SCIENCE AND SOCIETY

The neural basis of humour processing

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Abstract | Humour is a vital component of human socio-affective and cognitive functioning. Recent advances in neuroscience have enabled researchers to explore this human attribute in children and adults. Humour seems to engage a core network of cortical and subcortical structures, including temporo-occipito-parietal areas involved in detecting and resolving incongruity (mismatch between expected and presented stimuli); and the mesocorticolimbic dopaminergic system and the amygdala, key structures for reward and salience processing. Examining personality effects and sex differences in the neural correlates of humour may aid in understanding typical human behaviour and the neural mechanisms underlying neuropsychiatric disorders, which can have dramatic effects on the capacity to experience social reward.

Laughter occurs in all cultures worldwide and is a universal component of the human experience[1,2]. In human infants, laughter is one of the first social vocalizations[3], and laughter's early onset (at approximately 4 months of age) in response to the actions of others suggests that it has innate components[1,2,4]. In contrast to laughter, which is generally understood to be a reflex-like physiological–behavioural response, humour is believed to represent a rather complex higher-order emotional process[5]. Specifically, "humour is a broad term that refers to anything that people say or do that is considered funny and tends to make others laugh, as well as the mental processes that go into both creating and perceiving such an amusing stimulus, and also the affective response in the enjoyment of it" (REF. 6). Despite such multiple usages and definitions of humour, nearly all of us can easily recognize humour when we experience it[7,8].

There are many theories that explain the pervasive role of humour in society. Among these, three theories are related to the functional role of humour in a proximal (psychology and physiology) or ultimate (natural selection) sense. According to the superiority theory, aggression is regarded as an essential component of humour, particularly so if playful[6]. In line with this theory, a central function of humour is to maintain social order and to reinforce social bonding[9] by allowing people to express disagreeable feelings in a more positive way. A related theory, tension-relief, conceptualizes humour as a mechanism for physiological release of tension[6]. Hence, people experience humour and engage in laughter because it dispels pent-up stress[9]. Another potential role of humour in society is suggested by linking it with sexual selection theory[10,11]. In so doing, humour is proposed to act as a fitness indicator that provides mating partners with information about underlying mate quality, especially for women judging men. In addition to these three theories on the functional role of humour, one prominent cognitive humour theory attempts to account for how people understand humour. The 'incongruity detection and resolution' theory suggests that humour requires two elements: the introduction of incongruity, created by the simultaneous presence of two habitually incompatible elements, which produces an unexpected violation of expectations, convention, fact or intention, and results in cognitive arousal; and incongruity resolution associated with amusement[6,12–14]. Together, these frameworks for humour point to the breadth and depth of humour's role and functionality in human experience.

Here, we propose that rigorous scientific study of the neural basis of humour will shed light on the importance of humour to the human experience. Our understanding of how individual variation influences communication and adaptation (both in health and in illnesses in which humour may be adversely affected; for example, brain disorders such as autism, major depression and schizophrenia) may also be enhanced through brain-based research. The aim of this article is to provide a comprehensive summary of the recent functional MRI (fMRI) findings that shed light on the neurobiological basis of humour appreciation in humans and to outline directions for future research. We provide a brief overview of the relevant mental and social operations that are inherent to humour processing, followed by a detailed discussion of brain-based fMRI studies that examine humour and its potential clinical relevance. We conclude with a brief summary and offer perspectives on the future direction of neuroscientific studies of humour.

Evolution and benefits of humour

Humour can lead to positive emotion[15] and is thought to serve important evolutionary socio-emotional purposes. Extant findings highlight its key role in building and maintaining relationships, emotional health and cognitive function[6]. Humour helps us to communicate ideas, attract partners, boost mood and cope in times of trauma and stress[16–22]. These beneficial manifestations are complemented at the physiological level, with humour acting as a natural stress antagonist that can potentially enhance the cardiovascular, immune and endocrine systems[23–27]. Examples of such positive effects of humour on physiology include faster cardiovascular recovery, decreased cortisol levels after stress and improved natural killer cell activity. Furthermore, as a prototypical positive human cognitive state, humour can increase life satisfaction by building resilience[28]. Resilience is defined as the ability of most people, when exposed to extraordinary levels of stress and trauma, to maintain normal psychological and physical functioning and avoid serious mental illness[29]. Although the above work provides some evidence that humour can have healing effects, it is important to recognize that more rigorous research is still needed, particularly studies including control groups and applying established (psychological) definitions of humour[30,31].

Although we share some of the basic properties underlying laughter and smiling with other hominids, mainly related to their association with a social safety and play signal (BOX 1), humour defined as mental play with words and objects and conceptualized as "enjoying incongruity" (REF. 32) is recognized as a human-specific characteristic[4].

Given these considerations, it is surprising that far less research attention is paid to elucidating the development and function of positive emotional states in humans, such as those attained through humour, than of basic negative emotional states such as fear[33–35] (but also see REF. 26).

