The frontal lobes are necessary for 'theory of mind'

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Summary

Patients with limited focal frontal and nonfrontal lesions were tested for visual perspective taking and detecting deception. Frontal lobe lesions impaired the ability to infer mental states in others, with dissociation of performance within the frontal lobes. Lesions throughout the frontal lobe, with some suggestion of a more important role for the right frontal lobe, were associated with impaired

visual perspective taking. Medial frontal lesions, particularly right ventral, impaired detection of deception. The former may require cognitive processes of the lateral and superior medial frontal regions, the latter affective connections of the ventral medial frontal with amygdala and other limbic regions.

Keywords: frontal lobes; self-awareness; theory of mind; perspective taking; deception

Abbreviations: BF = bifrontal; LF = left frontal; LNF = left nonfrontal; RF = right frontal; RNF = right nonfrontal

Introduction

Humans and only a few species of great apes (Gallup, 1985) may be capable of 'metarepresentation' (Leslie and Frith, 1987) within cognitive processes. Metacognitive faculties are awareness of one's own mental states, beliefs, attitudes and experiences, the relationship between these and external events, and also of the mental states of others and the implications for their motives and intentions (Frith, 1989; Gallup, 1998a). These metacognitive abilities emerge with maturation as an individual develops a 'theory of mind': an awareness of the likely content of other people's minds (Perner and Wimmer, 1988; Wellman and Woolley, 1990).

Several brain regions have been implicated in theory of mind, particularly in the right hemisphere. Right hemisphere damage may impair the pragmatic, nonlinguistic aspects of communication, blunt empathy, and diminish understanding of sarcasm and irony, all capacities that appear to require inference or attribution (Alpert *et al.*, 1980; McDonald, 1993; Siegal *et al.*, 1996; Bowden and Beeman, 1998; Winner *et al.*, 1998; Happé *et al.*, 1999). None of these studies have implicated a specific area within the right hemisphere.

The frontal lobes may contribute to theory of mind. Investigations of the development of theory of mind in children implicate a role for the frontal lobes (Ozonoff *et al.*,

1991; Gallup, 1998b). Mirror self-recognition and mental state attribution emerge in the second year of life, and the frontal cortex is developing more rapidly than any other part of the brain at that age (Milner, 1967).

The frontal lobes have also long been considered to play a special role in human behaviour, with damage in this region affecting not only high level cognitive functions but also social behaviour, personality, personal memories and self-awareness (Alexander *et al.*, 1979; Brazzelli *et al.*, 1994; Damasio, 1994; Adolphs *et al.*, 1995; Channon and Crawford, 1999; Rogers *et al.*, 1999a, b; Stuss *et al.*, 2001). While these reports suggest impairment in making mental state attributions, theory of mind in such patients has been directly tested in controlled experiments only once (Stone *et al.*, 1998); in this study, patients with unilateral right frontal damage or nonfrontal lesions were not included.

A distinct role for a particular region of the frontal lobes in theory of mind can be anticipated based on specific lesion correlation with disturbed social behaviour and personality changes. Damage to the left or right orbitofrontal/ventral medial areas consistently causes personality changes including indifference, impaired social judgement, diminished affective responsiveness, impaired pragmatics, deficient self-

regulation, and inability to associate social situations with personal affective markers (Nauta, 1973; Stuss and Benson, 1983; Kaczmarek, 1984). The right frontal lobe is involved in humour appreciation, self-awareness, self-face recognition, and episodic (personal, affect-laden autobiographical) memory (Stuss, 1991; Fink *et al.*, 1996; Wheeler *et al.*, 1997; Levine *et al.*, 1998; Craik *et al.*, 1999; Keenan *et al.*, 1999; Shammi and Stuss, 1999).

Functional imaging data also suggests a role of the frontal lobes in theory of mind. Fletcher and colleagues found activation in the left medial frontal area (specifically Brodmann area 8) when subjects had to consider the thoughts and feelings of characters in comparison to control tasks where the characters' thoughts and feelings were irrelevant (Fletcher *et al.*, 1995). Goel and colleagues also found left medial frontal lobe, as well as left temporal lobe, activation in a PET study when inferential reasoning about the beliefs and intentions of others was required (Goel *et al.*, 1995).

