

A Review of Functional Imaging Studies on Category Specificity

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Abstract

■ A review of 20 functional imaging studies that compared visual processing of natural objects and artifacts in normal subjects is presented. The studies included fulfilled three criteria: (i) they used pictures as stimuli, (ii) they were based on direct contrasts between categories, and (iii) they reported findings in Talairach space. Not a single area is consistently activated for a given category across all studies. In contrast, 11 out of 29 regions are reported activated by both artifacts and natural objects. It is argued that the inconsistency is unlikely to reflect differences between studies in task re-

quirements alone. Rather, the most likely causes of the inconsistency are: (i) adoption of liberal statistical thresholds that may yield false-positive activations, (ii) limited sensitivity due to few observations, and (iii) failure to match categories on confounding variables such as familiarity and visual complexity. Of the most consistent activations found, none appear to be selective for natural objects or artifacts. The findings reviewed are compatible with theories of category specificity that assume a widely distributed conceptual system not organized by category. ■

INTRODUCTION

Some of the more remarkable impairments that can follow brain damage are the selective disturbances in the ability to recognize or comprehend certain categories of objects but not others; the so-called category-specific disorders. Usually, these disorders affect the recognition or comprehension of natural objects (e.g., animals and plants), whereas the recognition or comprehension of artifacts (e.g., furniture and kitchen utensils) is relatively preserved. Although more infrequent, the reverse pattern is also on record (for reviews, see Capitani, Laiacina, Mahon, & Caramazza, 2003; Humphreys & Forde, 2001; Gainotti, 2000; Caramazza & Shelton, 1998). This suggests that natural objects and artifacts may be processed differently in the brain.

Numerous patients with category-specific disorders have been reported since the seminal descriptions by Warrington and Shallice (1984) and Warrington and McCarthy (1983), but the explanations of these deficits remain controversial (Caramazza & Mahon, 2006; Laws, 2005) as do their neural causes (Tyler et al., 2003). There are at least two reasons for this: (i) category-specific disorders can occur as a consequence of disturbance at different functional levels (structural, semantic, lexical), which make them rather heterogenous (Rosazza et al., 2003; Humphreys & Forde, 2001), and (ii) the cerebral damage associated with the disorders seldom conforms

to functionally homogenous anatomical systems, which make theoretical interpretations based on lesion analysis complicated (for a recent attempt, see Gainotti, 2002).

The explanations advanced to account for category-specific disorders can be grouped into three general classes (Caramazza & Mahon, 2003): the sensory/functional account, the correlated-feature account, and the domain-specific account. A comprehensive discussion and evaluation of these accounts, which would require extensive review of studies with both patients and normal subjects, is beyond the scope of this article. Instead, the focus will be on relevant evidence from functional imaging studies with normal subjects (positron emission tomography and functional magnetic resonance imaging). Evidence from this source has become increasingly prevalent in the discussion of category specificity in recent years. Nevertheless, there are few reviews focusing on functional imaging and category specificity and the three reviews which have been published so far included studies on both word and picture processing (Devlin, Russell, et al., 2002; Price & Friston, 2002; Joseph, 2001) as well as face processing (Joseph, 2001). Because word and picture processing may yield different effects of category, this mixture of studies may have contributed to the lack of consistency observed in these reviews.

The main objective of this article is to assess the degree of consistency for functional imaging studies examining category specificity in normal subjects when the comparison is limited to studies of picture processing. Secondly, it will be evaluated whether the three

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general accounts of category specificity mentioned are consistent with the findings reported. Although the present study is narrower in scope than previous ones, it provides an up-to-date review, as 12 of the 20 studies included were not considered in any of the previous reviews.

