



The dissociation of color from form and function knowledge

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We report on two brain-damaged subjects who exhibit the uncommon pattern of loss of object color knowledge, but spared color perception and naming. The subject P.C.O., as in previously reported patients, is also impaired in processing other perceptual and functional properties of objects. I.O.C., in contrast, is the first subject on record to have impaired object color knowledge, but spared knowledge of object form, size and function. This pattern of performance is consistent with the view that semantic information about color and other perceptual properties of objects is grounded in modality-specific systems. Lesion analysis suggests that such grounding requires the integrity of the mesial temporal regions of the left hemisphere.

How we interact with objects in the world often depends on what colors we perceive them to have, and on how those perceived colors accord with what we know to be the normal or 'canonical' colors of the objects in question. Thus, we do not eat green strawberries, we drink water only if it is colorless, and we stop for red traffic lights. These complex behaviors depend on the integrity of neural mechanisms involved in processing color as such, as well as mechanisms that combine information about color with other types of information about an object's representation, such as its form.

The early stages of color processing in humans have been extensively studied, both in neuropsychological studies of patients with achromatopsia (loss of color vision following brain damage)^{1–4} and in neuroimaging studies with neurologically intact subjects^{5–8}. Studies have documented achromatopsia associated with both relative sparing of form^{9–11} and the reverse dissociation—that is, relative sparing of color with respect to form¹². These complementary observations suggest that the early processing of color and form are functionally independent. Analysis of the lesions associated with achromatopsia and the results of neuroimaging studies suggest a critical involvement of temporo-occipital structures in the early processing of color. The relevant structures are located in the lateral bank of the collateral sulcus⁶, considered analogous to area V4 in the monkey. However, the exact involvement and location of V4 in the human brain remain controversial^{13,14}.

Considerably less is known about the neural mechanisms involved in processing color as a stored property of an object ('object color knowledge'). This is partly because neurological patients are rarely encountered who exhibit a loss of object color knowledge, but spared perception, recognition and naming of colors^{15–17}. Of the three recent cases that have been reported, the evidence for a dissociation between loss of color knowledge and spared color perception and recognition is ambiguous in two (G.G. and A.V.)¹⁶ and anecdotal in a third (R.M.)¹⁷. Nonetheless, when contrasted with observations of patients with achor-

matopsia but spared object color knowledge^{9,11}, these reports demonstrate that the mechanisms underlying color perception and naming are separable from those representing knowledge of the canonical color of objects. However, in all these cases, knowledge of other stored properties of objects was damaged along with object color knowledge. Both G.G. and A.V.¹⁶ suffered from damage to object form knowledge, as shown by their poor performance in object-decision tasks and by their failure to produce crucial details of the form of objects in drawing tasks; R.M.¹⁷ exhibited a generalized imagery deficit. Therefore, it is not possible to determine, based on these reports, whether the observed loss of object color information resulted from damage specifically to stored knowledge of object color, or whether it was attributable to a general loss of the stored properties of objects. Nonetheless, the dissociation between spared ability to name color probes and impaired ability (whatever its basis) to access object color knowledge provides evidence for the functional independence of color knowledge (for example, that a colored patch is yellow) and object color knowledge (for example, that the canonical color of bananas is yellow).

The anatomical substrate of object color knowledge has also been investigated. All reported cases of loss of object color knowledge but spared color vision suffered from damage involving (but not restricted to) the left temporal lobe^{16,17}. However, this observation is of limited usefulness because, as argued above, the nature of the functional cause of the object color knowledge impairment in these patients is unclear. Neuroimaging studies also converge in suggesting that the temporal lobe is somehow implicated in representing object color knowledge, but contrast in attributing a critical role to the left inferotemporal region^{5,18} or to bilateral mesial occipitotemporal and dorsal occipital (and perhaps also right frontal) structures⁷.

Here we report evidence that may help to resolve some of these issues. We describe two brain-damaged subjects (P.C.O. and I.O.C.) who exhibit damaged object color knowledge and unim-

Table 1. Performance obtained by P.C.O., I.O.C. and S.L.A. on tasks evaluating the ability to perceive colors, and to recognize and name color probes.

	P.C.O.	I.O.C.	S.L.A.
Ishihara color blindness plates	N/A	14/17 (0.82)	N/A
Farnsworth-Munsell hue	flawless	minor errors	flawless
Color sorting	20/20 (1.00)	N/A	20/20
Color name comprehension	24/24 (1.00)	N/A	24/24
Color naming	24/24 (1.00)	17/17 (1.00)	24/24

Percentages are in parentheses. N/A, not administered.

paired color perception. Crucially, one of these subjects (I.O.C.) displays spared knowledge of object form and function; this was never previously reported in a patient who has difficulties with object color. The performance of these patients is compared to that of a control patient (S.L.A.) who has a left occipital lesion but no observable cognitive deficit. S.L.A. served as control for P.C.O. Her results are reported but not discussed in the text.

