

Normal Body Perception despite the Loss of Right Fusiform Gyrus

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Abstract

■ Human extrastriate cortex contains functional regions that are selective for particular categories such as faces, bodies, and places, but it is unclear whether these category-selective regions are necessary for normal perception of their preferred stimuli. One of these regions is the right fusiform body area (FBA), which is selectively involved in body perception. Do loss of the right fusiform gyrus and the absence of the right FBA

necessarily lead to deficits in body perception? Here we report the performance of Galen, a brain-damaged patient who lost the right fusiform gyrus and has no right FBA, on eight tasks of body perception. Despite his lesion, Galen showed normal performance on all tasks. Galen's results demonstrate that damage to the right fusiform gyrus and the lack of the right FBA do not necessarily lead to persisting deficits in body perception. ■

INTRODUCTION

Category-selective regions have been a central issue in cognitive neuroscience in the last 15 years. These functionally defined extrastriate areas respond more strongly to particular visual categories such as faces, bodies, and scenes than to other objects and control images (Kanwisher, 2010). Despite numerous imaging studies demonstrating that these regions are strongly activated by their “preferred” stimuli (Kanwisher, 2010) and TMS studies indicating a causal role for these regions (Dilks, Julian, Paunov, & Kanwisher, 2013; Pitcher, Walsh, Yovel, & Duchaine, 2007; Urgesi, Berlucchi, & Aglioti, 2004), a fundamental question remains open: Are category-selective regions necessary for normal perception of their preferred stimuli? Specifically, does the loss of an anatomical structure that contains a category-selective region necessarily impair perception of the region's preferred stimuli?

Studies of patients with damage to a category-selective region who suffer from deficits with the preferred category (Barton, 2008; Gaillard et al., 2006; Epstein, De Yoe, Press, & Kanwisher, 2001) suggest that these regions are required for normal perception. One example is a Japanese patient who had a small lesion in the region of the right fusiform face area (FFA; Kanwisher, McDermott, & Chun, 1997) and exhibited severe prosopagnosia (Wada & Yamamoto, 2001). This case is often cited to argue that the right FFA is not only involved in but is actually necessary for normal face recognition (Kanwisher, 2010; Spiridon & Kanwisher,

2002). However, typical lesion studies are likely to support the idea that category-selective regions are critical because patients who come to the attention of researchers tend to be those who suffer from visual impairments. Patients with lesions to a category-selective region who are not impaired might exist, but they are likely to go unnoticed. However, if such cases exist, these patients would demonstrate that a lesion to a category-selective region does not necessarily lead to perceptual deficits with the preferred stimuli.

Here we report such a patient. Galen, a 31-year-old right-handed man, lost the right fusiform gyrus following an arteriovenous malformation resection in the right temporal lobe. Galen did not show any voxels in the right fusiform body area (FBA; Peelen & Downing, 2005; Schwarzlose, Baker, & Kanwisher, 2005), which is a category-selective region that responds more strongly to bodies and body parts than to control images. He did, however, exhibit a left FBA and bilateral extrastriate body areas (EBAs; Downing, Jiang, Shuman, & Kanwisher, 2001), another set of functional regions that are body selective. FBA is thought to be important for many aspects of body perception (Downing & Peelen, 2011). Like FFA, FBA is larger and more consistently found in the right hemisphere than in the left hemisphere (Taylor, Wiggett, & Downing, 2007; Schwarzlose et al., 2005).

The loss of Galen's right fusiform gyrus and the absence of his right FBA motivated us to systematically investigate his body perception. We tested Galen with eight behavioral tasks that measure various aspects of body perception. A *t* test for single-case studies (Crawford & Howell, 1998) was used to compare Galen's accuracy and RT to those of controls.

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METHODS

Patient Description

Galen is a right-handed male physician who was 31 years old when last tested. He was first reported in Susilo, Yovel, Barton, and Duchaine (2013). In 2004, Galen underwent surgery to excise an arteriovenous malformation in the right temporal lobe, after which he noticed face recognition problems. Galen majored in English before attending medical school. He was working at a Veterans Administration hospital when we tested him. Formal testing in our laboratory confirmed his prosopagnosia (Susilo et al., 2013).

High-resolution MR images of Galen's brain showed a lesion extending from the middle occipital lobe to the lateral parahippocampal gyrus in the right hemisphere, encompassing a large part of his right occipitotemporal lobe and the fusiform gyrus. A small lesion was also present in the right cerebellum.

Galen was tested behaviorally on two occasions in a quiet room in the Veterans Administration hospital where he worked. The body detection, body shape discrimination, body posture discrimination, and body sex discrimination tasks were administered in June 2012, whereas the tasks assessing body identity discrimination, body expression discrimination, and body identity recognition were administered in August 2013. Galen's body posture discrimination data have been reported as part of a different investigation (Susilo et al., 2013).

