Humour appreciation: a role of the right frontal lobe

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Summary
Humour occupies a special place in human social interactions. The brain regions and the potential psychological processes underlying humour appreciation were investigated by testing patients who had focal damage in various areas of the brain. A specific brain region, the right frontal lobe, most disrupted the ability to appreciate humour. The individuals with damage in this brain region also reacted less, with diminished physical or emotional responses (laughter, smiling). Performance on the humour appreciation tests used were correlated in a distinct pattern with tests assessing cognitive processes. The ability to hold information in mind (working memory) was related to both verbal (jokes) and non-verbal (cartoon) tests of humour appreciation. In addition, the demands of the specific type of humour test were related in a logical manner to cognitive processes, verbal humour being associated with verbal abstraction ability and mental shifting and cartoon humour being related to the abilities to focus attention to details and to visually search the environment. The ability of the right frontal lobe may be unique in integrating cognitive and affective information, an integration relevant for other complex human abilities, such as episodic memory and self-awareness.

Keywords: humour; right frontal lobe; working memory; verbal abstraction; mental shifting

‘Men will confess to treason, murder, arson, false teeth, or a wig. How many of them will own up to a lack of humour?’
Frank Moore Colby, 1997

Introduction
Humour plays a powerful and unique role in human life, with wide-ranging effects on many aspects of functioning. Humour is a basic ingredient of binding in society; it provides an effective means of communicating a wide range of ideas, feelings and opinions (Brownell and Gardner, 1988). Humour is therapeutic, providing a mechanism for coping with daily stressors (Lefcourt and Martin, 1986) and having positive effects on the immune (Lefcourt et al., 1990) and central nervous (Fry, 1992) systems. It is such a key element in the human behavioural repertoire that it is considered to be a defining human attribute (Nahemow, 1986). In fact it is so highly valued and desired that very few people are willing to admit to a lack of a sense of humour (Omwake, 1937; Allport, 1961).

Previous research investigating the effects of brain damage on humour has pointed to the role of the right hemisphere in the ability to appreciate humour. Gardner et al. (1975) found that both left and right hemisphere patients were impaired in their ability to detect the most humorous cartoon in a cartoon array. However, a different order of difficulty across items and a different profile of mirth responses differentiated right from left hemisphere patients. That is, while left hemisphere patients behaved in a manner similar to normal subjects, right hemisphere patients showed much more variability in mirth and a dissociation between their cognitive and affective responses. Wapner et al. (1981) found that, in comparison with normal subjects, right hemisphere patients showed a reduced ability to offer a reasonable explanation for cartoon humour and chose both a significantly lower percentage of correct choices of the funniest caption from among four possible captions and the greatest percentage of non sequitur endings as funniest. They concluded that the result with non sequiturs suggests that the right hemisphere patients recognize the importance of the form of a joke but they have difficulty fully interpreting a joke’s content. Another series of studies (Brownell et al., 1983; Bihrlle et al., 1986) found that damage to the right hemisphere selectively affected patients’ ability to process one of two major components of humour: the ability to revise an initial interpretation in order to integrate a sentence back with what came earlier in a discourse. That is, patients with right hemisphere damage showed a preserved sensitivity to the surprise element of
humour and a diminished ability to establish coherence. They seemed to retain an appreciation of simpler, slapstick humour that does not require integration of content across sentences. The impairment of right hemisphere-damaged patients in the comprehension of humour is further supported by Dagge and Hartje (1985), whose study indicated that these patients had general difficulties with the processing of humour. Although these studies indicate that the right hemisphere is important in humour appreciation, they do not provide further anatomical specificity.

Extending these initial efforts of pioneers in the study of humour, we investigated whether brain damage affects the ability to appreciate humour, whether dysfunction in specific cognitive processes is related to deficient humour appreciation, and whether there is a specific brain region or a neural network that is especially relevant. To do this, we studied patients who had an acquired single focal brain lesion restricted to an identified brain region. These patients, and comparable neurologically intact control subjects, were administered several tests which were directed to different aspects of humour, or processes that might affect humour appreciation (see Methods). First, tests of humour appreciation were administered. Two tests assessed the ability to appreciate verbal humorous statements and more formal verbal jokes. Cartoons that depended on visual details and not verbal captions for their humour were administered to provide a potential comparison of verbal and non-verbal aspects of humour. In addition to asking patients to rate how funny these items were, the patients were videotaped (with informed consent) to examine objectively their spontaneous affective responses (laughter, smiles). The second step was to control for extraneous factors that might influence results. Thus, we administered general psychological tests that provide a measure of basic abilities necessary to complete tasks involving language and perception. Finally, psychological tests which assessed cognitive functions that might be necessary for humour appreciation were given. Some of these measures were inherent in the humour tasks themselves, and others were assessed by standard neuropsychological measures.

