Impaired face and body perception in developmental prosopagnosia

Ruthger Righart* and Beatrice de Gelder*†‡

*Cognitive and Affective Neurosciences Laboratory, Tilburg University, 5037 AB, Tilburg, The Netherlands; and †Martinos Center for Biomedical Imaging, Massachusetts General Hospital, Harvard Medical School, Charlestown, MA 02129

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Prosopagnosia is a deficit in face recognition in the presence of relatively normal object recognition. Together with older lesion studies, recent brain-imaging results provide evidence for the closely related representations of faces and objects and, more recently, for brain areas sensitive to faces and bodies. This evidence raises the issue of whether developmental prosopagnosics may also have an impairment in encoding bodies. We investigated the first stages of face, body, and object perception in four developmental prosopagnosics by comparing event-related potentials to canonically and upside-down presented stimuli. Normal configural encoding was absent in three of four developmental prosopagnosics for faces at the P1 and for both faces and bodies at the N170 component. Our results demonstrate that prosopagnosics do not have this normal processing routine readily available for faces or bodies. A profound face recognition deficit characteristic of developmental prosopagnosia may not necessarily originate in a category-specific face recognition deficit in the initial stages of development. It may also have its roots in anomalous processing of the configuration, a visual routine that is important for other stimuli besides faces. Faces and bodies trigger configuration-based visual strategies that are crucial in initial stages of stimulus encoding but also serve to bootstrap the acquisition of more feature-based visual skills that progressively build up in the course of development.

face configuration | inversion effect | N170

Prosopagnosia is a relatively rare deficit in the basic ability to recognize a person by the face in the presence of normal recognition of personal identity by voice, gait, clothing, and other features. When prosopagnosia occurs in normal adults as a consequence of brain damage, it is most often associated with lesions in the occipito-temporal brain regions (1–6). In other cases, there is no evidence of brain damage, and the exact etiology of face recognition deficits is unknown (7–9). The pattern of deficits in acquired and developmental prosopagnosia is similar as far as some basic aspects of face processing are concerned (10). But in analogy with developmental dyslexia, the term developmental prosopagnosia is best used for the latter cases, because at present the congenital basis is not known.

From the few cases studied in detail, it seems that a critical problem concerns configural perception, usually defined as the processing routine whereby the whole face is represented at a glance (11). Its hallmark is the inversion effect (12), a dramatic drop in recognition performance when a face is presented upside-down. The notion is that upside-down presentation blocks encoding of the face as a whole (its configural properties) and makes observers shift to a feature-based perceptual routine instead (12–14). Neuropsychological studies have shown that prosopagnosics do not process the face image as an integrated whole or a configuration, but use a feature-based recognition procedure instead and seem to attend to facial features in a serial fashion. This problem is reflected in their laborious processing of normally oriented faces (4–6, 10, 15–20). As a consequence, performance on upright faces is often the same, or even worse than performance on inverted faces (10, 15–17), and in some cases this performance can even lead to a paradoxical inversion effect, as when upside-down faces are easier to match than normally oriented ones (10, 16).

Event-related potentials (ERPs) provide a technique particularly well suited to investigate these early stages. It has already been used in investigations of normal face recognition and in a few cases of prosopagnosia. A well known ERP component, the N170 (a negative waveform observed in the 150- to 200-ms time window), is sensitive to stimulus orientation. Whether the N170 indexes only face perception is still a matter of debate (21–23), as is to a lesser extent, the category specificity of an earlier component the P1 (23–25). Many studies have observed an increase of the P1 (23, 25) and N170 amplitude (21–23) for faces compared with nonface objects, but others found no category difference when faces were compared with objects (e.g., cars; refs. 26 and 27).

Investigations of the N170 in the very few single-case studies of prosopagnosia are so far inconclusive. For some prosopagnosic cases, the N170 did not show the characteristic increased amplitude for faces as compared with objects (28–31), whereas for other cases an increase of the N170 for faces relative to objects was reported much as in normal subjects (31, 32). This lack of consistency may be related to the heterogeneous nature of developmental disorders like prosopagnosia and is in line with mixed results obtained in behavioral (9, 20, 33) and functional MRI studies (34–36), mostly of single patients.