Functional Localizer

Control Participants

Five neurologically intact participants (aged 19–42, three women) participated as controls. All participants were screened for MRI scanning and provided informed written consent in accordance with the protocols approved by Committee for the Protection of Human Participants of Dartmouth College. They were either paid or received course credit for their participation.

Procedure

We used dynamic stimuli (Pitcher, Dilks, Saxe, Triantafyllou, & Kanwisher, 2011) to localize the body-selective regions. Each participant completed three localizer runs. Each run comprised 10 blocks of 12-sec video clips interleaved with 12-sec fixation blocks. Five categories of stimuli were presented: faces, objects, scrambled objects, headless bodies, and scenes. Each category was presented twice within each run. Within each block, participants passively viewed six video clips (1500 msec per clip, with a 500-msec ISI) randomly selected from 60 clips of each category. Stimuli were presented using Superlab 4.5.3 (www.superlab.com/) and presented to participants via a Panasonic

DT-4000U DLP projector (resolution = 1024×768 ; refresh rate = 60 Hz) at the rear of the scanner.

Participants were scanned on a 3.0-T Phillips MR scanner (Philips Medical Systems, Bothell, WA) with a SENSE (sensitivity encoding) 32-channel head coil. At the beginning of the scan, an anatomical volume was acquired using a high-resolution 3-D magnetization-prepared rapid gradient-echo sequence (220 slices, field of view = 240 mm, acquisition matrix = 256×256 , voxel size = $1 \times 0.94 \times 0.94 \text{ mm}^3$).

Functional images were collected using echo-planar functional images (repetition time = 2000 msec, echo time = 35 msec, flip angle = 90° , voxel size = $3 \times 3 \times 3 \text{ mm}^3$). Each volume consisted of 36 interleaved 3-mm-thick slices with 0-mm interslice gap. The slice volume was adjusted to cover most of the brain including the entire temporal lobe and aligned with each participant's AC–PC line to reduce susceptibility artifacts (Ojemann et al., 1997).

Imaging data were analyzed using the AFNI software package (Cox, 1996). Before statistical analysis, the first two volumes of each run were discarded to allow for magnetic saturation effects, and each volume was registered to the third volume of the first run. The EPI data were warped to align with the anatomical data and transformed to a standard space in the Talairach template (Talairach & Tournoux, 1988). Each volume was blurred with a 4-mm FWHM Gaussian kernel. Time series of each run were scaled by the mean of the baseline before passing onto the deconvolution analysis. Detrending and motion correction were carried out by including trends and head motion as regressors in the regression model. Repetition times with excessive motion ($>0.3 \text{ mm}$) were removed.

A general linear model procedure was used for ROI analysis. Body-selective regions were identified with a “bodies > objects” contrast.

Behavioral Testing

Control Participants

A total of 139 participants provided control data. All had normal or corrected-to-normal vision and received course credit or reimbursement. Participants were tested in our laboratory at Dartmouth College, except for the body detection task where they were tested in our previous laboratory at University College London. All participants gave consent in accordance with the approved ethics requirement. Detailed information about control participants for each task is described below.

Body Perception Tasks

There were eight tasks of body perception. The stimuli and procedure for each task are described below. All tasks were administered on a 13-in. MacBookPro

(1024 × 768 resolution) using SuperLab 4.5. Galen and control participants were seated approximately 50–70 cm from the computer screen (depending on the task) without chin rest.

Detection. *CONTROL PARTICIPANTS.* Nineteen individuals from the University College London community (11 women, 7 men, ages 19–39; the sex information of one participant was missing) participated for course credit or reimbursement.

STIMULI AND PROCEDURE. This task was identical in format to the face detection task in Garrido, Duchaine, and Nakayama (2008), except we used bodies instead of faces. Each trial showed a 5 × 5 array (25 images total) of animals, objects, food, and landscapes, with or without a body (Figure 1). At about 50-cm viewing distance, the array subtended 14° of visual angle. Participants were told to press “b” as quickly as possible if they saw a body in the display or not respond if they did not see a body. The next trial began following response or after 8 sec had passed. There were 37 trials, with 25 body-present and 12 body-absent. Two practice trials were provided at the beginning. Hits and false alarms were calculated to compute *a*-prime (we could not compute *d*-prime because many controls had perfect hits and no false alarms; McMillan & Creelman, 1990). RT for hits was also computed. In addition, we computed an inverse efficiency score, which combines both *a*-prime and RT using the formula [inverse efficiency = RT/*a*-prime]. This composite measure is suitable for use when accuracy performance is high (Bruyer & Brysbaert, 2011).

