Three-Dimensional Representations of Objects in Dorsal Cortex are Dissociable from Those in Ventral Cortex

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Abstract
An established conceptualization of visual cortical function is one in which ventral regions mediate object perception while dorsal regions support spatial information processing and visually guided action. This division has been contested by evidence showing that dorsal regions are also engaged in the representation of object shape, even when actions are not required. The critical question is whether these dorsal, object-based representations are dissociable from ventral representations, and whether they play a functional role in object recognition. We examined the neural and behavioral profile of patients with impairments in object recognition following ventral cortex damage. In a functional magnetic resonance imaging experiment, the blood oxygen level-dependent response in the ventral, but not dorsal, cortex of the patients evinced less sensitivity to object 3D structure compared with that of healthy controls. Consistently, in psychophysics experiments, the patients exhibited significant impairments in object perception, but still revealed residual sensitivity to object-based structural information. Together, these findings suggest that, although in the intact system there is considerable crosstalk between dorsal and ventral cortices, object representations in dorsal cortex can be computed independently from those in ventral cortex. While dorsal representations alone are unable to support normal object perception, they can, nevertheless, support a coarse description of object structural information.

Key words: 3D perception, impossible objects, object agnosia, object recognition, two visual systems

Introduction
Standard conceptualizations of the organization of the visual cortical system espouse a segregation between ventral cortex, which mediates object recognition, and dorsal cortex, which supports spatial representations (Ungerleider and Mishkin 1982) and goal-directed actions (Goodale and Milner 1992). Consistent with this distinction, many studies have confirmed that ventral cortical regions are highly sensitive to object shape and are invariant to changes in viewpoint or retinal size (Gross et al. 1972; Desimone et al. 1984; Malach et al. 1995; Booth and Rolls 1998; Grill-Spector et al. 1999; Kourtzi and Kanwisher 2000). More surprising, then, is the evidence that object-selective responses are also observed in dorsal cortical regions, even for tasks that do not involve visually guided actions. These responses were initially attributed to attentional or intentional processes, (Grill-Spector et al. 1999; Kourtzi and Kanwisher 2000). However, recent studies have shown that these responses are largely independent of image transformation (Konen and Kastner 2008) and support object-related spatial processing (Xu 2009; Bettencourt and Xu 2013; Zachariou et al. 2014; Freud, Rosenthal, et al. 2015).

The involvement of the dorsal cortex in object perception is also in-line with behavioral and imaging studies that show that...
action observation can facilitate object perception (Helbig et al. 2006; and also see Creem and Proffitt 2001), and that this process is supported by parietal regions in the dorsal cortex that modulate the activation profile in portions of the ventral cortex (Kiefer et al. 2011, Sim et al. 2015). The existence of such crosstalk was also established by anatomical investigations that showed that the vertical occipital fasciculus travels between the ventral and dorsal cortices and provides the structural infrastructure for the crosstalk between the two systems (Yeatman et al. 2014).

Despite the considerable evidence that suggests that the dorsal cortex is involved in object perception, the nature of such representations and their behavioral significance are not yet clear. One possibility is that the object representations in dorsal regions are merely the result of feedforward signals from the object representations in ventral cortex. An alternative possibility is that the dorsal representations are dissociable from ventral cortex and can be computed independently of the ventral representations, that is, they can be generated in the absence of the input from the ventral cortex.

To adjudicate between these alternatives, we employed neuroimaging and behavioral measures to examine whether individuals, with a lesion to ventral cortex (Fig. 1) and impaired object recognition, still evince sensitivity to object structural information. These patients all suffer from visual object agnosia (see Table 1 for case descriptions), a deficit in object recognition which is not attributed to a general loss of knowledge about objects or to impaired intelligence (Farah 1994). This deficit is usually observed after ventrolateral or ventromedial occipitotemporal cortex lesions (e.g., Goodale et al. 1991; Karnath et al. 2009; Konen et al. 2011). Importantly, dorsal cortex is intact in these individuals, thereby providing the opportunity to explore object representations in dorsal cortex largely without the contribution of ventral cortex. If dorsal representations are sufficiently sensitive to object structural information, then the dorsal cortex of the agnosia patients should evince differential sensitivity to visual displays that either obey or violate the legality of objects’ spatial structure. This sensitivity should continue to be apparent in behavioral tasks even if the patients’ overall perceptual performance is impaired relative to controls.

To assay the sensitivity of dorsal object representations, we employed pictures of possible and impossible objects (Penrose and Penrose 1958; Fig. 1). Contrasting these 2 classes of objects is informative: in contrast with possible objects, in impossible objects, there are inconsistencies between global and local information, that is, while the local cues are valid, the resulting 3D global structure is incoherent (shown from an accidental viewpoint) and violates the legality of the structure of real-world objects. Thus, although global depth cues may be extracted rapidly and effortlessly (Di Luca et al. 2004), the contradicting sources of global and local information cannot be resolved and observers are highly sensitive to these violations (Shuwairi et al. 2007; Regolin et al. 2011; Freud, Avidan, et al. 2015). Moreover, as we have shown in a recent functional magnetic resonance imaging (fMRI) study, there is greater activation for impossible than possible objects in both ventral and dorsal cortices (Freud, Rosenthal, et al. 2015) and thus, this contrast can serve as a probe of the sensitivity of dorsal cortex to object structure.

**Structural scans**

**Visual agnosia patients**

**Visual form agnosia**

**Brain-damaged controls**

![Figure 1](http://cercor.oxfordjournals.org/ at Acquisitions Dept/Hunt Library on October 22, 2015 http://cercor.oxfordjournals.org/)
Materials and Methods

Participants

All participants gave written informed consent to participate, and the protocol was approved by the Institutional Review Board, Carnegie Mellon University (CMU) and by the ethics committee of Ben-Gurion University of the Negev. The patients and a subset of control participants were tested in Pittsburgh and the remaining control participants were tested in Israel. Patients were tested either at the university or in their home.