Our first goal was to measure face, body, and object processing by using homogeneous stimulus sets. This approach departs from the more common procedure of many normal and neuropsychological investigations of category specificity comparing performance on a set of faces against that on a set of other objects. We used homogeneous sets of images of normal oriented stimuli and upside-down stimuli of the same category to measure the inversion effect (16), the procedure best-suited given that object categories differ in low-level features to which ERP recordings are particularly sensitive and that these low-level features may result in artefacts (25).

A more important goal was to use these stimuli to measure whether configural face processing was impaired, and if so, whether the impairment was restricted to faces or also existed for other canonically oriented objects. Inverted face stimuli have been used frequently in neurologically intact viewers. Face inversion delays and increases the P1 and N170 peak in adolescent and adult participants irrespective of task conditions, which is especially observed for the N170 measured on right-hemisphere electrodes [see supporting information (SI) Table 2].

Face inversion using ERPs has, to our knowledge, only been studied once before in developmental prosopagnosia (37), and

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Abbreviation: ERP, event-related potential.

‡To whom correspondence should be addressed. E-mail: degelder@nmr.mgh.harvard.edu.

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Table 1. Assessment of face recognition in four developmental prosopagnosics

Test	Correct responses (response times, ms)				
	Controls	G.R.	C.B.	H.V.	J.S.
Benton Face Recognition	45.4	40	31	40	40
Warrington Face Memory	44 (1,778)	36†(4,037‡)	37*(4,573‡)	41 (3,853‡)	32‡(1,961)
Faces upright	63.3 (1,146)	62 (3,054‡)	63 (3,458†)	63 (2,840‡)	58‡(3,232‡)
Faces inverted	62.0 (1,526)	64 (4,302‡)	57†(5,400‡)	62 (3,640‡)	58*(3,641‡)
Shoes upright	62.5 (978)	63 (2,074‡)	63 (2,836†)	64 (1,757‡)	64 (2,456‡)
Shoes inverted	62.8 (1,069)	62 (2,082‡)	63 (2,559‡)	64 (1,689‡)	64 (1,651*)
Face parts upright	62.7 (1,562)	59†(4,165‡)	55‡(4,539‡)	60*(4,446‡)	63 (2,748‡)
Face parts inverted	62.0 (1,755)	58*(3,809‡)	51‡(5,067‡)	63 (4,130‡)	60 (2,690‡)
House parts upright	62.7 (1,192)	64 (2,191‡)	64 (2,966‡)	62 (1,703‡)	63 (1,278)
House parts inverted	63.2 (1,132)	64 (2,324‡)	63 (3,061‡)	62 (1,593‡)	64 (1,422*)

For a description of the task see *Methods*. Comparisons of prosopagnosic cases with control group were calculated by *z*-scores. *, $P < 0.05$; †, $P < 0.01$; ‡, $P < 0.001$. Control group: Warrington Face Memory, $n = 25$ (18–27 yr); faces and shoes, $n = 11$ (18–28 yr); face and house parts, $n = 21$ (18–29 yr). Maximum possible score for Benton Face Recognition was 54, for Warrington Face Memory 50, and for the other tests 64.

this single prosopagnosic case did not show the normal inversion effect on the N170. That study did not include a critical comparison of face and object inversion effects, which is essential in view of the fact that prosopagnosia is a relative deficit, which also to some extent affects recognition for other object categories. Our approach consisted of comparing the inversion effect obtained for each category. Comparing the effect of inversion thus provides a measure of face specificity that is reasonably free of low-level visual confounds.

Whole faces and objects have been used in previous studies of prosopagnosia focusing on the N170, but bodies are a novel kind of stimuli. Similar to faces, which have discrete parts (e.g., eyes, nose) in a specific spatial arrangement (e.g., two eyes above a nose), bodies are characterized by parts in a specific configuration (arms above legs). Faces and bodies are among the very first biological motion stimuli that confronts the newborn (38). Recent studies have underscored some important similarities between faces and bodies. For both categories, error rates and response times (39), as well as N170 latencies and amplitudes (40), increase as a consequence of body inversion. Consistent with this finding, there is considerable overlap in the functional neuroanatomy of processing faces and bodies. The middle part of the fusiform gyrus is involved in face and body perception (41, 42), and lesions have been linked to deficits in configural processing in prosopagnosia (6).

