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Functional and Anatomical Decomposition of Face Processing: Evidence from Prosopagnosia and PET Study of Normal Subjects [and Discussion]

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Functional and anatomical decomposition of face processing: evidence from prosopagnosia and PET study of normal subjects

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[Plate 1]

SUMMARY

Studies of brain-damaged patients have revealed the existence of a selective impairment of face processing, prosopagnosia, resulting from lesions at different loci in the occipital and temporal lobes. The lesions are often extensive, and it is unclear what functional aspects of face processing are normally served by the damaged areas, and whether they are uniquely devoted to the processing of faces. These issues are further addressed through a combined magnetic resonance imaging (MRI) and positron emission tomography (PET) study of regional cerebral blood flow (rCBF) in normal subjects performing different tasks of face and object processing. The results indicate different patterns of cerebral activation depending on the requirements of the tasks within the processing of faces, as well as a clear dissociation of the neural substrates underlying face and object processing. These results are compared with radiological data from prosopagnosic patients, and are put in relation with the patterns of deficits observed in the patients as a function of the location of their lesions. Together, the findings offer new evidence regarding the functional neuroanatomy of face and object processing.

1. INTRODUCTION

People often express surprise and incredulity when they learn that the perception and recognition of faces are the object of intense research. What is there to investigate, they ask, and how could such natural activities as identifying a friend, recognizing an emotion, appreciating the beauty of a face, that call for no particular skills, raise any questions of scientific interest? There are indeed many factors that deprive the processing of faces of the usual characteristics of an object of scientific scrutiny. It is an effortless act performed as a matter of course and at a speed typical of an automatism. It is a function acquired very early during development and requiring no formal training, and it does not need to be cultivated or improved through special techniques as we feel no particular urge to achieve higher proficiency. It does not involve any thinking and it only occasionally fails us. There seem to be no limits to the number of faces that we can recognize and, as we make new acquaintances and as new actors or politicians become public figures, their faces are quickly learned and identified without obliterating the memories of already known faces. In addition, perceiving and recognizing faces is a private experience, uncommunicable to others, and we are not in the habit of sharing our impressions as to how we process the faces of people. Yet we are also convinced that every one is endowed with the capacity to identify faces, and, when we pass by an acquaintance who shows no sign that he recognizes us, we attribute this failure to his being too absorbed in his thoughts rather than to his being unable to recognize faces. Indeed, those rare individuals who, as a result of brain damage, have become unable to identify the faces of persons they know, try and manage to keep their deficit hidden from others lest they be judged insane.

At a first approximation, these inherent characteristics of face processing could fit the defining properties of 'modules' outlined by Fodor (1983). Perceivers have little conscious awareness of the operations underlying the processing of faces, and they do not even know what physical attributes of the face they rely on when they derive specific information about an individual from a facial representation. That is, face processing is 'cognitively impenetrable', which makes its internal workings unmodifiable, opaque, and not easily amenable to experimental decomposition. Further, face processing is 'informationally encapsulated'; we perceive photographic, caricatural, or schematic, facial representations as faces, even though we are aware that such representations are not real faces. In addition, there is evidence that face processing is domain specific, as it calls for operations unlike those inherent in the processing of other visual objects, and that it is innately specified, as newborns exhibit a remarkable ability to respond to facial representations. Finally, focal cortical damage may produce a selective impairment of face processing, suggesting the existence of neural structures specifically, and perhaps uniquely, devoted to the processing of faces.

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The automaticity, proficiency, and apparently modular organization, of face processing are part of the challenge of investigating a function that is so deeply incrusted in our cognitive capabilities that one easily fails to see the questions raised by its realization and to discern the intricate operations that must be implemented for a perceived face to become meaningful. These seemingly effortless operations attest to the efficiency of the cerebral apparatus subserving this function, but also make the cognitive and neural architectures sustaining face processing harder to penetrate and understand. However, not all aspects of face processing are 'cognitively impenetrable', and recent advances in cognitive science have pushed the limits of explorability of mental functions by seeking to define their particular purposes and the operational principles of their component processes, and to specify the nature, the goals, and the logical order of the steps to be achieved for their realization.

2. FUNCTIONAL DECOMPOSITION OF FACE PROCESSING

The human face holds a special place among visual objects. Any social animal must possess the capacity to differentiate and recognize members of its group and, in humans, the face is the most distinctive attribute for indexing identity reliably. For the face to assume such an indexing role, the processing organism must be endowed with structures and mechanisms adapted to performing the operations required by this function, which implies a structural and cognitive architecture different from that required in processing other objects that do not play such a role. The main purpose of face perception and recognition is to provide the perceiver with a faithful description of facial representations that can be categorized and processed so as to guide interactions with others. This entails a series of constraints on the organism to accommodate the perceptual, cognitive, and social demands inherent in the processing of faces that must be discriminative, accurate, quick, and lead to pertinent information about the bearer of the face.