While imaging studies suggest involvement of different brain regions, they do not indicate which areas are necessary. No study has directly examined theory of mind in patients with limited focal lesions in distinct frontal and nonfrontal regions of the brain, or included frontal patients with damage to left, right or ventral medial regions within the frontal lobes. This is essential to verify whether the frontal lobes are uniquely related to theory of mind, and if distinct regions (particularly right) contribute to different processes related to theory of mind. We studied patients with well-defined focal and limited brain lesions in frontal and nonfrontal regions to assess which brain regions are necessary for two mental state attribution tasks: visual perspective taking, and deception. Both of these tasks have been considered to be theory of mind tasks, but the cognitive demands of the tasks are not equivalent. Differences between the two tasks may be revealed by assessing patients with lesions in different frontal locations.

Methods

Subjects

A total of 32 patients with focal lesions in frontal and nonfrontal brain regions were tested. Damage for all patient groups occurred in adulthood. Cases with a history of diffuse brain damage, history of psychiatric illness or other neurological disorder, significant comprehension problems or notable neglect were excluded. All patients were fluent in English, and had no difficulty understanding the task demands. All gave informed consent to participate in the study which was approved by the Joint Baycrest Centre/ University of Toronto Research Ethics and Scientific Review Committee.

Demographic information is presented in Table 1.

All patients had CT or MRI. For inclusion, lesions had to be limited to frontal or nonfrontal regions. Frontal could include cases with deep frontal white matter and dorsal striatum (all due to subcortical middle cerebral artery infarctions). Previous research has demonstrated similar consequences of dorsolateral frontal and dorsal caudate lesions (Godefroy et al., 1992; Mega and Alexander, 1994; Stuss et al., 1994). There are strong, well-defined, functional and anatomical linkages between dorsolateral frontal lobe and caudate (Alexander et al., 1986). Minor overlap of lesion (<25%) or a minor secondary lesion was allowed. In order to obtain a sufficient number of focal lesion patients representative of different brain regions, patients with different aetiologies (stroke, haemorrhage, lobectomy, tumour and trauma) were accepted provided the damage was circumscribed. For example, for trauma patients (important for the composition of the bifrontal group) there had to be no evidence of significant diffuse axonal injury. Lesions were localized with standard atlases and transferred to template following Damasio and Damasio (Damasio and Damasio, 1989).

Analysis of lesion site relationships to performance on the experimental task followed four steps. First, to demonstrate a general effect of frontal damage, subjects were grouped simply as frontal (n = 19), nonfrontal (n = 13) and control (14 age and education equivalent control subjects). Secondly, to probe for more specific regional effects, groups were divided by site of lesion into right frontal (RF, n = 4), left frontal (LF, n = 8), bifrontal (BF, n = 7), right nonfrontal (RNF, n = 5) and left nonfrontal (LNF, n = 8) groups. Thirdly, to clarify possible tendencies for frontal laterality effects, the BF group was added to each unilateral frontal group, thus producing 11 patients with right frontal damage and 15 with left frontal damage. Each of these groups was separately compared with all other groups. The rationale for this approach was based on our previous findings that lesions in the inferior or superior medial frontal regions could be comparable to the effects after right or left frontal lobe damage, depending on the function being tested (Stuss et al., 1998, 2000). Fourthly, to investigate, at least tentatively given the small numbers, whether unique regions were critical for these tasks, each discrete frontal region (Stuss et al., 1995) was scored for the presence or absence of any lesion. Correlations of performance with these more specific regions were completed.

There was no group difference for the size of lesion [F(4,18) = 1.13, P = 0.37]. Time since injury was at least 3 months (range 3–146). There was a significant difference between groups on this measure [F(4,27) = 3.71, P = 0.02]: (RF = 7 months (SD = 4.83); LF = 6.3 (2.19); BF = 17.4 (22.4); RNF = 48.4 (26.1); LNF = 58.5 (57.3). A post hoc Tukey test revealed a significant difference between the LF and LNF groups, but this difference was not considered relevant since neither of these two groups were impaired on the tasks.

