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The Inverted Face Inversion Effect in Prosopagnosia: Evidence for Mandatory, Face-specific Perceptual Mechanisms

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Does the human visual system contain a specialized system for face recognition, not used for the recognition of other objects? This question was addressed using the "face inversion effect" which refers to the loss of our normal proficiency at face perception when faces are inverted. We found that a prosopagnosic subject paradoxically performed better at matching inverted faces than upright faces, the opposite of the normal "face inversion effect". The fact that his impairment was most pronounced with the stimuli for which normal subjects show the greatest proficiency in face perception provides evidence of a neurologically localized module for upright face recognition in humans. An additional implication of these data is that specialized systems may control behavior even when they are malfunctioning and therefore maladeaptive, consistent with the mandatory operation of such systems according to the "modularity" hypothesis of the cognitive architecture.

Face inversion Face recognition Modularity Prosopagnosia

Is face recognition accomplished using a specialized subsystem of the visual system, or are faces recognized in the same way as other objects? Single unit recordings in nonhuman primates have revealed populations of cells that respond selectively to faces, in some cases responding differentially to particular faces, suggesting a role for these cells in face recognition (e.g. Bruce, Desimone & Gross, 1981; Perret, Rolls & Caan, 1982; Baylis, Rolls & Leonard, 1985; see Desimone, 1991 for a recent review). However, faces may not be unique visual stimuli in this regard, as cells have also been found that respond to nonface objects, although the selectivity and strength of such responses is weaker (Baylis *et al.*, 1985). The interpretation of the "face cell" literature with respect to the question posed at the outset is further complicated by the observation that monkey's face recognition performance is not seriously impaired when the area richest in face cells, the superior temporal sulcus, is ablated bilaterally (Heywood & Cowey, 1992).

Potentially the strongest evidence of a specialized neural system dedicated to face recognition comes from human prosopagnosia. Prosopagnosia is the apparently selective impairment of face recognition following brain damage. Although such individuals frequently manifest some slight difficulty with the recognition of common objects, particularly in pictures, they appear far more impaired at face recognition, failing to recognize friends and close family members by sight. Although prosopagnosia is most naturally explained by damage to a specialized face processor, an alternative interpretation is possible, and is indeed frequently offered in the modern neuropsychology literature.

Proponents of the more parsimonious view, that there is a single visual recognition system for faces and nonface objects, have pointed out that faces may be more difficult to recognize than most objects because faces are more complex than many other objects and very similar to one another (e.g. Brown, 1972; Damasio, Damasio & Van Hoesen, 1982; Gloning, Gloning, Jellinger & Quatember, 1970; Mesulam, 1987). From this point of view, it is plausible that prosopagnosia results from mild damage to a general-purpose object recognition system.

Distinguishing between these two accounts of prosopagnosia requires that the prosopagnosic's performance on faces and nonface control stimuli be assessed relative to normal subjects. In this way it is possible to determine whether prosopagnosics are disproportionately impaired at face recognition. Several recent studies have attempted to assess the true selectivity of prosopagnosia by comparing recognition performance with faces and nonface objects whose difficulty level for normal subjects is known.

Grusser, Kirchkoff and Naumann (1990) devised a recognition memory test with photographs of faces

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and art nouveau vases, and administered it to a variety of brain-damaged patients and control subjects. They found that, relative to normal control subjects, patients performed worse on the faces, although there was no significant different between left and right hemisphere damage, or between the different aphasia-types of the left hemisphere group. This finding suggests that faces may be differentially vulnerable to brain damage in general. However, none of the patients tested had prosopagnosia, or even lesions in temporo-occipital cortex, the territory associated with prosopagnosia. McNeil and Warrington (1993) compared the recognition performance of a prosopagnosic subject with human and sheep faces, and found the prosopagnosic impaired only with human faces. In an experiment with a different prosopagnosic subject, Farah, Klein and Levinson (1995) used a variety of common objects (chairs, scissors etc.) in one experiment and eyeglass frames in another experiment as the nonface objects, and again found the prosopagnosic to be more impaired with faces, relative to normal control subjects.

The results of these studies challenge the hypothesis that prosopagnosia is a mild or moderate impairment of general-purpose face recognition, with faces most vulnerable simply because they are overall harder than nonface objects. However, a proponent of single-system, general-purpose object recognition might still question whether the faces and nonface objects used in these experiments were equivalently difficult on all relevant dimensions. For example, perhaps faces are harder than eyeglass frames on the dimension of inter-item similarity, but easier on the dimension of acuity. In this case prosopagnosia might not be face-specific, but simply a general impairment of individuating highly similar patterns.