Patients with Visual Agnosia

Five premorbidly normal right-handed individuals participated in these experiments. After a lesion sustained in adulthood (except for CR who was aged 16 years at the lesion onset), all individuals are impaired at visual perception. Table 1 briefly summarizes the biographical and neurological history for each patient; additional information about the etiology of the lesions and about the structural scan is available in the Supplementary Material and in previous publications (Mapelli and Behrmann 1997; Vecera and Behrmann 1997; Gauthier et al. 1999; Marotta et al. 2001; Marotta et al. 2002; Behrmann and Kimchi 2003; Rosenthal and Behrmann 2006; Behrmann and Williams 2007; Nishimura et al. 2010; Konen et al. 2011; Behrmann and Plaut 2014; Gilaie-Dotan et al. 2013, 2015).

Brain-Damaged Controls

Two additional patients who sustained brain damage were tested, one with damage to the left ventral cortex (GB), and the other with damage to the right parietal lobe (KL) (Fig. 1, bottom panel). GB has an upper right visual field quadrantanopia and pure alexia. KL does not reveal any perceptual difficulties. Neither of these patients is impaired in object recognition. More detailed information is available in the Supplementary Material and in previous publications (Mapelli and Behrmann 1997; Vecera and Behrmann 1997; Gauthier et al. 1999; Marotta et al. 2001; Marotta et al. 2002; Behrmann and Kimchi 2003; Rosenthal and Behrmann 2006; Behrmann and Williams 2007; Nishimura et al. 2010; Konen et al. 2011; Behrmann and Plaut 2014; Gilaie-Dotan et al. 2013, 2015).

Healthy Controls

A group of 10 healthy participants participated in the behavioral study, with 2 controls matched to each visual agnosia patient on age and handedness. Three of the matched control participants for CR and SM also participated in the fMRI experiment. Two additional matched controls were recruited for the fMRI study and also completed the behavioral session. These latter participants were not included in the behavioral experiments analysis to maintain an equal number (2) of matched controls for each patient.

Stimuli

Stimuli were 71 pairs of grayscale line-drawings of possible and impossible objects that had been used in previous studies (Freud, Avidan, et al. 2013; Freud, Ganel, et al. 2013, 2015; Freud, Avidan, et al. 2015; Freud, Rosenthal, et al. 2015). For each possible object, an impossible object was derived by altering one or a few features, resulting in a modification of the object’s global structure from possible to impossible (Fig. 2). Low-level features were equivalent between object categories as shown by statistical
comparisons showing equivalence in the overall number of pixels and the number of pixels that defined edges ($t$'s < 1).

**Procedure**

**fMRI Experiment.** General procedure. Three patients (CR, SM, and RN) and 5 matched controls completed a MRI session that was conducted before the behavioral session described below. This session included a 3D anatomical scan, 2 localizer runs, and 4 experimental runs. The data from RN were not analyzed due to excessive head movements. Additionally, to obtain a broader distribution of data from control participants, we included the data from an identical experiment that was performed in a different scanner and with young controls (age = 26 ± 1.5) (Experiment 1a; Freud, Rosenthal, et al. 2015). A preliminary analysis ensured that no differences were observed between the two control groups in terms of sensitivity to object possibility (at CMU versus Freud, Rosenthal, et al. 2015 scanned in Soroka Medical Center; $F$s < 1) and, thus, we merged the control data.

**MRI setup.** Participants were scanned in a 3T head scanner (Verio, Siemens) at Carnegie Mellon University. Details of the scanning parameters and of visual stimulation setup are described in the Supplementary Material.

Localizer scan. Participants were presented with a standard blocked-design localizer experiment used for delineating object selective regions. Stimuli were presented in 10-sec blocks, each comprised of 20 images. The stimuli in a given block were from a specific visual category (faces, houses, musical instruments, novel objects, or scrambled objects). Note that we used this large variety of object categories to remain consistent with other studies that perform localization of object–selectivity. To maintain their attention, participants performed a one-back task (responding by button press to a consecutive repeat of the same stimulus) and there was one image repetition within each block.

Possible/impossible scans. Participants completed 4 runs in which they viewed 30 blocks of possible and 30 blocks of impossible objects. Each 20 s blocks was comprised of 8 stimuli, each presented for 2000 ms followed by 500 ms fixation. Participants performed a one-back task and there was one image repetition within each block.

**Data Analysis**

fMRI data were processed using BrainVoyager 2.6 QX software (BrainInnovations, Maastricht, the Netherlands. RRID: nif-0000-00274) and complementary in-house software written in Matlab (The MathWorks, Inc., Natick, MA, USA. RRID: nlx_153890). Preprocessing included 3D-motion correction and filtering of low temporal frequencies (slow drift) and was followed by concatenation of the 4 experimental runs for each participant. No spatial smoothing was applied.

**Selection of Regions of Interest**

For each subject (i.e., patients and controls), regions of interest (ROIs) were defined individually based on the localizer scans at a significance level of at least q(FDR) < 0.05. As in our previous study (Freud, Rosenthal, et al. 2015), object-selective regions were defined by the contrast of (novel objects + musical instruments) > scrambled objects. The regions that were selected as ROIs were shown to be selective to objects and to 3D structure of objects in previous studies. The lateral occipital complex (LOC) (Malach et al. 1995) is the best known and well-studied object selective region. Importantly, this region was also found to be involved in 3D perception (e.g., Moore and Engle 2001). Another ventral region, the ITS, was also identified by previous studies, as an object selective region (e.g., Hasson et al. 2003) and was therefore included in the current study. Additionally, 2 dorsal regions were defined as ROIs, the transverse occipital sulcus (TOS), which is usually known as a scene selective region (Hasson et al. 2003) but is also responsive to spatial properties of objects (Troiani et al. 2014) and the posterior parietal cortex (PPC), which is involved in the perception of objects’ spatial features (Faillenot et al. 1999) and supports object individuation (Bettencourt and Xu 2013). Supplementary Table 1 includes the mean Talairach coordinates of the selected ROIs and the mean cluster size for the controls and separately for CR and SM.