Most objects are processed in terms of the physical characteristics that define the properties of a given basic category (Rosch *et al.* 1976), irrespective of the unique attributes of a particular instance. On the other hand, each face can be classified into a variety of categories that correspond to diverse properties of the individual, such as age, gender, race, emotion, etc., and, with respect to identity, is treated as different within the category of faces so as to detect its uniqueness and individuality. What makes the processing of faces a complex process is, on the one hand, the different perceptual combinations of facial attributes that must be performed depending on the information to be accessed about an individual, and, on the other hand, the need to extract, from a configuration common to all faces, the particularities that make each face unique. This implies refined perceptual mechanisms capable of achieving a faithful structural representation from which specific patterns of variations within faces can be detected and subtle differences among faces can be discriminated to isolate the attributes that uniquely define each face (Sergent 1989). Each representation must then be stored reliably, and this imposes added constraints on the processing organism given the large number of faces that have to be remembered and the variety of appearances each face can take. For a face to be perceived as familiar, further operations must be implemented to make contact between perceived and stored facial representations, and these operations are concerned with extracting the physiognomic invariants embedded in a given facial representation. Additional processes must then be performed for a face to be recognized as that of a specific individual, and these involved the reactivation of biographic (episodic, semantic, emotional) information related to that face and without which it would remain the face of a stranger (see Bruce & Young (1986) for a detailed description of this model of face recognition).

3. ANATOMICAL DECOMPOSITION OF FACE PROCESSING

Face recognition thus engages a series of operations, different from those inherent in recognizing objects, and whereas the functional organization of the underlying operations has been formally described on the basis of behavioural and simulation studies (e.g. Burton *et al.* 1990), a detailed specification of the neuroanatomical substrates of these operations has been difficult to achieve. The only source of information bearing on this issue has so far been the study of prosopagnosic patients. The correlation between, on the one hand, the behavioural impairments related to the inability to process faces and, on the other hand, the location of the lesion, has offered the opportunity to identify cortical areas the damage of which produces prosopagnosia (Meadows 1974; Damasio *et al.* 1990). It is currently believed that damage to both posterior hemispheres is required for the occurrence of prosopagnosia and, although it is acknowledged that the right hemisphere plays a more crucial role in face processing than does the left hemisphere, it has not yet been possible to identify the actual contribution of each hemisphere to this function, nor the specific operations performed by the involved structures within each hemisphere. In addition, the reliance on data from neurological patients to infer the structural and functional organization of the neural substrates normally underlying face recognition is confronted with a series of theoretical and methodological difficulties.

Inquiring about the location of the lesions responsible for prosopagnosia and asking which cortical areas underlie the normal processes inherent in face recognition are distinct questions that may not have the same answers. A focal cerebral damage may have detrimental effects on the functioning of distant areas and, within an injured brain, local structural integrity does not guarantee normal functioning (Sergent 1984). Alternatively, a particular area may perform operations the outcome of which normally serves as input to other areas and without which the latter may

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not be able to perform its specific operations (see Warrington & Taylor 1978). Therefore, the actual contribution of a cerebral structure to a function may not be revealed in a damaged brain if operations taking place at earlier stages cannot be performed as a result of damage to an area normally mediating these operations. A given area may also participate in the realization of a function without its participation being either necessary or sufficient, such that its destruction would not result in impaired processing. Studies of prosopagnosic patients may thus not provide an exhaustive picture of the neurofunctional anatomy of face recognition.

In addition, because the lesions responsible for prosopagnosia are often extensive and not restricted to well delineated cytoarchitectonic areas, it is unclear what cortical regions are critically involved in the processing of faces, what functional aspects of face processing are served by the involved areas, and whether these areas are uniquely devoted to the processing of faces. Moreover, there is such a large variability among patients in the aetiology and location of the damage associated with the occurrence of prosopagnosia that it has been difficult to achieve a comprehensive view of the biological architecture of face recognition. For instance, even though the ventro-medial occipito-temporal junction of the right hemisphere has been considered a critical area in the processing of faces, cases have been reported in whom the lesion did not invade this particular area (e.g. Damasio *et al.* 1982; Michel *et al.* 1989; Sergent & Poncet 1990). It is not even clear whether the engagement of both hemispheres is required for the normal processing of faces, and, although it is commonly held that bilateral lesions are necessary for the occurrence of prosopagnosia (e.g. Damasio *et al.* 1982), several cases have been reported with damage restricted to the right hemisphere (De Renzi 1986; Landis *et al.* 1988; Michel *et al.* 1989). Research on commissurotomized patients (Levy *et al.* 1973; Sergent 1990) and on normal subjects (Sergent 1986) has produced results suggesting that the left hemisphere is not a silent partner in face processing and may be equipped with the necessary structures to perform all the operations from perception to identification. However, the particular conditions under which face processing is examined in these subjects, with few, expected, and repeatedly presented, faces may reveal competences the emergence of which is entirely dependent on the experimental procedures. With respect to the associated deficits, it has not yet been established if the non-facial impairments accompanying prosopagnosia result from a common basis to the processing of faces and the other deficient functions or reflect adjacent cortical territories respectively dedicated to different functions but conjointly damaged.

It thus seems that the knowledge and understanding of the anatomical substrates of face recognition cannot be entirely achieved on the sole basis of radiological data from prosopagnosic patients, and findings of hemisphere asymmetry in face processing obtained in commissurotomized and normal subjects are at best equivocal.