Functional neuroanatomy of humour

During the past 15 years, several fMRI studies (predominantly in adults) have probed the neural substrates of humour appreciation in humans (TABLE 1). In these studies, the stimulus modalities used can be fundamentally dissociated into two groups: verbal and visual. Verbal stimuli comprise either written or auditory information and can be further differentiated into phonological versus semantic jokes, funny versus nonsense or 'garden path' punchlines, and (non)funny versus (un)ambiguous sentences versus noise. In turn, visual stimuli differ mainly according to their manner of presentation, which can be static (for example, cartoon images) or dynamic (for example, short movie clips) (also see BOX 2). Accordingly, humour appreciation has been found to activate a large set of cortical and subcortical brain areas subserving many cognitive and emotional functions (see below and FIG. 1). Similar activation patterns seem to emerge when using parametric data analysis procedures to capture brain areas in which humour processing positively correlates with subjective funniness ratings (FIG. 2; TABLE 1). This is in agreement with results from one fMRI investigation[36] showing that subjective funniness rating or labelling during humour appreciation does not disrupt the brain's response to humour but even seems to have sustaining effects, particularly in brain regions associated with emotion.

Despite the use of various stimulus modalities recruiting distinct brain areas in a task-specific manner, as well as the application of different analysis approaches (main effects contrasts versus parametric modulation), there is a convergence of the findings indicating two dissociable, albeit interdependent, core processes of humour appreciation in humans.

A cognitive component is reliably associated with (residual[30]) incongruity detection and resolution, which is also referred to as humour comprehension in a recent verbal humour processing model[14]. This cognitive component is thought to rely fundamentally on basic visual, auditory and/or verbal processing (in a task- and stimulus-modality-dependent manner), as maintained by activity in the visual and auditory cortices; and on the activation of language and semantic knowledge areas, including the (particularly left) inferior frontal gyrus (IFG; Brodmann area 45 (BA45), BA46 and BA47) and the temporal pole (TP; BA38). In the case of stimuli requiring the juxtaposition of mental states (theory of mind (ToM)), humour comprehension will also recruit activity in cortical midline structures, including the medial prefrontal cortex (mPFC), posterior cingulate cortex (PCC) and precuneus (PREC), as well as the (anterior and posterior) superior temporal gyrus (STG) and superior temporal sulcus (STS). Finally, because incongruity can also involve error detection or monitoring, dorsal anterior cingulate cortex (ACC) activation has been reported in such contexts (for references, see TABLE 1). After a thorough review of the literature, we suggest that all of these mechanisms converge towards a core processing area of incongruity detection and resolution, which not only includes the temporo-parietal junction (TPJ; BA22, BA39 and BA40) but also extends ventrally into the temporo-occipito-parietal junction (TOPJ; BA37, BA39 and BA40)[37]. This area of the human brain receives multimodal input from different sensory afferents and is also known to be activated during self-related processing and ToM. Furthermore, it is involved in the detection of unexpected stimuli of behavioural relevance and linked

Box 1 | **The evolution of humour in humans: genetic and cultural influences**

Humour in humans is thought to be tightly linked structurally and conceptually with the expression of Duchenne laughter[1], a genetically predisposed[4,91] and inherently positive emotion that elicits 'genuine' or 'real' smiles[92]. Derived from the primate relaxed open-mouth play face[93], such Duchenne laughter is primarily elicited in situations in which a sudden unexpected change in events occurs within a safe social surrounding. This includes 'rough-and-tumble' play, tickling, physical mishaps and pleasant surprise in infants (for example, a 'peek-a-boo' face expressed by a parent), which are referred to as 'proto-humour' (REF. 11). By contrast, Duchenne laughter elicited by incongruity-based conceptual humour, primarily in adults, is associated with 'formal' attempts at inducing laughter[11]. However, proto-humour and Duchenne laughter are often tightly linked with one another. Darwin associated humour with "tickling of the mind" (REF. 94), and there seems to be a relationship between the propensity to laugh when tickled and to laugh at and use humour (in adults)[95]. Together, the spontaneous laughter of human infants, tickling and formal adult humour all share what is essentially a phylogenetically and ontogenetically conserved structure and context, referred to as non-serious social incongruity[11].

Despite their evolutionary origin being linked with genetic predispositions, Duchenne laughter and humour are not considered to be completely resistant to modulatory influence. In this context, cultural norms and related learning mechanisms are mentioned as key shaping factors[11]. A good illustration of such relations is the cultural variation observed in the subject matter of humour, which can vary from toilet- and sex-based humour to political humour and span a wide spectrum of cultural institutions and customs[11]. Furthermore, it is known that learning processes within different cultures strongly influence the context, frequency, intensity and expression of laughter as a function of display rules and varying norms and customs[11]. Along these lines, the comparison of three studies investigating the genetic versus environmental components of humour in adult monozygotic versus dizygotic twins from the United Kingdom, Australia and North America is noteworthy[96]. The principal measure was individual differences in humour expression according to four distinct humour styles, of which two are positive (affiliative and self-enhancing) and two are negative (aggressive and self-defeating). The results revealed that, for studied twins from Australia and the United Kingdom, additive genetic and environmental factors accounted for the variance in all four humour styles. For twins from North America, additive genetic and environmental factors accounted for the variance in the two positive humour styles but not for the two negative humour styles, for which variance was accounted for solely by environmental factors. Such findings probably demonstrate cross-cultural differences in what are deemed to be acceptable uses of humour and suggest that there is more cultural pressure surrounding negative rather than positive humour. However, future studies from different cultures are needed to confirm and extend these findings.