There were no significant age differences among the groups [RF = 54 years of age, SD = 12.9; LF = 57 (7.5); BF = 50 (15.5); RNF = 46 (16.2); LNF = 49 (15.7); control = 52 (14.9)]. There were no significant group

Table 1	Summary of	demographic	information an	d neuropsycholo	gical tests
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Group	Age (years)	Education	NARTa	Token ^b	BNT ^c	FAS ^d	Semantice	DS-F ^f	DS-B ^g	BDI ^h	VPA–Total ⁱ
Right frontal n	54.25	12.75	105.18	42.5	48.5	37.5	15.25	5.25	5.25	7.0	16.0
	4	4	4	4	4	4	4	4	4	4	4
Left frontal <i>n</i>	57.38	13.25	105.08	41.63	52.0	21.0	13.0	6.5	4.63	2.25	13.5
	8	8	8	8	8	8	8	8	8	8	16
Bifrontal <i>n</i>	49.57	10.57	100.27	40.75	48.71	26.57	13.43	6.71	4.57	6.29	15.4
	7	7	7	4	7	7	7	7	7	7	5
Right nonfrontal <i>n</i>	46.20	12.0	106.43	44.0	55.6	37.8	19.8	7.0	4.8	4.0	16.8
	5	5	5	5	5	5	5	5	5	5	5
Left nonfrontal <i>n</i>	48.88	13.0	102.16	40.75	47.5	26.75	15.13	5.5	4.25	4.125	13.63
	8	8	8	8	8	8	8	8	8	8	8
Control <i>n</i>	52.0	14.36	113.26	43.54	56.71	46.29	22.43	7.07	5.36	2.15	18.0
	14	14	14	13	14	14	14	14	14	13	14

^aNART = National Adult Reading Test; ^bToken = Token Test; ^cBNT = Boston Naming Test; ^dFAS = Verbal Fluency—Letters, FAS; ^cSemantic = Semantic Fluency—Category, Animals; ^fDS-F = Digit Span Forward; ^gDS-B = Digit Span Backward; ^hBDI = Beck Depression Inventory; ⁱVPA-Total = Verbal Paired Associates—Total Score.

differences for years of education, although there was a trend [F(5,40) = 2.35, P = 0.06]. There was a significant difference on the level of premorbid intelligence as estimated by the National Adult Reading Test [F(5,40) = 2.57, P = 0.04]. A post hoc test revealed the BF (IQ = 100) group had a significantly lower score than the control (IQ = 113) group. When these measures were used as covariates in the statistical analyses, the results did not alter. Moreover, all groups clearly had adequate intelligence to perform the tasks as demonstrated in the baseline task, and intelligence is a factor in these measures only at the extremes (Happé, 1995). There were no significant differences among the groups on the Beck Depression Inventory.

Tasks and procedure

For all conditions, the subject's task was to choose the cup under which he/she thought an object had been hidden. The tasks were presented in a fixed order. Subjects normally responded quickly. If no response was made within 15 s, they were prompted to make a choice. This seldom occurred.

Visual perspective taking

The purpose of the visual perspective study was to examine the ability to infer visual experience in others. Tasks with greater or lesser degree of inference requirement were administered. A Baseline task was first administered, followed by two visual perspective tasks (Direct Inference and Transfer Inference), the latter requiring a higher level inference. The procedures in the Transfer Inference condition were varied deliberately to determine whether different manipulations designed to produce comparable results on visual perspective taking would produce similar results for purposes of establishing convergent or construct validation.

The examiner and subject were seated on opposite sides of a table. On the table between the examiner and the subject was a small wooden frame 29 inches high and 33 inches wide. The frame held a curtain such that the subject could not see over or around the frame when the curtain was closed. Five ordinary 8 oz white Styrofoam coffee cups, situated on the examiner's side of the frame and inverted to hide an object, were used for the visual perspective taking task. The cups were placed on a sponge pad to minimize any noise from the placement of the cups. On each trial a soft flexible sponge ball, ~1 inch in circumference, was hidden under one of the cups. In the Baseline and Direct Inference conditions, large wrap-around safety type glasses were used as described below. One pair of glasses was painted with black flat paint to make them opaque. Sponge was placed on the frame of the glasses so that it was impossible to see around the sides.

In the Baseline condition, the curtain was open for all trials. The examiner explained to the subject that, for each trial, he or she would be invited to put on a different pair of glasses, one being clear and the other totally opaque. Starting with the clear glasses, the glasses were alternated for each of six trials. For each trial, the examiner 'hid' the ball under one of five cups, and then asked the subject to remove the glasses and point to the cup where he or she thought the ball was hidden. The subject was instructed to make a response each time, even if he or she was not sure.