Results

Neuropsychological Testing. All prosopagnosic participants (G.R., C.B., H.V., and J.S.) underwent comprehensive neuropsychological testing. None of the participants made a consistent number of errors on more than one subtest of the Birmingham Object Recognition Battery (58). However, three of four prosopagnosics (G.R., C.B., and J.S.) scored poorly on the object decision task, requiring the viewer to decide whether the image is that of a real as opposed to an imaginary object (G.R., 22/32 and 27/32; C.B., 20/32 and 23/32; J.S., 23/32 and 24/32; scores for hard and easy versions of task, respectively. Each score is 2 SD below the mean of the control group, (except the score of G.R. on the easy version), which may relate to face and object recognition problems in developmental prosopagnosia as found in previous studies (10, 33).

Table 1 shows results of the face recognition tests. In summary, all prosopagnosics scored below average on the Benton Face Recognition Test (43). For the Warrington Face Memory task (44) the accuracies for G.R. ($z = -2.40$), C.B. ($z = -2.09$), and J.S. ($z = -3.60$) were significantly below mean. H.V. ($z = 4.64$), G.R. ($z = 5.05$), and C.B. ($z = 6.25$) have prolonged response times.

Face and object recognition deficits were tested with a matching task with upright and inverted stimulus presentation. Overall, latencies were high ($z > 3.00$) as observed previously with another case (17). G.R. and C.B. showed a normal pattern of delayed responses to inverted faces as compared with upright faces ($z > 3.00$). H.V. showed a slight delay ($z = 1.70$), and J.S. fell within the normal range ($z = 0.12$). J.S. ($z = -5.05$) and C.B. ($z = -2.08$) showed a paradoxical inversion effect, that is, shorter response times for inverted than upright shoes.

Feature matching was tested by the faces and houses task (for details see ref. 17). G.R. ($z = -2.76$), C.B. ($z = -5.73$), and H.V. ($z = -2.02$) showed lower accuracies for matching face parts. Response times for upright faces were slower than in the control group ($z > 3.00$). Response times for houses were delayed for G.R. and C.B. (both $z > 3.00$) and H.V. ($z = 2.90$). Most importantly, paradoxical inversion was observed for faces. Response times were faster for inverted than upright faces for G.R. ($z = -2.95$), H.V. ($z = -2.74$), and J.S. ($z = -1.35$).

ERPs. Performance on the orientation–decision task (upright versus inverted) during ERP recordings was nearly flawless (all > 90%). Fig. 1 shows the ERP waveforms for the N170 component. Fig. 2 shows the effects of inversion on the P1 and N170. We report data where deviation from the control group occurs for at least three cases.

P1 latency. The control group showed a main effect for stimulus [$F(2,10) = 4.67, P < 0.05$]. Latencies for faces (115 ms) and shoes (117 ms) were both longer than for bodies (105 ms) ($P < 0.05$ and < 0.01, respectively). This main effect was qualified by an interaction with orientation [$F(2,10) = 7.80, P < 0.01$]. Latencies were prolonged for inverted (116 ms) over upright faces (113 ms). No differences were found as a consequence of body inversion (upright, 105 ms; inverted, 105 ms). Latencies for inverted shoes (115 ms) were shorter than upright shoes (119 ms) ($P < 0.05$). No effects were observed for prosopagnosics.