Table 1 | **List of all fMRI (and one PET) studies on humour in humans included in the meta-analyses***

Stimulus modality	Contrast depicted	Summary of main findings	Refs
Studies including main effects of humour contrasts			
Visual static	ToM cartoon versus non-ToM cartoon	Activity during ToM stories and ToM cartoons overlapped in the mPFC (paracingulate cortex)	102
Verbal written versus visual static	ToM versus non-ToM for stories versus cartoons		
Visual static versus verbal written	ToM versus non-ToM for cartoons versus stories		
Verbal auditory	Semantic funny versus non-funny	The processing of semantic versus phonological jokes produced differential activity in the posterior MTG, posterior ITG and IPG but overlapped in the vmPFC	100
	Phonological funny versus non-funny		
	Semantic versus phonological funny		
	Phonological versus semantic funny		
	Funny versus baseline (semantic and phonological)		
Visual dynamic	Natural amusement funny versus instructed smiling non-funny	Laughter or smile induced by visual comics (as opposed to voluntary movement) increased activity in the visual cortex, ATP, uncus, OFC and mPFC	103 (PET study)
Visual static	Funny versus non-funny	Humour increased activity in the TOC, IFG, ATP, SMA, dACC, mesocorticolimbic reward areas, hypothalamus and AMG	104
Visual dynamic	Humour comprehension	Humour comprehension ('getting the joke') entailed increased activity in the inferior frontal and posterior cortices, whereas humour elaboration (experience of mirth) activated the insula and AMG	105
	Humour elaboration		
Visual dynamic	Funny versus non-funny	Passive viewing of funny (versus neutral) films led to increased activity in the insula, ATP, STG, MTG and CUN	36
Visual static	ToM versus physical cartoons	ToM (versus physical) cartoons entailed increased activity in the PREC, IPL and MTG (in healthy control individuals only)	69
Visual static	Funny versus non-funny	Humour (versus neutral) increased BOLD signal change in the FG, STG, MTG, IFG and cerebellum	106
Visual static with caption	Humour for language-based gag versus sight gag	High-level visual areas activated more strongly during visual humour; classic language areas activated more strongly during language-dependent humour; a common network activated for both types of humour comprising the AMG and midbrain (associated with amusement)	97
Visual static without caption	Humour for sight gag versus language-based gag		
Visual static overall	Funny versus non-funny		
Visual static	Funny versus non-funny	Humour (versus neutral) entailed stronger BOLD signal change in the sensorimotor cortex, SMA, PFC, TOPJ, MTG, ATP, AMG, PHG, thalamus, putamen, midbrain and cerebellum	107
Visual static	ToM versus semantic versus visual puns versus irresolvable incongruity	Semantic puns and incongruity resolution activated a (left-sided) network including the TPJ, IFG and vmPFC; visual puns showed more activity in the extrastriate cortex; ToM cartoons increased activation in the SFG, mPFC, TPJ, aSTS, ATP and FG	98
Visual static	Incongruity resolution versus nonsense	Incongruity resolution (versus nonsense) recruited the mPFC, SFG and TPJ	58
Visual static	Cartoon versus neutral	Humour (versus neutral) increased activity in the angular gyrus, SFG, ACC, PREC, thalamus, MTG and cerebellum	63
Visual dynamic	High versus low funniness	High (versus low funny) clips elicited stronger activation in the mesocorticolimbic areas, TPJ, SMA and IFG	108
Verbal auditory	Funny versus non-funny	Humour (versus neutral) increased BOLD signal change in the MTG, midbrain, AMG, cingulate, visual cortex, ATP, OFC, FG, IFG, SFG and ACC	109
Visual dynamic (children)	Funny versus non-funny	Funny (versus non-funny) movies increased activity in the TOPJ and midbrain; funny (versus positive) movies entailed stronger activity in the STG and SMG	37
	Funny versus positive		
Verbal written	Funny versus 'garden path'	Funny (versus 'garden path') sentences increased activity in the AMG, midbrain and PHG	101
Verbal written	Funny versus nonsense	Funny (versus nonsense) sentences entailed stronger activity in the SFG and IPL	14

Table 1 (cont.) | **List of all fMRI (and one PET) studies on humour in humans included in the meta-analyses***