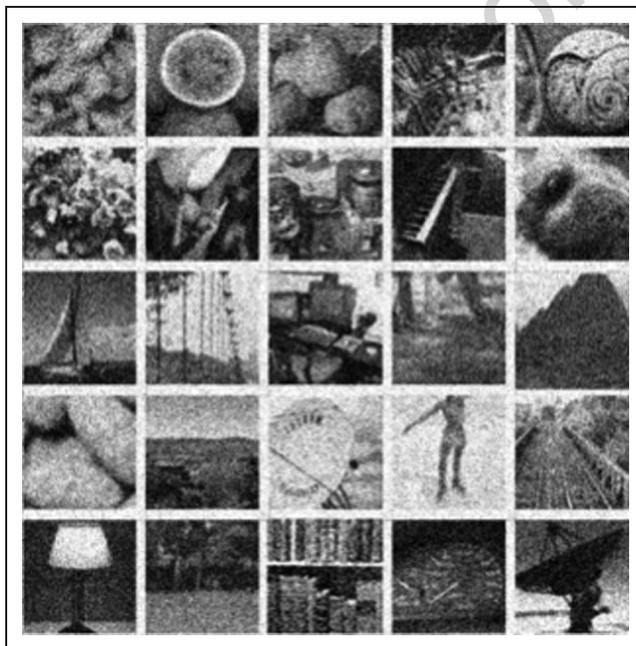


Figure 1. An example stimulus in the detection task. The body image is on fourth row, fourth column.

Shape discrimination. *CONTROL PARTICIPANTS.* Twenty individuals from the Dartmouth community (11 women, ages 18–34) participated for course credit or reimbursement.

STIMULI AND PROCEDURE. The task used body stimuli drawn from the set used in Pitcher, Charles, Devlin, Walsh, and Duchaine (2009). The stimuli were headless male bodies created using Poser software and then morphed to create several body continua. Each trial presented a pair of bodies one after another for 250 msec each with an ISI of 500 msec that included a Gaussian mask for 250 msec. The first body was always shown at the center of the screen, whereas the second body was presented slightly below the center and to either the left or right. At roughly 50-cm viewing distance, the stimuli subtended 2.5° by 6.7° visual angle. The bodies in a pair were either the same or differed by one of four morph levels: 50% (10 trials), 70% (20 trials), 80% (20 trials), or 100% (10 trials). Participants were instructed to press “s” if the bodies were the same or to press “d” if the bodies were different. There were 120 trials in total (60 same trials, 60 different trials). Six practice trials were provided at the beginning. The dependent measures were *d*-prime and RT.

Sex discrimination. *CONTROL PARTICIPANTS.* Twenty Dartmouth undergraduates (15 women, ages 18–21) participated for course credit.

STIMULI AND PROCEDURE. The components for the stimuli were two headless young men (M1, M2) and two women (F1, F2) created using Poser. Four sex continua were made by morphing all possible pairs of male and female participants (M1/F1, M1/F2, M2/F1, M2/F2). At about 50 cm viewing distance, the bodies subtended 5.3° by 5.3° visual angle. A trial showed two bodies from the same continuum one after another at 250 msec each with an ISI of 500 msec. The first body was shown at the center of the screen, whereas the second body appeared randomly at one of four locations 5° from the center (up left, up right, down left, down right). Each body pair was shown twice in reverse order (e.g., M1/F2_0% and M1/F2_30%, then M1/F2_30% and M1/F2_0%). Participants were asked to decide which body looked more masculine and to press “f” if they thought it was the first body or “s” if they thought it was the second body. There were a total of 96 trials, along with six practice trials at the beginning. The dependent measures were proportion correct and RT.

Posture discrimination (faceless and headless). *CONTROLS PARTICIPANTS.* Control data were provided by participants previously tested in Susilo et al. (2013) (13 women, ages 18–27).

STIMULI AND PROCEDURE. The tasks and Galen’s data were reported in Susilo et al. (2013), and the tasks were

identical to those in Yovel, Pelc, and Lubetzky (2010). Participants had to make same–different judgments on 144 sequentially presented pairs of faceless and headless bodies shown in separate blocks. All participants completed the headless bodies block first. Pairs of bodies differed either in head (when present), arm, or leg posture. Upright and inverted trials (72 each) were mixed in each block, but only upright trials were analyzed for the current study. The dependent measures were d-prime and RT.

Identity discrimination. CONTROL PARTICIPANTS. Twenty new individuals from the Dartmouth community (13 women, ages 18–26) took part for course credit or reimbursement.