**Univariate Analysis**

The 4 runs of each participant were concatenated and analyzed using a general linear model (GLM) and possible and impossible objects were contrasted to identify whether a region is sensitive.
to object possibility. Next, for each participant and each ROI, we used the mean β-weights for possible and impossible objects to calculate a ratio measuring the selectivity to possible/impossible objects:

\[
\frac{\text{Possible/impossible selectivity ratio}}{= \frac{(\text{Beta weight}_{\text{impossible objects}} - \text{Beta weight}_{\text{possible objects}})}{(\text{Beta weight}_{\text{impossible objects}} + \text{Beta weight}_{\text{possible objects}})}}.
\]

Positive values indicate that impossible objects elicit greater activation compared with possible objects while negative values indicate the opposite. Zero indicates equivalent activation for the 2 object categories.

To compare between the patients and controls, we conducted a bootstrapping analysis which consisted of 10,000 iterations in which the data from 12 healthy controls were randomly sampled with replacement, and their object possibility sensitivity indices were averaged. This analysis yielded a distribution of the mean selectivity index for each ROI and the mean selectivity index of the patients was compared with this distribution. To establish the statistical significance of the difference between controls and patients, we calculated the 99% confidence interval (CI) of the obtained bootstrap distribution of the mean.

**Behavioral Experiments**

**General Procedure**

The behavioral session included 4 experiments. In all experiments, practice was first given and feedback provided. During the experiment, trials were self-initiated and no feedback was provided.

**Experiment 1—same/different classification with matched objects.** Participants made speeded same/different judgments on 80 trials in which pairs of objects were presented. Half of the pairs were of the same object (possible/impossible) and half were of different objects. The “different” trials were of possible and matched impossible objects that differed from each other by few features. The first object in half of these trials was of the possible version, while in the remaining trials the first object was of the impossible version.

On each trial, the first object was presented for 3000 ms, followed by a mask screen (500 ms) that was composed of scrambled (400 fragments) objects. The second object was then presented until the participant provided a response (Fig. 4A).

**Experiment 2—depth comparison of spatial information.** One green and one red dot were superimposed on the stimuli and participants were required to judge which of the 2 markers was located closer in depth to the participant. The dots were located at the same position for the matched possible and impossible object (Fig. 4B). The assignment of the dots was counterbalanced across stimuli such that for half of the stimuli, the closer dot was lower in the vertical plane and for the other half the closer dot was higher in the vertical plane. Subject agreement about the close/far spatial location of the dots was validated in a prior pilot study. The experiment included 142 stimuli (half possible and half impossible). Each stimulus was presented until participants provided a response and was then followed by a masking screen that was presented for 500 ms.

**Experiment 3—possible/impossible classifications.** Participants were instructed to classify object possibility (Schacter et al. 1990). Possible objects were defined as objects that could legitimately exist in 3D space, while impossible objects were defined as objects that could not exist in 3D space. The experiments included the stimuli used in Experiment 2. Stimuli were presented until participant response and then followed by a mask shown for 500 ms (Fig. 4C).

**Experiment 4—same/different classification with nonmatched objects.** This last experiment serves as a control experiment to offer some specificity on the mechanisms that mediate the advantage for possible over impossible objects. The procedure was similar to Experiment 1, however the “different” trials were of two objects that remarkable differed from each other. Half of these trials were of a possible object, while the remaining trials were constituted from impossible object. The logic here is that because the two objects in a pair, when they differ, are so easily discriminable as being different, there is no need to compute a complex 3D shape (discrimination can be based on simple features, computed in a 2D description). The prediction is that even if the control participants perform better than the patients, there should be no interaction with object type.

**Results**

**Functional MRI**

**fMRI Experiment**

To examine the sensitivity of the dorsal and ventral cortices to object structural information in individuals with a lesion to the occipitotemporal cortex, we analyzed the fMRI response in the ventral and the dorsal cortices of 2 patients with visual agnosia and 12 healthy controls.

**Behavioral Results During fMRI Scanning**

Accuracy was high in both patients and controls, with better performance for the controls regardless of object category single-case analyses (Crawford and Garthwaite 2002): \(t’s > 2.1, P < 0.06\). No differences were found between possible and impossible objects \(F_{1,9} = 2.5, P > 0.1\). Unsurprisingly, reaction times (RT) were slower for the patients than the controls [single-case analyses: \(t’s = 2.05, P < 0.07\) but were similar across object categories \(F < 1, \text{ns}\) (Table 2). Thus, any differences in the fMRI signal between possible and impossible objects could not obviously be attributed to the fact that signal was summed over a longer activation period in one condition (or participant group) over the other.