RESULTS

The results are organized into three sections, reporting on the patients' abilities to recognize and name colors, to process knowledge of object color, and to process knowledge of other properties of objects. Comparable but not identical tasks were given to the three subjects.

Perception, recognition and naming of color probes

P.C.O. flawlessly matched color probes, pointed to color probes named by the examiner, named the colors of probes, and arranged them in the Farnsworth hue test¹⁹ (Table 1).

I.O.C. named 17/17 color probes. She named the embedded numbers in 14/17 (0.82) Ishihara plates²⁰ (the errors reflected her anomia; she misread 3 as 8, 97 as 87, and 45 as 48), and made minor arrangement errors, well within the normal range, in the Farnsworth hue test¹⁹. Because color-blind subjects fail to read most numbers in Ishihara plates and exhibit specific patterns of incorrect color arrangement in the Farnsworth hue task, neither of which was demonstrated in I.O.C., these results rule out achromatopsia and other disorders of color processing in this patient (Table 1).

Object color knowledge

Having established that both P.C.O. and I.O.C. had essentially normal color perception, we now report on the tasks tapping knowledge of object color. In these tasks, objects with canonical colors (for example, blood) were presented, and subjects were asked to say whether or not a color presented by the examiner was appropriate for a given object or they were asked to produce the canonical color of the object.

Subject P.C.O. completed two object-color verification tasks. In the auditory/auditory task, she was asked to decide whether or not a color name and an object name pronounced by the examiner matched. ("Can a canary be yellow?" "Can a lion be red?") In the visual/auditory task, she was asked to say whether or

not the object depicted in a black-and-white drawing could have the color named by the examiner (for example, picture of a lemon: "Can this be yellow?"). In both tasks, each object was paired once with the correct color and once with a highly implausible color (for example, blue for a lemon). In all of these tasks, chance responding would result in 0.50 accuracy. Overall, P.C.O. produced 45/80 (0.56) correct responses. Performance on the two tasks was comparably poor (auditory/auditory, 27/40 correct; visual/auditory, 18/40 correct; $\chi^2 = 3.251$; NS). Collapsing across tasks, P.C.O. produced significantly fewer correct responses to animals (6/23, 0.26) than to fruits and vegetables (18/29, 0.62) or to artifacts (21/28, 0.75; $\chi^2 = 5.313$, $p < 0.05$ and 10.243, $p < 0.001$, respectively).

In two object-color attribution tasks, P.C.O. was asked to produce the name of the canonical color associated with an object named by the examiner (auditory/verbal) or to select from a set of 24 colored crayons the one corresponding to the canonical color of an object depicted in a black-and-white line drawing (visual/visual). Only responses that were obviously incorrect were scored as errors (for example, elephant, 'red'). Overall, P.C.O. produced 56/115 (0.49) correct responses. Accuracy was comparable on the auditory/verbal (30/53) and the visual/visual tasks (26/62; $\chi^2 = 1.909$; NS). Collapsing across tasks, she produced correct responses for 2/29 (0.07) animals, 24/34 (0.71) fruits and vegetables, and 29/51 (0.57) inanimate objects. Once again, animals caused more difficulty than fruits and vegetables ($\chi^2 = 23.632$; $p < 0.001$) and artifacts ($\chi^2 = 18.018$; $p < 0.001$).

In a third color attribution task, P.C.O. was asked to name a picture, and then to produce its canonical color. She provided the correct color name for 27/40 (0.67) pictures she named correctly, but did so for only 5/28 (0.18) pictures she failed to name correctly ($\chi^2 = 14.361$; $p < 0.001$). This result indicates a correlation between naming performance and object color knowledge, as was the case for patients G.G. and A.V. (ref. 16).

Subject I.O.C. performed two object-color verification tasks. In the visual/auditory task, the examiner presented a black-and-white drawing of an object (for example, a banana), while naming a color that was correct (yellow), related (orange) or unrelated (purple) to the target. In the visual/visual task, the examiner presented the colored drawing of an object. The color could be correct (a green frog), related (a yellow frog) or unrelated (a blue frog). In both cases, the subject's task was to say whether the color was appropriate for the picture. I.O.C. responded correctly on only 80/114 (0.70) and 130/174 (0.75) of the trials in the visual/auditory and in the visual/visual task, respectively ($\chi^2 = 0.507$, NS).