P1 amplitude. The control group showed a main effect for stimulus [$F(2,10) = 21.86$, $P < 0.01$] on measures of the P1 amplitude. Amplitudes were largest for faces (5.81 μV) and shoes (5.62 μV), which differed significantly from bodies (3.12 μV). An interaction was observed between stimulus and orientation [$F(2,10) = 4.81$, $P < 0.05$]. Although both faces and bodies showed more positive amplitudes for inverted than upright stimuli, the difference was only significant for faces ($P < 0.01$). The P1 amplitudes for faces and bodies were increased for all prosopagnosics relative to the control group. Importantly, Fig. 2 illustrates that

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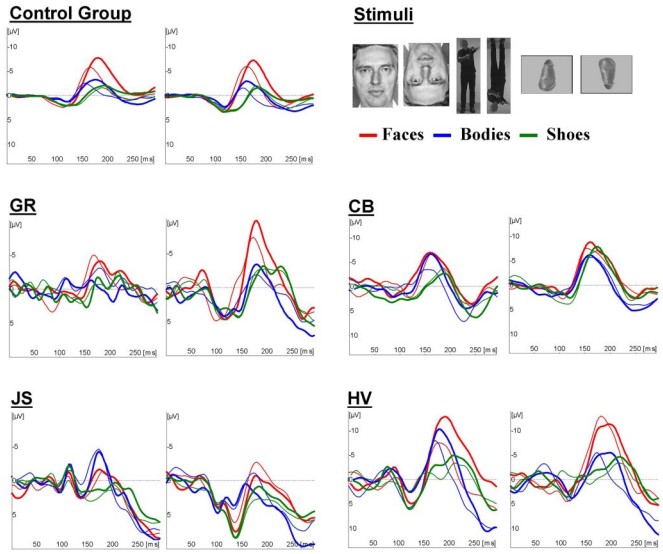

Fig. 1. ERP waveforms. The N170 response for prosopagnosics against control group ($n = 12$) at electrodes P7 and P8 is shown. Thin lines represent upright stimuli and thick lines represent inverted stimuli. Negative voltages are plotted upward.

three prosopagnosics (H.V., G.R., and C.B.) have a paradoxical inversion for faces.

N170 latency. The control group showed a main effect of stimulus [$F(2,10) = 12.84$, $P < 0.01$]. Latencies for bodies (159 ms) were significantly shorter than for faces (172 ms) ($P < 0.001$) and shoes (179 ms) ($P < 0.05$), whereas faces did not differ from shoes ($P > 0.05$). An interaction was found with orientation [$F(2,10) = 15.42$, $P < 0.001$]. Latencies were prolonged for inverted faces (178 ms) and inverted bodies (164 ms) as compared with upright faces (165 ms) ($P < 0.01$) and upright bodies (155 ms) ($P < 0.001$), but not for inverted shoes (175 ms) compared with upright shoes (179 ms) ($P > 0.05$). N170 latencies were longer for bodies than for shoes for all prosopagnosics. Effects of face-inversion differed from the control group for all cases. Three of four prosopagnosics (J.S., H.V., and C.B.) showed a paradoxical inversion effect for faces (Fig. 2).

N170 amplitude. The control group showed a main effect for stimulus [$F(1,11) = 24.16$, $P < 0.001$]. Amplitudes were most negative for faces (-5.95 μV), intermediate for bodies (-2.87 μV), and smallest for shoes (-0.78 μV) (all $P < 0.01$). There was a main effect of orientation [$F(1,11) = 9.14$, $P < 0.05$], with inverted stimuli showing larger amplitudes than upright stimuli (faces upright, -5.45 μV; faces inverted, -6.44 μV; bodies upright, -2.54 μV; bodies inverted, -3.19 μV; shoes upright, -0.70 μV; shoes inverted, -0.86 μV). The N170 amplitudes of faces were smaller than the N170 amplitudes of bodies for J.S. and H.V.; amplitudes of faces were smaller than shoes for J.S. and C.B.. However, a paradoxical inversion effect was observed for three of four cases for bodies (J.S., H.V., and C.B.).