4. DIVERSITY OF FACE-PROCESSING BREAKDOWN IN PROSOPAGNOSIA

The study of prosopagnosic patients has none the less provided important information about the cognitive and anatomical architecture of face processing. In particular, it has shown that the same behavioural deficit – an inability to experience a feeling of familiarity at the view of faces of known persons, and therefore, to identify them – can result from damage at different locations in cerebral structures and can be produced by a breakdown at different stages of processing. Thus, a disruption of one of these stages is sufficient to disable the whole face-recognition system, but it does not necessarily affect all operations on facial representations. Table 1 illustrates this point and shows the results of a series of tests conducted on four prosopagnosic patients (Sergent & Signoret 1991). In addition to standard intellectual and memory tests, the patients were subjected to tasks of object recognition (naming an object seen from a canonical or a non-canonical perspective), gender categorization (telling men apart from women, using faces of individuals with short hair), age estimation (categorizing faces into one of five classes of age), recognition of facial emotion (naming the emotion expressed by a face, using the six basic emotions), matching different views of the same faces, which requires the extraction of the physiognomic invariants, and identifying famous people by their faces.

Whereas all were severely impaired at identifying faces and none had visual object agnosia, they exhibited different patterns of performance on tasks that call for the processing of various facial properties regardless of identity. For instance, patient R.M. was defective at all aspects of face processing, even being unable to realize that two identical photographs of the same face represented the same individual, yet he had no difficulty in differentiating and identifying instances of another category of visual objects such as cars, giving the correct make, model, and year of fabrication of 172 out of 210 pictures of cars that were presented to him, a performance that none of the normal subjects that have so far been tested on this task has yet achieved. Neither R.M. nor patient P.M. were able to extract the physiognomic invariants of faces, whereas the other two patients (P.C. and P.V.) performed this operation well above chance. In fact, P.V. was not significantly impaired as long as the familiarity and identity of the faces were irrelevant to processing, and for example, she could easily realize that two different views of her own face represented the same person but she was not aware that they were her own. Yet, in addition to her prosopagnosia, she was unable to recognize such famous monuments as the Eiffel Tower or the Arc de Triomphe.

These different patterns of deficits thus reflect a break-down at different levels in the steps leading from the perception to the identification of faces, suggesting that the integrity of several functional stages is necessary for the recognition of faces. In some patients (e.g. R.M.), the disturbance lies at the structural encoding stage; in others (e.g. P.M.), it lies

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Table 1. *Performance of prosopagnosic and control subjects on face and object processing tasks*

	P.C.	P.M.	P.V.	R.M.	controls (range)
WAIS verbal	114	108	102	103	
memory quotient	109	111	98	112	
object recognition (canonical)	52/54	54/54	52/54	52/54	50–54
object recognition (non-canonical)	24/54	18/54	—	23/54	45–54
gender categorization	38/50	31/50[a]	43/50	18/50[a]	43–50
age estimation	17/20	16/20	17/20	4/20[a]	16–20
face emotion	12/24	8/24[a]	18/24	6/24[a]	18–24
physiognomic inv.	14/24	4/24[a]	17/24	2/24[a]	16–24
face recognition	7/100	4/100	2/100	0/100	94–100

[a] Performance not different from chance.
Underlined: performance lower than the lowest performance of control subjects.

beyond this stage but affects the operations by which the physiognomic invariants contained in a facial configuration are extracted; still in others (e.g. P.C. and P.V.), it spares the latter stage but affects the operations whereby a properly elaborated perceived facial configuration reactivates the pertinent memories related to that face. It must be noted, however, that, even if the nature of the prosopagnosic disturbance reflects an impairment at different cognitive loci across patients, the actual impairment does not always fall so neatly into the well delineated steps of face-recognition models, and the results of P.M. and P.C. (see table 1) indicate that the break down may affect to varying extent several of the underlying stages of face processing.

5. PET STUDY OF FACE PROCESSING IN NORMAL SUBJECTS

Recent advances in brain-imaging techniques for measuring blood flow within cerebral structures have made possible the visualization of the neuronal substrates of cognitive abilities in normal subjects, thus providing the opportunity to infer the neuroanatomy of a given function without interference from the dynamic effects of a cortical lesion on the functioning of the whole brain. One such technique, developed by Raichle, Fox, Posner and their colleagues (Petersen *et al.* 1988; Posner *et al.* 1988), is based on positron emission tomography (PET) of regional cerebral blood flow (rCBF), using a short lived radioisotope such as [^{15}O] H_2O as a blood flow tracer, and successive and complementary tasks allowing, through a method of subtraction, a comparison of the localization and level of cerebral activation as a function of the specific processing demands inherent in the experimental tasks. This technique was recently applied on seven normal volunteers subjected to a series of control and experimental tasks involving the processing of faces and objects (Sergent *et al.* 1991). The basic procedure was the same as that used by Posner *et al.* (1988), with two additional features. One of the difficulties inherent in the interpretation of PET results lies in the localization of the foci of activation in the cerebral structures. In this study, functional data from PET scans were superimposed on structural data from MRI scans obtained from each subject. This procedure (Evans *et al.* 1988) offers the opportunity to compare the localization of foci of activation in the normal brain with the site of the lesions in the brains of prosopagnosic patients. In addition, to ensure that the subjects were effectively performing the requested tasks, they had to respond manually to the presented stimuli, thus providing data about the speed and accuracy of their responses.

