG,[a] temporal pole	L	44/45/38	<0.001	1457	4.73	(−50, 16, 20)
SMA proper,[a] pre-SMA, dACC	L	6/32	<0.017	218	3.47	(−2, 5, 62)
Ventral striatum,[a] NAcc, anterior thalamus, VTA, hypothalamus, and amygdala	L/R	–	<0.001	1406	4.71	(−10, −2, 4)

Only clusters with an extent threshold of p < 0.05 corrected for whole brain are reported. Stereotaxic coordinates and Brodmann areas as in Talairach and Tournoux (1988) atlas space.

Abbreviations: SMA, supplementary motor area; NAcc, nucleus accumbens; VTA, ventral tegmentum area; dACC, dorsal anterior cingulate cortex; IFG, inferior frontal gyrus.
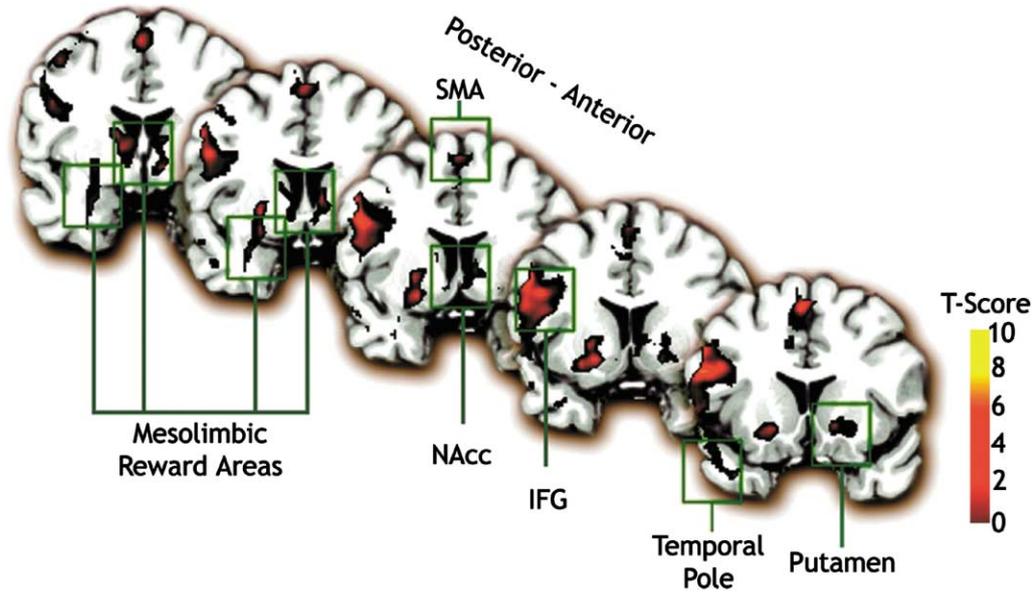
[a] Denotes peak activation.

Figure 3. Composite Montage Showing Activated Regions Covarying with Degree of Humor Intensity

Significant clusters of activation were determined using the joint expected probability distribution (Poline et al., 1997), with height ($p < 0.05$) and extent threshold ($p < 0.01$) corrected at the whole-brain level. Results showed activation in the left temporo-occipital junction: peak Talairach coordinates: x, y, z; -46, -65, -14; $Z = 5.73$, BA 19/37; left IFG: -51, 9, 27; $Z = 4.92$; BA 9/44/45. Again this cluster extended ventrally to the temporal pole (TP) (BA 38). A cluster was also found in the medial SMA proper: -2, 18, 51; $Z = 4.22$; BA 6/8. A final cluster was also observed encompassing the mesolimbic doperminergic system: -8, -33, -7; $Z = 4.01$. This clusters also extended to the right IFG (BA 44).

stimulated, induces laughter accompanied by a feeling of mirth (i.e., positive emotion) (Arroyo et al., 1993). In view of these observations, this region may be involved in the incongruent, or surprising (Brownell et al., 1983), elements of a joke, and thus may play a pivotal role in the early stages of the humor network.