METHODS

Criteria for Inclusion

The present review is not an exhaustive review of all functional imaging studies on category specificity. In order to make comparisons across studies sensible, studies to be included had to fulfill three criteria:

1. The stimuli should be pictures and pictures only. Studies in which no separate analysis is given for pictures (e.g., Devlin, Moore, et al., 2002) or in which pictures and words were presented simultaneously (e.g., Rogers, Hocking, Mechelli, Patterson, & Price, 2005; Moore & Price, 1999: Experiment 2) were not included. The rationale behind this criterion is that processing of words and pictures may give rise to different effects of category or different magnitudes of category effects which make comparisons across modalities complicated. For example, Price, Noppeney, Phillips, and Devlin (2003) reported that category effects in the posterior fusiform gyri were present for pictures but not for words¹ (see also Noppeney, Price, Penny, & Friston, 2006). Similarly, in reaction time studies, classification of pictures as either “natural” or “manmade” is typically faster for natural objects compared with artifacts (Kiefer, 2001; Price & Humphreys, 1989), whereas the same effect for words is more modest (Riddoch & Humphreys, 1987). Indeed, category effects that are present during picture processing may be heavily influenced if words are also presented in the task (Låg, 2005).

2. The studies should be based on direct comparisons of natural objects and artifacts. Hence, studies where natural objects and artifacts were compared with something other than stimuli from the opposite category (e.g., faces or fractals) were excluded (e.g., Grabowski, Damasio, & Damasio, 1998²). The reason for this criterion is that activations which are not based on direct comparisons between natural objects and artifacts cannot be assumed to be specific to these categories. Differences that seem to be present when one compares each category with a common (noncategorical) baseline task (indirect comparisons) could turn out not to be significantly different if the categories are compared directly.

3. In order to be anatomically comparable, the studies should report activations in Talairach space³ (Talairach & Tournoux, 1988). Only one study did not fulfill this criterion (Spitzer, Kwong, Kennedy, Rosen, & Belliveau, 1995). It should be noted that studies are not necessarily directly comparable just because they report

Talairach coordinates. For instance, the standard brain used in SPM95 and SPM96 differs considerably in size, making direct comparison between coordinates impossible. As most studies included in the present review reported coordinates on the basis of the MNI-SPM96 implementation (Friston et al., 1995) of the stereotatic atlas of Talairach and Tournoux (1988), the coordinates reported in Table 1 are all MNI-Talairach coordinates. Studies that reported coordinates on the basis of Talairach and Tournoux were adjusted to MNI-Talairach coordinates using the procedure described by Matthew Brett (URL: <http://www.mrc-cbu.cam.ac.uk/Imaging/mnispac.html>). This was the case for the studies reported by Damasio, Tranel, Grabowski, Adolphs, and Damasio, (2004), Whatmough, Chertkow, Murtha, and Hanratty (2002), Smith et al. (2001), and Martin, Wiggs, Ungerleider, and Haxby (1996).

Based on these criteria, 20 studies were identified: Gerlach, Law, and Paulson (2006), Mechelli, Sartori, Orlandi, and Price (2006), Moss, Rodd, Stamatakis, Bright, and Tyler (2005), Damasio et al. (2004), Gerlach, Law, and Paulson (2004), Tyler et al. (2003), Chao, Weisberg, and Martin (2002), Gerlach, Aaside, et al. (2002), Whatmough et al. (2002), Smith et al. (2001), Okada et al. (2000), Chao and Martin (2000), Gerlach, Law, Gade, and Paulson (2000), Gorno-Tempini, Cipolotti, and Price (2000), Chao, Haxby, and Martin (1999), Gerlach, Law, Gade, and Paulson (1999), Moore and Price (1999), Perani et al. (1999), Martin et al. (1996) and Gerlach (Appendix A).⁴ The results of the studies are summarized in Table 1 and displayed graphically in Figure 1. Additional information regarding the studies, such as number of subjects scanned, and so forth, can be found in Appendix B.