In the two inference conditions, the examiner had two assistants (the same assistants were used across all tasks). For the Direct Inference condition, each assistant was placed to the right or left of the examiner behind the frame such that it was obvious the assistants had the potential to see the ball being hidden when the curtain was closed. The curtain was closed when the examiner hid the ball and opened when the subject was requested to point to the cup where he or

she thought the ball was hidden. Since the subject could not see the ball being hidden, they were told to rely on the assistants for help. The assistants were in clear view of the subject to ensure that it was evident who was wearing the clear or opaque glasses. For each trial, the assistants alternated the type of glasses they wore as they 'looked' at the ball being hidden by the examiner under one of the five cups. After the examiner hid the ball, and the curtain was opened, the assistants removed their glasses. The assistant who had worn the clear glasses pointed to the cup where the ball was indeed hidden, and at the same time, the one who had worn the opaque glasses pointed to one of the other cups. This was pre-arranged so that the assistant with the opaque glasses did not point accidentally to the correct cup. The subject had to use his/her own experience with the glasses to infer which of the two assistants was pointing to the cup under which the object was hidden. The subject then selected where he or she thought the object was.

The Transfer Inference condition was identical to the previous condition with one exception. Instead of using glasses, the two assistants alternated their position for each trial, one sitting on the side of the examiner and able to see where the ball was hidden, and the other sitting beside the subject and not able to see where the ball had been hidden. The inference in this condition was based on the ability of the subject to use the knowledge of the location of the assistant in relation to the examiner or him/herself. After the ball was hidden the two assistants returned to the same positions on the sides of the table behind the frame, analogous to the Direct Inference condition. After the examiner opened the curtain, each assistant pointed to different cups, with the assistant who had sat next to the examiner pointing to the correct cup. If subjects made three or more errors on either the Direct Inference or Transfer Inference tasks, that condition was then repeated using a coin instead of a sponge ball.

Deception condition

The Deception task, in which an assistant always pointed to the cup where the ball was not hidden, was designed to assess an individual's ability to infer that someone was trying to deceive them. Only two cups were used, one assistant was involved, and the object hidden was a 25-cent coin. The assistant was decided upon in a random fashion. The subject kept the money for correct responses, and the assistant received it for incorrect responses made by the subject. On each trial, the curtain was closed when the coin was hidden. The assistant stayed on the side of the examiner, viewing what the examiner did. After the money was hidden and the curtain opened, the assistant always pointed to the wrong cup, the one without the hidden money, and the subject pointed to the cup he/she thought the ball was under. This condition was discontinued after five consecutive correct responses, or 14 trials.

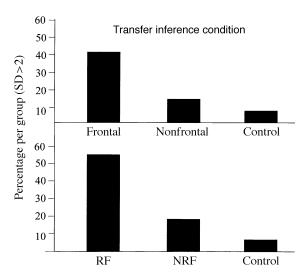


Fig. 1 Visual perspective taking. The proportion of individuals in different groups who committed more errors than the control group, based on 2 SD, on the visual perspective taking task. When patients were compared with the presence of pathology in frontal and nonfrontal regions, the results approached significance (P=0.056; top half of the figure). When the directed hypothesis of right frontal involvement was examined by comparing all patients with right frontal (RF) lobe damage to those patients without such damage (NRF) and the control group, a significant effect implicating the right frontal lobe was revealed (P=0.021; bottom half of the figure).

Results

There were no group differences for the Baseline condition, or the Direct Inference condition [F(5,40) = 0.54, P > 0.75]. Patients understood and could perform the task, even when they had to make a first level inference based on a direct visual experience. The only significant visual perspective difference occurred for the next level of inference, the Transfer Inference condition. More frontal patients made one or more errors (based on 2 SD) on this task than any other group (frontal patients = 42%; nonfrontal = 15%; control = 7%) [Fisher's exact two-tail test P = 0.056]. The comparison of RF, LF, BF, RNF, LNF and control subgroup analysis was not significant [F(5,40) = 0.87, P = 0.51]. However, when all patients with right frontal lobe damage (RF and BF) were compared with all other patients and the control group, there was a significant group main effect (Fisher's, P = 0.026). This was also significant if the RF and BF groups were compared with the LF, nonfrontal and control groups (Fisher's exact two-tail tests, P = 0.05). Further analysis showed that more patients with right frontal involvement (RF or BF) made errors than control subjects (Fisher's, P = 0.021). No significant difference was found when LF and BF groups combined were compared with the other groups. The percentage of individuals in each group who were impaired in the Transfer Inference task were: RF = 50%, LF = 25%, BF = 57%, RNF = 20%, LNF = 13%. For the Transfer Inference task, there was a general frontal effect, with suggestion of a more important role for the right frontal region (see Fig. 1). There were, however, no significant