The largest area of cortical activation occurred in the left lateral IFG (BA 44), including Broca's area, possibly reflecting the language-based decoding of the stimuli. The vast amount of literature has implicated the IFG in word perception and production (e.g., Price et al., 1996), although it is now commonly believed that the IFG is a polymodal language region, involved in numerous aspects of language processing, including semantic and sentence processing (for review, see Gernsbacher and Kaschak, 2003). This cluster also proceeded ventrally to the temporal pole (BA 38). Although the temporal pole is highly prone to susceptibility artifact and resultant signal loss (Ojemann et al., 1997), leaving its role in

cognitive functions somewhat of an enigma (Cabeza and Nyberg, 2000), it is thought that this region is involved in lexical retrieval and is a major storehouse for semantic knowledge (Damasio et al., 1996; Mummery et al., 2000). One interpretation is that these regions may constitute a frontal-temporal network involved in integrating language and long-term memory (Goel, 2003). Such a network would presumably be needed to comprehend and find the cartoon jokes funny.

Collectively, the temporo-occipital junction, IFG, and temporal pole are of particular theoretical interest as they fit well with Suls' influential *incongruity-resolution model* of joke appreciation, which posits that a cartoon is found funny via a two-stage process. First, the joke recipient finds their expectation is incongruous with the cartoon caption. Second, the joke recipient revises their initial interpretation to accommodate the caption and the rest of the cartoon, thus establishing coherence (Suls, 1972). It is an appealing conceptualization that
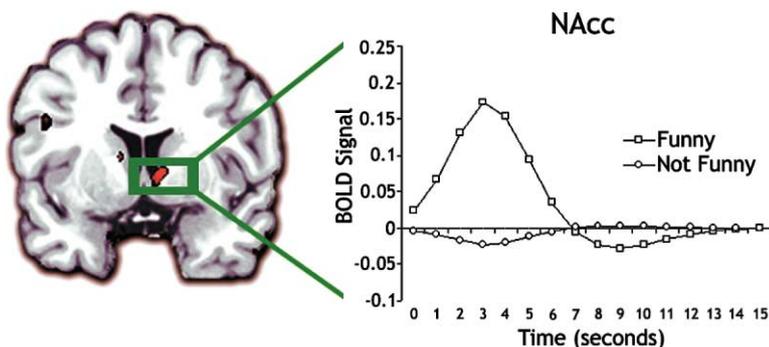

Figure 4. Averaged Time Series for Funny Compared to Nonfunny Activity in the Right NAcc

Stereotaxic coordinates: x, y, z; 6, 2, -4; $p < 0.0001$.

the temporo-occipital junction detects incongruence as suggested in previous studies of humor and laughter (Goel and Dolan, 2001; Iwase et al., 2002), while more anterior regions, including Broca's area and the temporal pole, ascertain linguistic coherence.

Engagement of the left SMA proper (BA 6) and pre-SMA are likely to reflect motor aspects of expressive laughter. Intraoperative electrical stimulation of the left pre-SMA has been shown to elicit smiles and laughter (Fried et al., 1998). Recent neuroimaging studies also have shown increased activation in the bilateral SMA proper to be correlated with laughter (Iwase et al., 2002; Osaka et al., 2003). In the present study, the SMA proper cluster also extended to the adjacent dACC, a multifaceted structure implicated in reward-based decision making, attention allocation, and laughter (Arroyo et al., 1993; Bush et al., 2002; Osaka et al., 2003; Procyk et al., 2000). Particularly compelling is that ictal laughter (i.e., gelastic seizures) has been shown to arise from a circumscribed region encompassing the SMA and dACC (Chassagnon et al., 2003). It is also intriguing to note that both SMA proper and dACC receive rich dopamine input via ascending mesocortical projections from the ventral striatum (Bates and Goldman-Rakic, 1993; Dum and Strick, 1993), suggesting that these regions play an extended role in the dopaminergic reward network associated with humor appreciation.

A novel finding of this study relates to the detection of a humor-specific cluster that encompassed several subcortical structures, including the amygdala, ventral striatum/NAcc, ventral tegmental area (VTA), anterior thalamus, and the subadjacent hypothalamus (see Table 1 and Figure 2). These regions constitute the core of the subcortical dopaminergic reward network, beginning in the VTA, where cell bodies of dopamine neurons are located, and projecting rostrally to striatal, limbic, and frontal lobe terminal fields (Schultz, 2000). Functional connectivity within this network of subcortical regions has been demonstrated in oral amphetamine (Devous et al., 2001) and cocaine (Breiter and Rosen, 1999) infusion studies, reflecting the prominent role of dopaminergic signaling in drug rewards.