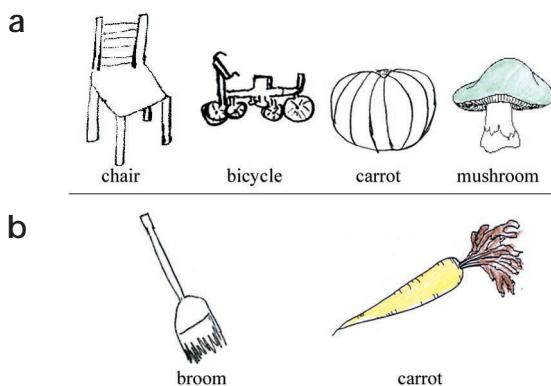


Fig. 1. Examples of the drawing and object-coloring performance of patients P.C.O. and I.O.C. In the drawing task, P.C.O. (a) produced correct responses (chair), distortions of the target response (bicycle), semantic substitutions (carrot), or unrecognizable drawings. I.O.C. (b) produced correct depictions (broom) or complete omissions. In the coloring task, both subjects colored common objects incorrectly.



I.O.C. performed poorly in three variants of an object-color attribution task. She was presented with black-and-white drawings of objects or with object names, and had to color the drawings or to name the canonical colors of the objects. She correctly colored only 16/38 (0.42) pictures, and she correctly produced the canonical color names for 20/38 (0.52) black and white pictures and for 25/38 (0.66) orally named objects. I.O.C. also performed poorly on a version of these tasks (with a new set of items) that was designed to compare the effects of semantic category. She was significantly more accurate with natural objects (41/54, 0.76) than with man-made objects (22/54, 0.41; $\chi^2 = 12.343$; $p < 0.001$). Overall, she produced 63/108 (0.58) correct responses, as compared to an average performance of 97% correct by three matched control subjects.

To evaluate the relationship between naming ability and object color knowledge, I.O.C. was asked to color 21 black-and-white line drawings by selecting an appropriate crayon from an array of 24 (Fig. 1). Her performance was again very poor (7/21 correct). After coloring the drawing, she was asked to name it. I.O.C. correctly named 13/21 (0.62) objects. She colored equally poorly objects she named correctly (4/13, 0.31) and objects she failed to name (3/8, 0.37; $\chi^2 = 0.025$; NS). I.O.C. was significantly less accurate than P.C.O. in coloring correctly named objects ($\chi^2 = 4.044$; $p < 0.05$) but did not differ from P.C.O. when coloring objects she could not name ($\chi^2 = 0.485$; $p = \text{NS}$). Unlike P.C.O. (and G.G. and A.V.¹⁶), there was no correlation between I.O.C.'s performance on object coloring and object naming (Table 2).

Knowledge of color and other properties of objects

The results reported so far demonstrate that P.C.O. and I.O.C., like G.G., A.V.¹⁶ and R.M.¹⁷, exhibit loss of object color knowledge, but spared color perception, recognition and naming. We now present their performance in tasks that explored the status of other types of knowledge about objects. With the exception of drawing tasks, all the tasks reported on here required a yes/no decision or a selection between two alternatives. Hence, chance responding would yield a 0.50 hit rate.

Subject P.C.O. scored 80/128 (0.62) correct in an object decision task²¹, indicating a severe deficit in recognizing the forms of objects. In a task in which she had to say which of two similar-sized objects was bigger, she was equally impaired with animals (45/60 correct, 0.75) and artifacts (46/60, 0.77).

P.C.O. performed just as poorly in other tasks that required her to decide whether named animals and artifacts had specific properties. Questions probed knowledge of color, other perceptual properties (form, size, material) and non-perceptual properties (category membership, function, environment, encyclopedic knowledge). For example, P.C.O. was asked the following questions: "Is a lemon yellow?", "Is a baseball square?" and "Is a pencil made of glass?" Collapsing across categories (animals and artifacts), she responded correctly to 25/38 (0.66) questions about color, 156/214 (0.73) questions about other perceptual properties and 205/320 (0.64) questions about non-visual properties ($\chi^2 = 4.615$; $df = 2$; NS). Collapsing across properties, P.C.O. produced significantly fewer correct responses to questions about animals (156/240, 0.65) than to questions about artifacts (230/276,

Table 2. Correct responses produced in tasks that required the ability to process object color knowledge.