Stimulus modality	Contrast depicted	Summary of main findings	Refs
Visual dynamic (children)	Funny versus non-funny	Funny (versus neutral) entailed increased activity in the IPL, midbrain and bilateral PCG	46
	Funny versus positive	Funny (versus positive) entailed stronger activity in the STG, TPJ, midbrain, pSTS and OCC	
Studies including parametric modulation of funniness			
Verbal auditory	Funny versus baseline	Activity in the vmPFC overlapping for both phonological and semantic jokes correlated positively with funniness ratings	100
Visual static	Funny versus non-funny	Activity in response to humour in the mesocorticolimbic areas, IFG, ATP and TOC correlated positively with funniness ratings	104
Visual dynamic	Funny versus non-funny	BOLD signal change to funny films correlated positively with funniness ratings in the SFG, IFG, ACC, insula, STG, thalamus, caudate, putamen and cerebellum	36
Visual static	Funny versus non-funny	BOLD signal change to humour correlated positively with funniness ratings in the cerebellum, FG, STG, IFG, MTG, AMG and PHG	106
Visual static	Funny versus non-funny	Increased scores of funniness correlated positively with brain activity in response to humour in the STS, MTG, mesocorticolimbic areas, hippocampus, STG, SFG and cingulate	97
Visual static	Funny versus non-funny	Positive correlation between funniness ratings and humour appreciation in the mPFC, insula, basal ganglia, STG and cerebellum	110
Visual static	Funny versus neutral	Funniness ratings correlated positively with humour activity in the SFG, ACC and lingual gyrus	63
Visual dynamic	High versus low funny	Activity in response to funny movies correlated positively with funniness ratings in the cerebellum, TPJ, SMA, mesocorticolimbic areas, STS, PHG, ITG, AMG, motor cortex and ATP	108

ACC, anterior cingulate cortex; AMG, amygdala; aSTS, anterior STS; ATP, anterior temporal pole; BOLD, blood-oxygen-level-dependent; CUN, cuneus; dACC, dorsal ACC; FG, fusiform gyrus; fMRI, functional MRI; IFG, inferior frontal gyrus; IPG, inferior pre-central gyrus; IPL, inferior parietal lobule; ITG, inferior temporal gyrus; mPFC, medial PFC; MTG, middle temporal gyrus; OCC, occipital cortex; OFC, orbitofrontal cortex; PCG, post-central gyrus; PET, positron emission tomography; PFC, prefrontal cortex; PHG, parahippocampal gyrus; PREC, precuneus; pSTS, posterior STS; SFG, superior frontal gyrus; SMA, supplementary motor area; SMG, supramarginal gyrus; STG, superior temporal gyrus; STS, superior temporal sulcus; TOC, temporo-occipital cortex; ToM, theory of mind; TOPJ, temporo-occipito-parietal junction; TPJ, temporo-parietal junction; vmPFC, ventral mPFC. *The investigations are separated into those using a main effects contrast approach (FIG. 1) and those using a parametric modulation analysis with subjective funniness scores (FIG. 2). Some studies included both types of analyses. The stimulus modality used, principal contrast (or contrasts) and main findings are also listed. Studies are sorted by year of publication, ascending.

to increased connectivity with ventral frontoparietal areas associated with attention and decision making[38–41]. The TOPJ therefore seems ideally suited for incongruity detection and resolution. However, it should be noted that incongruity detection and resolution have not yet been functionally and anatomically dissociated, because they occur in rapid temporal succession (virtually at the same time), making it difficult to separate them with current fMRI methods. Investigations using electroencephalography or magnetoencephalography might be better suited to address this issue[42–44].

An emotional component is also consistently found to be involved in humour appreciation. Although this emotional component recruits the insula, the ventral ACC and the supplementary motor area (SMA), it is primarily associated with increased activity in mesocorticolimbic dopaminergic brain areas (that is, the ventral tegmental area, substantia nigra, nucleus accumbens, ventral striatum and ventral mPFC) (FIG. 1). Changes in the blood-oxygen-level-dependent (BOLD) signal in mesocorticolimbic dopaminergic areas are known to increase during various reward-related responses[45], and such activations are also commonly reported by means of correlational analyses with subjective funniness ratings (FIG. 2; TABLE 1). Accordingly, this is generally understood to represent a positive feeling of mirth or reward in the course of humour appreciation, which is also referred to as humour elaboration[14]. The exact nature of positivity associated with humour, however, is not yet completely understood. This is probably for several reasons. First, increased subjective ratings of funniness also correlate with BOLD signal change during humour processing in cognitive areas comprising the TPJ, TP, mPFC, ACC, PCC and PREC (FIG. 2). Therefore, heightened funniness scores could also be linked to humour properties other than the basic sense of reward typically linked with dopaminergic signalling. Second, and related to this notion, most neuroimaging studies of humour appreciation compare funny stimuli to a neutral control condition but not to a similarly positive state without humour. There are only two investigations to date that used such a positive-state control[37,46]. Although these studies were conducted in children, they show evidence that humour appreciation differs from a more generalized response to reward; this difference is probably related to the satisfaction of detecting and resolving the incompatible elements of humour. More extensive testing of optimal control conditions for humour studies is required.

Humour is also reliably associated with activation of the amygdala (FIGS 1,2). Although the human amygdala is known to be involved in reward-related mechanisms[47], its functional profile is more comprehensively understood to resemble a relevance detector[48–50]. The amygdala is attributed a key role in selecting from a constant incoming stream of diverse information those inputs that are most relevant to the goals or intentions of the organism at a given moment in time. Such

Box 2 | **Different types of humour used in fMRI research**

The extant literature using functional MRI (fMRI) to study humour includes different types of stimuli for humour induction. Below is a summary of the most prominent categories, which are dissociated by stimulus modality (verbal versus visual) and presentation mode (static versus dynamic).