Inverted faces are an ideal type of nonface control stimulus for testing this hypothesis. They are equivalent to upright faces in virtually all physical stimulus parameters, such as spatial frequency, complexity, and inter-item similarity. Nevertheless, a large body of research on the "face inversion effect" (see Valentine, 1988) suggests that inverted faces are not perceived and recognized using the same processes as upright faces: inverted faces are harder for normal subjects to learn as measured by recognition performance, and harder to perceive as measured by simultaneous matching performance. The inferior performance with inverted faces can be interpreted in terms of the specialization of face recognition processes for upright faces. Further evidence linking the face inversion effect to the operation of a specialized face processor which takes only upright faces as input comes from developmental studies, laterality studies, and studies of the nature of face representation. For example, Carey and Diamond (1977) report that the inversion effect is absent in young children, but as face recognition matures it also becomes vulnerable to the inversion effect. The right hemisphere, which is generally reported to be superior to the left at face recognition, also shows a more pronounced face inversion effect (Leehey, Carey, Diamond & Cahn, 1978). Although faces are encoded into memory holistically (i.e. without explicitly represented parts), inverted faces are not; they appear to be represented with the same degree of part decomposition as nonface objects such as houses (Tanaka & Farah, 1993). In sum, even though upright and inverted faces are identical in every way except their orientation, it appears that upright faces engage the processes by which we normally recognize faces and inverted faces do not, or do so to a lesser extent.

In the present study, we assessed the face inversion effect in a prosopagnosic subject, in order to test the hypothesis of face-specific perceptual mechanisms in humans. We reasoned that if the prosopagnosic's underlying impairment was not face-specific, then he would show a normal face inversion effect. In contrast, if he had suffered some degree of damage to neural tissue implementing a face-specific processor, he would show an absent or attenuated face inversion effect, thus providing evidence for the existence of a functionally and anatomically distinct system for perceiving faces. Previous neuropsychological research with nonprosopagnosic brain-damaged subjects has found mixed results with inverted faces. Yin (1970) tested nonprosopagnosic right hemisphere-damaged subjects with upright and inverted faces and found a diminished face inversion effect, whereas Grusser *et al.* (1990) report that their nonprosopagnosic brain-damaged subjects performed consistently worse with inverted faces than with upright, particularly the right hemisphere-damaged subjects.

METHODS

Subjects

The prosopagnosic subject was LH, a 40 yr-old man who has been prosopagnosic since an automobile accident 20 yr earlier. When tested during his recovery, his verbal IQ was 132 and his performance IQ was 93. His main residual impairment is in face recognition. He is profoundly prosopagnosic, unable to recognize friends, neighbors or even his wife and children without extra-facial cues. His recognition of real objects and pictures is only mildly impaired, and his recognition of printed words is good. His ability to match faces is within the normal range, and he produces easily recognizable copies of unrecognized drawings, placing him in the category of associative (rather than apperceptive) visual agnosics. Brain damage from the accident and subsequent surgery consists of bilateral occipitotemporal lesions, and right frontal and anterior temporal lesions. For additional neuropsychological information please see Levine, Calvanio and Wolfe (1980).

Note that research on prosopagnosia is generally confined to single case studies because of the rarity of the syndrome. It would of course be desirable to test the generality of our results with other prosopagnosics. Nevertheless, clear-cut and reliable findings obtained with LH can function as an "existence proof" at the very least, and given that he was entirely normal prior to his injury in adulthood (i.e. he was a successful college student, and had no history of developmental, neurological or psychological abnormality), we believe it is reasonable to assume that conclusions regarding the organization of his visual system can be applied to the human visual system in general.

Normal subjects were also tested, in order to verify that the experimental paradigm would elicit the face inversion effect in nonprosopagnosics. These subjects were recruited from the undergraduate populations of Carnegie Mellon University and the University of Pennsylvania.

Materials

Stimuli consisted of 15 different sketch-like depictions of male faces, created using the Mac-a-Mug program and differing from one another only in their internal features. These were paired to create 15 "same" pairs and 15 "different" pairs, for a total of 30 pairs. In all studies to be described, these pairs occurred equally often upright and inverted. Thus, 60 trials comprises one replication of all trial types. For studies run on a computer, faces subtended a visual angle of approx. 16 × 12 deg at a typical viewing distance, and subjects responded "same" or "different" by pushing labeled keys on the keyboard. For studies using laser-printed sheets of paper, the visual angle was approx. 14 × 10 deg, and the subject said "same" or "different".

Procedure

Because of the profound face recognition impairment in prosopagnosia, we assessed face processing using a face matching task rather than a recognition task. LH and normal subjects were tested in a sequential matching task, in which an unfamiliar face was presented, followed by a brief interstimulus interval (ISI), followed by a second face, to which the subject responded "same" or "different". The first and second faces of a trial were always in the same orientation, and upright and inverted trials were randomly intermixed.