Subject P.C.O.	Animals	Plant life	Inanimate	Total
Color verification	6/23 (0.26)	18/29 (0.62)	21/28 (0.75)	45/80 (0.56)
Color attribution	2/29 (0.07)	24/34 (0.71)	29/51 (0.57)	56/115 (0.49)
Subject I.O.C.				
Color verification	Correct	Related	Unrelated	Total
Visual/Auditory	28/38 (0.74)	16/38 (0.42)	36/38 (0.95)	80/114 (0.70)
Visual/Visual	33/58 (0.57)	43/58 (0.74)	54/58 (0.93)	130/174 (0.75)
Visual/Visual (normal control)	54/58 (0.93)	56/58 (0.97)	56/58 (0.97)	165/174 (0.95)
	Natural objects	Man-made objects		Total
Color attribution	41/54 (0.76)	22/54 (0.41)		63/108 (0.58)
Control's average (<i>n</i> = 3)	18/18 (1.00)	17/18 (0.94)		35/36 (0.97)
Subject S.L.A.				
	Animals	Plant life	Inanimate	Total
Color verification	29/29 (1.00)	28/29 (0.97)	28/28 (1.00)	79/80 (0.99)
Color attribution	29/29 (1.00)	34/34 (1.00)	51/51 (1.00)	115/115 (1.00)

Percentages are in parentheses.

0.83; $\chi^2 = 21.932$; $p < 0.001$). This difference was significant for each of the three attribute types ($0.001 < p < 0.025$).

P.C.O. was also impaired in a physical attribute task that tapped knowledge of size, color, texture and presence/absence of legs for animals and artifacts ("Which is red, a tomato or a tangerine?" "Which is shorter, a pig or a horse?" "Which has legs, a cat or a trout?"). She responded correctly to 70/84 (0.83) animals and 73/84 (0.87) artifacts. For both categories, she was significantly less accurate with color (15/24, 0.62) than with other physical properties (128/144, 0.89; $\chi^2 = 9.322$; $p < 0.001$).

Finally, P.C.O. was asked to draw 128 objects named by the examiner. Two independent judges, blind to the goal of the study, scored her responses; disagreements were resolved by a third judge. Using these criteria, 40 (0.31) responses were scored as correct, 10 (0.08) as semantic errors (drawing a kettle for a funnel), and 78 (0.61) as uninterpretable. The latter drawings typically lacked details crucial for distinguishing among items of the same category (Fig. 1).

This subject demonstrated widespread damage to semantic properties of objects, regardless of whether they were living or nonliving things and regardless of whether the knowledge that was assessed concerned perceptual or functional properties.

Subject I.O.C. was given an object decision task that contained equal numbers of real animals, chimeric animals, real artifacts and chimeric artifacts (*n* = 30 for each). Her response accuracy (114/120, or 0.95) compared favorably with the average performance (87% correct) for a group of normal aged controls²². She also responded correctly to 54/60 (0.90) items in the size judgment task (a normal control scored 58/60 correct; $\chi^2 = 1.205$; NS). I.O.C. completed property judgment and physical attribute tasks identical in structure to the ones used with P.C.O., except that questions about object color were not included. She was comparably accurate in property judgments with questions about visual form (113/121, 0.93) and non-visual attributes (130/142, 0.96). Three control subjects responded correctly on average to 118/121 (0.98) visual and to 125/142 (0.88) non-visual properties. In the physical attribute task, I.O.C. provided the correct response to 65/67 (0.97) stimuli.

Table 3. Performance obtained by P.C.O., I.O.C. and S.L.A. and normal controls on tasks tapping knowledge of stored properties of objects.

	P.C.O.	I.O.C.	S.L.A.	Normal subjects
Reality judgments	80/128 (0.63)	114/120 (0.95)	121/128 (0.95)	104/120 (0.87)
Judgments of stored properties				
Size judgments	91/120 (0.76)	54/60 (0.90)	120/120 (1.00)	58/60 (0.97)
Property judgments				
Color	25/38 (0.66)	N/A	38/38 (1.00)	N/A
Visual (form, size, texture, etc.)	156/214 (0.73)	113/121 (0.93)	205/214 (0.96)	118/121 (0.98)
Non-visual (category, function, etc.)	205/320 (0.64)	130/142 (0.96)	315/320 (0.98)	125/142 (0.88)
Physical attributes	141/168 (0.84)	65/67 (0.90)	168/168 (1.00)	N/A
Perceptual properties	N/A	208/236 (0.88)	N/A	200/236 (0.85)

Same numbers of items denote administration of the same task to different subjects. Percentages are in parentheses. N/A, not administered.

In another perceptual property judgment task tapping various modalities (for example, table: "Does it have a flat surface? Is it soft to touch?"), I.O.C. produced 208/236 correct responses (0.88)—a level of performance similar to that of three matched control subjects (85% correct).

In a drawing task, I.O.C. produced clearly recognizable drawings for 27/32 named objects (0.84). The only errors were instances in which she failed to produce any response at all (for example, padlock: "I don't know what a padlock is"; rolling pin: "I can see it, but I cannot draw it"; Fig. 1).

Overall, I.O.C.'s results demonstrate that object color knowledge can be damaged in the context of remarkably spared knowledge of other perceptual and functional properties of object representation (Table 3).

