Something funny happened to reward

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The human reward system has been shown to be activated by a wide range of reinforcers, including food, money, sex, drugs, and beauty. Now, a recent fMRI study has found mesolimbic reward activation associated with humorous cartoons, providing a neurobiological link between theories of humour and hedonic processes in the brain.

Two cows were standing in a field, and one said to the other, 'Those humans are sure getting worked up about this mad cow disease. It is an unfortunate state of affairs. What do you think?' To which the other replied, 'Don't ask me. I'm a chicken.'

Was this joke funny? Before you answer, let's ask your nucleus accumbens; it may surprise you. It is with some trepidation that we venture into the neuroscience of humour, for as the American essayist, E.B. White said, 'Humor can be dissected, as a frog can, but the thing dies in the process and the innards are discouraging to any but the pure scientific mind' [1]. And although few people might wish to dissect frogs, without humour, the human condition might resemble a drab landscape of cognition punctuated by the firings of a morose limbic system. Nothing is sacred from the peering view of the cognitive neuroscientist, with his fancy magnetic resonance imaging machines and his pocket supercomputers crunching away gigabytes of data. Which brings us to a recent paper that has reported, for the first time, activation of mesolimbic reward centers by humour - scientists have found the funny bone in the brain.

Imaging the neural substrates of humour

Using fMRI, Allan Reiss and his colleagues at Stanford University measured the brain response in sixteen volunteers who were exposed to humorous cartoons in the scanner [2]. In an event-related design, the subjects categorized the cartoons as 'Funny' or 'Not Funny', and these categories were subsequently used with each subject to determine which brain regions were relatively activated by humour. The cartoons were culled from published jokes exemplified by the Bizarro series, known for its eccentric and twisted outlook on contemporary society (Figure 1). To control for the visual and language elements of the stimuli, Reiss et al. digitally removed the funny element from a subset of the cartoons. Funny cartoons, when compared with non-funny cartoons, activated a cortical network that included the left temporo-occipital junction, inferior frontal gyrus, supplementary motor area (SMA), and a subcortical network including the ventral striatum, nucleus accumbens, anterior thalamus, ventral tegmentum, hypothalamus and amygdala.

Although the Stanford group was not the first to use brain imaging in the study of humour, they were the first to report reward system activation. A previous fMRI study from University College London reported differential activations in a cortical network, especially the left inferior frontal gyrus with phonological juxtapositions (puns) and bilateral temporal lobe activation with semantic juxtaposition (one line jokes) [3]. When these stimuli were categorized based on funniness, only the ventral medial prefrontal cortex and cerebellum were found to be activated by the funny jokes. Also, a group at Kyoto University recently reported activation of the premotor/SMA, visual cortex, and cerebellar vermis in response to onomatopoeic words mimicking laughter [4]. Neither the UCL nor the Kyoto groups reported mesolimbic reward activations with humour.

Reward, incongruity and humour

The Stanford group's report of humour-induced activation of the mesolimbic reward system is significant because it provides the first tentative link to the hedonic aspects of humour. It would be premature to conclude that the activation of the mesolimbic regions represented the pleasurable component of humour, but if nothing else the mesolimbic activation probably signaled some form of saliency to the subject [5]. The lack of previous reports of mesolimbic activation to humour is surprising and may represent insufficent power to detect activations in a

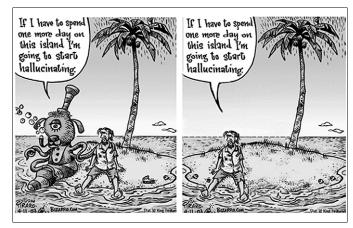


Figure 1. Example of a funny cartoon and (right) the same cartoon with the funny cues omitted, as used in the Mobbs, Reiss *et al.* study [2]. © 2003) Dan Piraro. Reprinted with permission of Bizarro cartoons (www.kingfeatures.com/features/comics/bizarro/about.htm)

region of the brain notoriously susceptible to fMRI artifact, but this seems unlikely given the similarity of sample size in all of the studies. If mesolimbic activation can be taken as an index of humour, then maybe the Stanford experiment was the funniest of the bunch. Humour is contextual. Just as watching a comic on television is nowhere near as funny as in person, Bizarro cartoons may have been funnier than witicisms. Although the UCL group associated ventromedial PFC activation with the affective component of puns, how this differed from the Stanford report of meosolimbic activation is not clear. Cultural attitudes towards humour aside, the difference may lie in the nature the stimuli. Puns can be funny, but they are also painful; as Edgar Allan Poe wrote, 'The goodness of your true pun is in the direct ratio of its intolerability' [6].

There is much to be excited about the mesolimbic activation with humour because this finding provides a neurobiological bridge to psychological theories of humour. Longstanding theories of humour have relied on cognitive judgments, notably variants of 'Incongruity Theory' [7], like Suls' two-stage model of registering surprise followed by the reestablishment of coherence [8]. The evidence for the cortical basis of such models has been inconsistent [9,10]. But especially when it comes to reward, incongruity detection appears to be a function at which the mesolimbic dopamine system excels [11,12], and the Stanford study lends credence to this idea. Of course there are other theories of humour, ranging from the expression of superiority [13] to the relief of suppressed internal conflict [14] to the correction of social injustices [15]. No imaging study has explored these very complex but undeniable aspects of humour. Indeed, the social function of humour may underlie the hedonic component. Any discussion of humour would be incomplete without at least the mention of sex, and here we find an area ripe for further research. The behavioral output of humour, laughter, is sexually dimorphic [16], suggesting what could be a fascinating study of gender differences in the brain response to humour.

Laughter

This brings us to a Jamesian notion that without laughter, there is no humour [17]. Although James spoke of fear and the running of bears, with the exception of the UCL study, all of the humour findings indicated SMA activation, suggesting a strong motor component to humour. It is an empirical question; we do not know which subjects, if any, had a smile on their face, but this would be easy to measure in future studies. Laughter and all of its premotor correlates warrant further investigation, for although we tend to think that only humans laugh, compelling evidence suggests that at least chimpanzees have the equivalent

of laughter and probably a sense of humour for the incongruous [18]. But the most important function of laughter is the social bond that it creates with other people. To the extent that humour induces laughter, or vice versa, humour is more of a social phenomenon than a cognitive one (the mad cow joke is funnier in person – if you do not believe me, then we can discuss it over a hamburger).

It is fortunate that three groups on three continents have studied humour with brain imaging. Despite the differences in methodology, the intersection of common regions of activation, both across modalities and cultures creates an exciting platform to launch a deeper investigation of humour. Everyone loves to laugh, and it is high time to understand why. Which reminds me, a man walked into a bar with his pet monkey....

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