The hypothesis was that patients with damage in the frontal regions would be more impaired on the humour tests than those with lesions elsewhere in the brain. Specifically, our expectation was that it is right frontal damage and not frontal lobe damage or right hemisphere damage irrespective of locus (as indicated in previous research) that is critical in producing deficits on humour tests. Such a finding would provide further specificity in terms of the brain region within the right hemisphere that is critical for the appreciation of humour. This hypothesis was supported by literature indicating the role of the right frontal lobe in non-literal language (Alexander et al., 1989), personality and emotions (Stuss and Benson, 1983; Stuss et al., 1992) and self-awareness (Stuss, 1991), all of which we believed were related to humour appreciation. We further hypothesized that certain cognitive processes would relate in a logical manner to the appreciation of humour, i.e. working memory, verbal abstraction ability and mental shifting would be related to the appreciation of verbal humour, while working memory and the ability to efficiently conduct a visual search and focus attention to relevant details would be related to non-verbal humour appreciation.

**Methods**

**Subjects**

Twenty-one consenting individuals between the ages of 18 and 70 years (mean age 49.4 years, SD = 13.1; mean years of education 13.05; SD = 2.8) with single focal brain damage (as assessed by CT or MRI) restricted to the frontal (right, left or bilateral) and non-frontal (right or left) regions were compared with a sex-, age- and education-matched normal control group (n = 10; mean age 49.8 years, SD = 13.6; mean years of education = 14.8, SD = 2.7) (Table 1). All patients and control subjects who participated in the study gave informed consent and ethical approval was granted by a joint ethics committee from the University of Toronto and from Baycrest Centre for Geriatric Care. All were conversationally fluent in English. All participants were right-handed. Damage in all cases was sustained in adulthood. Cases with diffuse brain damage, a history of multiple events or a history of a psychiatric illness were excluded. All lesions were carefully documented according to the atlas of Damasio and Damasio (1989). Lesion volume was quantified using a pixel tabulation method. For each patient, for each axial slice in which a lesion was evident, the size of the lesion was quantified by superimposing the lesion on a constant pixel diagram and counting the number of pixels. This provided a method of comparing lesion sizes across groups.

**Tests of humour**

All tests of humour appreciation were developed by pretesting stimuli using normal control subjects. Only those stimuli that were rated by these subjects as being unambiguously humorous were included in the final version of the tests.

**Appreciation of humorous verbal statements**

Each individual rated on a five-point scale how funny they found each of 21 humorous and seven neutral written statements. Examples of humorous statements: (i) Sign in a Hong Kong tailor’s shop: ‘Please have a fit upstairs’. (ii) In a Tokyo hotel: ‘Guests are invited to take advantage of the chambermaid’. Thirty-five items were pretested using 10 normal subjects. Only those items that were rated as being funny by at least eight of the 10 control subjects were included in the final test.

**Joke and story completion**

The incongruity-resolution model of humour (Suls, 1972) involves the ability to detect surprise (the incongruity between
Table 1  Demographic and lesion information

<table>
<thead>
<tr>
<th>ID number</th>
<th>Number of years</th>
<th>Aetiology</th>
<th>Size of lesion*</th>
<th>Lesion site</th>
<th>Age (years)</th>
<th>Years of education</th>
<th>Vocabulary</th>
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<td></td>
<td></td>
<td>Left</td>
<td>Right</td>
<td></td>
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</tr>
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<tr>
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<td>11</td>
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</table>

*Lesion size was quantified in the following manner. For each patient, each axial slice for which a lesion was evident was measured. The relative size of the lesion was quantified by superimposing the lesion on a constant pixel diagram and counting the number of pixels. † NA = not available; after the patients had been tested and placed into lesion groups based on neurological records and scans, the original brain scans were lost for subsequent analysis. Therefore, quantification of lesion size could not be completed for these two patients in the posterior group. ‡ This group consisted of patients not included in the specific anatomical localization analysis as they did not fully meet the criteria for either the impaired or unimpaired frontal subjects (see text).

the joke stem and the punch-line) and then to resolve the incongruity by establishing coherence of the punch-line with the joke. The Joke and Story Completion test was the same as that used by Brownell et al. (1983) and was used with permission of the authors. This test was included in order to replicate previous research as well as to extend it, i.e. to investigate whether further specificity of results might be available in terms of the lesion within the right hemisphere that might be correlated with impaired performance on this task.