DISCUSSION

Subjects P.C.O. and I.O.C. were unable to say whether a named color or a color patch was the appropriate color for an object, to produce the correct color name for an object or to select the appropriate crayon or pencil to color it, despite essentially normal ability to arrange color patches by hue and to recognize and name

color probes. This rarely documented pattern confirms previous reports^{16,17} and complements the observed sparing of object color knowledge in achromatopsia^{9,11}. Taken together with PET studies showing that distinct neural structures are active in perceiving color and retrieving object color knowledge^{5,7}, these neuropsychological observations demonstrate that the perception, recognition and naming of color are dissociable from access to object color knowledge.

In previous reports^{16,17}, damage to object color knowledge was found to co-occur with damage to other stored properties of objects. A.V. and G.G. performed poorly on object decision and object

drawing tasks; this pattern suggests damage to object form knowledge. P.C.O. exhibited a similar pattern of impairment; although she was most severely impaired in tasks that probed object color knowledge, she also performed quite poorly with other properties of objects, including object form, size, texture and functional information (environment, use, encyclopedic knowledge). Because several kinds of properties of objects are impaired along with color in these cases, it is impossible to determine whether object color knowledge is subject to selective damage—and, by extension, whether it is functionally and anatomically distinct from other knowledge about objects. In other words, the failure of patients like P.C.O., A.V. and G.G. may be a consequence of general damage to structures that underlie conceptual knowledge, rather than specific damage to areas involved in retrieving the canonical colors of objects.

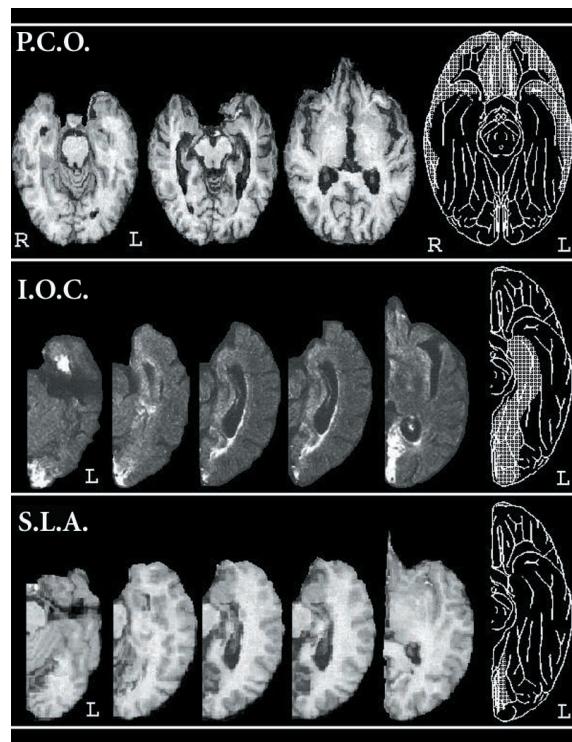


Fig. 2. Representative axial MRI sections and schematic representation of mesial temporal and temporo-occipital damage for the three subjects. Sulcal patterns were used as landmarks to locate and reconstruct each lesion³⁷. Subject P.C.O. (T1-weighted image) presents with diffuse atrophy and several patchy lesions, mostly involving the white matter contiguous to the cortex, in both hemispheres. Lesions are more extensive in the left than in the right hemisphere, and are essentially symmetrical. There is extensive involvement of the temporal pole and of the inferolateral temporal regions (that is, middle and inferior temporal gyri), of the pre-frontal convexity, and of the anterior, medial and lateral orbital gyri. Damage is less extensive in the parietal lobe and in the superior-rostral insula; both hippocampi are atrophic. No lesions could be detected in the mesial temporal gyri. Subjects I.O.C. (FLAIR image; middle), and S.L.A. (T1-weighted image; bottom) exhibit lesions restricted to the left temporal and occipital lobes and left hippocampal atrophy. In I.O.C., the lesion includes the calcarine cortex, the lingual gyrus, the isthmus and a small portion of the adjacent posterior cingulate gyrus, the parahippocampal gyrus and the rostro-medial portion of the fusiform gyrus, including also part of the ventral portion of the temporal pole. Damage is less extensive in S.L.A., whose lesion involves the lingual gyrus (except for its rostral-ventral portion), and the rostral section of the cuneus, up to the inferior sagittal sulcus. It includes the caudal bank of the parieto-occipital fissure and continues into the anterior calcarine sulcus. The left posterior forceps major of the corpus callosum is also partly damaged.



A distinctly different pattern of performance was obtained for I.O.C., who is severely impaired in accessing object color knowledge, in spite of essentially spared access to other perceptual and functional knowledge. This profile supports the notion that object color and other stored properties of objects are represented autonomously. It also invites the conclusion that the co-occurrence of deficits documented in previous cases is not functionally determined and may result from damage to contiguous neural structures involved in processing object color and form.