**Univariate Analysis**

Object-selective ROIs in the occipitotemporal (LOC, ITS) and occipitoparietal (TOS, PPC) cortices were defined in each hemisphere (Fig. 3A). A GLM analysis was conducted using the data from the controls, separately for each object-selective region. The weights for possible and impossible objects were calculated and subjected to repeated-measures analysis of variance (ANOVA) with ROI, hemisphere and object possibility as within-subject variables. This analysis revealed robust effects of object possibility, with greater activity for impossible compared with possible objects \(F_{1,11} = 52.35, \eta^2_p = 0.82, P < 0.001\), and planned comparisons confirmed that all object selective regions exhibited a similar pattern \(F_{1,11} = 10.0, P < 0.01\). Additionally, an interaction was observed between hemisphere and possibility \(F_{1,11} = 9.26, \eta^2_p = 0.45, P < 0.05\), with stronger sensitivity to object impossibility in the right than left hemisphere, a finding that is consistent with the lateralization of object-based spatial information processing to the right hemisphere (e.g., Ditunno and Mann 1990; Farah 1994; Harris and Miniussi 2003; Zacks et al. 2003).
We analyzed the data from the patients in the same way but, first, we ensured that a reliable signal could be derived from the ROIs. For SM, because his lesion overlapped the right ITS, no activation was observed in this region in the localizer scans. For CR, although the right ITS was defined in the localizer, no reliable signal was obtained from this ROI in the experimental runs, and therefore this ROI was excluded from further analysis. All other regions exhibited normal event-related activation profiles and were used in subsequent analyses (see Supplementary Fig. 1).

To compare the BOLD profile of the two patients to the control group, we conducted a bootstrapping analysis of the distribution of normal sensitivity indices to object possibility in each ROI for the controls: sensitivity to object impossibility (greater response to impossible objects) is defined as a value greater than zero (see Materials and Methods for details). This analysis revealed that, in all dorsal ROIs, patients exhibited sensitivity to object possibility and it was equivalent to that of the controls (see Fig. 3B). In contrast, in the ventral regions, for the patients, 2 of the 3 sampled ROIs did not show sensitivity to object structure: this was true in both the left LOC [mean patients = −0.01, mean controls = 0.05, P < 0.01, 99% CI (0.02, 0.09)] and left ITS [mean patients = 0.001, mean controls = 0.05, P < 0.01, 99% CI (0.02, 0.08)]. The mean sensitivity in the right LOC was in the normal range [mean patients = 0.04, mean controls = 0.05, 99% CI (0.02, 0.09)] as a result of SM’s sensitivity to object possibility in this ROI. This LOC region is posterior to SM’s lesion, which might account for his preserved sensitivity. A similar bootstrapping analysis that equalized the number of controls to patients by sampling just 2 controls in each iteration yielded a similar pattern of results.

In addition to the group-level analysis, we performed single-case analyses using the revised standardized difference test (RSDT) (Crawford and Garthwaite 2005) which tests whether the difference between an individual’s standardized score on 2 conditions (possible versus impossible) is significantly different from the difference observed in the control sample. The RSDT confirmed that SM was significantly impaired in his sensitivity to object possibility in the left ITS [t(11) = 2.11, P = 0.05], while CR exhibited reduced sensitivity to object possibility in the left LOC.

Table 2 The behavioral performance during the fMRI scan

<table>
<thead>
<tr>
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<th>Accuracy</th>
<th>RTs</th>
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<tbody>
<tr>
<td></td>
<td>Possible</td>
<td>Impossible</td>
</tr>
<tr>
<td>Controls</td>
<td>98.8% (+0.009%)</td>
<td>100% (+0%)</td>
</tr>
<tr>
<td>SM</td>
<td>92%</td>
<td>90%</td>
</tr>
<tr>
<td>CR</td>
<td>94%</td>
<td>100%</td>
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Note: The performance of the patients was compared with the controls using a single-case analysis (see text for details). *indicates a marginal effect (P < 0.1). **indicates a significant effect (P < 0.05).

Figure 3. fMRI experiment. (A) ROI definition—ROIs were defined based on an independent localizer. The averaged ROIs are presented on inflated hemispheres of representative subject. (B) For each ROI, a distribution of the mean differences between the beta weights of impossible and possible objects was created (see text for details). The red vertical lines represent the 99% CI of the mean. The red dot in each graph represents the mean sensitivity index of the patients. For controls, all objects’ elective regions exhibited stronger activation for impossible compared with possible objects as evident from the CI that did not include zero. In contrast, for CR and SM dorsal ROIs were still sensitive to object possibility while most of the ventral ROIs were insensitive to structural information.
The results of the fMRI experiment confirm that, as expected, visual agnosia is accompanied by reduced neural selectivity to 3D structure in the ventral cortex. More importantly, the results show, for the first time, that the fMRI signal in dorsal cortex reflects sensitivity to 3D object structural information equivalent to that of the controls. This finding provides strong support for the claim that object representations in dorsal cortex are independent of those in ventral cortex.

Before reaching this conclusion definitively, however, we explore 2 alternative interpretations. One possibility is that the sensitivity to 3D object structural information is a product of the left hemisphere ventral regions. This can be ruled out as CR has bilateral lesions and SM, who has a unilateral right lesion, also exhibited impaired sensitivity in his intact left ventral cortex (see Konen et al. 2011 as well).

A second possibility is that the sensitivity noted in the dorsal cortex in the patients was mediated by the observed residual ventral sensitivity and perhaps, then, is not entirely independent. To evaluate this possibility, we applied a Bayesian method that enables us to determine whether sensitivity to object impossibility in dorsal ROIs was still preserved in the patients even after the residual ventral sensitivity was accounted for as a covariate (Crawford et al. 2011). The results confirmed that, in all dorsal ROIs, there was no difference in sensitivity to structural information between the patients and the controls (Ps > 0.3). The only exception was the right PPC of SM that exhibited marginal oversensitivity compared with the controls (Z-ccc = 4.6, P = 0.07).

Behavioral Experiments

The results of the fMRI experiment suggest that representations in the dorsal ROIs are sensitive to object structure in patients with a lesion to ventral cortex. These findings provide novel evidence for the functional dissociations of object representations in dorsal cortex. If these dorsal representations play a functional role in perception, then we might predict a behavioral difference to possible versus impossible objects in these patients even though their object perception accuracy may be lower than that of controls.