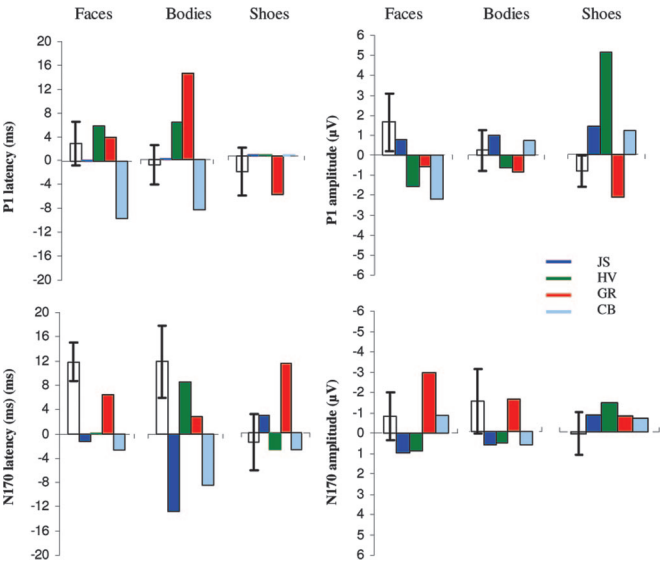

Fig. 2. Inversion effects for P1 and N170 component on right hemisphere electrodes. P1 and N170 latencies (ms) and amplitudes (μV) were pooled over right-hemisphere electrodes for prosopagnosic individuals against the control group (confidence interval 95%). Normal inversion occurs when amplitudes/latencies are greater for inverted than upright stimuli (i.e., above the dotted axis). Paradoxical inversion occurs when amplitudes/latencies are smaller for inverted than upright stimuli (i.e, underneath the dotted axis).

Discussion

We investigated configuration-based processing of faces, bodies, and shoes in four prosopagnosics by measuring ERPs to upright and inverted stimulus presentation. Our results suggest a major deficit in this processing routine for faces and bodies. Overall, we observed anomalous inversion effects for three of four prosopagnosics.

The N170 for Canonically Oriented Stimuli. Although a relative absence of an increased N170 amplitude for faces as compared with objects may relate to face recognition problems (28–30), other cases of prosopagnosia have not shown this pattern (31, 32). One explanation of this diverse pattern again observed here may be that the N170 is, in addition to the encoding of the whole face, related to the perception of facial features and may reflect the extent to which a featural strategy is adopted. For example, attention to the eye region (21, 45) or perception of distorted faces (46, 47) increases the N170 amplitude. Consistent with this finding, some cases of prosopagnosia may show normal or even increased N170 amplitudes caused by featural processing. Thus the finding of reduced N170 amplitudes is related to earlier reports in the literature, but its interpretation should not be overstated. Because the absolute amplitude of the N170 may be a function of stimulus properties, the inversion effect provides a more stringent index of configural face processing.

The N170 for Inverted Stimuli. In three of four developmental prosopagnosics the normal inversion effect is absent for both faces and bodies. This result replicates the previous findings for face processing in one developmental prosopagnosic (37), but now generalizes this finding to a larger group, and most importantly, it shows that it extends to body stimuli. The absence of inversion effects on the N170 suggests an inflexible use of this feature-based strategy for both upright and inverted faces and bodies in prosopagnosia. In line with this result, the behavioral results for matching face parts showed that the prosopagnosics did not show a normal inversion effect.

A unique finding is that the inversion effect was also absent for face stimuli on the P1 amplitude. It has been observed that the P1 amplitude is increased for faces as compared with objects, and that the amplitude increases by face inversion (23). The P1 inversion sensitivity may also be related to the role of the inferior occipital gyrus in face and body processing, and anomalous activation in this area is known to contribute to face deficits (34). Future studies may show how specific this inversion effect is in normal face processing and how specific the absence is in developmental prosopagnosia.