Along with two control tasks (passive fixation of a lit screen and passive fixation of unfamiliar faces), the subjects performed four two-choice reaction-time tasks: (i) a grating-orientation discrimination; (ii) a male–female face categorization; (iii) a face identification, in which they categorized familiar faces as politicians or actors; and (iv) an object categorization, in which they classified objects into living or non-living categories. The three tasks involving either face or object processing were exactly the same as those performed by the four prosopagnosic patients. The

Description of plate 1

Figure 1. Foci of activation superimposed on magnetic resonance images of the subjects' brains (the numbers on the bottom left of the images correspond to the slice level on the dorso-ventral axis, following Talairach & Tournoux (1988) stereotaxic atlas). Gratings: gratings minus fixation; (a) activation at the level of the occipital cortex; (b) activation at the level of the left sensori-motor cortex resulting from the subjects' right-hand response in the experimental tasks. Face Gender: face gender minus fixation; slices are 3 mm apart, in ascending order, starting at slice level −8 mm. Face identity: (a) face identity minus gender; (b) face identity minus fixation, in ascending order, starting at slice level −23 mm. Object: object-recognition minus gratings; (a) absence of activation of the anterior temporal cortex; (b) activation of the left occipito-temporal cortex and the left temporal area 21.

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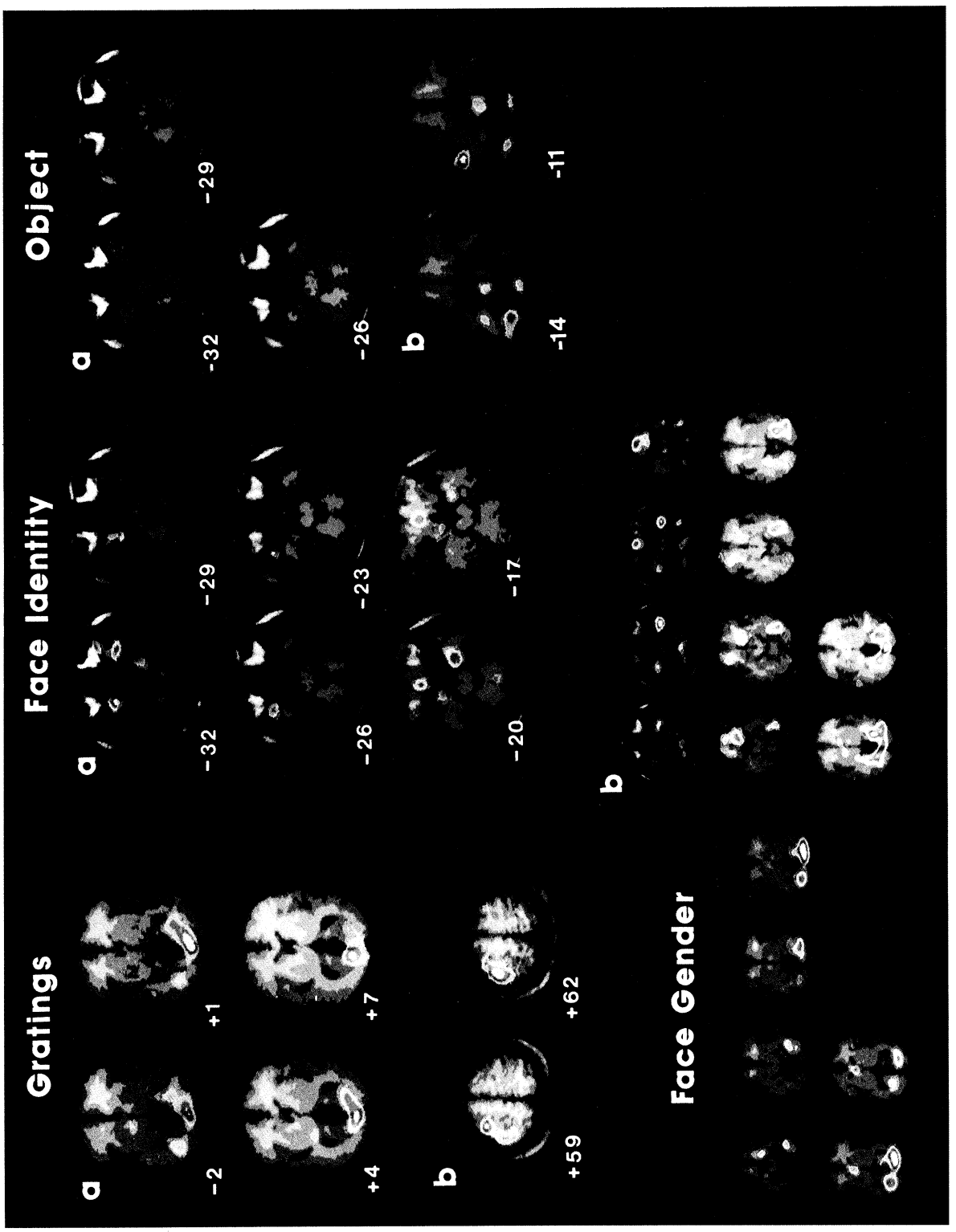

Figure 1. For description see opposite.

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main findings of the PET experiment are described in figure 1 that presents the foci of activation in four of the tasks, superimposed on a MR image of the subjects' brains.