We evaluated the patients’ sensitivity to the coherence of structural information in a series of psychophysical tasks that varied in their perceptual requirements. Two additional patients with visual agnosia participated in these experiments (n = 4). Comparisons were made between the patients versus two groups of controls, individuals with no neurological damage and two patients who are not agnostic and have brain damage to regions outside of right ventral cortex.

**Experiment 1: Same–Different Classifications (matched objects)**

Experiment 1 utilized a task that could be completed solely on the basis of 2D information but, at the same time, demanded fine-grained processing. Participants performed same–different classifications on pairs of possible and impossible objects (Fig. 4A, left panel). To enforce detailed processing of the stimuli, the differences between stimuli were minor even in the “different” trials (see Materials and Methods for details). In this task, a representation is generated from the first object, which is later compared with the second, on-screen object. Thus, to the extent that structural information is processed in this task, better performance is predicted for trials in which a possible object was presented as the first object compared with trials in which the first object was impossible and a coherent representation could not be generated (Schacter et al. 1990; Soldan et al. 2009; Freud, Hadad, et al. 2015; Freud et al. 2015). Additionally, it was predicted that patients with visual agnosia would be impaired on this task compared with healthy controls, but, would nevertheless show preserved sensitivity to object possibility which may rely on the intact dorsal object representations.

In this experiment, object possibility was orthogonal to the task (same/different judgement) at hand, and therefore sensitivity could be calculated independently for possible and impossible objects (note that analysis of the raw data, which included both object type (possible–impossible) and trial type (same–different) yielded similar results, with better accuracy and faster RTs for possible objects, regardless of experimental group. Yet, patients showed better performance in the “same trials” mirroring a perceptual bias. Importantly, the d’ analysis, is not affected by this perceptual bias, and reflects the perceptual sensitivity to object possibility.) Repeated-measures ANOVA revealed a robust difference between the groups, with better performance for the matched controls than the patients [F(1,12) = 44.97, ηp² = 0.78, P < 0.001]. However, despite a quantitative trend in this direction, no advantage was observed for trials primed by possible compared with impossible objects [F(1,12) = 2.23, P = 0.16], with no interaction with group [F(1,12) < 1] (Fig. 4A).

Single-case analyses (Crawford and Garthwaite 2002; Crawford et al. 2010) confirmed that all patients were impaired in their overall performance [t’s > 2.67, P < 0.05], while the brain-damaged controls performed equivalently to healthy controls [t’s < 1]. Additionally, the inferential methods for comparing 2 single cases (Crawford et al. 2010), showed that brain-damaged controls performed better from the agnostic patient [t’s > 2.26, P < 0.05], excluding EC [t’s < 1.68, P > 0.1].

Despite the absence of an effect for object type in terms of d’ scores, RT analysis revealed a main effect of object possibility [F(1,12) = 8.28, ηp² = 0.4 P < 0.001] with faster RTs for trials primed by possible objects. Importantly, this effect was evident to a similar extent in the patients and the control groups as shown by the lack of an interaction between group and object possibility [F(1,11) < 1]. Specifically, all patients exhibited faster RTs for possible compared with impossible objects, excluding RN who performed slightly faster (5 ms) for impossible objects, but might have traded speed and accuracy as he had a considerably better d’ score for possible than impossible objects. To assess the similarity of each patient’s RT to the controls with respect to sensitivity to object possibility, we applied the RSTD analysis and confirmed that all patients performed within the normal range [t’s < 1.3, P > 0.2].

Despite the lack of interaction between the groups and the descriptive statics that showed the advantage for possible objects in all patients, we wanted to ensure that the patient group was statistically significantly better for possible compared with impossible objects. However, the utilization of simple comparisons for 4 subjects is highly unreliable. Therefore, we applied a randomization analysis, which consisted of 10 000 iterations in which the data from each patient was sampled with replacement, and was randomly assigned to the different conditions (i.e., possible or impossible). This method yielded 10 000 random samples, which were based on the patients’ data. Next, we subtracted the “impossible” condition from the “possible” condition to create the random distribution of the possibility advantage and calculated the 95% CI of this distribution. Finally, we examined whether the results obtained in the experiment exceeded the CI and therefore deviated from the random distribution.

The randomization analysis confirmed that the patients had better sensitivity for possible objects compared with impossible
Figure 4. Experiments 1–4 design (left panel) and results (middle and right panels). The data of each agnostic patient (RN, SM, CR, and EC) and brain-damaged controls (KL and GB) is plotted separately in addition to the average results for the patients and matched controls. Agnostic patients, matched controls and brain-damaged controls are, respectively, designated by squares, circles, and triangles. Error bars across all figures represent CIs for the main effect of object possibility as calculated for repeated-measures ANOVAs ([armaz and Hollands 2009). (A) Experiment 1: Participants performed same/different classifications on pairs of objects which were physically highly similar. Object possibility was orthogonal to the task, and sensitivity was calculated independently for possible (gray) and impossible (black) objects. The overall performance of the matched controls was better (middle panel), but sensitivity to object possibility was equivalent between the two groups (right panel). (B) Experiment 2: participants performed depth classifications—which dot is closer in depth—the red (black in figure) dot or the green dot (white in figure). Overall, matched controls performed better than patients (middle panel). Both groups exhibited superior performance for possible compared with impossible objects (right panel). (C) Experiment 3: participants performed overt possible/impossible classifications. Patients had only minimal awareness to object 3D structure possibility while matched control exhibited high sensitivity to this information. (D) Experiment 4: Participants performed same/different classifications on pairs of objects which were physically obviously different. Overall, matched controls performed better than patients (middle panel). Both groups exhibited similar performance for possible and impossible objects (right panel).
objects [mean $d'$ advantage = 0.24, mean random advantage = 0.001, $P < 0.05$, 95% CI (−0.18, 0.18)] and this was also true in terms of RTs [mean RT difference = 120 ms, mean random RT difference = 0.48 ms, $P < 0.05$, 95% CI (−120, 119 ms)] (note that analysis of the raw data, which included both object type (possible-impossible) and trial type (same-different) yielded similar results, with better accuracy and faster RTs for possible objects, regardless of experimental group. Yet, patients showed better performance in the “same trials” mirroring a perceptual bias. Importantly, the $d'$ analysis, is not affected by this perceptual bias, and reflects the perceptual sensitivity to object possibility).