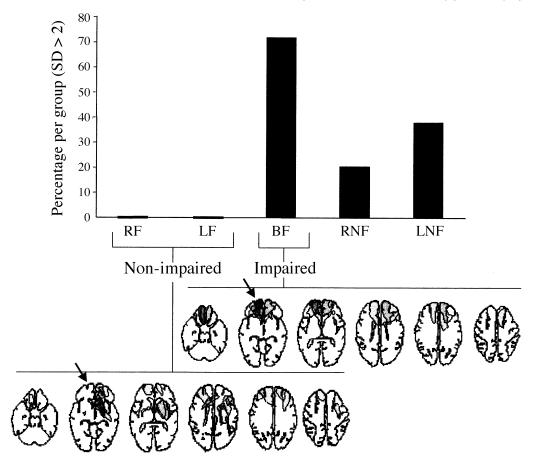


Fig. 2 Deception task. The top half of the figure illustrates the percentage of each patient group that exceeded the control group error performance by more than 2 SD. Only patients with bifrontal lesions were significantly impaired. The bottom half of the figure contrasts the overlap of lesion locations for patients with unilateral left and right frontal lesions to the bifrontal group. The arrows highlight the major group anatomical difference in the right ventral medial frontal region. Left and right sides are reversed.

correlations of performance with more specific lesion localization. Using a coin or a ball did not make a significant difference on the results.

For the Deception task, there was no general frontal lobe lesion effect (Fisher's, P = 0.30). As above, when LF and BF groups were combined and compared with other groups, no significant difference was found. Comparable to the Transfer Inference task, there was a significant group effect when the combined RF and BF groups were compared with the LF, nonfrontal and control groups (Fisher's, P < 0.05). However, these results were more robust for the full subgroup ANOVA (analysis of variance) for both the number of correct responses out of 14 trials [F(5,40) = 4.8, P = 0.002] and the number of the first five consecutive correct trials [F(5,40) = 3.5, P = 0.01]. The group with RF lesions performed as well as or better than the control group but the BF group was significantly worse than the RF and control groups. The percentage of individuals in each patient group whose mean number of errors exceeded the control group by 2 SD were: RF = 0; LF = 0; BF = 71%; RNF = 20%; LNF = 38%. When the three frontal groups were compared on this error measure, a significant difference was found

(Fisher's exact two-tail test, P = 0.007). The BF group was significantly more impaired than the LF group (Fisher's, P = 0.007).

The importance of medial areas for the Deception task, particularly on the right, was confirmed by Φ correlation of lesion location with number of errors (see also Fig. 2). No significant correlation was found with left unilateral lesions. The right medial (both inferior and superior) frontal areas and right anterior cingulate were significantly correlated with the number of errors [r=0.75, P=0.003; r=0.66, P=0.009; r=0.545, P=0.029, respectively].

Discussion

Theory of mind is related to the frontal lobes. The experimental tasks were structured such that the subjects could recognize the peculiar inference and deception requirements. Deficits could not be attributed to other factors such as depression, level of IQ or years of education, since there were either no significant group differences, or adding the scores as covariates did not alter results. Motivation and effort were good. The tasks on which significant differences

were found made modest cognitive, linguistic and memory demands. On an adequately unambiguous level, the tasks demand first order attributions: to infer the experiences of others based on simple perspective taking and to recognize the deception of others.

The processes measured by the two tests, Transfer Inference and Deception, may be related to different parts of the frontal lobes. Bifrontal lesions, which overwhelmingly involve medial regions, impaired performance on the deception task. The right medial lesion was most statistically significant, but the results do not differentiate conclusively between inferior or superior medial areas. There was less specificity of lesion location within the frontal lobes for the Transfer Inference task, although there was some suggestion for a greater role for the right frontal region. Lesions of the left frontal lobe played no role in the Deception task, and had the least effect on the Transfer Inference task. Our results confirm and extend those of Stone and colleagues, who revealed that patients with inferior medial damage but not left dorsolateral pathology were impaired on theory of mind tasks (Stone et al., 1998). Their study did not include patients with unilateral right frontal damage.