Static visual stimuli

Visual pun. This kind of humour uses visual resemblance as the main element inducing incongruity, which is usually achieved by one (or more) part of an image having different possible meanings. In the provided example (see the figure, part **a**), the diagonal line can stand for the sea (activated through the fin) or the mountain (activated through the skis).

Semantic pun. Such humour is based on pure semantic relations and not visual resemblance (as in a visual pun). In the provided example (see the figure, part **b**), the patient has died, which can be seen on the monitor in the form of an angel flying away. There is no visual resemblance between the angel and the expected flatline, which indicates no heartbeat on an electrocardiogram.

Theory of mind humour. In contrast to visual and semantic puns, this kind of humour requires mentalizing abilities in order to get the joke. In the given example (see the figure, part **c**), one has to understand that the woman does not know what will happen to her, whereas the man does; such discrepancy in subjective knowledge represents the central element of incongruity.

Language-dependent visual humour. Under certain circumstances, incongruity during visual humour perception is introduced through the image caption and not the image (that is, the drawing, cartoon, and so on). This is differentiated from 'sight gags' containing a legend that are still experienced as funny when the caption is removed[97].

Control conditions for static visual humour usually consist of images with an irresolvable incongruity[98] or stimuli in which the incongruent (funny) element has been removed[97].

Dynamic visual stimuli

Such humour is usually presented by means of short movie clips, taken either from professional comedy programmes or from amateur footage, including scenes in which humans and/or animals display unusual behaviour and/or the shown action takes an unexpected (incongruous) twist. Some studies use full-length episodes of a comedy series, in which humour will not be purely visual: there will also be an incompatibility between behaviour and speech comparable to language-dependent visual humour (see above).

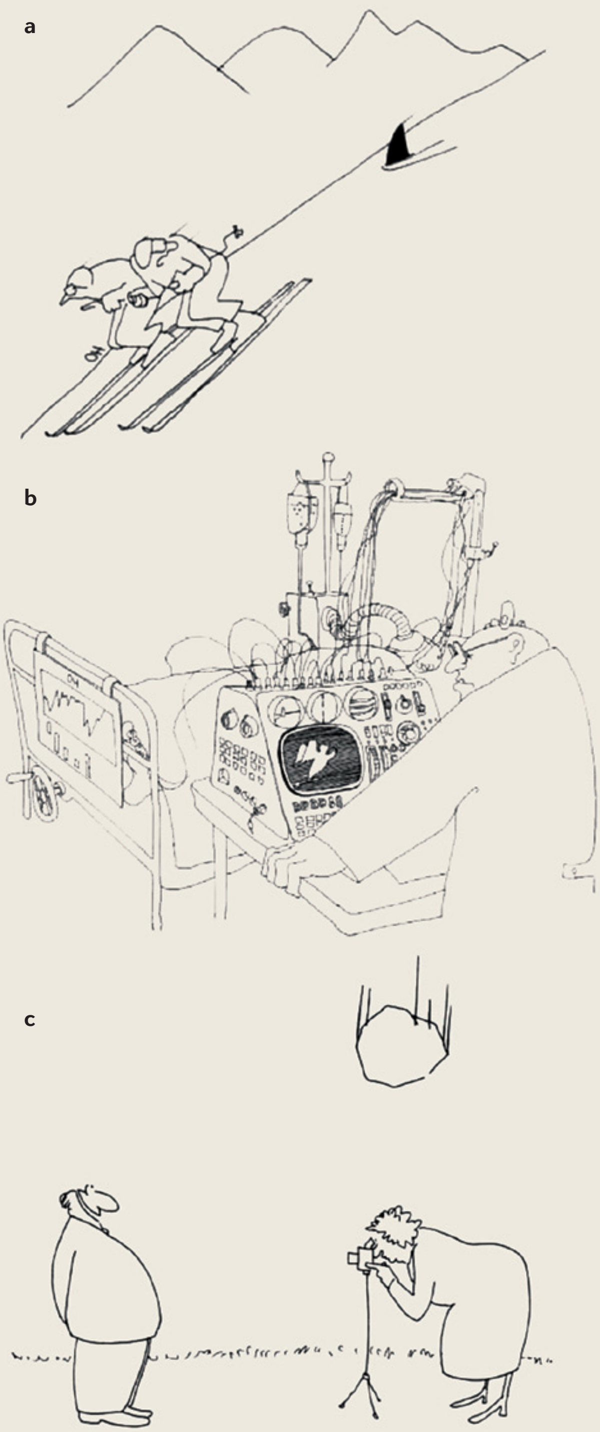
Control stimuli normally include comparable 'neutral' scenes with no funny elements. In rare cases, positive or rewarding but non-funny scenes have been used as more appropriate controls[37,46,61].

Verbal stimuli

There is a wide variety of verbal jokes that originate from different structural levels of language[99]. These are phonetic, (lexico-)semantic, morphological, phraseological and syntactical. Phonetic and semantic jokes are the main types of jokes used in fMRI humour research.