The incongruity-resolution model of humour was tested by a series of joke stems presented in a written format, followed by four possible ending types: the funny punch-line; a logical (coherent) but not surprising ending; a surprising but not logical conclusion (slapstick); and a fourth possible ending which was not funny or coherent (a ‘no sense’ non sequitur). The participants were instructed to complete the joke stems by selecting one ending from among the four choices provided, the one that they thought was the original punch-line or the correct, funny ending. For example: The neighbourhood borrower approached Mr Smith at noon on Sunday and inquired ‘Say, Smith, are you using your lawnmower this afternoon?’ ‘Yes, I am’ Smith replied warily. Then the neighbourhood borrower answered: (i) ‘Oops!’ as the rake he walked on barely missed his face; (ii) ‘Fine, then you won’t be wanting your golf clubs—I’ll just borrow them’; (iii) ‘Oh well, can I borrow it when you’re done, then?’; (iv) ‘The birds are always eating my grass seed’.

The Story completion, with no funny punch-line presented, required just the completion of the stem. That is, for the Story condition, the participants were instructed to complete the stem by selecting from among the three possible endings (logical and straightforward; logical but unrelated; humorous non sequitur) the one that had the same main idea as the rest of the story, i.e. the one that completed the story in a logical way. This controlled for the ability to establish a coherent narrative story that was not humorous.

Non-verbal cartoon appreciation

Laughter in response to a cartoon without a verbal caption requires the detection and analysis of a specific detail in the
cartoon which provides the ‘twist’ to the context of the cartoon. This was tested by providing four similar drawings, only one of which had a funny detail. In the other three, a similar detail was altered but the change did not evoke humour. For example, the four pictures showed a man opening a closet door to get out his golf clubs. In the funny cartoon, instead of golf clubs, the golf bag contained a rake, spade and similar garden equipment. Three other identical pictures were presented in a 2×2 array, all of which contained non-humorous details such as an empty golf bag or a bag with golf clubs. As with the Appreciation of Humorous Verbal Statements test, the items were pretested using 10 normal subjects and 10 items that were rated as being funny by at least eight of the 10 subjects were included in the final test.

Dependent measurements were (i) the number of correct responses on the Joke and Story Completion test and the Non-verbal Cartoon test, (ii) funniness ratings on all tests defined as the individual’s rating of how funny the item was, using a five-point scale, and (iii) number of mirth responses. That is, humour in all tasks was measured not only by correct responses or ratings, but also by the individual’s spontaneous reactions—smiling (defined as the observation of the movement of the respondent’s lips upwards while looking at the stimulus—an evident smile) and laughter (defined as an audible response accompanied by smiling).

Cognitive functions associated with humour
A series of neuropsychological tests were administered for two reasons. They assured us that a loss of humour could not be attributed to some more basic cognitive disturbance, such as an inability to understand language or to see the details in the cartoons. In addition, by correlating performance on the psychological tests with humour performance, the results indicate which abilities may be necessary for specific tests of humour. The humour tests required several abilities: language, abstract reasoning, visual search and assessment of detail, shifting concepts, and ability to keep in mind the story so that the punch-line can be connected with the stem. The tests administered were the Token test and Boston Naming Test, the Gorham Proverbs Test, Judgement of Line Orientation, the Embedded Figures Test, the Wisconsin Card Sorting Test, the Alpha Span Test, the Trail-Making Test, and the Letter Cancellation Test.

Results
The results were first analysed by grouping patients according to the standard anatomical classification method by comparing each focal lesion group (i.e. right frontal, left frontal, bifrontal, right posterior and left posterior) to the matched control group. Multiple group comparisons were performed using Kruskal–Wallis ANOVA (analysis of variance), while comparisons involving two groups were performed with Mann–Whitney U–Wilcoxon rank sum W tests. The right frontal (Z = -2.38, P < 0.02; Z = -2.30, P < 0.02; Z = -2.78, P < 0.005) and bifrontal (Z = -2.12, P < 0.03; Z = -2.12, P < 0.03; Z = -2.79, P < 0.005) groups were impaired on all three humour tests. The left frontal (Z = -3.09, P < 0.00) and the right posterior (Z = -2.87, P < 0.00) groups were impaired only on the Cartoon Array test. The left posterior group was not impaired on any task.