The dissociation of object color from object form knowledge in I.O.C. nicely complements the observation of achromatopsia with spared perception of form¹⁰. Furthermore, when these cases are taken together with reports of partial sparing of color perception associated with complete loss of form perception¹², they suggest that color and form processing are autonomous at all levels of representation. The patterns of performance documented in our subjects allow plausible inferences about the neural basis of color and object color knowledge.

We may first conclude that the mesial temporal structures of the left hemisphere are specifically involved in representing or accessing object color knowledge. The region putatively involved would include the ventral-rostral portions of the lingual gyrus, the rostro-medial aspect of the fusiform gyrus, the isthmus and the parahippocampal gyrus. (It is possible that only some of these areas will prove to be crucial for object color knowledge.) These structures were impaired in I.O.C., but spared in S.L.A., who did not exhibit cognitive damage. In the light of previous neuroimaging studies of object color knowledge^{5,18}, it is interesting to observe that the left inferolateral temporal region was intact in I.O.C., whereas it was lesioned in P.C.O., who suffers from a widespread conceptual deficit. Consistent with neuroimaging studies of semantic processing²³, these observations suggest that the left inferotemporal cortex might represent conceptual information, and not specifically object color information. Another conclusion afforded by our data is that the computations underlying color recognition and color naming are implemented bilaterally in the fusiform and lingual gyrus, probably by portions of these lobes located rostrally to those activated by color perception⁶. This possibility is suggested by the observation that in subjects with damaged object color knowledge and spared naming and recognition of color probes, these structures were intact in the right hemisphere (I.O.C., R.M.¹⁷ and possibly G.G.¹⁶) or bilaterally (P.C.O. and possibly A.V.¹⁶).

The observation that access to object color knowledge can be damaged independently of access to object form knowledge is consistent with those theories of the organization of conceptual knowledge that assume that such knowledge is distributed across various 'modality'-specific systems, such as visual, auditory, motor, functional and verbal systems^{24,25}. However, consideration of other aspects of our subjects' performance and various results on category-specific semantic deficits²⁶ provide little support for a strictly modality-specific organization of conceptual knowledge.

There is now ample evidence that the categories of animals, fruits and vegetables, and artifacts can each be damaged independently of the others^{26,27}. To account for these dissociations, modality-specific theories of conceptual knowledge have assumed that visual properties are crucial for the representation of living things and that functional attributes are particularly important for the representation of artifacts. Thus, damage to the visual semantic subsystem should result in disproportionate damage to the living things category. Furthermore, selective damage to color knowledge would be expected to disproportionately affect the recognition and naming of fruits, vegetables and flowers, because

these kinds of objects share many structural properties and are differentiated primarily by color^{25,28}.

These expectations have not been borne out by empirical observation. A selective deficit in processing living things is not always associated with disproportionate difficulty in processing their visual attributes^{22,29-32}. Moreover, there are reports of subjects who are selectively impaired in processing the visual attributes of objects, but who are not also disproportionately impaired in processing living things^{30,33}. More importantly in the present context, I.O.C., who is selectively impaired in accessing object color knowledge, does not exhibit selective difficulties in processing fruits and vegetables, or animals³⁴.

How do we reconcile the findings that access to object color knowledge can be damaged independently of access to other object properties and that particular semantic categories can each be damaged or spared selectively? Here we consider one speculative possibility. Suppose that conceptual information is organized into broad semantic domains (conspecifics, animals, plant life and perhaps tools), each subserved by distinct neural networks²². According to this view, domain-specific conceptual representations are distinct from domain-general, modality-specific perceptual representations. The latter representations are organized into modality-specific systems, which have the function of 'grounding' modality-independent representations stored in the conceptual system^{35,36}; one of these modality-specific systems is specialized for color. Thus, I.O.C. would represent a case of disconnection between the modality-specific color knowledge system and the domain-specific systems of conceptual knowledge.

Regardless of which functional architecture of the conceptual system will ultimately prove most satisfactory in accounting for the patterns of semantic category-specific deficits, the results obtained with I.O.C. clearly establish that information about object form knowledge is dissociable from object color knowledge. Furthermore, the data we report here suggest that semantic information about the perceptual properties of objects must be grounded in modality-specific neural systems. The system that subserves the representation of color knowledge would seem to require the integrity of mesial temporal regions of the left hemisphere.

METHODS

Subjects. Subjects P.C.O. and S.L.A. were native speakers of Italian; subject I.O.C. was a native American-English speaker. Tasks differed for the three subjects in the number of items, but were otherwise identical or very similar in structure. S.L.A. served as a control for P.C.O.; normal subjects were used as controls for I.O.C. For all subjects, lesion reconstruction was based on a sulcal brain map³⁷.