Explanatory Comments to Table 1

One hundred twenty-three individual peaks were reported in the 20 studies. To make an overview possible, only one peak coordinate is listed for a given region across studies. This coordinate represents the mean of the peak coordinates reported in all studies where activation was found within a given region (the region being one of 29 regions listed in Table 1). The coordinates listed in Table 1 therefore represent gross estimates. This procedure was found sufficient for the present purpose as it increased the chances of finding commonalities across studies. It also eliminated the problem of what to do with studies where more than one peak is reported for a given region. In the case that two or more peaks are found for a given comparison in a given study, they were simply entered as individual data points for that region when the mean was computed. Although this procedure arguably does lead to gross estimates of location, it is not clear whether a more precise specification can in fact be obtained given that the studies vary considerably in the significance threshold

Table 1.

	<i>L. Anterior Cingulate (BA 24/32)</i>	<i>R. Anterior Cingulate (BA 24/32)</i>	<i>L. Dorsolateral Frontal (BA 6/44/45)</i>	<i>L. Inferior Frontal (BA 45/46/47)</i>	<i>R. Inferior Frontal (BA 45/46/47)</i>	<i>L. Middle Frontal (BA 11)</i>	<i>L. Superior Temporal (BA 22)</i>
	$x = -6 (-12/-4),$ $y = 35 (52/16),$ $z = 19(38/0)$	$x = 6 (3/8),$ $y = 3 (22/-16),$ $z = 44 (47/40)$	$x = -48 (-64/-44),$ $y = 5 (9/-1),$ $z = 22(32/8)$	$x = -49 (-58/-41),$ $y = 26 (36/13),$ $z = 5 (16/-12)$	$x = 37 (36/37),$ $y = 20 (22/10),$ $z = -12 (-12/-11)$	$x = -35 (-44/-30),$ $y = 45 (52/38),$ $z = -19(-18/-20)$	$x = -43 (-43/-42),$ $y = -61 (-59/-63),$ $z = 14(19/8)$
Chao et al. (1999)	-	-	-	-	-	-	T > A
Chao & Martin (2000)	//	//	T > A	?	-	-	?
Chao et al. (2002)	//	//	T > A	//	//	//	//
Damasio et al. (2004)	//	//	//	//	//	//	//
Martin et al. (1996)	T > A	//	T > A	//	//	//	//
Okada et al. (2000)	//	//	//	T > A	//	//	//
Perani et al. (1999)	//	//	T > A	//	//	//	//
Whatmough et al. (2002)	T > A	T > A	//	//	//	//	//
Gerlach et al. (1999)	//	//	//	//	//	//	//
Gerlach et al. (2000)	M > N	//	M > N	M > N	//	M > N	//
Gerlach et al. (2002a)	//	//	//	//	//	//	//
Gerlach et al. (2004)	-	-	-	-	-	-	-
Gerlach et al. (2006)	-	-	-	-	//	-	-
Gerlach (Appendix A)	N > M	N > M	//	//	N > M	//	//
Gorno-Tempini et al. (2000)	//	//	//	//	//	//	//
Mechelli et al. (2006)	//	//	//	//	//	//	//
Moore & Price (1999)	//	//	//	//	//	//	//
Moss et al. (2005)	//	//	//	//	//	//	//
Smith et al. (2001)	//	//	//	N > M	N > M	//	//
Tyler et al. (2003)	//	//	//	//	//	//	//
Total	4/17: 3M/1N	2/17: 1M/1N	5/17: 5M	3/16: 2M/1N	2/17: 2N	1/16: 1M	1/17: 1M

Table 1. (continued)