Phonetic jokes. The most commonly used underlying principle is ambiguity caused by an identical or very similar pattern of sounds conveying different meanings. For example: "Why did the golfer wear two sets of pants? He got a hole in one." (REF. 100).

Semantic jokes. In this type of humour, there is either a deviation against lexico-semantic rules or a violation at the pragmatic communicative level that introduces ambiguities in the interpretation of the described situation. This can be achieved by the use of synonyms or antonyms (words with the same or opposite meaning, respectively), homonyms (phonetically identical but semantically different words), polysemy (in which a lexical item has a range of different meanings) or paronymy (in which words sound similar but mean different things)[99].



Different baselines have been used for verbal jokes. Usually, the punchline is exchanged with a logical or congruent statement. However, in some cases, the punchline has been modified to include either nonsense or 'garden path'-like elements; the latter introduces non-funny and irresolvable incongruity[14,101].

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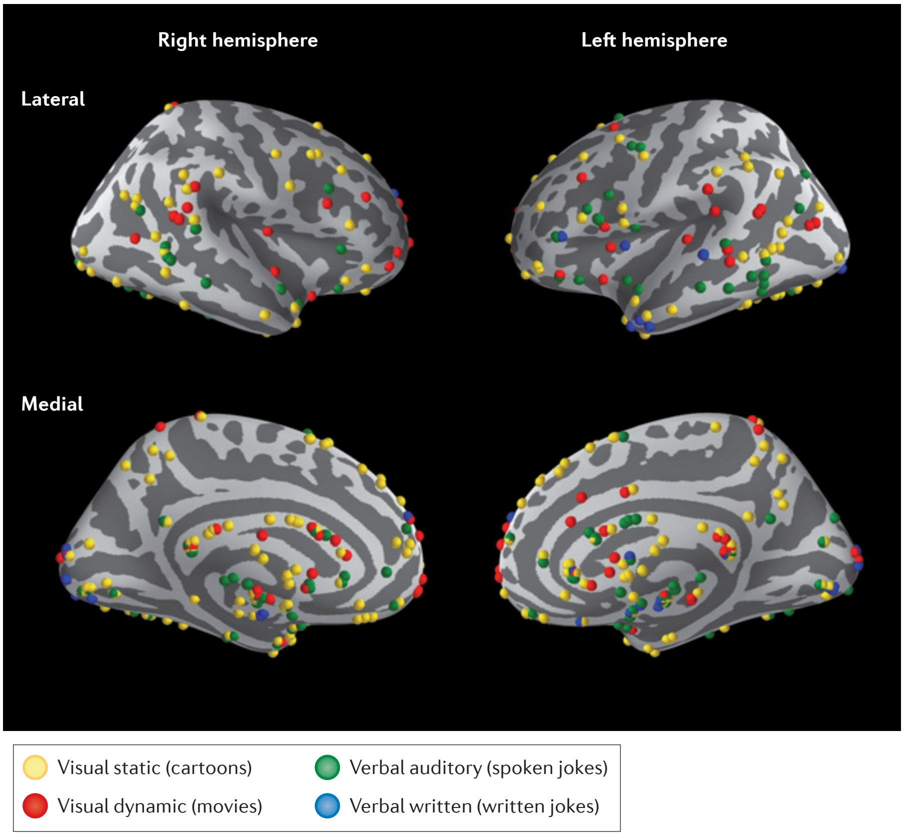

Figure 1 | **Meta-analysis of activations during humour processing.** The meta-analysis results in the figure show that humour processing recruits a large set of cortical and subcortical brain areas that maintain both the cognitive and the emotional components of humour in a stimulus modality- and task-dependent manner. Literature review suggests that humour appreciation converges on two core processes: 'incongruity detection and resolution', as maintained by the temporo-occipito-parietal junction; and reward and salience processing involving mesocorticolimbic areas and the amygdala. Each sphere represents peak coordinates of reported activation clusters from humour studies using functional MRI (TABLE 1) in Talairach coordinates, projected on a template single-subject flattened structural brain image. Computed contrasts to derive these activations include funny versus non-funny, theory of mind (ToM) funny versus non-ToM funny, semantic funny versus phonological funny (and vice versa), natural amusement versus instructed smiling, language funny versus 'sight gag' funny (and vice versa), funny versus irresolvable incongruity, incongruity resolution versus nonsense, funny versus positive, and funny versus 'garden path' (for a definition of humour conditions, please refer to BOX 2).

'biological value' seems to be prominently related to the processing of salience, significance, ambiguity and unpredictability[50]. Accordingly, humour appreciation is likely to activate the amygdala because it contains not only several of the above processing components related to basic incongruity detection and resolution but also a positive interaction signal with high intrinsic social significance. Amygdala involvement in humour appreciation therefore underscores the importance of humour as a social process for humans and highlights the susceptibility of this process to various moderating influences, such as personality, sex and the presence of neuropsychiatric disorders that modify the biological value of humour.