Subject P.C.O., a 30-year-old woman with a university degree, was tested 9 months after onset of a probable encephalitis of undiagnosed nature. Ambidextrous for most everyday activities, she writes with her right hand. No elementary motor, sensory, visual or auditory deficits were detected (MRI results, Fig. 2, top).

P.C.O. scored within the normal range on visuo-spatial and praxis tasks and on Raven's Colored Progressive Matrices. Short-term verbal memory was reduced. Speech was fluent and grammatically correct. Language evaluation³⁸ showed spared grammatical abilities and severe lexical-semantic damage that was more pronounced for nouns than for verbs. In an auditory word-picture verification task (chance accuracy, 0.50), P.C.O. responded correctly to 27/46 (0.54) natural objects, 127/183 (0.69) inanimate objects and 26/30 (0.87) body parts. Performance was significantly poorer on natural objects than on body parts ($\chi^2 = 5.471$; $df = 1$; $p < 0.025$). In picture naming, P.C.O. produced correct responses to 21/98 (0.21) natural objects, 61/118 (0.52) inanimate objects and 26/42 (0.62) body parts. Performance was significantly less accurate for natural kinds than for either inanimate objects ($\chi^2 = 19.559$; $p < 0.001$) or body parts ($\chi^2 = 19.822$; $p < 0.001$).



Subject I.O.C. (for details, see ref. 34), a right-handed 56-year-old with two years of college education, suffered a stroke in the left posterior or cerebral artery territory (Fig. 2, middle). Neurological examination revealed mild left hemiparesis. I.O.C. has lost vision in her left eye and has only foveal vision in her right eye.

In the previous report, a severe anomia was demonstrated for all noun categories except body parts, in the presence of largely spared comprehension. In a difficult comprehension task, I.O.C. performed roughly equally for animals (0.63), fruits and vegetables (0.75) and artifacts (0.69) (chance performance, 0.50 correct). This subject is a letter-by-letter reader.

Subject S.L.A., a right-handed 28-year old with a university degree, was tested 6 months after onset of a left posterior cerebral artery ischemia (Fig. 2, bottom), resulting in a right homonymous hemianopia. She completed the same language examination³⁸ and experimental tasks administered to P.C.O. She showed no cognitive deficits, except for a very mildly reduced ability to learn word lists.