The deficit in visual perspective taking after frontal lobe damage represents a disorder of representing another's perceptions based on one's own experiences. The cognitive processes of the frontal regions likely play a neural network role in this metarepresentation. perhaps a more important role played specifically by the superior medial and right lateral area. However, the impairment in perspective taking deficit does not appear to be a direct consequence of such cognitive deficits. The fact that the right frontal lobe is critical for selecting among competing choices (Deiber et al., 1991; Frith et al., 1991) cannot explain our results. Both tasks required a response choice, yet different brain regions were involved for both tasks. An important role in working memory has also been attributed to the dorsolateral frontal region, with the right frontal lobe active for non-verbal working memory (Bechara et al., 1998). However, each trial of the visual perspective taking task was based on immediate experience, without any substantial working memory demands. Even if slight demands on working memory are made with visual perspective taking, the impaired capacity requires no more working memory than the direct inference condition that was normal.

Deficits in attention, particularly sustained attention, have been reported after right frontal lobe damage. It is possible that all of the activity of the indirect inference task (assistants moving around, screen opening and closing) distracted attention. However, the distraction caused by the acts of coming and going in the Transfer Inference condition does not appear to be notably greater than the changing of glasses, and screen opening and closing, in the Direct Inference condition in which no impairment was observed. Moreover, an impaired attention explanation is not consistent with the unilateral right and left frontal lesioned patients' excellent performance on the deception task.

That bilateral, particularly right, orbital/medial, lesions might impair patients' capacity to incorporate the experience of another's deceptions into their own plans is consistent with existing knowledge about damage to this region. Lesions in this area result in a failure to activate relevant somatic markers so that past emotional experience can be used to guide response options (Bechara et al., 1997). Guessing is a method of approximating future consequences of current choices, and guessing increased activity predominantly in the right orbitofrontal region (Elliott et al., 1999). Impairment after ventral frontal lesions in certain switching tasks (Dias et al., 1996), and reversal learning, are related to reinforcement, suggesting a potential common role of affective feedback. None of these have been specifically related to the right frontal ventral medial area, a brain region implicated in personal, self-reflective capabilities. This orbitofrontal, ventral medial area is also critical for selfregulated social and cognitive behaviours despite normal performance on standard IQ and frontal lobe tests (Eslinger and Damasio, 1985; Levine et al., 1999).

Is another interpretation possible? The ability to detect deception in a simple laboratory game was impaired in patients with bilateral orbital/medial frontal lesions, but not greatly affected by unilateral frontal lesions. Although it might appear that this deficit is due to an impairment in reversal learning, that is not the case. In our task, the object was hidden in a random order, and as a consequence there was no relation between where the object appeared and the subject's previous response. It may be, therefore, that this is indeed based on learning, but it requires functions beyond that normally considered in reversal learning. To the extent that learning is involved, the subject has to infer (learn) that the *person* is deceiving them, and therefore must choose the opposite cup. We consider such an inference to be a classic instance of theory of mind.

Our results identify the brain regions necessary for some components of a theory of mind, and demonstrate the neural complexity underlying different facets of metacognitive faculties. The frontal lobes are essential, with the right frontal lobe perhaps particularly critical, maybe because of its central role in the neural network for social cognition, including inferences about feelings of others and empathy for those feelings. The ventral medial frontal regions are also important, perhaps because connections with the amygdala and other limbic structures give them a key role in the neural network for behavioural modulation based upon emotions and drives (Pandya and Yeterian, 1996). It is difficult to dissociate social cognitive processes from behavioural expression of those processes, but these data from patients with focal lesions provide support for such a dissociation.

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References

Adolphs R, Tranel D, Damasio H, Damasio AR. Fear and the human amygdala. J Neurosci 1995; 15: 5879–91.

Alexander MP, Stuss DT, Benson DF. Capgras syndrome: a reduplicative phenomenon. Neurology 1979; 29: 334–9.

Alexander GE, DeLong MR, Strick PL. Parallel organization of functionally segregated circuits linking basal ganglia and cortex. [Review] Annu Rev Neurosci 1986; 9: 357–81.

Alpert M, Cohen NL, Martz M, Robinson C. Electro-encephalographic analysis: a methodology for evaluating psychotherapeutic process. Psychiatry Res 1980; 2: 323–9.

Bechara A, Damasio H, Tranel D, Damasio AR. Deciding advantageously before knowing the advantageous strategy. Science 1997; 275: 1293–5.

Bechara A, Damasio H, Tranel D, Anderson SW. Dissociation of working memory from decision making within the human prefrontal cortex. J Neurosci 1998; 18: 428–37.