Personality, sex and brain disorder

Considerable evidence from data in adults indicates that humour is linked with positive individual, as well as group, outcomes[6,11,20,22,51–53]. Conversely, humour perception has been observed to be reduced in conditions associated with negative mood states, such as major depression[54], and in people suffering from social anxiety[55]. One way to investigate such associations is to examine brain activity in response to humour as a function of personality traits that are risk factors for psychopathology, such as introversion–extraversion and neuroticism[56]. To date, two fMRI investigations in adults[57,58] have used such an approach. Preliminary results showed that positive traits such as emotional stability (the opposite of neuroticism) and experience seeking (related to extraversion) may enhance humour processing, as indicated by increased activity in the lateral prefrontal and temporal cortices, hippocampus and mesocorticolimbic circuits. Conversely, high introversion has been found to correlate with amygdala activity during humour appreciation. These preliminary data indicate that both cognitive and emotional processes during humour appreciation can be moderated by personality traits in adults and are in agreement with behavioural data showing that extraversion is related to the amount of positive affect in response to humour[59,60]. Comparable data from earlier developmental stages are scarce, but a recent study provides preliminary evidence that, in 6–13-year-old children, humour processing is already moderated by temperament traits such as emotionality, shyness and sociability[61]. Overall, these findings suggest that humour appreciation may be susceptible to individual differences in personality in both children and adults, highlighting the need for further research into the developmental trajectories of this uniquely human positive cognitive state by means of larger cross-sectional and/or longitudinal studies.

The findings noted above are complemented by data from two fMRI investigations probing sex differences in adult humour processing[62,63]. The first study showed that the TOPJ, TP and IFG were activated during humour appreciation in both sexes. However, activity in the IFG was stronger in females, who displayed additional BOLD signal change in mesocorticolimbic reward areas. These findings were interpreted as indicating a greater degree of executive processing and language-based decoding, as well as a greater reward network response and possibly less reward expectation in females[62]. The notion of stronger emotional reactivity in females during humour perception was supported by the second study in adults[63]. An examination of sex differences in humour appreciation in 22 children (aged 6–13 years) found similar activation patterns to those reported in adults[46]. Stronger activity in the midbrain and amygdala in response to humour was observed in girls compared with boys, who in turn displayed stronger activation in the ventral mPFC. This supports the notion of increased reward response and salience in girls, perhaps owing to less reward anticipation during the task. Overall, such emerging data on sex differences in humour appreciation in both adults and children support the fitness indicator hypothesis of humour

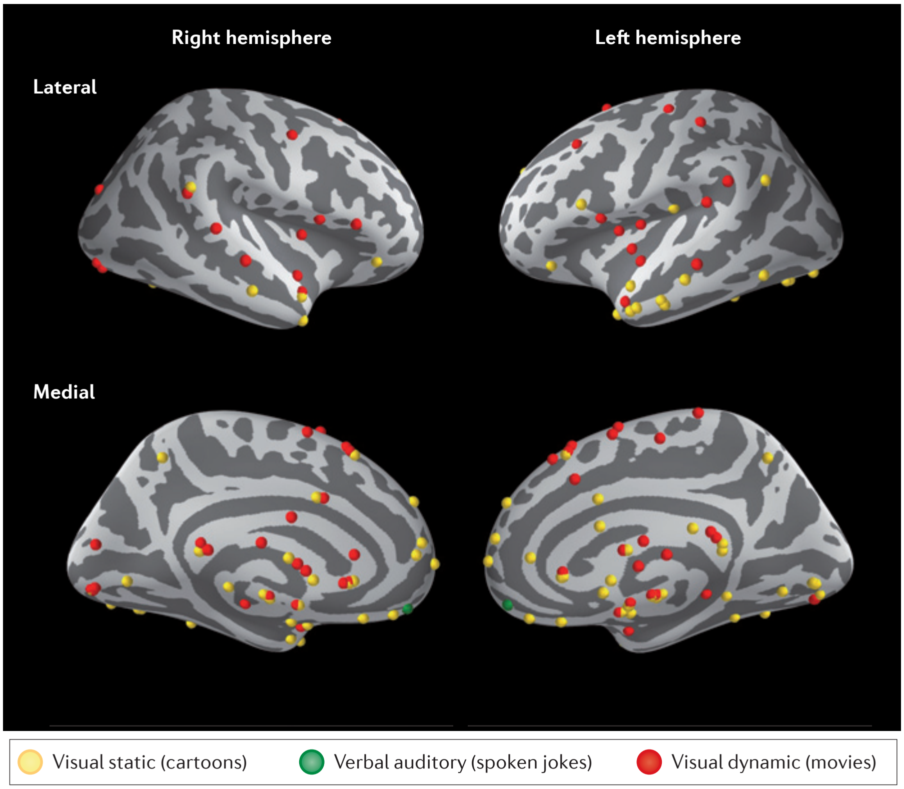

Figure 2 | **Meta-analysis of activations involving parametric modulation of humour.** The meta-analysis results in the figure show that the degree of funniness reported by participants positively correlates with brain activity in response to humour in a large set of cortical and subcortical brain areas maintaining both the cognitive and the emotional components of humour. These areas include the temporo-parietal junction, mesocorticolimbic circuit and amygdala. Each sphere represents peak coordinates of reported activation clusters from humour studies using functional MRI (TABLE 1) in Talairach coordinates, projected on a template flattened structural brain image. Parametric modulation analyses were always based on funny versus non-funny contrasts.

function related to sexual selection theory (see above and REF. 11) by illustrating that females may be more receptive to, and display less reward expectation from, humour, regardless of age. Further research to confirm and extend such findings is needed.