Of these several components of the reward system, the NAcc has been consistently implicated in psychologically and psychopharmalogically driven rewards (Breiter et al., 2001; Breiter and Rosen, 1999; Knutson et al., 2001). In the present study, the time series analysis revealed a pronounced increase in activation during funny cartoons, when compared to nonfunny cartoons (see Figure 4). Modulation of the NAcc by funny cartoons was also confirmed in the post hoc covariate analysis showing that activity in this region increases with the degree of humor intensity (see Figure 3). In addition, humor-elicited NAcc activation converges with findings from fMRI studies across a number of psychologically rewarding tasks, suggesting that this structure is involved in the processing of a diverse number of stimuli with rewarding characteristics (Aharon et al., 2001; Breiter et al., 2001; Breiter and Rosen, 1999; Erk et al., 2002; Goel and Dolan, 2001; Rilling et al., 2002). Although we cannot exclude other intervening factors (e.g., novelty), in light of prior fMRI and physiological studies implicating NAcc modulation in self-reported happiness (Knutson et al., 2001) and cocaine/amphetamine-induced euphoria in humans (Breiter and Rosen, 1999; Drevets et al., 2001), it is reasonable to conclude that the NAcc activation observed in the present study reflects the hedonic feeling that accompanies humor. Further investigations, however, are needed to unravel the discrete nexus between NAcc activation and rewarding aspects of humor.

The presence of left amygdala activation also presents a compelling finding. The amygdala is an integral component of the dopamine reward system, providing excitatory innervation to the NAcc (Price and Amaral, 1981). Comparative studies have demonstrated that discrete ablation of the amygdala produces conspicuous impairments in stimulus-reward learning (for review, see Baxter and Murray, 2002). In humans, the amygdala, while classically associated with negative emotions, has also been implicated in reward magnitude (Pratt and Mizumori, 1998), laughter (Iwase et al., 2002), and processing of pleasurable emotions (Yang et al., 2002). Furthermore, the finding of amygdala activation is of clinical interest, as this region has been implicated in the pathological features of many affective disorders. Diminished dopaminergic tone in the amygdala has been implicated in the emotional memory dysfunction and anhedonia observed in depression (Nestler et al., 2002) and the "affective flattening" seen in Parkinson's disease (Tessitore et al., 2002). Conceptually, connections between the amygdala and ventral striatum may provide new insight into the symptomatology of psychiatric disorders with hypodopaminergic underpinnings.

In summary, our results provide compelling new evidence that subcortical, dopaminergic structures may play a key role in the hedonic aspects of humor. We also, in part, replicate previous findings related to the cortical, presumably cognitive and motor, aspects of humor and laughter. These findings also make modest steps toward elucidating the neural basis of salutary aspects of humor that may lead to a better understanding of the putative psychological and physiological benefits of a good sense of humor.

Experimental Procedures

Subjects
Sixteen young, healthy, adult subjects (mean age, 22.4 ± 1.8; range, 20–26 years; 7 males, 9 females) participated in this study. All subjects spoke native English, were right-handed (as measured by the Edinburgh Handedness Inventory; Oldfield, 1971), and were screened for history of psychiatric or neurological problems using the Symptom Checklist-90-R (Derogatis, 1977). Subjects were deemed eligible only if scores were within one standard deviation of the mean normative standardized sample. All experimental procedures complied with the guidelines of the human subjects committee at Stanford University School of Medicine. Written informed consent was obtained from each subject.

Stimuli: Rating of Cartoons
Subjects, similar in age and background to the experimental subjects, chose 42 of the funniest cartoons from a portfolio of approximately 130 cartoons. In addition, each cartoon was rated for simplicity (i.e., how easy the jokes were to comprehend) and visual clarity. Of the final 42 cartoons, 36 of the funny cartoons were captioned, compared to 37 of the nonfunny stimuli. The majority of the cartoons were of the violation-of-expectation type (cf. Herzog and Larwin, 1988). The final 42 funny cartoons were compared to 42 nonfunny cartoons (i.e., funny cues omitted) in the scanner. Nonfunny cartoons were also matched to funny cartoons for luminance and visual

elements (i.e., geometrical complexity). No cartoon was shown twice.