Grouping patients by gross anatomical regions, while the most common approach in group brain–behaviour studies, does not address the potential specificity of localization of frontal lobe functioning. By documenting the location of the brain lesion, by testing individuals with damage in different brain regions, and by grouping individuals by their performance and investigating the brain correlates (Stuss et al., 1994, 1998), it is possible to examine if a particular brain region is more salient to a specific humour function—in this case humour appreciation. So as not to confound verbal and non-verbal aspects, we limited this analysis to the verbal tasks. We used two measures that had revealed the most significant differences on the original patient groupings as the criteria to differentiate the frontal patients into impaired and unimpaired groups: (i) the difference score, i.e. the difference in funniness rating between humorous and neutral items; and (ii) the number of correct items on the Joke Completion test. The impaired group consisted of frontal lobe patients whose scores on both measures fell one standard deviation below that of the control participants. The unimpaired group consisted of frontal patients whose performance was comparable to that of normal participants. Three frontal patients did not meet the strict criteria of impairment on both measures, and were not included in this analysis. The two new frontal groups (unimpaired, impaired) were then compared with the control group (in the original analysis neither posterior group was significantly impaired on these verbal tasks and no posterior patients met the ‘impaired’ criteria).

When the lesions within the unimpaired and impaired frontal damaged groups were superimposed for comparison (Fig. 1), it was evident that most patients who were impaired had lesions involving the right frontal region, involving superior, rostral, primarily polar, regions, particularly areas 8 and 9. The patients with right frontal damage failed to distinguish adequately between humorous and neutral verbal stimuli on the Appreciation of Verbal Humour Statements test (Z = -3.1, P < 0.002), and were significantly impaired in choosing correct, funny punch-lines to incomplete verbal joke stems (Z = -3.41, P < 0.001). The impairment in these patients was quite specific. In the Joke and Story Completion Test (see Methods), when required to provide a logical conclusion to a non-humorous story they correctly selected the logical ending. There was no problem in simple logic. Moreover, these patients with right anterior frontal damage still understood the necessity for surprise in humour, which they demonstrated by selecting ‘slapstick’ endings instead of the correct punch-line (Z = -2.6; P < 0.009). Once they had registered this surprise, however, they could not then
establish the cognitive coherence between the punch-line and the body of the joke to appreciate the true humour present in the joke. Earlier studies had suggested such a defect in right hemisphere-damaged patients, but these studies had not differentiated the importance of lesion location within the right hemisphere (Brownell et al., 1983; Bihrl et al., 1986). Our results specify where in the right hemisphere the greatest deficit occurs; right frontal pathology is critical in producing a deficit in humour appreciation.

These results reveal a double dissociation within the right hemisphere. Damage in the right posterior part of the brain did not produce a deficit in humour appreciation (Fig. 1). There appears to be a very specific brain–behaviour association of humour appreciation within the right frontal lobe: the right anterior (somewhat more superior) region (Fig. 2). There is suggestion of a possible dissociation within the right frontal lobe as well, although the sample size is small. Patient 2053 had the third-largest right frontal lesion, yet was in the unimpaired group. Examination of the lesion location in this patient indicated that the right frontal lesion was inferior medial while those in the impaired group had more superior polar involvement.

The presence or absence of a deficit observed on the humour tests in the impaired group was not attributable to chronicity or size of their lesions (Table 1). There were no significant differences between the impaired and non-impaired frontal groups in size ($Z = -0.428; P < 0.66$) or chronicity of lesions ($Z = -0.329; P < 0.74$).

The above tests reflected how the subjects rated the jokes as being funny, or what decision they made concerning what was humorous. There is a second type of measurement—physical reaction. This measure related more to spontaneous affective responsiveness. Only patients with right frontal lobe damage displayed significantly muted physical–emotional responses to the humorous stimuli; a lack of responsiveness was evident for all tasks ($Z = -2.42, P < 0.01$).

On the Non-verbal Cartoon Appreciation test, all patient groups were impaired compared with the control group except the left posterior lesion group. The difficulty of most groups with this test might reflect the complexity and multiplicity of processes required for this task. Due to the inability of this test to clearly discriminate within frontal patients, performance on this test was not included for further analysis in terms of lesion location within the frontal group.