The results of Experiment 1 suggest that, notwithstanding the lesion to the ventral cortex, patients with visual agnosia still process structural information and retain sensitivity to the validity of object structure. Although patients exhibited highly impaired performance in the perceptual task, they were as sensitive to object possibility as the controls.

**Experiment 2: Depth Comparison of Spatial Information**

Experiment 1 revealed that, despite their reduced accuracy in object perception, the patients were still sensitive to the legality of object structure. Because, arguably, this task does not necessarily demand the processing of the object as a whole, the observed sensitivity to object possibility might reflect the patients’ intact local processing of the structural violations that differentiate between object categories. To explore whether the observed sensitivity is a product of structural representation of objects per se, in Experiment 2, two dots were superimposed on each object and participants decided which dot is closer to the observer in depth (Fig. 3B, left panel). The dots were always located in different locations of the object to enforce the processing of the object as a whole.

Consistent with the results of Experiment 1, with $d'$ as the dependent measure, patients were less accurate than controls [$F_{1,12} = 13.99, \eta^2 = 0.53, P < 0.05$] and this was true for all patients, as reflected in the single-case statistics [$t's > 2.63; P < 0.05$], with the exception of CR [$t < 1$]. The two brain-damaged controls performed as well as the healthy control group [$t's < 1$] (Fig. 3B, middle panel), and significantly better than the agnostic patients [$t's > 2.097, P < 0.06$] excluding CR [$t < 1$].

The ANOVA also revealed an additional main effect with better performance for possible compared with impossible objects [$F_{1,12} = 5.56, \eta^2 = 0.31, P < 0.05$]. Importantly, this superiority was observed to a similar extent for the patients and controls, as evident from the lack of interaction between group and object possibility [$F_{1,12} < 1$; Fig. 3B, right panel]. Specifically, all patients exhibited greater sensitivity to possible compared with impossible objects, excluding SM who showed similar sensitivity levels to the two object categories in terms of $d'$, but exhibited slower RTs for impossible objects compared with possible objects (note that SM exhibited a similar pattern in Experiment 1). The RSAT analysis showed that none of the patients was different from the controls in terms of sensitivity to object possibility in this task [$t's < 1$].

RT analysis revealed a similar trend with faster responses for possible compared with impossible objects [$F_{1,12} = 3.13, \eta^2 = 0.2, P = 0.1$], and with no interaction between object possibility and group [$F_{1,12} = 1.59, P > 0.2$]. Brain-damaged controls also showed the same pattern with faster RTs for possible (1954 ms) compared with impossible objects (2060 ms) (see Supplementary Fig. 3), and this did not differ from the other groups [$t's < 1$].

To validate the advantage for possible over impossible objects, we applied the randomization analysis similarly to Experiment 1. This analysis revealed significantly better sensitivity for possible over impossible objects for the patients [mean $d'$ advantage = 0.32, mean random advantage = 0.001, $P < 0.05$, 95% CI (−0.27, 0.27)], while a marginal effect was also observed in terms of RTs [mean RT difference = 43 ms, mean random RT difference = 0.14 ms, $P = 0.06$, 95% CI (−44, 44 ms)].

These findings replicate and extend the results of Experiment 1, albeit in a task that required computation of structural object-based information: patients with visual agnosia still evinced sensitivity to object structural information despite their overall impairment in object perception. This preserved sensitivity might be mediated by the intact dorsal object representations uncovered in the fMRI experiment. This finding suggests that, although these dorsal representations are insufficient to support normal object perception, they may suffice to support sensitivity to structural, likely spatial, object information.

**Experiment 3: Possible/Impossible Classifications**

The ability to classify an object as possible or impossible requires a fine-grained representation of object 3D structure. Specifically, object impossibility is a product of the inconsistency between local and global cues: only when the inconsistency of these contradicting pieces of information becomes apparent can participants label the image as impossible. Based on previous studies (e.g., Delvenne et al. 2004; Turnbull et al. 2004), we predicted that, despite the observed sensitivity to object possibility in Experiments 1 and 2, patients with visual agnosia will be impaired in the possibility classification task.

Participants were shown a single image and were asked to indicate explicitly whether it was possible or not. The agnostic patients exhibited reduced sensitivity to the possible/impossible status of the objects, compared with matched controls [$F_{1,13} = 24.4, \eta^2 = 0.67, P < 0.001$] and this held true for every patient [$t's > 2.32; P < 0.05$]. The sensitivity of the two brain-damaged controls did not differ from that of the matched controls [$t's < 1.03; P > 0.5$] (Fig. 4C), however, their scores were found not to be statistically different from the patients [$t's < 1.42, P > 0.15$], excluding EC [$t's > 2.94, P < 0.01$]. There were no differences in RT between the agnostic patients and healthy controls [$F_{1,13} < 1$] nor between the agnostic patients and the brain-damaged controls [$t's < 1$] (see Supplementary Fig. 3).

The results of Experiment 3 showed that, despite the observed sensitivity to structural representation in Experiment 1 and 2, agnostic patients were unable to explicitly determine whether an object is possible or not. The apparent failure to integrate the 3D information for this purpose is likely an outcome of more ventral computations and sets a boundary on the nature of the dorsal object-based representations. These results indicate that the dorsal object representations may be necessary for, but are clearly insufficient for, the normal perception of object structure.