Several studies were carried out, with different subjects, modes of stimulus presentation, and durations of stimuli and ISIs as reported in Table 1.

RESULTS

The first study was undertaken to verify that our task would elicit the face inversion effect in normal subjects. As shown in Table 1, subjects were reliably more accurate and faster at matching upright than inverted faces.

LH was the subject of the second study. Although he is able to match faces, he does so slowly and with more difficulty than a normal subject. Therefore, longer exposure durations and a shorter ISI were used. As shown in Table 1, LH was significantly more accurate with inverted faces. This outcome was not among the alternatives we had considered. We had assumed that if he had an impaired face processor, it would simply

TABLE 1

Study	Subject(s) and trials/subject	Mode of stimulus presentation	Presentation rates: stimulus 1 ISI stimulus 2	Accuracy				Reaction time (msec)			
				$\bar{X}_{upright}$	$\bar{X}_{inverted}$	χ^2/F value	P value	$\bar{X}_{upright}$	$\bar{X}_{inverted}$	F/t value	P value
1	16 control subjects $n = 300$	Macintosh II with CRT display	200 msec 3 sec 200 msec	87.8%	77.1%	$F = 34.491$	0.0001	950.911	1045.495	$F = 42.899$	0.0061
2	LH $n = 120$	Manual	10 sec 2 sec —*	76.7%	95.0%	$\chi^2 = 6.853$	0.0088	N/A	N/A	N/A	N/A
3	LH $n = 60$	Manual	5 sec 2 sec —*	80.0%	96.7%	$\chi^2 = 2.588$	0.1077	N/A	N/A	N/A	N/A
4	LH $n = 300$	Macintosh portable with LC display	—†	62.0%	68.0%	$\chi^2 = 0.938$	0.3329	1612.446	1529.525	$t = 1.432$	0.1555
5	LH $n = 300$	Macintosh II with CRT display	1.5 sec 1.5 sec 1.5 sec	58.0%	72.0%	$\chi^2 = 5.861$	0.0155	1702.179	1524.102	$t = 3.022$	0.0017
6	8 control subjects $n = 300$	Macintosh II with CRT display	1.5 sec 1.5 sec 1.5 sec	93.9%	82.2%	$F = 28.670$	0.0011	1085.701	1253.319	$F = 10.845$	0.0132

*LH was given unlimited time to view stimulus 2 during manual presentations.
†See text for explanation.

not be used in this task, leading to the prediction of an absent or attenuated face inversion effect. Instead, it appears he has an impaired face-specific processor, which is engaged by the upright but not the inverted faces, and used despite being disadvantageous.

To verify this counterintuitive result, we repeated the task in Study 3. The means were very similar to those of the second study, although the difference was not statistically significant. This is presumably because only half as many trials were completed. Combining the results of all testing so far with LH, the type II error probability of the inverted inversion effect is 0.001.

In a fourth study, we administered 300 trials of the experiment to LH using a Macintosh portable computer. We used longer exposure durations and a shorter ISI than the previous studies because of LH's difficulty in seeing the liquid crystal display, which was not backlit. The precise time durations have unfortunately been lost, but we include this study for the sake of completeness. Table 1 shows that his performance was indeed poorer than before, even with the altered timing. Although there are trends in both accuracy and reaction time consistent with his previous performance, neither effect is statistically reliable.

A fifth study was undertaken as a final test of the inversion effect with both a good quality display and a large number of trials. The exact design of the fourth study was replicated with a Mac II computer. Table 1 indicates that with the improved visual quality of the display, LH was able to perform well with relatively brief exposures, and again showed a significant inverted inversion effect in both accuracy and reaction time. Figure 1(a) shows his accuracy for upright and inverted faces.

Finally, in a sixth study normal subjects performed the task with the same display and timing as LH, and showed normal inversion effects in both accuracy and reaction time. Their mean accuracy for upright and inverted faces is shown in Fig. 1(b).