The perception of gratings, and the discrimination of their orientation signalled by a right-hand response, resulted in intense activation of the striate and extrastriate cortex of both hemispheres (figure 1, Gratings, a), and of the left pre- and post-rolandic areas corresponding to the cortical sensori-motor representation of the right hand (figure 1, Gratings, b). The gender-categorization task produced further activation essentially localized in the right lingual and posterior fusiform gyri, and these activated areas were more anterior and more ventral than those involved in the discrimination of the gratings. When the activation resulting from the gender-categorization was subtracted from that associated with the face-identification task, the remaining significant activation involved three main regions of the brain: (i) the medial fusiform gyrus (areas 19–37) of both hemispheres; (ii) the right parahippocampal gyrus (area 36) with no activation of the left homotopic area; and (iii) the anterior region of the temporal lobe of both hemispheres, including the temporal poles (see figure 1). However, when the activation generated by the object categorization task was subtracted from the activation associated with the performance of the face-identification task, the activation of the left fusiform gyrus was no longer apparent, suggesting that this area is involved in operations that are not specific to the processing of faces. The only involvement of the left hemisphere that could be related to the processing of faces as such was found in the most anterior region of the left temporal lobe (see figure 1). Finally, the recognition of objects engaged cerebral structures located in the left hemisphere, specifically the lateral temporo-occipital region (area 19–37) and the middle temporal gyrus (area 21). By contrast, there was no activation of the anterior temporal cortex nor of the parahippocampal gyrus during the object-recognition task, and there was, therefore, little overlap between the cerebral structures involved in face and object processing.

6. CONVERGING EVIDENCE FROM PROSOPAGNOSIA AND PET STUDY

The regional activation of cerebral structures identified in the PET study suggests that the processing of faces essentially involves ventro-medial regions of the right hemisphere, and three main areas appear to play a crucial role in the realization of this function. The right medial lingual and fusiform gyri, the right parahippocampal gyrus, and the anterior cortex of the temporal lobes. It may therefore be of interest to compare these findings with the site of the lesions responsible for prosopagnosia in the four patients whose performance on face and object recognition tasks was presented in table 1 and whose brain images are presented in figure 2. The examination of these images indicates a striking convergence of the radiological data from the patients and the loci of activation in the normal subjects. Except for P.V. who had a small lesion in the temporal pole of the left hemisphere, the localization of the lesion was restricted to the right hemisphere. More importantly, the cerebral damage affected different parts of the right hemisphere in the four patients, which concurs with the different patterns of deficits they exhibited. Thus, both R.M. and P.M. had lesions involving the right occipital cortex and the posterior part of the medial temporal cortex, and, as shown in table 1, they were defective at purely perceptual operations on facial representations. In contrast, P.C.'s lesion involved the white matter surrounding the right fusiform gyrus but did not affect the cortex of this gyrus, and, in P.V., the lesion involved the anterior half of the right temporal cortex comprising the parahippocampal gyrus. In the latter two patients, the capacity to perform perceptual operations on faces and to extract the physiognomic invariants was essentially spared, and their deficit reflected an inability to reactivate pertinent memories associated with a perceived face.

The pattern of findings emerging from the study of prosopagnosic patients and of normal subjects suggests that the processing of faces is subserved by an extensive neural network that encompasses most of the ventro-medial regions of the right hemisphere, from the occipital pole to the temporal pole. The right lingual and fusiform gyri participate in the perceptual operations concerned with the elaboration of a configurational representation of the face and the extraction of the physiognomic invariants that uniquely define each face. The right parahippocampal gyrus, which is an integral part of the limbic system and plays a pivotal role in distributing outputs from the hippocampus (Van Hoesen 1982), is involved in re-establishing the connections between facial representations and the pertinent biographical information that was activated and stored during earlier encounters with these faces. The involvement of the anterior temporal cortex may reflect the activation of this biographical information which is not exclusively related to faces but is essential for a face to become meaningful. It is unclear, at present, whether the contribution of the left anterior temporal cortex, evidenced in the PET study and suggested by the lesion of P.V., is a necessary requirement for the processing of faces, as lesions restricted to the right anterior temporal lobe may be sufficient to prevent retrieval of pertinent biographical information, not only from the presentation of faces but from the evocation of proper names (e.g. Ellis *et al.* 1989). It is noteworthy that no activation of the superior temporal sulcus, nor of the lateral infero-temporal cortex, in which cells selectively responsive to faces have been recorded in the monkey's brain, could be detected in the PET study. Moreover, damage to these areas in the human brain does not result in prosopagnosia (Damasio *et al.* 1990). On the basis of current findings, there seems to be no direct anatomical correspondence between the simian and the human neural substrates of face processing. In addition, both the results of the PET study and the findings from the prosopagnosic patients indicate that face and object processing are dissociable functions and do not rely on the same neural structures. The