STIMULI AND PROCEDURE. This match-to-sample task was developed in Robbins and Coltheart (2012). The stimuli were 18 images of nine White women in uniform black clothing and cropped so the head was not visible. Two images of each woman were used to reduce image-level similarity. Each trial presented a target body at the center of the screen for 250 msec, an ISI of 500 msec, and then two bodies to either side of fixation until response, one of which depicted a different image of the target body. Body pairs were chosen based on approximate similarity as determined in pilot studies. Bodies subtended 4.5° by 14.5° of visual angle when viewed from approximately 40 cm. Participants had to decide which of the two bodies matched the target body and press “1” for the body on the left or “2” for the body on the right. Each image was presented twice in separate blocks, resulting in a total of 36 trials. Two practice trials were given. Proportion correct and RT were computed.

Expression recognition. CONTROL PARTICIPANTS. A new group of 20 Dartmouth undergraduates (14 women, ages 18–23) were tested for course credit.

STIMULI AND PROCEDURE. The stimuli were a subset of body images developed and validated in the Bodily Expressive Action Stimulus Test (de Gelder & Van den Stock, 2011). For the task, we chose 100 images displaying one of four expressions: happy, angry, sad, or surprise (25 for each expression). Each trial presented an actor displaying one of the four expressions in grayscale with the face covered for 250 msec. Participants were asked to press “1” if they thought the actor was posing happy, “2” for angry, “3” for sad, and “4” for surprise. At 50-cm viewing distance, the images subtended 3.5° by 7.5° visual angle. Ten practice trials were provided. Proportion correct and RT were computed.

Identity recognition. CONTROL PARTICIPANTS. A new group of 20 Dartmouth undergraduates (14 women, ages 18–22) took part in exchange for course credit.

STIMULI AND PROCEDURE. This task was identical in format, design, and development to the Cambridge Face Memory

Test (Duchaine & Nakayama, 2006), except that bodies were used instead of faces. The stimuli were 51 Poser-generated grayscale images of male bodies with an occluder added to cover the genital area; six of these images were chosen as target bodies based on pilot testing. The task consisted of three sections totaling 72 trials (Figure 2). Each trial consisted of a three-alternative forced-choice item that required participants to identify a target body among