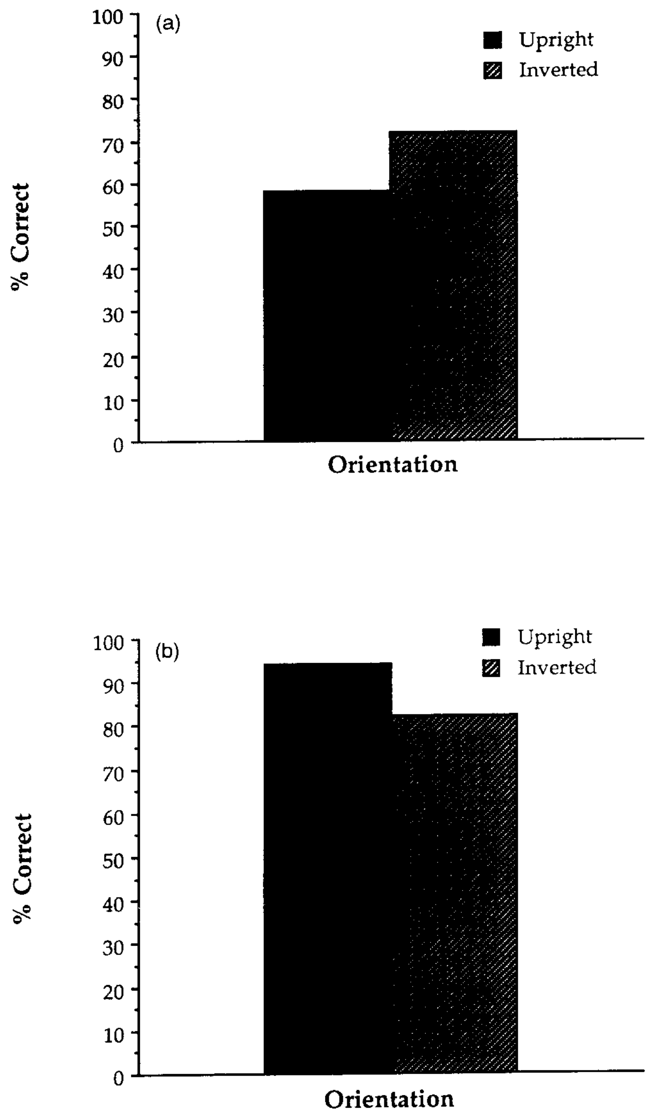

FIGURE 1. Performance of LH (a) and normal subjects (b) at matching upright and inverted faces, shown for 1.5 sec each with a 1.5 sec interface interval. Normal subjects show the classic "face inversion effect"; LH shows an inverted inversion effect.

DISCUSSION

Two major conclusions follow from LH's inverted inversion effect. First, LH's prosopagnosia results from damage to a specialized face recognition mechanism. Previous findings of impaired face recognition relative to nonface object recognition used objects (vases, eyeglass frames, animal faces) that were at least as difficult as faces overall, but that may have been less difficult than faces along some specific dimension such as complexity, inter-item similarity, or a particular range of spatial frequencies. Inverted faces are the perfect control stimulus from this point of view, and LH's disproportionate impairment on upright relative to inverted faces is therefore strong evidence that an impairment of face-specific processing mechanisms underlies his prosopagnosia. Assuming that LH was not anomalous prior to his injury, this in turn implies that the human visual system contains an anatomically distinct system that is functionally specialized for the perceptual analysis of faces. At the very least, it demonstrates that one apparently normal human had such a system.

Our second main conclusion concerns the apparently mandatory application of face-specific processing mechanisms. It may seem paradoxical that if LH can use general (i.e. nonface-specific) visual pattern perception mechanisms to perform inverted face matching at a particular level of accuracy, he cannot also use these mechanisms on upright faces with at least the same degree of success. A similar paradox was noted by McNeil and Warrington (1993) when discussing their subject who had attained good proficiency at recognizing sheep faces, but whose human face recognition remained poor. Why could he not treat human faces as he does sheep faces? In the case of LH, his superior performance at matching inverted faces relative to upright faces shows that he cannot even perceive (let alone develop recognition strategies for) upright faces using the more general visual pattern perception mechanisms that he applies to inverted faces.

The idea that specialized perceptual systems, or "modules" would operate mandatorily was suggested by Fodor (1983). He reasoned that this was a desirable feature for modules because it would enable them to complete their computations more quickly than if a decision whether or not to engage them was required before they could be engaged. The concept of dominance by a specialized but impaired brain system has been invoked to explain the discrepancy between right hemisphere linguistic competence as measured in left hemisphere-damaged aphasics and in split-brain patients (Zaidel, 1985). However, inter-patient variability is an alternative explanation (Gazzaniga, 1983). In the present case such an explanation is not possible as the critical contrast is within a single subject. LH's performance with inverted faces gives us a measure of his ability to match stimuli of the same complexity, inter-item similarity, spatial frequency, and so on as upright faces. The fact that he performed worse with upright faces demonstrates that his specialized face perception system was contributing to his performance even though it was impaired and clearly maladaptive. Therefore, the "inverted inversion effect" provides the most direct neuropsychological support available for Fodor's (1983) characterization of special-purpose modules as engaged mandatorily by their inputs.

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