We also examined in the present study whether independent measures of working memory, mental shifting and verbal abstraction would be correlated with performance on the humour appreciation tests. There were very specific correlations when all frontal subjects were considered. For the verbal task, there were significant correlations with measures of working memory (Alpha Span Test; $r = -0.74, P < 0.00$), mental shifting (Trail-Making Test, Part B; $r =$ 0.43, $P < 0.05$). The above tests reflected how the subjects rated the jokes as being funny, or what decision they made concerning what was humorous.
Fig. 2 Brain pathology relationships in humour appreciation. All the patients with focal frontal lesions were divided into those who were impaired (frontal lobe patients whose scores fell 1 SD below that of control participants’ scores on the verbal humour appreciation tests) and non-impaired (frontal lobe patients whose scores fell within 1 SD of control participants’ scores). The patients with non-frontal lobe lesions, left or right hemisphere, were not impaired. Within the impaired and non-impaired frontal damaged groups, the schematic description of each patient was overlapped. The right hemisphere is on the left. The two axial views, which illustrate a clear difference between the two groups, are highlighted. The impaired group of patients all had lesions that were in the right frontal lobe, particularly the more polar, somewhat more superior, region representing Brodmann areas 8, 9 and probably parts of 10.

Discussion
There are several major findings in our study. In the verbal humour tasks (Appreciation of Verbal Humorous Statements and Joke Completion test), individuals with lesions in the posterior brain regions were not impaired in their appreciation of the humour. If viewed according to hemispheric differences, it is damage to the right hemisphere and not the left that affects verbal humour appreciation. There is also a specificity of the relationship of humour appreciation within the right hemisphere, the right frontal patients alone being impaired. For the cartoon, non-verbal test all brain-damaged groups were impaired compared with the control group except for those with left posterior damage. The deficiencies were related to cognitive processes in a logical way. In addition, spontaneous affective responses were deficient in the right frontal group only for all measures.

Why the frontal lobes?
Brain damage to the frontal lobes, and not the posterior regions in our sample, did affect the ability to appreciate humour. There is a logic to this finding. Damage to the frontal lobes has historically been related to changes in personality, with striking effects on humour production and reactions. Such individuals have ‘Witzelsucht’ (addiction to telling jokes, usually inappropriate in content when they are produced), ‘moria’ (silly, euphoric behaviour) and inappropriate laughter (Stuss and Benson, 1986; Stuss et al., 1992). So striking are these changes in personality and behaviour that the patient with frontal lobe damage is considered to be not the same person as before. The most famous case, described by Harlow (1868), was Phineas Gage, who was so transformed that he was ‘no longer Gage’.

There are two excellent reasons for the consideration of the importance of the frontal lobes in humour. Anatomically, there are significant connections of the frontal lobes, particularly the polar and ventral/medial areas, with the other brain regions related to affective–emotional responsiveness (Nauta, 1973; Pandya and Barnes, 1987). The early observations of moria and Witzelsucht implicated the mesial–orbital region of the frontal lobe. The frontal lobes are also
crucial to the development of personality and a sense of self (Stuss and Benson, 1986; Stuss, 1991; Damasio, 1994).

Secondly, the frontal lobes have been closely linked with the type of cognitive processes that would be an integral part of humour appreciation. The frontal lobes have a particular role to play in narrative discourse, abstract/non-literal interpretation and indirect forms of communication such as irony, affective intonation and sarcasm (Alexander et al., 1989). This brain region is important to novel problem-solving; a major theory of humour, the incongruity-resolution model (Suls, 1972), considers humour appreciation as a problem-solving task in which the punch-line, which is incongruous with the body of the text, must be detected and then reconciled with the lead. In detecting humour in captionless cartoons, the pictorial environment must be scanned and the appropriate humorous details differentiated from the background. The ability of the brain to hold information on line during processing, a function called working memory and associated with the frontal lobes (Baddeley, 1986; Goldman-Rakic and Friedman, 1991), would be necessary for most jokes. Thus, there is some relation of these cognitive processes to humour appreciation. This may be a necessary but not sufficient condition for the uniqueness of the frontal–humour appreciation relationship.