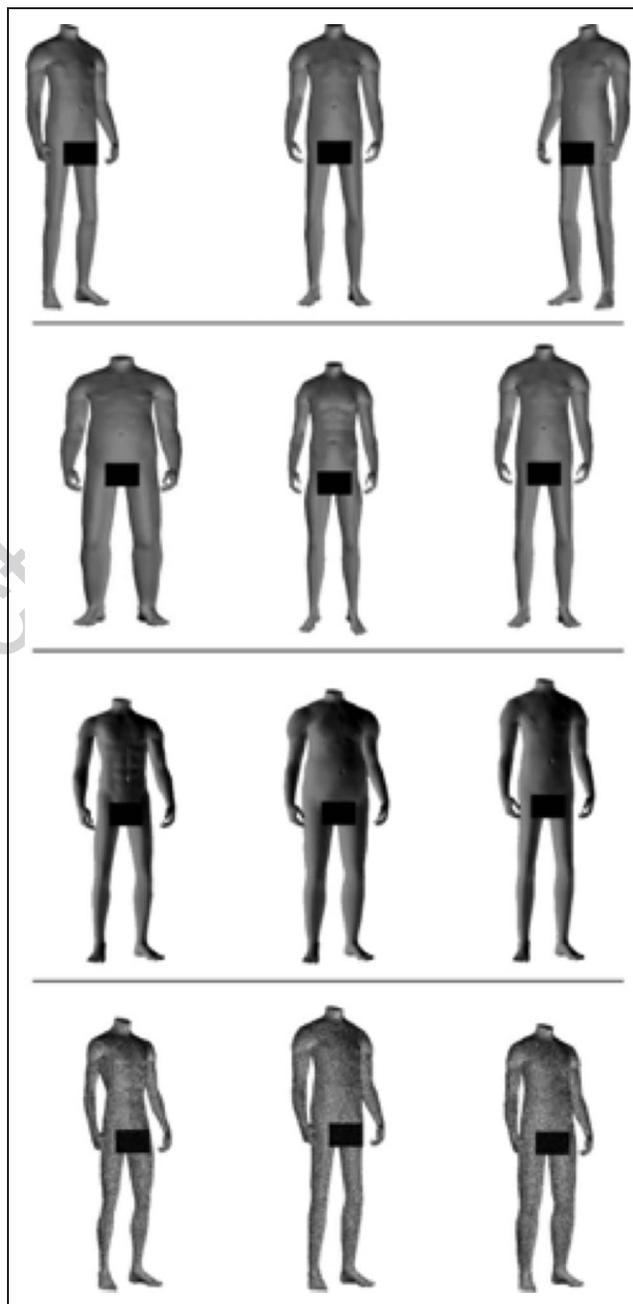
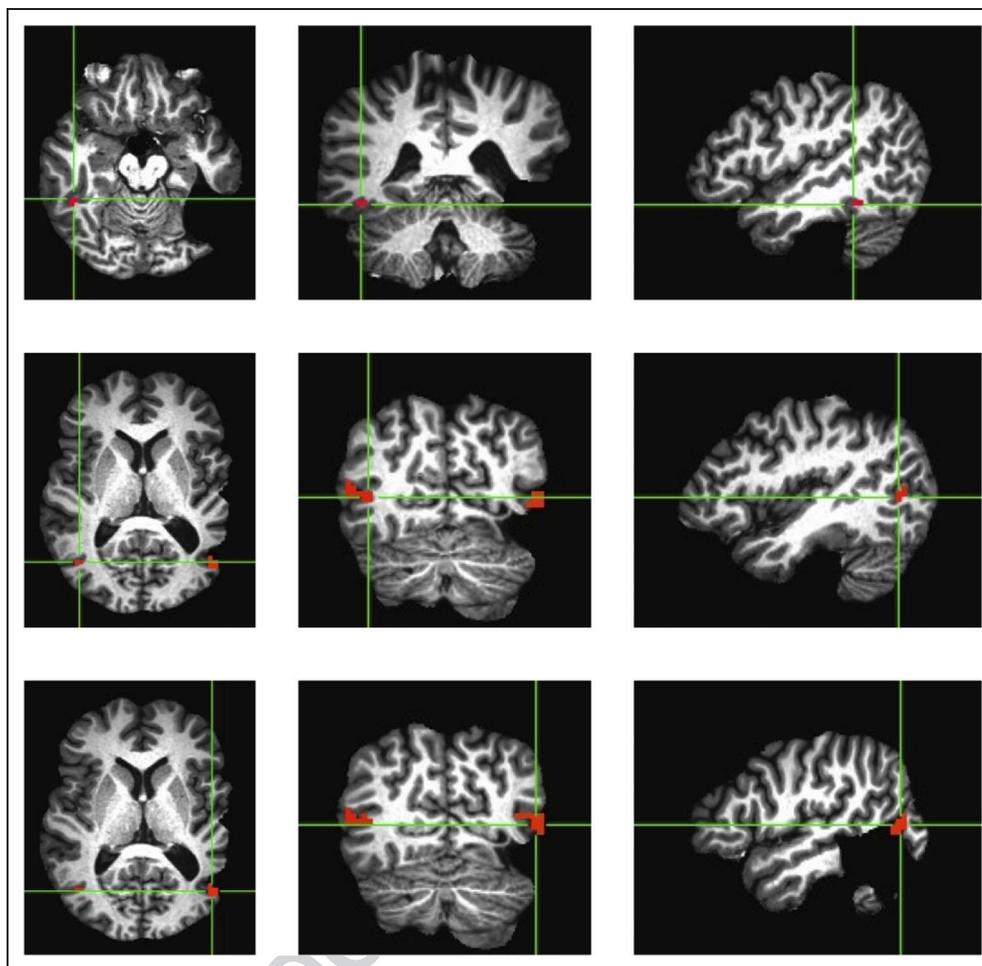


Figure 2. Example stimuli from the identity recognition task. The first row shows a target body in different viewpoints. The second row shows the same image of the target body with distractors. The third row shows a different image of the target body (different viewpoint and lighting) with distractors. The final row shows yet another different image of the target body with noise added to all stimuli.

Figure 3. Galen’s body-selective regions. Columns from left to right show axial, coronal, and sagittal planes. Rows from top to bottom shows left FBA, left EBA, and right EBA (indicated by the green crosses). Notice the absence of the right fusiform gyrus.



two distractors. The first section introduced each target body in three views (-30° , 0° , 30°), after which three test trials immediately followed for a total of 18 trials. At the end of this section, a review slide showing the six target bodies in 0° viewpoints was shown for 20 sec. In the second section each target body appeared five times for a total of 30 trials. The trials showed novel images of the bodies that differed from those learned in the introduction (-45° , -15° , 15° , and 45°) and lighting that resulted in different shadows. At the end of the section, the review slide was again shown for 20 sec. The final section presented 24 trials, and each target body appeared

four times. Gaussian noise was added to the body images in this section to increase difficulty and minimize reliance on particular body features.