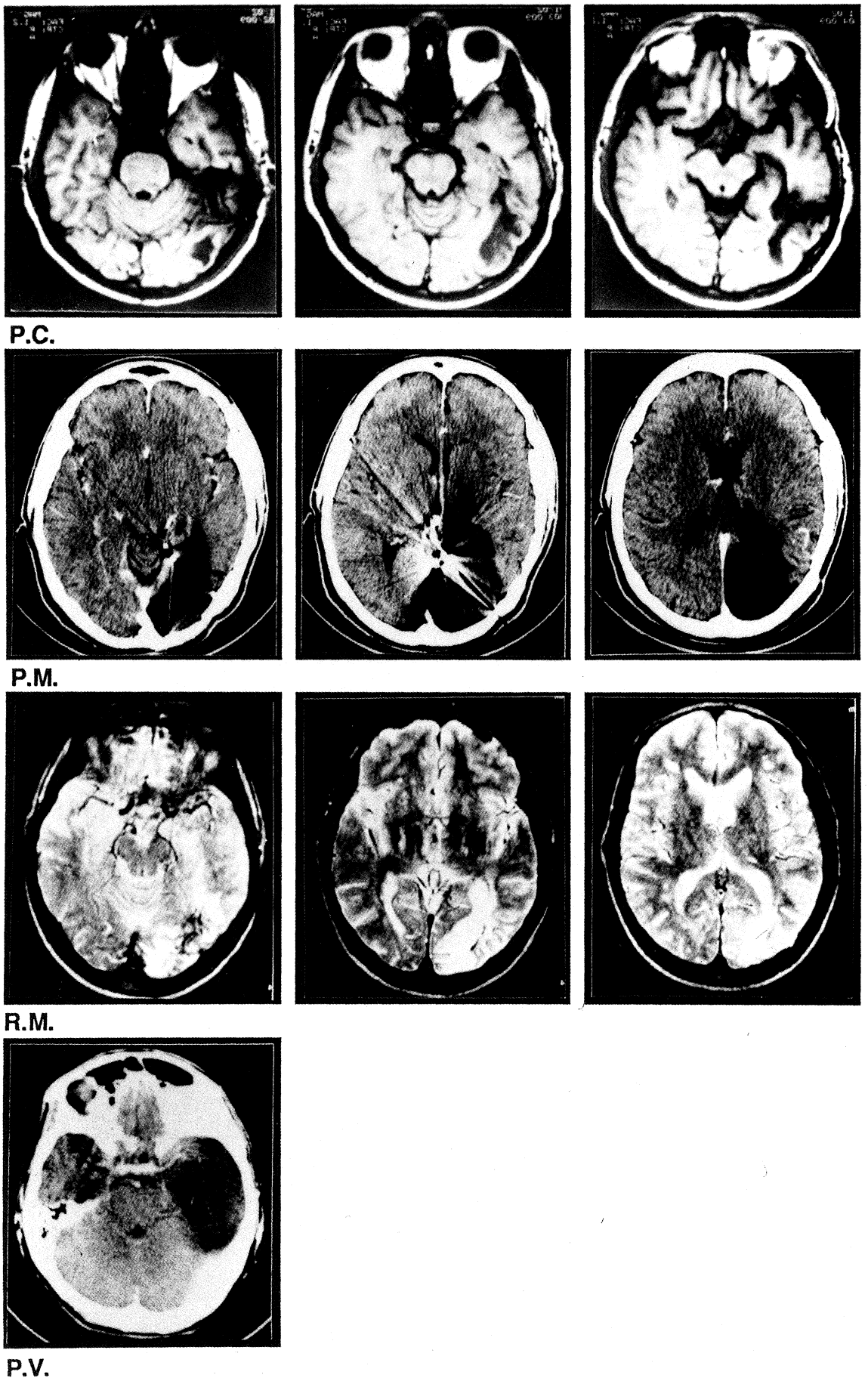

Figure 2. Radiological data of the four prosopagnosic patients.

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frequent observation of a joint deficit of these two functions is likely to result from a bilateral posterior lesion, but each deficit occurs separately in the case of unilateral damage.

The functional architecture of the brain is designed to accommodate the cognitive demands of the multitude of operations that have to be performed to adapt to the environment. With respect to face processing, the stringent perceptual demands, made necessary by the common format of all faces that differ in subtle variations in their configurations, call for structures capable of performing quick and reliable differentiations; the need to access relevant personal information about these faces for their recognition also requires the involvement of structures able to relate facial representations to their pertinent memories. Although other categories of objects carry with them similar processing demands, it is unclear at present whether they rely on the same structures as those underlying face processing. There is no logical reason why they should not, but we are still far from having deciphered the logic of the brain.

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Discussion

V. Bruce (*Department of Psychology, University of Nottingham, U.K.*). The prosopagnosic patients Dr Sergent described were all impaired in their recognition of non-canonical views of objects. What is her view of the relation between this impairment and their impairments in the processing of faces?

J. Sergent. Actually, only three of the four patients were subjected to a test of recognition of objects presented from a non-canonical perspective, as P.V. was not examined on this task. This is obviously unfortunate, because no perceptual impairment could be detected in P.V., presumably as a result of the location of her lesion in the anterior part of the temporal lobes, and her performance on this test would have yielded crucial information. None the less, not all prosopagnosic patients display an impaired recognition of non-canonical views of objects (see, for example, Sergent & Villemure (1989), suggesting that the two impairments are not necessarily concomitant. Yet their association had already been pointed out by Landis *et al.* (1988) and the present findings concur with their observation. It would be necessary to identify the underlying operations conjointly involved in the recognition of faces and non-canonical views of objects in order to uncover the reason for the frequent association of their impairments. The suggestion that a deficit in axis

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transformation underlies the failure to recognize unusual views of objects (Humphreys & Riddoch 1984) does not apply to prosopagnosia as there should be no difficulty in retrieving the major axis of a face. In fact, prosopagnosic patients can perform as well as normal subjects on tasks that require the recognition of disoriented objects or letters (Sergent & Signoret 1991). An alternative interpretation of the failure to recognize unusual views of objects (Warrington & James 1986) is based on the suggestion that a minimal set of distinctive features of the objects must be retrieved for recognition and that a larger set is required for right-hemisphere damaged patients. Such an interpretation does not seem to apply either to the impairment of prosopagnosic patients, as they do not perform better when presented with caricatures of faces which typically highlight the distinctive features uniquely characteristic of a face (Sergent & Signoret 1991).