From the viewpoint of anatomical connections and cognitive processes, then, the frontal lobes are a logical area to consider as playing a major role in humour appreciation and expression. Our results demonstrate in a more objective experimental way what has been suspected on clinical grounds. The fascination is not with this frontal lobe–behaviour association; the emphasis is the specificity found within the frontal lobes.

Why the right frontal lobe?
The humour appreciation ability was quite directly related to a specific brain region: the anterior portion of the right frontal lobe. This entire story has profound implications—the right frontal lobe has been (and in some cases still is) considered as the most silent of brain areas. In contrast, it may represent one of the most important of human brain regions. This finding may also add evidence that a neural region (or more likely a distributed system) has a reasonable correspondence with a very complex human mental state. Humour impairment is not caused by brain damage irrespective of locus. The few major studies of humour in patients with brain lesions reported the major deficits in patients who had right hemisphere brain damage (Gardner et al., 1975; Brownell et al., 1983; Bihrlle et al., 1986). Our data have refined these results: within the right hemisphere there is specificity of function and localization related to humour. Pathology in the right frontal lobe, specifically the superior, anterior (polar) region, correlated with deficits in humour appreciation.

Several sources of information corroborate the importance of the right frontal lobe in humour. First, the main role of the right hemisphere in indirect interpretation, and organizing and integrating information, is probably related to the right frontal lobe (Alexander et al., 1989). Secondly, humour appreciation appears to require interpretation of current information in the light of an individual’s past experience. Such a personal re-enactment would require several processes. It requires episodic memory, the remembering of personally experienced events. Recent PET studies of memory, summarized as the ‘hemispheric encoding/retrieval asymmetry’ (HERA) model, emphasize the salient role of the right frontal lobe in retrieval of information of past personal events (e.g. Tulving et al., 1994). According to this HERA model of prefrontal activation, the left prefrontal cortex is differentially more involved with semantic retrieval and episodic encoding, whereas the right prefrontal cortex is more involved with episodic retrieval. This personal re-enactment through episodic memory is closely related to autonoetic consciousness, an awareness of self. It has been postulated recently that the development and maintenance of self-awareness is dependent on the frontal lobes (Stuss and Benson, 1986; Damasio, 1994), particularly the right frontal lobes (Wheeler et al., 1997; Stuss et al., 1999). The connectivity with brain regions related to affect and feelings has been hypothesized to play a major role in some of these functions (Stuss, 1991). Thus, the right frontal lobe appears particularly relevant to the integration of information, episodic memory and self-awareness, all of which have at least apparent relationship to humour appreciation.

We are not arguing for the localization of humour to this relatively discrete brain region. That would be phrenological folly. We are, however, postulating that the confluence of the massive evolution of the frontal lobes in man; the presence within the frontal lobes of important functions necessary for humour; the role of the frontal lobes in the integration of cognition and affect; and the almost unique representation within the frontal lobes of information deriving from the affective limbic system and the feelings associated with body states (Nauta, 1973) provide the humus (‘humereal’ bedding) for the development of humour. Our results in the patients we tested suggest that, in the neural network of the limbic affective system, the right frontal lobe plays a pre-eminent role in the appreciation of humour. The possibility that, because of the limitations of human brain studies, we are tapping only one aspect of a larger anatomical region, such as the bilateral frontal polar region, cannot be excluded. This would be more compatible with other suggestions including the importance of ventral–medial areas (Damasio, 1994). An alternative hypothesis is that our experimental methods were fortunate in selectively tapping one aspect of a larger distributed cortical and subcortical network related to humour appreciation, affective expression, mood and self-awareness. Areas 10 and anterior 9, for all their morphological simplicity (Barbas, 1995), might be considered a connective precursor to these highest human behaviours. Its importance may lie not in its morphological development, but its central interconnecting role with regions essential to the interaction
of thinking, and affectively reacting (Pandya and Yeterian, 1996). Area 10 is reciprocally connected with the medial and orbital frontal cortex, areas 46 and 8, and the multimodal area of the superior temporal sulcus (Barbas and Pandya, 1989; Seltzer and Pandya, 1989; Pandya and Yeterian, 1996). The superior temporal sulcus does have a role in facial grimacing (Rolls, 1990).