RESULTS

Functional Localizer

Galen showed three body-selective regions: the left FBA and bilateral EBA (Figure 3). He did not show any response in the vicinity of the right FBA, in contrast to all five controls who showed it. Table 1 compared the coordinates and

Table 1. Talairach Coordinates and Cluster Size of Functionally Localized Body-selective Areas in Galen and Control Participants

	Controls		Galen	
	Coordinates	Cluster Size (mm^3)	Coordinates	Cluster Size (mm^3)
Right FBA	-41 ± 2 , 43 ± 5 , -11 ± 10	729	Missing	Missing
Left FBA	41 ± 4 , 43 ± 3 , -13 ± 3	594	47 , 41 , -12	81
Right EBA	-43 ± 3 , 72 ± 5 , 6 ± 4	2916	-51 , 66 , 6	1188
Left EBA	48 ± 5 , 74 ± 5 , 7 ± 3	2943	53 , 66 , 12	1485

Reported clusters are significant at p (uncorrected) $< .01$.

cluster size of Galen's body-selective areas with those of controls. The locations of Galen's left FBA and bilateral EBA fall within the range of normal participants.

To further assess whether Galen's right FBA is completely absent, we used a more lenient uncorrected threshold and calculated a probabilistic map of body-selective activation in normal participants. Each individual participant's right FBA (bodies > objects) is overlaid on top of one another, creating a probabilistic overlap map. We then placed the probabilistic map on Galen's anatomical scan to illustrate the relationship between the positions of Galen's lesion and the right FBAs in the controls (both aligned to Talairach template; Figure 4). There is little overlap between Galen's brain tissue and the right FBA of control participants.

Behavioral Testing

Figure 5 shows Galen's performance across eight tasks. The bottom right table displays his t values for each task, each of which is compared with a critical cutoff (Crawford & Howell, 1998). We used one-tailed tests because we predicted the presence of deficits a priori. For the detection task, a one-tailed test at 0.05 level with 18 degrees of freedom results in a cutoff of -1.734 . For all other tasks, a one-tailed test at 0.05 level with 19 degrees of freedom results in cutoff of -1.729 . As can be seen in the table, all of Galen's t values are above the cutoff. Galen showed somewhat poor performance on detection (t values of -1.39 for RT and -1.36 for inverse efficiency score), but this performance is still well above the threshold for impairment.

DISCUSSION

This study is concerned with the question of whether category-selective regions in the human extrastriate cortex are critical for perception of their preferred stimuli. Specifically, we asked whether damage to the right fusiform

gyrus and the lack of the right FBA necessarily lead to impaired body perception. To address this question we tested Galen, a brain-damaged patient who underwent a resection that lesioned the right fusiform gyrus and who failed to show any voxels in the right FBA. Galen completed eight tasks of various aspects of body perception. He performed normally on all of them, demonstrating that body perception can be normal despite the loss of the right fusiform gyrus and the lack of the right FBA.

Several alternative accounts are unlikely to explain Galen's normal performance. One possibility is that our tasks might not be sensitive enough to pick up subtle deficits. This appears unlikely because all tasks were free from floor and ceiling effects and because Galen's RTs were all within the normal range. Another possibility is that our tasks might not have engaged the body-selective regions, but two of them have been shown to activate such regions in previous studies (Brandman & Yovel, 2012; Pitcher et al., 2009). Moreover, the other tasks used body stimuli that are comparable to stimuli typically used to localize body-selective regions (Downing & Peelen, 2011). Finally, it is unlikely that our localizer failed to identify Galen's right FBA. The same localizer successfully identified his left FBA and the EBA bilaterally, and the right FBA was absent even when we used a very liberal threshold. In addition, our probabilistic map shows that the surgical resection removed the portion of the right fusiform gyrus where the right FBA is commonly found.

Does Galen's performance imply that the right FBA does not contribute to body perception in normal participants? We believe it does not, because many studies indicate that the right FBA is strongly engaged in many tasks of body perception (see Downing & Peelen, 2011, for a review). A group lesion study even suggests that the area where the right FBA is typically found is causally involved in body perception (Moro et al., 2008). What our study indicates is that the loss of the right fusiform gyrus that contains the right FBA does not necessarily lead to persistent deficits with body perception.