Prosopagnosia from a Developmental Perspective. As noted, none of the participants reported any neurological problems, which was

confirmed for two prosopagnosics by MRI scans.[§] Therefore, one needs a developmental perspective on the acquisition of normal face recognition, as configural perception of faces develops gradually during childhood (13, 14, 49–52). For example, Carey and Diamond (14) have shown that 6-year-old children were equally fast on recognizing inverted and upright faces, whereas 10-year-old children were somewhat delayed on inverted faces but still less so than adults, suggesting that they rely more on configural properties than younger children [see also Mondloch *et al.* (51)]. These behavioral data are consistent with the developmental trends that were found in the ERP data. A study by Itier and Taylor (53) suggests that the inversion effect on the N170 amplitude increases during childhood. Young children (8–13 years) showed no inversion effect on the N170 amplitude, whereas the older groups (14–16 years) showed a tendency for an inversion effect, and a group of adults showed a strong inversion effect on the N170 amplitude. The pattern of the ERP data for the developmental prosopagnosics is similar to that of the youngest children (8–9 years) (see also ref. 54). The results suggests that anomalies in the initial visual processing stages in infancy may hinder the acquisition of configural processing skills and may gradually translate as face recognition deficits in adulthood. Previous studies have reported that in addition to face recognition, deficits in prosopagnosia may extend to nonface objects, although so far a close comparison as now done here has not been undertaken (4, 8, 10, 16, 20, 33, 56). In line with these studies, our results suggest that configural processing is impaired for faces and bodies. This finding is in line with data showing that bodies contain important configural properties, and body inversion affects recognition performance negatively (39) and generates a larger and delayed N170 for faces and bodies alike (40).[¶]

The similarity between anomalous face and body processing may indicate a common developmental origin. Faces and bodies represent the earliest stimuli the infant is exposed to, and their special status may be in part related to this exposure. Possibly, configural processing is related to the sensitivity for relating structure and motion early in development, as movement is a potent trigger for segmentation. The characteristic shape and associated movement represented by bodies may be a potent trigger for form perception in the immature visual system of the neonate (55). For example, by 5 months of age infants are sensitive to a point-light walker as compared with a random pattern of moving dots for upright displays only (38).

Conclusions

Using ERP measurements, this study shows that the inversion effect of faces and bodies is either absent or paradoxical in developmental prosopagnosia. This finding extends previous behavioral findings of paradoxical inversion effects and now traces these to early processing stages measured at not only the N170 but also at the P1 level, and in addition to faces and bodies. The lack of an inversion effect on the N170 (rather than its absolute amplitude) appears as an important diagnostic marker of developmental prosopagnosia. To the extent that the later stages of face recognition rely relatively more on initial stages of encoding configuration, problems with face recognition emerge as the more dominant, but they are not the single deficit of developmental prosopagnosics.

[§]Van den Stock, J., van de Riet, W. A. C., de Gelder, B., 14th Meeting of the Cognitive Neuroscience Society, May 5–9, 2007, New York, NY.

[¶]Meeren, H. K. M., Hadjikhani, N., Ahlfors, S. P., Hämäläinen, M. S., de Gelder, B., 36th Annual Meeting of the Society for Neuroscience, Oct. 14–18, 2006, Atlanta, GA.

Methods

Case Histories. Prosopagnosics were recruited after they had contacted us through our web site or after reports in the media. All participants reported lifelong problems in recognizing people and complained of difficulties when meeting familiar persons unexpectedly. All were tested on an extensive face recognition battery (see below). All participants gave informed consent according to the Declaration of Helsinki. We report here four developmental prosopagnosics representing a fairly homogeneous group reflecting the variability inevitably existing in developmental disorders with hitherto-unknown etiology.

J.S., a 40-year-old man, is an orchestra conductor. He is not able to recognize the members of his orchestra, a problem that is aggravated by the uniform dress code. He reports no neurological problems, except very occasional epileptic seizures (two to three over the last 5 years). G.R. is a 48-year-old woman with lifelong face recognition problems. C.B. is a 27-year-old woman, who reports having had face recognition problems all of her life. H.V., a 41-year-old man, has had face recognition problems all of his life. None of them report neurological incidences, and the anatomical brain scans of H.V. and G.R. show a neurologically intact brain.

Neuropsychological Testing. Visual object recognition and face recognition were tested with standard clinical test batteries in sessions preceding the electroencephalography measurements. Face recognition was tested with the Benton Face Recognition Test (43) and the Warrington Face Memory Test (44). To obtain information about speed-accuracy tradeoff, we used a computerized version of the latter test. Basic visual functions were tested by using subtests (line length, size, orientation, gap, minimal feature match, foreshortened views, and object decision) from the Birmingham Object Recognition Battery (57).