A third possibility might be that both faces and unusual views of objects make perceptual demands that call for the ability first to derive featural invariants from a given representation regardless of perspective and second to establish the proper relations among these invariants so as to achieve an adequate configuration of the structure of the face or the object. Whether faces and unusual views of objects share underlying processing structures for their recognition is still unknown, but this is certainly a possibility worth studying. Conjointly, the deficit may very well be exacerbated by a non-specific impairment in perceptual processing whereby right-hemisphere damage, irrespective of its locus within the posterior region of this hemisphere, reduces the capacity to operate on visual information that lacks its usual contrast and resolution. If the source of the association of the two impairments lies in the latter two deficits, the conjoint occurrence of impaired recognition of faces and unusual views of objects should then depend on the cognitive locus of the prosopagnosic disturbance, and one would predict that patient P.V. should show no deficit in recognizing non-canonical views of objects.

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E.T. Rolls (*Department of Experimental Psychology, University of Oxford, U.K.*). I would be interested to know where, as accurately as possible, in the right anterior temporal lobe region, activation occurs to (passively seen) faces, as this region might be the area in human subjects which corresponds to some of the more anterior and ventral temporal lobe sites in which face-selective neurons are found in macaques.

J. Sergent. At present, there is no answer to this question. The subjects were tested in a passive face-viewing condition in the PET study, using faces of unfamiliar people, but the paterns of cerebral activation associated with this condition did not result in any activation change when compared with the grating condition. When compared with the fixation-control condition, this passive face-viewing resulted in significant bilateral blood-flow changes only in the striate cortex and lingual gyrus, but not beyond. This illustrates two types of problems inherent in cognitive ^{15}O PET studies, one methodological, the other technical.

From a methodological standpoint, the use of a passive-viewing condition, especially when data must be averaged across subjects to increase the signal-to-noise ratio, prevents any control over the actual cerebral state of the subjects who are not constrained to perform any specific task. In the case of faces which lend themselves to so many diverse operations, one cannot guarantee homogeneity of processing during a passive condition, with the consequence that different cortical areas may be activated across subjects, making it impossible to obtain a reliable group difference between a control and a passive-viewing condition. It seems that passive-viewing (or listening or sensing) conditions are unlikely to provide relevant results and will produce discrepant findings across studies as well as many failures to replicate across laboratories. This problem extends to the situation where a passive condition is designed as a control for an experimental condition. Because activation changes between a control and an experimental condition necessarily reflect relative rather than absolute patterns of cortical involvement in a given task, the actual activation obtained in a control condition plays a crucial role in the identification of the activation associated with the experimental condition. If subjects are let free to perform any cognitive operation in a (passive) control condition, it will not be possible to know what underlies an observed activation increase in the experimental condition.

From a technical standpoint, absence of activation change does not mean absence of activity, and there are several factors that may prevent a given area that would be expected to participate in a task from attaining the required increase in blood flow from one condition to another. For instance, not all cerebral areas may have the same activation threshold. If an area has a low threshold, as might be the case of the hippocampus, blood-flow increase may be relatively small and insufficient to achieve statistical significance. Or a control condition may raise activation in a given area even if its participation is not indispensable, which could hide its actual participation in a task to which its contribution is indispensable.

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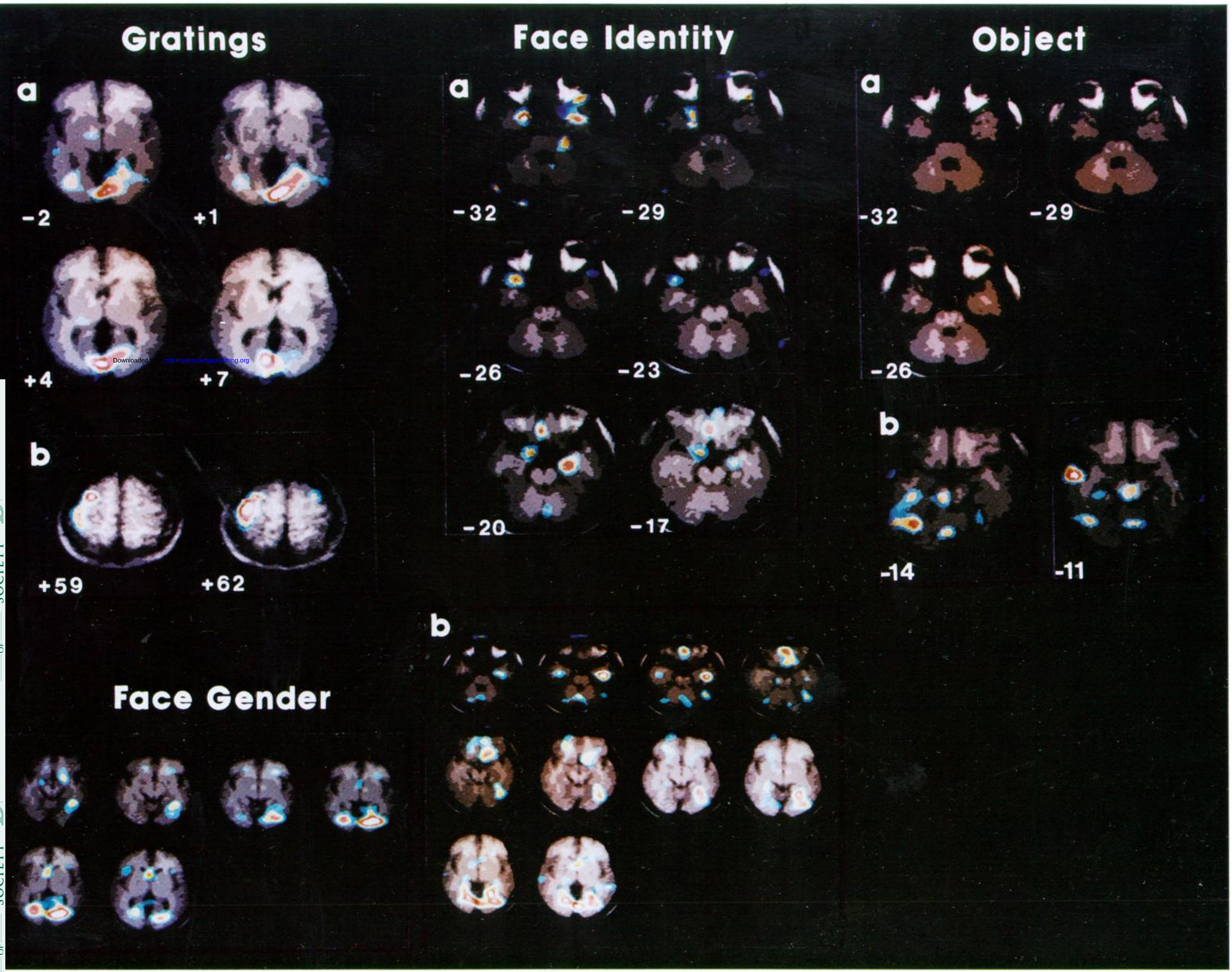