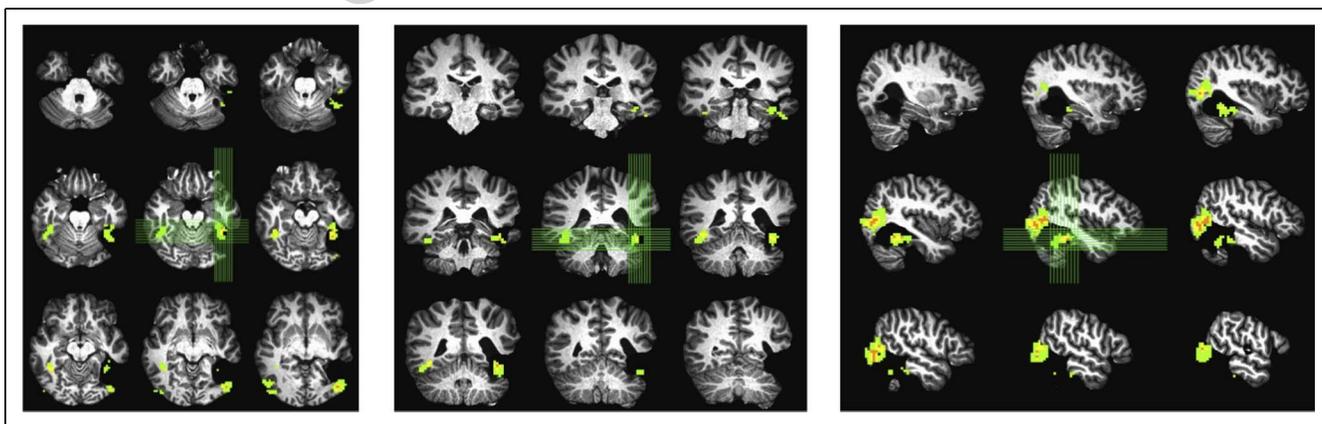


Figure 4. The probabilistic map of body-selective activation in control participants overlaid on Galen's anatomical scan. Nine slices from each plane around the location of right FBA were shown: (left) axial (more inferior to more superior), (center) coronal (more anterior to more posterior), and (right) sagittal (more medial to more lateral). The color displayed the overlap percentage. The green line indicates where the slices were taken.