Participants were tested with additional computerized face and object recognition experiments previously developed to investigate different aspects of face recognition in normal people and prosopagnosia patients. To examine face inversion effects against similar effects for nonface objects, the faces and shoes task was used (16). Participants were requested to select the correct probe that corresponds with the target face. The target was always a frontal picture, and the two probes underneath consisted of pictures in three-quarter profile. Faces and shoes were presented upright and inverted (for details of stimulus construction and previous results see refs. 10 and 16). Feature-based matching was tested with a face-parts and a house-parts matching task, which required participants to match a face part (i.e., mouth or eyes) to a corresponding part in the whole target face. In a second test, house parts (i.e., door or upper window) had to be matched to a corresponding part in the whole house. Faces and houses were presented upright and inverted (for further details see refs. 10, 17, and 48). Participants were instructed to respond as accurately and rapidly as possible. Accuracy and mean response times were calculated for each test. Data of the control group were normalized, and z-scores were obtained for each prosopagnosic participant (cut-off $z = 1.65$).

ERPs. Control participants in the ERP study were 12 undergraduate students aged 18–26 years (40) with an educational level and socioeconomic status similar to that of the prosopagnosic individuals and an age range comparable to other studies in the literature (see SI Table 2).

Stimulus categories were bodies, faces, and shoes, and they were presented upright or inverted. The faces in the body stimuli were blurred with an opaque gray patch to minimize face processing (40). The viewing angular size of the stimuli ranged from 9.6° to 10° vertical and 3.4° to 7.9° horizontal. Stimuli were presented for 500 ms and immediately followed by a central

fixation cross lasting 500–1,500 ms. The experiment comprised three blocks each containing the three stimulus categories (240 trials per block). Half of the stimuli were presented upright, and the other half was presented inverted. Each condition contained 60 trials. A delayed-response procedure was used to avoid influence from motor activity. Participants were requested to decide whether the stimulus was presented upright or inverted, using two designated buttons after termination of the fixation cross. The number of trials was increased to improve the signal-to-noise ratio for prosopagnosic participants. The experiment comprised six blocks of 144 trials using 72 trials per condition.

Electroencephalogram was recorded at a sampling rate of 256 Hz (0.1–30 Hz, 24 dB per octave) from 49 electrodes by using active Ag-AgCl electrodes (BioSemi Active, Amsterdam, The Netherlands) mounted in an elastic cap, referenced to an additional active electrode (common mode sense) during recording. After electro-oculography correction, epochs with amplitudes exceeding $\pm 100\ \mu V$ at any channel were automatically rejected (for further details see ref. 40). Unlike our previous study (40), we used only neutral stimuli and not emotional expressions. The number of trials after artifact removal was equally balanced across conditions. The average number of trials per participant ranged from 52 to 60 for the control group and 53 to 69 for the prosopagnosics trials per condition.

Our ERP analyses concentrated on the P1 and N170 component, and their peak latency and amplitude were scored in a window of 80–140 and 140–200 ms, respectively. Peaks for P1 were scored at electrode positions O1/2 and PO3/4, and for N170 they were scored at electrode positions P7/8, P5/6, PO7/8. Multivariate analyses for repeated measures were performed for the control group with the factors stimulus (bodies, faces, shoes), orientation (upright, inverted), hemisphere (left, right), and electrode position.

Peak latencies and amplitudes for normally oriented faces were compared with the other categories (e.g., bodies, shoes) by calculating difference scores between each of the stimulus categories to test for category selective effects on the P1 and N170 (28, 29). Inversion effects were calculated by subtracting the scores for inverted stimuli from upright stimuli (see Fig. 2). Peak latencies and amplitudes were pooled for electrodes over each hemisphere (58). Confidence intervals of 95% were calculated for each condition in the control group (20, 21) to determine whether normal upright stimuli differed in latency and amplitude and whether inversion was normal [i.e., latency or amplitude for inverted $>$ upright), absent (inverted $=$ upright) or paradoxical (inverted $<$ upright)].

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