Bowden EM, Beeman MJ. Getting the right idea: semantic activation in the right hemisphere may help solve insight problems. Psychol Sci 1998; 9: 435–40.

Brazzelli M, Colombo N, Della Sala S, Spinnler H. Spared and impaired cognitive abilities after bilateral frontal damage. Cortex 1994; 30: 27–51.

Channon S, Crawford S. Problem-solving in real-life-type situations: the effects of anterior and posterior lesions on performance. Neuropsychologia 1999; 37: 757–70.

Craik FIM, Moroz TM, Moscovitch M, Stuss DT, Winocur G, Tulving E, et al. In search of the self: a positron emission tomography study. Psychol Sci 1999; 10: 26–34.

Damasio AR. Descartes' error and the future of human life. Sci Am 1994; 271: 144.

Damasio H, Damasio AR. Lesion analysis in neuropsychology. New York: Oxford University Press; 1989.

Deiber MP, Passingham RE, Colebatch JG, Friston KJ, Nixon PD, Frackowiak RS. Cortical areas and the selection of movement: a study with positron emission tomography. Exp Brain Res 1991; 84: 393–402.

Dias R, Robbins TW, Roberts AC. Dissociation in prefrontal cortex of affective and attentional shifts. Nature 1996; 380: 69–72.

Elliott R, Rees G, Dolan RJ. Ventromedial prefrontal cortex mediates guessing. Neuropsychologia 1999; 37: 403–11.

Eslinger PJ, Damasio AR. Severe disturbance of higher cognition after bilateral frontal lobe ablation: patient EVR. Neurology 1985; 35: 1731–41.

Fink GR, Markowitsch HJ, Reinkemeier M, Bruckbauer T, Kessler J, Heiss W-D. Cerebral representation of one's own past: neural networks involved in autobiographical memory. J Neurosci 1996; 16: 4275–82.

Fletcher PC, Happé F, Frith U, Baker SC, Dolan RJ, Frackowiak RS, et al. Other minds in the brain: a functional imaging study of 'theory of mind' in story comprehension. Cognition 1995; 57: 109–28.

Frith U. A new look at language and communication in autism. [Review] Br J Disord Commun 1989; 24: 123–50.

Frith CD, Friston K, Liddle PF, Frackowiak RS. Willed action and the prefrontal cortex in man: a study with PET. Proc R Soc Lond B Biol Sci 1991; 244: 241–6.

Gallup GG Jr. Do minds exist in species other than our own? Neurosci Biobehav Rev 1985; 9: 631–41.

Gallup GG Jr. Self-awareness and the evolution of social intelligence. Behav Proc 1998a; 42: 239–47.

Gallup GG Jr. Can animals empathize? Sci Am Presents 1998b; 9 (4 spec ed): 66–71.

Godefroy O, Rousseaux M, Leys D, Destee A, Scheltens P, Pruvo JP. Frontal lobe dysfunction in unilateral lenticulostriate infarcts. Prominent role of cortical lesions. Arch Neurol 1992; 49: 1285–9.

Goel V, Grafman J, Sadato N, Hallett M. Modeling other minds. Neuroreport 1995; 6: 1741–6.

Happé FG. The role of age and verbal ability in the theory of mind task performance of subjects with autism. Child Dev 1995; 66: 843–55.

Happé F, Brownell H, Winner E. Acquired 'theory of mind' impairments following stroke. Cognition 1999; 70: 211-40.

Kaczmarek BL. Neurolinguistic analysis of verbal utterances in patients with focal lesions of frontal lobes. Brain Lang 1984; 21: 52–8.

Keenan JP, McCutcheon B, Freund S, Gallup GG Jr, Sanders G, Pascual-Leone A. Left hand advantage in a self-face recognition task. Neuropsychologia 1999; 37: 1421–5.

Leslie AM, Frith U. Metarepresentation and autism: how not to lose one's marbles. Cognition 1987; 27: 291–4.

Levine B, Black SE, Cabeza R, Sinden M, McIntosh AR, Toth JP, et al. Episodic memory and the self in a case of isolated retrograde amnesia. Brain 1998; 121: 1951–73.

Levine B, Freedman M, Dawson D, Black S, Stuss D. Ventral frontal contribution to self-regulation: convergence of episodic memory and inhibition. Neurocase 1999; 5: 263–75.