Behavioural, imaging and brain lesion findings associated with humour and psychopathology have also been published. For example, one line of research reports deficient humour processing in autism[64–67]. These results are linked to the individual's difficulties in understanding the social aspect of humour requiring ToM and, more generally, in integrating cognitive and affective information. Prominent neural substrates for such functions are the TPJ and (right) IFG, the activity of which has been found to be altered in people with autism[64,66,67].

Other research indicates impaired humour appreciation in schizophrenia[68–71]. Affected individuals display reduced humour recognition associated with impaired ToM abilities and diminished mPFC activity in response to jokes requiring the attribution of mental states (BOX 2). Therefore, in both autism and schizophrenia, humour appreciation deficits seem to be predominantly related to disturbed ToM and/or socio-emotional integration mechanisms, and thus cognitive humour processing (see above). In accordance with such findings, there are data from patients with focal brain damage linking humour-processing deficits with impaired (right) frontal lobe function[67].

Finally, a link between altered humour appreciation and cataplexy has been noted[72,73]. Cataplexy refers to episodes of sudden and transient loss of muscle tone triggered by strong emotions, usually occurring in association with the complex sleep–wake disorder called narcolepsy. Results from fMRI investigations in patients suffering from cataplexy converge in suggesting an overdrive of the emotional humour circuitry (ventral striatum and amygdala), which might be linked with a compensatory suppression of hypothalamus activity by cortical inhibitory regions.

Taken together, these data on personality, sex differences and psychopathological conditions associated with humour appreciation demonstrate the psychological, psychiatric or even neurological variation related to both the cognitive and the emotional components of humour. Moreover, many of these effects can be observed in both adults and young children. Such findings highlight the clinical relevance of investigating humour appreciation by means of neuroimaging methods at different developmental stages.

Conclusions and perspective

Humour is a ubiquitous component of human cognition, communication and interaction. It has numerous potential beneficial effects on personal, psychological and physical well-being, and positively influences social and group processes.

On a functional neuroanatomical basis, humour appreciation recruits a wide range of brain areas, which differentially activate as a function of distinct humour-inducing stimulus modalities and task requirements. Nonetheless, all of these auxiliary mechanisms seem to converge towards two core processes of humour appreciation: incongruity detection and resolution (the cognitive component); and a feeling of mirth or reward (the emotional component). Whereas the cognitive component seems to rely principally on activity in the TOPJ, the emotional component appears to involve mesocorticolimbic dopaminergic pathways and the amygdala. Our perspective is that none of the regions or networks underlying human humour appreciation (for example, sensory processing, working memory, incongruity detection and resolution, and reward) evolved individually or in concert with another expressly for that function. Rather, the combination of several of these regions and/or networks in the service of humour appreciation became increasingly prominent in human society because of its importance in processing social information. Although the differentiation between cognitive and emotional components of humour is not new[1], evidence from recent neuroimaging studies strongly supports this differentiation.

Future studies focused on the neuroscience of humour should address several outstanding areas of research. Perhaps most importantly, more data are needed to elucidate the development of humour throughout the human lifespan and its modulation by various factors such as culture, personality, sex, age and intelligence quotient (IQ). Such investigations are particularly desirable if they incorporate longitudinal study designs. However, we add the caveat that the current fMRI scanner environment limits the extent to which humour can be studied, particularly in comparison to naturalistic settings. Other functional imaging modalities, such as functional near-infrared spectroscopy[74–76], might provide methodological advantages from this standpoint. It also seems vital to extend existing data with research using appropriate control conditions and differentiating between incongruity detection and resolution, and 'proto-humour' versus 'formal' humour (BOX 1). Such experiments will shed more light on the neural bases of human humour appreciation. In addition, we note that the present article emphasizes the clinical relevance of humour related to neuropsychiatric disorders (such as autism, schizophrenia, anxiety, depression and cataplexy). However, there are many more domains in which the positive relationship between humour and coping and resilience could be more extensively explored in the future. As briefly mentioned above, it has been suggested that humour exerts many beneficial effects on physical and mental health, which is of potential interest in several medical settings, including procedures with ill children, older individuals or those in palliative care[19,77–82]. Furthermore, humour-based (psycho)therapy and counselling may help to promote healthy relationships in general, including marriage and family settings in particular[83–86]. Finally, the use of humour has been suggested to be beneficial in education for both learning and testing, as well as in the workplace, where it can enhance social functioning, ease negotiation and mediation, and support leadership[87–90]. Such preliminary findings on the beneficial effects of humour on physical and mental health need to be further evaluated under stringent scientific conditions. A deeper understanding of the neural bases of humour appreciation nonetheless seems relevant for many different contexts, and has the potential to positively affect the well-being of a wide range of individuals.

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