Experimental Design

Subjects were told to respond with a press of a button on a keypad if they found the cartoon funny (Figure 1A) or not (Figure 1B). Before entering the MRI scanner, subjects were reminded that the study was not a judgment of cartoons, but a test of how funny they found the cartoons. Subjects also were reminded not to move their heads if they laughed. Once in the scanner, subjects were first presented with the word "ready". Upon pressing a button, the word "rest" appeared for 2 s followed by 28 s of a black screen. Subsequently, each subject was presented with 42 cartoons previously rated as being funny and 42 cartoons rated as not funny. Stimuli were presented in an event-related fMRI paradigm with each cartoon being presented in random order for 6000 ms. A jittered interstimulus interval (ISI) was used, varying between 2000, 4000, and 6000 ms and counterbalanced across funny and nonfunny events (as rated in the pilot study). Data were collected in a single session lasting 15 min and 4 s, consisting of 84 events using a TR 2000 ms and random, counterbalance jitter of 2 TR.

Following the scan, each subject was asked to rate each cartoon for humor intensity (i.e., degree of funniness) on a 1 to 10 scale, with 1 being least funny and 10 being most funny. Those considered nonfunny were given a zero. The individual means (for all funny jokes) ranged from 3.7 to 8 with a group mean of 6.4 ± 1.8. These subjective funniness ratings were then used to parametrically covary funniness with associated linear changes in BOLD signal intensity. To accomplish this, time points (n frames) corresponding to cartoon presentation were labeled with each subject's corresponding rating from 1 to 10. The n frames corresponding to the ISI and jokes considered nonfunny were scored as zero.

fMRI Acquisition

Images were acquired on a 3 T GE Signa scanner using a standard GE whole-head coil. The scanner runs on an LX platform, with gradients in "Mini-CRM" configuration (35 mT/m, SR 190 mT/m/s), and has a Magnex 3 T 80 cm magnet. A custom-built head holder was used to prevent head movement associated with laughter. To maximize magnetic field inhomogeneity, an automatic shim was applied. 28 axial slices (4 mm thick, 0.5 mm skip) parallel to the anterior and posterior commissure (AC-PC) covering the whole brain were imaged with a temporal resolution of 2 s using a T2* weighted gradient echo spiral pulse sequence (TR = 2000 ms, TE = 30 ms, flip angle = 80° and 1 interleave) (Glover and Lai, 1998). The field of view (FOV) was 200 × 200 mm^2, and the matrix size was 64 × 64, giving an in-plane spatial resolution of 3.125 mm. Tasks were programmed using Psyscope (Cohan et al., 1993). Commencement and synchronization between scan and task were accomplished using TTL pulse distribution to the scanner timing microprocessor board from a CMU Button Box (http://psyscope.psy.cmu.edu) linked to a G3 Macintosh.

fMRI Analysis

Inverse Fourier Transform was used to reconstruct images for each of the 450 n frame time points into 64 × 64 × 18 image matrices (voxel size: 3.75 × 3.75 × 7 mm). Statistical parametric mapping (SPM99; http://www.fil.ion.ucl.ac.uk/spm/spm99.html) was used to preprocess all fMRI data. Images were corrected for movement using least square minimization without higher-order corrections for spin history and normalized to stereotaxic Talairach coordinates (Talairach and Tournoux, 1988). Images were then resampled every 22 mm using sinc interpolation and smoothed with a 4 mm Gaussian kernel to decrease spatial noise.

Statistical Analysis

For each subject, voxel-wise activation during funny events compared to nonhumorous events was determined using multiple univariate regression analysis with correction for temporal autocorrelations in the fMRI data (Friston et al., 1995). Confounding effects of fluctuations in global mean were removed by proportional scaling, and low-frequency noise was removed with a high pass filter (0.5 cycles/min). A regressor waveform for each condition, convolved

with a 6 s delay Poisson function accounting for delay and dispersion in the hemodynamic response, was used to compute voxel-wise t statistics, which were then normalized to z scores to provide a statistical measure of activation that is independent of sample size. Subsequently, a random-effects model (Holmes and Friston, 1998) was used to determine which brain regions showed greater activation during funny compared to nonfunny events across the group of subjects. Contrast images generated from the individual subject analyses were analyzed using a general linear model to determine voxel-wise t statistics. A one-way t test was then used to determine group activation for the conditions of interest. Finally, the t statistics were normalized to z scores, and significant clusters of activation were determined using the joint expected probability distribution (Poline et al., 1997) with height (p < 0.01) and extent (p < 0.05) thresholds corrected at the whole-brain level. Activation foci were superimposed on high-resolution T1-weighted images and their locations interpreted using universal neuroanatomical landmarks (Duvernoy, 1991; Mai et al., 1997; Talairach and Tournoux, 1988).

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