McDonald S. Pragmatic language skills after closed head injury: ability to meet the informational needs of the listener. Brain Lang 1993; 44: 28–46.

Mega MS, Alexander MP. Subcortical aphasia: the core profile of capsulostriatal infarction. Neurology 1994; 44: 1824–9.

Milner E. Human neural and behavioral development. Springfield (IL): Charles C. Thomas; 1967.

Nauta WJH. Connections of the frontal lobe with the limbic system. In: Laitinen LV, Livingston KE, editors. Surgical approaches in psychiatry. Baltimore: University Park Press; 1973.p. 303–14.

Ozonoff S, Pennington BF, Rogers SJ. Executive function deficits in high-functioning autistic individuals: relationship to theory of mind. J Child Psychol Psychiatry 1991; 32: 1081–105.

Pandya DN, Yeterian EH. Comparison of prefrontal architecture and connections. Philos Trans R Soc Lond B Biol Sci 1996; 351: 1423–32.

Perner J, Wimmer H. Misinformation and unexpected change: testing the development of epistemic-state attribution. Psychol Res 1988; 50: 191–7.

Rogers RD, Everitt BJ, Baldacchino A, Blackshaw AJ, Swainson R, Wynne K, et al. Dissociable deficits in the decision-making cognition of chronic amphetamine abusers, opiate abusers, patients with focal damage to prefrontal cortex, and tryptophan-depleted normal volunteers: evidence for monoaminergic mechanisms. Neuropsychopharmacology 1999a; 20: 322–39.

Rogers RD, Own AM, Middleton HC, Williams EJ, Pickard JD, Sahakian BJ, et al. Choosing between small, likely rewards and large unlikely rewards activates inferior and orbital prefrontal cortex. J Neuroscience 1999b: 20: 9029–38.

Shammi P, Stuss DT. Humour appreciation: a role of the right frontal lobe. Brain 1999; 122: 657-66.

Siegal M, Carrington J, Radel M. Theory of mind and pragmatic understanding following right hemisphere damage. Brain Lang 1996; 53: 40–50.

Stone VE, Baron-Cohen S, Knight RT. Frontal lobe contributions to theory of mind. J Cogn Neurosci 1998; 10: 640–56.

Stuss DT. Self, awareness and the frontal lobes: a neuropsychological perspective. In: Strauss J, Goethals GR, editors. The self: interdisciplinary approaches. New York: Springler-Verlag; 1991. p. 255–78.

Stuss DT, Alexander MP, Palumbo CL, Buckle L, Sayer L, Pogue J.

Organizational strategies of patients with unilateral or bilateral frontal lobe injury in word list learning tasks. Neuropsychology 1994; 8: 355–73.

Stuss DT, Benson DF. Emotional concomitants of psychosurgery. In: Heilman KM, Satz, P, editors. Advances in neuropsychology and behavioral neurology. New York: Guilford Press; 1983. p. 111–40.

Stuss DT, Shallice T, Alexander MP, Picton TW. A multidisciplinary approach to anterior attentional functions. [Review] Ann N Y Acad Sci 1995; 769: 191–211.

Stuss DT, Alexander MP, Sayer L, Palumbo C, Franchi D, Dempster R, et al. The effects of focal anterior and posterior brain lesions on verbal fluency. JINS 1998; 4: 265–78.

Stuss DT, Levine B, Alexander MP, Hong J, Palumbo C, Hamer L, et al. Wisconsin Card Sorting Test performance in patients with focal frontal and posterior brain damage: Effects of lesion location and test structure on separable cognitive processes. Neuropsychologia 2000; 38: 388–402.

Stuss DT, Picton TW, Alexander MP. Consciousness, self-awareness and the frontal lobes. In: Salloway S, Malloy P, Duffy J, editors. The frontal lobes and neuropsychiatric illness. Washington (DC): American Psychiatric Press. In press 2001.

Wellman HM, Woolley JD. From simple desires to ordinary beliefs: the early development of everyday psychology. Cognition 1990; 35: 245–75.

Wheeler MA, Stuss DT, Tulving E. Toward a theory of episodic memory: the frontal lobes and autonoetic consciousness. Psychol Bull 1997; 121: 331–54.

Winner E, Brownell H, Happe F, Blum A, Pincus D. Distinguishing lies from jokes: theory of mind deficits and discourse interpretation in right hemisphere brain-damaged patients. Brain Lang 1998; 62: 89–106.

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