**Experiment 4: Same-Different Classifications (Nonmatched Objects)**

The behavioral results presented so far have shown that sensitivity to object 3D structure is observed even when ventral cortex is impaired. Based on this finding, we suggest that the dorsal cortex can mediate 3D object representations and these are potentially dissociable from ventral object representations. We have argued that the dorsal representations contribute to 3D processing and it is this sensitivity to spatial geometric structure that gives rise to the advantage for possible over impossible objects. It is the case, however, that this observed advantage might arise for other reasons such as object complexity (i.e., number of junctions, lines etc.). Despite the fact that our stimulus set is highly controlled for such factors (see Materials and Methods), we wanted to ensure that the observed advantage for possible objects, truly reflects 3D processing mechanisms. To this end, participants...
performed a same-different task, but unlike Experiment 1, stimuli in the “different” trials were obviously different (Fig. 4D, left panel). Hence, this task could be performed based on coarse differences between objects (i.e., 2D properties) and did not require fine-grained processing of the 3D properties of the stimuli.

As in previous experiments, overall, patients were impaired compared with controls \( [F_{1,18} = 4.5, \eta^2_p = 0.27, P = 0.05] \) reflecting their perceptual, ventral-related, difficulties. Single-case analysis showed that SM and CR were within the normal range while the other patients were impaired even on this simple task \( [t' > 2.01, P < 0.07] \). More importantly for the purpose of the current experiment, similar performance was found for the 2 object categories with no interaction with group \( [F_s < 1] \) (Fig. 4D). Repeated-measures ANOVA on the RT data did not reveal any significant effects \( [F_s < 1] \) (see Supplementary Fig. 3).

The results of Experiment 4 indicates that the advantage found in Experiments 1 and 2 for possible objects does not rely on 2D shape properties and, rather, is more specifically related to the processing of 3D information.

**Experiment 5—The Representation of Object Structural Information in Visual Form Agnosia**

Although, in the imaging analysis, we attempted to rule out the idea that the sensitivity to object 3D structure might have been mediated by residual functionality of the ventral cortex by using ventral stream activity as a covariate, here we provide additional evidence to rule out the claim that the dorsal representations are a result of ventral signal propagation. The approach is to report data from a final patient, JW, a patient who has especially marked visual form agnosia following widespread anoxic damage affecting the occipitotemporal lobes bilaterally (Mapelli and Behrmann 1997; Vecera and Behrmann 1997; Rosenthal and Behrmann 2006). JW is profoundly impaired in his perceptual abilities even relative to the patients described above. Given the substantial ventral lesion, if JW reveals any sensitivity to object structural information, it is unlikely to be the product of residual functionality of the ventral cortex, licensing us to conclude that the object representations in dorsal cortex are independent and functionally relevant.

We were unable to obtain imaging data from JW, as we could not confirm definitively that his replacement mitral valve was not ferromagnetic. Nevertheless a lesion of a similar magnitude in another patient, dramatically reduces object-selective activation in the ventral cortex (James et al. 2003).

**Experiment 5a: Same-Different Classifications (Matched Results)**

JW had significantly lower \( d' \) in this task, relative to the healthy controls \( [t = 5.2, P < 0.001] \). The inferential methods (Crawford et al. 2010) showed that his performance did not differ from the other visual agnosia patients \( [t' > 1.9, P > 0.08] \), which may be accounted for by a floor effect. Remarkably, however, JW still exhibited greater sensitivity to possible than impossible objects, and this was within the normal range in terms of sensitivity to object possibility \( [RSDT: t = 1.2, P = 0.25] \) (Fig. 5A).

The RT analysis showed that JW was significantly slower than both the healthy controls \( [t = 7.28, P < 0.0001] \) and all the agnosia patients \( [t' > 4.7, P < 0.01] \), confirming his perceptual difficulties. Notably his RT, too, was faster for possible than impossible objects, and his sensitivity to object possibility fell in the normal range \( [RSDT: t = 1.05, P = 0.31] \) (see Supplementary Fig. 4). As the number of correct trials was small, we re-analyzed the RT data using all trials and faster RTs were still evident for possible over impossible objects (possible: 3657 ms; impossible: 4202 ms).

**Experiment 5b: Depth Comparison of Spatial Information**

Based on \( d' \), JW’s performance was significantly impaired relative to controls \( [t = 10.9, P < 0.0001] \) and all the agnosia patients \( [t' > 5.35, P < 0.001] \) (Fig. 5B). Despite his profoundly impaired performance, JW retained sensitivity to object possibility similarly to the healthy controls \( [t < 1] \). This reduced \( d' \) but preserved sensitivity to object structure was also mirrored in the RT data. JW was significantly slower than the healthy controls \( [t = 9.4, P < 0.001] \) and also slower than each patient \( [t' > 6.09, P < 0.001] \). Nevertheless, he was even more sensitive than the healthy controls to object possibility with faster RT for possible objects \( [RSDT: t = 2.915, P < 0.05] \) (see Supplementary Fig. 4) and this was true even when all trials were included (possible objects 8757 ms; impossible objects 10165 ms).

**Experiment 5c: Possible/Impossible Classifications**

As expected, JW was unable to classify objects as possible or impossible (Fig. 5C); his \( d' \) was significantly lower than the controls \( [t = 5, P < 0.001] \) and marginally lower than the other patients \( [t' < 1.82, P < 0.1] \), excluding EC \( [t < 1] \). RT analysis showed no differences between JW and the controls or the other patients \( [t < 1.26, P > 0.2] \) (see Supplementary Fig. 4).
Discussion

The goal of the present study was to determine the nature of object representations in the dorsal regions of the visual cortex. While previous studies have demonstrated that these regions are sensitive to object shape (Konen and Kastner 2008; Xu 2009; Bettencourt and Xu 2013; Freud, Rosenthal, et al. 2015) and interact closely with ventral cortex to aid recognition (Kiefer et al. 2011; Sim et al. 2015), it is unclear whether these representations result from a cascade of signals from ventral cortex, or whether they are dissociable from ventral representations and independently computed.