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1. Cavanagh, P. *et al.* Complete sparing of high-contrast color input to motion perception in cortical color blindness. *Nat. Neurosci.* **1**, 242–247 (1998).
2. Heywood, C. A., Wilson, B. & Cowey, A. A case study of cortical colour "blindness" with relatively intact achromatic discrimination. *J. Neurol. Neurosurg. Psychiatry* **50**, 22–29 (1987).
3. Meadows, J.C. Disturbed perception of colour associated with localized cerebral lesions. *Brain* **97**, 615–632 (1974).
4. Zeki, S. A century of cerebral achromatopsia. *Brain* **113**, 1721–1777 (1990).
5. Chao, L. I. & Martin, A. Cortical regions associated with perceiving, naming and knowing about colors. *J. Cogn. Neurosci.* **11**, 25–35 (1999).
6. McKeefry, D. & Zeki, S. The position and topography of the human colour centre as revealed by functional magnetic resonance imaging. *Brain* **120**, 2229–2242 (1997).
7. Zeki, S. & Marini, L. Three cortical stages of color processing in the human brain. *Brain* **121**, 1669–1685 (1998).
8. Martin, A., Ungerleider, L. G. & Haxby, J. V. in *The New Cognitive Neurosciences* (ed. Gazzaniga, M.) 1023–1036 (MIT Press, Cambridge, Massachusetts, 2000).
9. Bartolomeo, P., Bachoud-Lévi, A.-C. & Denes, G. Preserved imagery for colours in a patient with cerebral achromatopsia. *Cortex* **33**, 369–378 (1977).
10. Bartolomeo, P. *et al.* Multiple-domain dissociation between impaired visual perception and preserved visual imagery in a patient with bilateral extrastriate lesions. *Neuropsychologia* **36**, 239–249 (1998).
11. Shuren, B. J., Brott, T. G., Scheft, B. K. & Houston, W. Preserved color imagery in an achromatopsic. *Neuropsychologia* **34**, 485–489 (1996).
12. Zeki, S., Aglioti, S., McKeefry, D. & Berlucchi, G. The neurological basis of conscious color perception in a blind patient. *Proc. Natl. Acad. Sci. USA* **96**, 14124–14129 (1999).
13. Cowey, A. & Heywood, C. A. There's more to colour than meets the eye. *Behav. Brain Res.* **71**, 89–100 (1995).
14. Hadjikani, N., Liu, A. K., Dale, A. M., Cavanagh, P. & Tootell, R. B. H. Retinotopy and color sensitivity in human visual cortical area V8. *Nat. Neurosci.* **1**, 235–241 (1998).
15. Davidoff, J. & Fodor, G. An annotated translation of Lewandowsky (1908) "Disconnection of the colour sense by focal disease of the brain." *Cognit. Neuropsychol.* **6**, 165–178 (1989).
16. Luzzatti, C. & Davidoff, J. Impaired retrieval of object-color knowledge with preserved color naming. *Neuropsychologia* **32**, 933–950 (1994).
17. Farah, M. J., Levine, D. N. & Calvano, R. A case study of mental imagery deficit. *Brain Cogn.* **8**, 147–164 (1988).
18. Martin, A., Haxby, J. V., Lalonde, F. M., Wiggs, C. L. & Ungerleider, L. G. Discrete cortical regions associated with knowledge of color and knowledge of action. *Science* **270**, 102–105 (1995).
19. Farnsworth, D. Farnsworth dichotomous test for colour-blindness. (Psychological Corporation, New York, 1947).
20. Ishihara, S. *Tests for Colour-Blindness* (Kanehara Shup, Tokyo, 1974).
21. Riddoch, M. J. & Humphreys, G. W. *BORB (Birmingham Object Recognition Battery)* (Lawrence Erlbaum Associates, Hove, UK, 1993).
22. Caramazza, A. & Shelton, J. R. Domain-specific knowledge systems in the brain: the animate-inanimate distinction. *J. Cogn. Neurosci.* **10**, 1–34 (1998).
23. Vandenberghe, R., Price, C. J., Wise, R., Josephs, O. & Frackowiak, R. S. J. Semantic system(s) for words or pictures: functional anatomy. *Nature* **383**, 254–256 (1996).
24. Allport, D. A. in *Current Perspectives in Dysphasia* (eds. Newman, S.K. & Epstein, R.) 207–244 (Churchill Livingstone, Edinburgh, 1985).
25. Warrington, E. K. & McCarthy, R. Categories of knowledge: further fractionations and an attempted integration. *Brain* **110**, 1273–1296 (1987).
26. Caramazza, A. The interpretation of semantic category-specific deficits: what do they reveal about the organization of conceptual knowledge in the brain? *Neurocase* **4**, 265–272 (1998).
27. Forde, E. M. E. & Humphreys, G. W. Category-specific recognition impairments: a review of important case studies and influential theories. *Aphasiology* **13**, 169–193 (1999).
28. Humphreys, G. W. & Forde, E. M. E. Hierarchies, similarity and interactivity in object recognition: on the multiplicity of 'category-specific' deficits in neuropsychological populations. *Brain Behav. Sci.* (in press).
29. Laiacona, M., Barbarotto, R. & Capitani, E. Perceptual and associative knowledge in category specific impairment of semantic memory: a study of two cases. *Cortex* **29**, 727–740 (1993).
30. Lambon Ralph, M. A., Howard, D., Nightingale, G. & Ellis, A. W. Are living and non-living category-specific deficits causally linked to impaired perceptual or associative knowledge? Evidence from a category-specific double dissociation. *Neurocase* **4**, 311–338 (1998).
31. Moss, H. E., Tyler, L. K., Durrant-Peatfield, M. & Bunn, E. M. Two eyes of a see-through: impaired and intact semantic knowledge in a case of selective deficit for living things. *Neurocase* **4**, 291–310 (1998).
32. Samson, D., Pillon, A. & De Wilde, V. Impaired knowledge of visual and non-visual attributes in a patient with a semantic impairment for living entities: a case of a true category-specific deficit. *Neurocase* **4**, 273–290 (1998).
33. Coltheart, M. *et al.* A semantic subsystem specific to the storage of information about the visual attributes of animate and inanimate objects. *Neurocase* **4**, 353–370 (1998).
34. Shelton, J. R., Fouch E. & Caramazza, A. The selective sparing of body part knowledge: a case study. *Neurocase* **4**, 339–352 (1998).
35. Jackendoff, R. On beyond zebra: the relation of linguistic and visual information. *Cognition* **26**, 89–114 (1987).
36. Miller, G. A. & Johnson-Laird, P. N. *Language and Perception* (Harvard Univ. Press, Cambridge, Massachusetts, 1976).
37. Economo, C. & Koskinas, G. N. *Die cytoarchitektonik der hirnrinde des erwachsenen menschen* (Springer, Wien, 1925).
38. Miceli, G., Laudanna, A., Burani, C. & Capasso, R. *Batteria per l'analisi dei deficit afasici* (CEPSAG, Roma, 1994).