The Neurology of Humour

A sense of humour is among our most cherished attributes. It eases the daily grind, promotes amity with our fellows and may even salve our hurts or confer reproductive success. 1 Laughter might be the ‘shortest distance between two people’, as averred by Victor Borge; awedingly humourless societies tend to disintegrate (think of Nazi Germany)1 and humour is feared by tyrants of all persuasions. In its more refined forms it is held up as a mark of discernment, but there can be very few of us who have not, from time to time, been reduced to fits of helpless mirth even in highly unsuitable situations. This underlines the extraordinary range and power of humour in its many genres. Despite its ubiquity as a phenomenon, the peculiarities of humour are often closely bound to time and place; the jokes of Euripides and Shakespeare have travelled less well than their tragedies and tastes in humour are heavily socially and culturally sanctioned. 1 On the other hand, certain humour motifs may be truly universal: from an evolutionary perspective, laughter is probably older than language1,4 and the destabilising properties of fruit peel were probably already drawing uncharitable sniggers among our cave-dwelling forebears. Though it is not clear that other animals possess humour, it is perhaps relevant that analogues of laughter and smiling in our primate relatives signal aggression or threat.5

In addition to its social and existential virtues, humour is of considerable interest as a cognitive neuropsychological phenomenon. Jokes typically entail the opposition of apparently incongruous elements that must be resolved in a surprising way:6 “These operations entail a number of cognitive processing stages and components. The process of resolution requiring the integration of conflicting alternatives is a model of frontal lobe function,”6 while the emotional payoff suggests an analogy with other phenomena (such as music) that link psychological expectations with the brain mechanisms of reward. 6 However, the neurobiological basis of humour remains largely obscure and the effects of brain disease on humour processing are poorly understood. Neurologists have taken an interest in the more extreme outward manifestations (like pathological affect and ‘ou rire prodromique’7) while largely ignoring the cognitive machinery behind them. Here we argue that this is a wasted opportunity, using examples in which alterations of humour are integral to neurological disease. We do not, however, wish to minimise the challenges inherent in attempting to study the neurology of humour.7,8,10 There is presently no standard, widely accepted cognitive model of humour processing, nor indeed any agreed terminology of the processes involved.8 Caution is therefore required in interpreting the published literature and this is compounded by the diversity of stimuli and paradigms that have been used to assess humour processing in health and disease.10,11,12 Furthermore, as is the case for all complex, multi-component cognitive processes, functional neuroimaging studies of humour (which delineate all brain areas involved in the relevant process) must be reconciled with clinical lesion studies (which identify areas critical for the process). In functional imaging work it is not always clear which contrasts should be employed to isolate specific components of humour processing and most imaging modalities lack the temporal resolution to capture the temporal staging of these components (this typically requires electrophysiological techniques).

In this review we highlight the many gaps in our current understanding of the neurology of humour and propose a framework for the systematic clinical analysis of humour cognition. Our focus here is on the brain mechanisms that process humour and the disorders that affect humour processing, rather than pathological affect and abnormal laughter, which are already well reviewed.10

Humour and the healthy brain

What happens in the brain when we ‘get’ a joke? Functional imaging studies in the healthy brain using stimuli as diverse as one-liners, sight gags, captionless cartoons, comic strips, Seinfeld, The Simpsons and stand-up comedy videos have implicated distributed cortical and subcortical networks in processing different aspects of humour perception and comprehension with separable cognitive, affective and social dimensions of the brain’s response. The temporo-parietal junction is engaged in the cognitive analysis of potentially humorous stimuli;10 this is consistent with a proposed role for this region in bringing stored expectations online10 and for processing socially relevant information more generally.11 This may be particularly pertinent to the basic humour associated with physical comedy (slapstick), which relies on the violation of physical or social norms. More widespread brain regions

Summary

• Functional imaging in the normal brain has implicated distributed cortical and subcortical networks in processing different aspects of humour perception and comprehension with separable cognitive, affective and social dimensions
• Impaired appreciation of humour is a feature of diverse developmental and acquired brain disorders
• Humour may present a useful model for studying certain complex behavioural functions of high clinical relevance: these include the resolution of ambiguity and incongruity, mentalising and empathy

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The barman says, ‘Is this some kind of joke?’

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Brain disorders and humour

Various brain disorders have been linked to disturbed understanding or appreciation of humour. Aside from their clinical relevance, such disturbances can (as with other complex neuropsychological functions) potentially reveal underlying critical brain substrates and cognitive architecture. However, much early work on the neurology of humour draws on a very broad anatomical distinction between the right and left cerebral hemispheres. Various brain disorders have been linked to impaired appreciation of humour, indicating that left hemisphere damage is more likely to affect the comprehension of humour that does not rely on mental inferences. A mentalising deficit is also likely to contribute to degraded humour processing in frontotemporal dementia.

Impaired appreciation of humour is a feature of diverse developmental and acquired disorders with more diffuse brain dysfunction, including autism spectrum disorders, schizophrenia, atypical lateral sclerosis, traumatic brain injury and Tourette’s syndrome.

Orbitofrontal cortex dysfunction may be a common theme linking these disorders with cases of focal brain damage and network disintegration in frontotemporal dementia. Certain disorders may produce specific cognitive deficits that impact on humour processing. The difficulty shown by patients with schizophrenia in interpreting sarcasm may at least partly reflect pitch processing difficulties while impaired mentalising in social phobia or Asperger’s syndrome impairs understanding of humour that depends on theory of mind, but not visual jokes or puns.

There have been few functional neuroimaging studies of humour processing in brain disease; in one MRI study with cartoon stimuli, individuals with cataplexy compared with healthy controls had heightened activation of subcortical reward circuitry, but in addition, increased engagement of inhibitory ‘circuitry in right inferior frontal gyrus, suggesting an intriguing disease model for the common experience of struggling to regain composure when we are ‘weak’ with laughter.

In Table 1, we present a simplified framework for assessing humour cognition that summarises functional neuroimaging evidence concerning the brain basis of humour with proposed clinical associations requiring substantiation in further work.

Future directions

Observations such as these in the healthy and damaged brain should encourage neurologists to enquire more systematically about their patients’ humour sensibilities and for cognitive scientists to develop frameworks that can reconcile lesion and functional neuroimaging work. It is clear that humour, as an aspect of brain function, is multi-dimensional and highly distributed. Admittedly no single cognitive model is ever likely to subsume the double entendres of Benny Hill, the acerbic social commentary of Peter Cook or Woody Allen, the sparkling wordplay of Wilde and Molieres, the
whimsical meanderings of Peanuts. Nevertheless, humour may present a useful model for studying certain complex behavioural functions of high clinical relevance: these include the resolution of ambiguity and incongruity mentalising and the exercise of empathy, and the putative ‘lexicon’ of jokes (particularly slapstick scenarios) that may be laid down in early childhood. These different dimensions of humour processing might be probed by customised stimuli that control for potentially confounding surface characteristics (for example, Figure 1). More broadly, if humour serves to debug inferential errors in our comprehension of the world, it might turn out to have a key role in the maintenance of cognitive well-being: perhaps the enduring appeal of Rabelais, the Pythons and Dali’s Aphroditeus: Telephone reflect such neural housekeeping by the absurd and the surreal. If it seems ironic to have two neurologists write on humour, perhaps a more compelling lead lies with literature, which is replete with melancholy clowns and the wisdom of fools. We hope the neuroscientific study of humour will help us to a better understanding of our patients and the predicaments they face, which do, after all, encompass some of the more grim and bitter ironies of medical practice.

REFERENCES