In addition to humour appreciation, which is a cognitive ability, the right frontal lobe may also be implicated in emotional responsiveness. In the present study, only patients with right frontal damage were impaired in displaying emotional responsiveness to humorous stimuli. The lack of mirth responses in right frontal patients is consistent with other literature which investigated either the effect of right hemisphere, or frontal lobe, damage on emotional expressiveness. Studies investigating facial expression of emotion in normal subjects and unilateral brain-damaged patients, and emotional reaction to humorous stimuli, have implicated the right hemisphere (Gardner et al., 1975; Borod and Koff, 1990; Borod, 1992). These studies did not investigate whether there was any difference within the right hemisphere. A second group of studies emphasize that the frontal lobes are also important in the production of facial expression (Kolb and Milner, 1981; Kolb and Taylor, 1988). Our results provide evidence that it is the right frontal region that may be most critically involved in appreciating humour and in mediating spontaneous facial expressions to emotional stimuli such as humour (see also Ross and Mesulam, 1979; Ross, 1993). The specific anatomical location or system remains to be identified. Our most impaired patients had superior polar lesions; in a previous study (Ross and Mesulam, 1979), the right frontal operculum was most relevant to emotional gesturing. Because of the difference in tasks, it is possible that each result represents a part of a distributed frontal system centred within the right frontal lobe.

There is an additional result of the right frontal patients’ abnormal emotional response: dissociation between their cognitive and affective responses to the humorous stimuli. That is, even when humorous stimuli were occasionally quantitatively rated by the right frontal patients as being funny and understanding of these items appeared to be reasonably adequate based on their explanations, they did not respond to these items with smiles or laughter, unlike normal participants and those with lesions in other brain regions. That is, while they may have grasped intermittently the cognitive basis of humour, they did not affectively respond. A similar dissociation was reported by Gardner et al. (1975) in right hemisphere patients. In the present study, only those with lesions involving the right frontal lobe displayed such a dissociation. Stuss and Benson (1983) reported a dissociation between language and action in emotional responding in prefrontal leucotomized patients. The present study indicates that right frontal damage is relevant to producing a dissociation between cognitive and affective responses.

Humour: a theory

Humour is a multifactorial function involving the integrated operation of several different processes. The frontal lobe is the ideal substrate to perform the integrative functions required for humour appreciation. It has been designated as a heteromodal cortex, responding to multiple stimuli, capable of interpreting internal stimuli or sensations as well as external sensory input (Mesulam, 1985). That is, it allows the individual to integrate ‘extrapersonal space’ with the ‘internal milieu’ (Mesulam, 1985). Nauta (1973) emphasized the extensive reciprocal anatomical connections of the frontal lobe, particularly with the limbic system, as the basis for its ability to re-represent exteroceptive (information from the outside world) and interoceptive (information from internal milieu/feeling) states. Barbas and Pandya (1989), reviewing the structural and anatomic relationships of the prefrontal cortex, indicated that this region provides the anatomic basis of cognitive–emotional interactions.

Thus, by virtue of the frontal lobe’s extensive reciprocal anatomical connections, as well as by being heteromodal in function, the frontal lobe provides the ideal substrate for integration at various levels of cognitive and affective functions. The correlation of cognitive processes with the different tests of humour attests to the necessity of cognitive functions. For instance, there were significant correlations between measures of working memory, mental flexibility, abstract ability and visual search with performance on humour appreciation tasks. While these cognitive operations are necessary, they are insufficient. Real humour appreciation requires an affective response. This very anterior area of the frontal lobes may enable the integration of cognition and affect. The amygdala may play an essential role in the affective responsiveness (Adolphs et al., 1995). There also appears to be hemispheric specialization for the type of integration necessary for humour appreciation, the right frontal region playing a dominant role. The right hemisphere’s holistic and simultaneous processing style has been considered important to humour (McGhee, 1983). The right frontal lobe also subserves retrieval of episodic memory (Tulving et al., 1994). At the highest level, the integration of cognitive with affective information in the right frontal lobe is critical to the highest and most evolved human cognitive functions, such as self-awareness (Prigatano, 1991a, b; Wheeler et al., 1997; Stuss et al., 1999) and humour.

Acknowledgements

We wish to thank H. Brownell for providing suggestions for test design and giving permission to use some of the test material, and D. Pandya and E. Tulving for providing advice on earlier drafts. The anatomical concepts were assisted enormously by discussions with D. Pandya. The project represents the successful University of Toronto Department of Psychology doctoral dissertation of the senior author. Funding for the project was provided by the Medical Research Council of Canada and the Ontario Mental Health Foundation.
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Received October 5, 1998. Revised December 2, 1998. Accepted December 8, 1998