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Figure 1. For description see opposite.

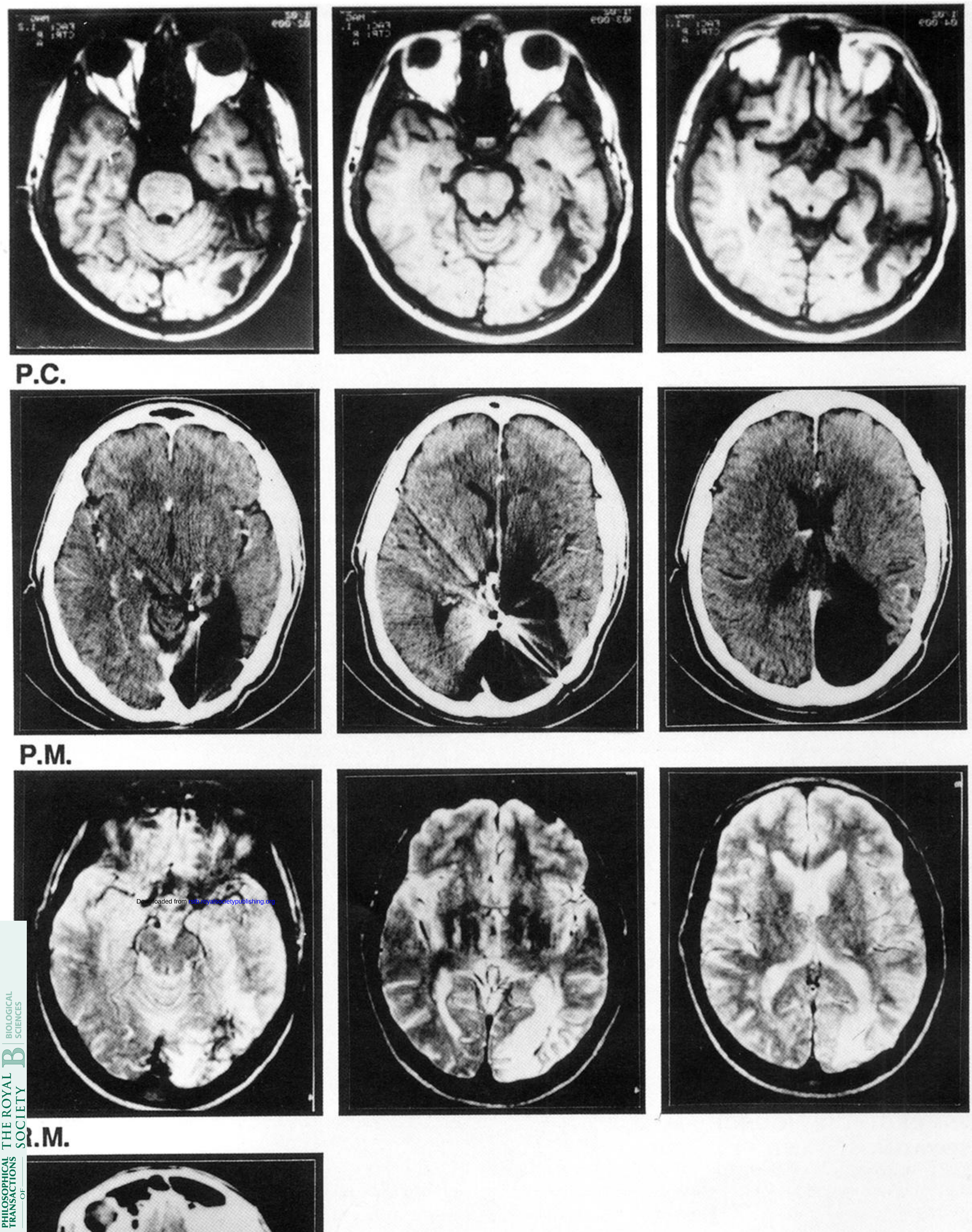

Figure 2. Radiological data of the four prosopagnosic patients.