To address this, we examined the neural and behavioral responses of 5 patients with visual agnosia, following a lesion to the ventral cortex, on a range of tasks that required the representation of object structural information. In the imaging results, despite a reduction of sensitivity to object structure in ventral regions, regions along the dorsal cortex evinced greater activation for impossible than for possible objects. Moreover, notwithstanding the profound perceptual impairments, the patients revealed behavioral sensitivity to the integrity of object structural information, evincing an advantage for geometrically coherent, possible objects over impossible objects. These findings lead us to conclude that dorsal representations are computed independently of ventral object representations. Moreover, the dorsal activation patterns capture representations of object structure and its legality.

However, a possible alternative explanation is one in which the dorsal activation is simply the cascade of whatever residual ventral function is available. Two lines of evidence make this alternative unlikely. The first is that the sensitivity to structural information in the dorsal cortex of the patients was found to be in the normal range even when the residual ventral cortex sensitivity served as a covariate. The second is that in a patient with profound visual-form agnosia following extensive bilateral occipitotemporal lesion, with minimal, if any, ventral cortex object functions, performance was still better for possible compared with impossible objects in two different tasks (i.e., Experiment 5a and 5b) to an equal extent as in the control individuals.

Together, these findings provide evidence that dorsal cortex, while disconnected or dissociated from ventral cortex, has sufficient object-based information. The question is whether the dorsal representations contribute to visual perception in normal participants. In the normal functioning brain, there are functional (e.g., Kiefer et al. 2011; Sim et al. 2015; Freud, Rosenthal, et al. 2015) and anatomical connections (Yeatman et al. 2014) between dorsal and ventral cortices and, thus, dorsal object representations are likely modulated and shaped by such connections (and the same may be true of ventral cortex). Nevertheless, our finding that 3D object representations can be generated in dorsal cortex even when ventral inputs are highly reduced and impaired suggests that such dorsal representations can be dissociated from and are not entirely reliant on ventral cortex.

The apparent dissociability of dorsal and ventral object representations raises a number of important questions for the interactivity of the ventral–dorsal modulations and for the temporal course of the activations. One possible scenario is that the initial computation of object representations begins (separately) in the dorsal and ventral cortices and only then the bidirectional connections modulate these emerging or existing representations. There are also questions about the weighting of the bidirectional connections and potential asymmetries in the strength of their modulations. These questions go beyond the scope of the current study and ought to be addressed in future investigations.

Finally, the apparent dissociability of dorsal object representations is consistent with findings showing that the dorsal portion of the LOC in visual agnosia patient retained sensitivity to objects presented tactualy but not visually (Allen and Humphreys 2009). Here, we extend this finding and show that a (perhaps partial) visual representation of object structure is generated in the dorsal cortex although ventral vision is highly impaired. The results we report here are also compatible with data from another imaging study, which includes patient SM (who is one of the participants in the present study) (Kassuba et al. in preparation). In that study, an fMRI adaptation paradigm revealed that SM’s visual responses to both 2D-objects and line drawings were impaired in all dorsal ROIs relative to healthy control subjects (and to a greater degree in the left than right hemisphere). However, responses to 3D-objects were comparable to the control group, suggesting that 3D structural information may be represented in parietal cortices.

The Behavioral Signature of Object Representations in the Dorsal Cortex

The imaging experiment demonstrated that the dorsal cortex of the visual agnosic patients was differentially activated by possible and impossible objects. Despite this, the patients were still profoundly impaired in various perceptual tasks, indicating that dorsal object representations are not sufficient for normal object perception. What then is the functional contribution of dorsal object representations?

The profound impairment in the object possibility classification task replicates previous studies with visual agnosia patients (Riddoch et al. 2003; Delvenne et al. 2004; Turnbull et al. 2004). However, because we used additional tasks in which the response was orthogonal to object possibility (e.g., red/green depth decision), we were able to uncover the sensitivity to 3D structural object information (for a similar idea see Farah et al. 1991) despite the reduced accuracy and increased RTs of the patients. These results suggest that the dissociable dorsal object representations might primarily be involved in deriving object structural information processing. This hypothesis is compatible with the importance of parietal regions for spatial and 3D information processing (e.g., Durand et al. 2009; Georgieva et al. 2009; Srivastava et al. 2009; Orban 2011; Verhoef et al. 2015). The key contribution of dorsal object representations, then, is in the derivation of the global geometry of objects.

Hemispheric Specialization in the Processing of Structural Information

The present results also point to potential differences between the 2 hemispheres in the processing of structural information. In particular, the fMRI experiment showed greater differential activation to impossible and possible objects in the right than left hemisphere. Moreover, while all the visual agnosia patients suffered from a right ventral lesion (except CR), GB, who suffered from a large unilateral lesion to her left ventral cortex showed neither a deficit in object perception nor any decrement in perceptual sensitivity to structural information.

This left–right hemispheric difference is compatible with previous studies that have documented right hemisphere specialization in tasks that require 3D rotations (Ditunno and Mann 1990; Harris and Minussi 2003). Furthermore, this specialization, especially in parietal regions, held only when the rotations were object-based, rather than viewer-based (Zacks et al. 2003).
Conclusions
The current study explored the nature and functional contribution of object representations in the dorsal cortex. Together, the imaging and behavioral findings suggest, for the first time, that the dorsal cortex can mediate visual information to generate dissociable object representations from the ventral cortex. These representations support the processing of object-related structural information, but are not sufficient for normal object perception.

Supplementary Material
Supplementary material can be found at: http://www.cercor.oxfordjournals.org/.

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Notes
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References