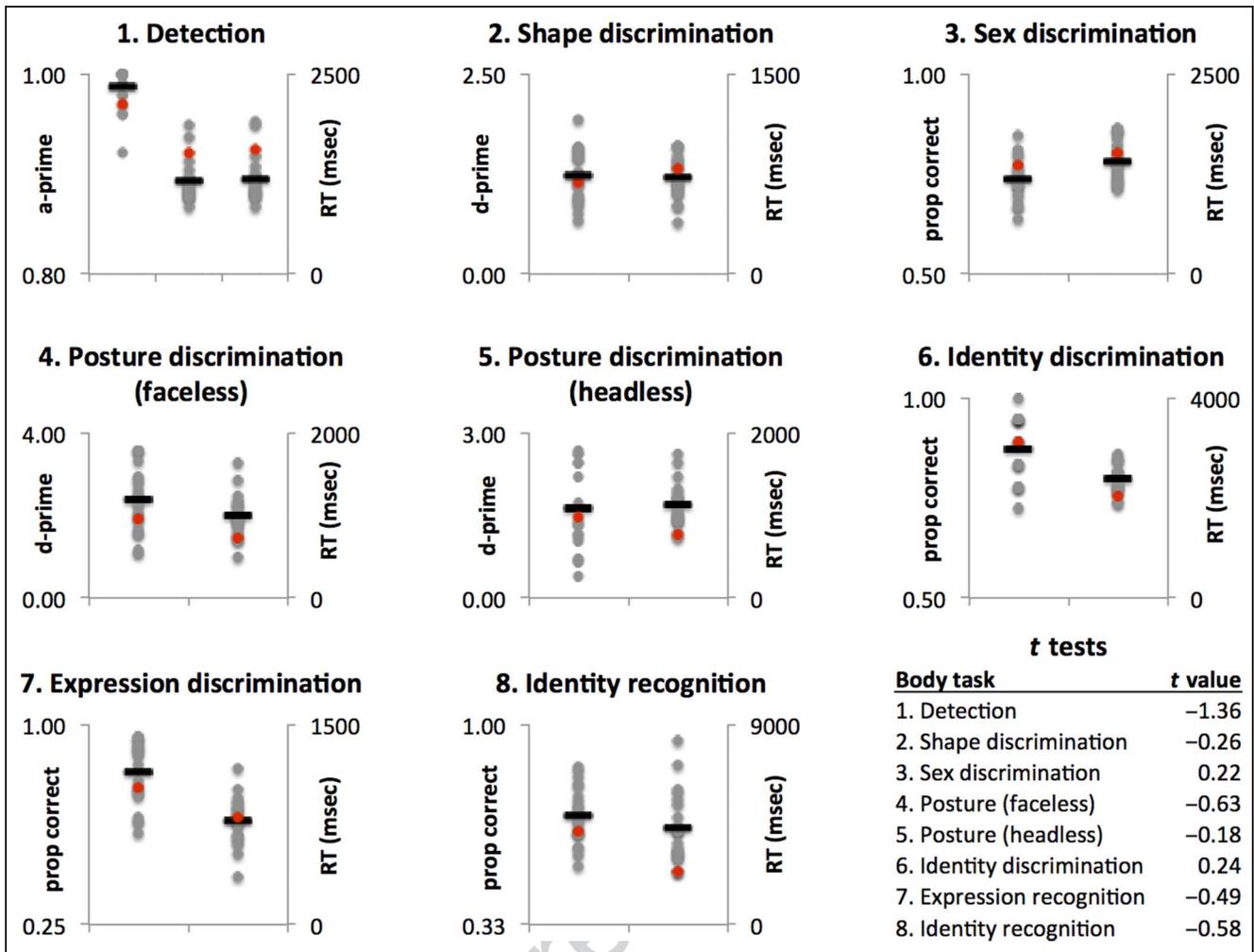


Figure 5. Galen's performance on eight tasks of body perception. Each panel plots an accuracy measure on the left and RT on the right, except Panel 1, which plots (from left to right) accuracy, RT, and inverse efficiency score. Red dots depict Galen, gray dots depict controls, and black bars depict control means. The bottom right table presents Galen's *t* values for the primary measure for each task; it was accuracy for all tasks, except the detection task, which used an inverse efficiency score.

Galen's normal body perception is interesting when considered in light of his prosopagnosia (Susilo et al., 2013). Galen is missing both the right FFA and the right FBA, yet he shows clear deficits with face recognition coupled with normal body recognition. Galen, however, failed to show normal activations in two face-selective regions, namely right FFA and right OFA (Yang, Susilo, & Duchaine, under review), whereas he was missing only one body-selective region. Another factor possibly contributing to this dissociation is that the right fusiform gyrus may be more important for face processing than body processing. This possibility is consistent with the smaller size of the right FBA relative to the right FFA in some studies (right FBA is about 50–60% of right FFA in Schwarzlose et al., 2005), although some studies have not found this difference (right FBA is about 80–140% of right FFA in Brandman & Yovel, 2010). Finally, although unilateral lesions are sufficient to produce prosopagnosia (Barton, 2008), perhaps they are not sufficient to impair body perception.

Our study has two limitations. First, we did not scan Galen before his resection. This leaves open the possibility that Galen may never have a right FBA, because the right FBA is not seen in every individual. Moreover, Galen's right fusiform gyrus may have been atypical before the surgery because of his arteriovenous malformation. But regardless of whether Galen had or did not have a right FBA in the past, his present results demonstrate that normal performance with bodies can co-occur in the absence of a right FBA. A second limitation is that our testing with Galen occurred years after the resection. This leaves open the possibility that Galen had body perception deficits but recovered from them. For example, recoveries of cognitive functions within months of neural insult are often reported in patients with spatial neglect (e.g., Corbetta, Kincade, Lewis, Snyder, & Sapir, 2005). Future studies that assess body perception immediately after surgery affecting body-selective regions are needed to address this issue decisively.

Our study raises two questions. First, what cortical regions might have subserved Galen's normal body perception? Consistent with the hypothesis that body perception is carried out primarily by body-selective regions (Kanwisher, 2010), Galen's left FBA and bilateral EBA might have compensated for his normal performance. Alternatively, motivated by the hypothesis that visual object perception is achieved in a largely distributed manner (Haxby et al., 2001), Galen's normal body perception might be subserved by both his remaining body-selective regions and other non-body-selective regions. A second question is more general: Which category-selective regions are critical for normal perception of their preferred stimuli? One possibility is that no single category-selective region is necessary and that the ventral visual cortex has sufficient flexibility to support visual object perception of any category when a category-selective region is damaged. This view is consistent with the notion that the general architecture of the ventral visual cortex is nonmodular (Haxby et al., 2001). However, evidence from patients who exhibit category-selective deficits (Barton, 2008; Gaillard et al., 2006; Epstein et al., 2001) and from TMS studies of category-selective regions (Dilks et al., 2013; Pitcher et al., 2007; Urgesi et al., 2004) suggest that at least some of these regions are critical. These considerations suggest that only some category-selective regions are critical for perception of their preferred stimuli. If so, it will be important to clarify which or what combinations of regions are critical and which are not (e.g., Dalrymple et al., 2011), because this might provide a clue to the organizing principles of ventral visual cortex.

In summary, our study demonstrates that damage to the right fusiform gyrus and the lack of the right FBA does not necessarily lead to persisting deficits with body perception. Although previous work indicates right FBA is important for body perception in normal participants, our study suggests its absence may be compensated for by other regions. Our study also shows that investigations of visual recognition that are motivated by lesions to category-selective regions are a valuable complement to the more traditional investigations that are motivated by behavioral deficits.

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Acknowledgments

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