	<i>R. Superior Temporal</i> (BA 22)	<i>L. Middle Temporal</i> (BA 21)	<i>R. Middle Temporal</i> (BA 21)	<i>L. Inferior Temporal</i> (BA 20)	<i>L. Inferior Parietal</i> (BA 40)	<i>R. Inferior Parietal</i> (BA 40)	<i>L. Anteromedial Temporal</i> (BA 28/34/38)
	$x = 50$ (43/57), $y = -50$ (-34/-61), $z = 17$ (22/12)	$x = -44$ (-47/-36), $y = -55$ (-52/-57), $z = 4$ (7/2)	$x = 49$ (40/60), $y = -56$ (-53/-62), $z = 4$ (6/10)	$x = -52$, $y = -16$, $z = -40$	$x = -36$ (-48/-30), $y = -41$ (-34/-47), $z = 47$ (56/42)	$x = 52$ (48/55), $y = -42$ (-31/-52), $z = 32$ (41/23)	$x = -17$ (-26/-10), $y = -1$ (5/-10), $z = -17$ (-13/-19)
Chao et al. (1999)	T > A	T > A	T > A	-	-	-	-
Chao & Martin (2000)	?	-	-	-	T > A	//	-
Chao et al. (2002)	T > A	T > A	//	//	T > A	//	//
Damasio et al. (2004)	//	//	//	//	//	T > A	//
Martin et al. (1996)	//	T > A	//	-	//	T > A	//
Okada et al. (2000)	//	//	//	//	T > A	//	//
Perani et al. (1999)	//	//	//	-	//	//	//
Whatmough et al. (2002)	//	//	//	//	//	//	//
Gerlach et al. (1999)	//	//	//	//	//	//	//
Gerlach et al. (2000)	//	//	//	M > N	//	//	//
Gerlach et al. (2002a)	//	//	//	//	//	//	//
Gerlach et al. (2004)	-	-	-	-	-	-	-
Gerlach et al. (2006)	-	//	//	//	-	-	//
Gerlach (Appendix A)	//	//	//	//	//	//	//
Gorno-Tempini et al. (2000)	//	//	//	//	//	//	//
Mechelli et al. (2006)	//	//	//	//	//	//	//
Moore & Price (1999)	//	//	N > M	//	//	//	N > M
Moss et al. (2005)	//	//	//	//	//	//	A > V & VF > T
Smith et al. (2001)	//	//	//	//	//	//	//
Tyler et al. (2003)	N > M	//	//	//	//	//	//
Total	3/17: 2M/1N	3/18: 3M	2/18: 1M/1N	1/15: 1M	3/17: 3M	2/17: 2M	2/17: 2N

Table 1. (continued)

	<i>R. Anteromedial Temporal (BA 28/34/38)</i>	<i>L. Lateral Fusiform (BA 37/20)</i>	<i>R. Lateral Fusiform (BA 37/20)</i>	<i>L. Medial Fusiform (BA 37/19)</i>	<i>R. Medial Fusiform (BA 37/19)</i>	<i>L. Lateral Occipital (BA 19)</i>	<i>R. Lateral Occipital (BA 19)</i>
	<i>x = 38, y = 12, z = -18</i>	<i>x = -40 (-50/-35), y = -55 (-42/-64), z = -16 (-8/-22)</i>	<i>x = 43 (36/56), y = -52 (-44/-59), z = -18 (-4/-24)</i>	<i>x = -25 (-28/-17), y = -54 (-47/-65), z = -13 (-5/-18)</i>	<i>x = 27 (22/32), y = -55 (-47/-65), z = -13 (-5/-19)</i>	<i>x = -38 (-46/-26), y = -80 (-68/-88), z = 7 (24/-4)</i>	<i>x = 46 (39/50), y = -75 (-68/-86), z = -3 (22/-15)</i>
Chao et al. (1999)	-	A > T	A > T	T > A	T > A	//	//
Chao & Martin (2000)	-	-	-	-	-	-	-
Chao et al. (2002)	//	A > T	A > T	T > A	T > A	A > T	A > T
Damasio et al. (2004)	//	A > T	A > T	//	//	A > T	//
Martin et al. (1996)	//	//	//	//	//	//	//
Okada et al. (2000)	//	T > A	A > T	//	//	T > A	A > T
Perani et al. (1999)	//	//	//	//	//	//	//
Whatmough et al. (2002)	//	//	A > T	T > A	T > A	//	//
Gerlach et al. (1999)	//	//	//	//	//	//	//
Gerlach et al. (2000)	//	N > M	//	//	//	//	//
Gerlach et al. (2002a)	//	//	N > M	//	//	//	//
Gerlach et al. (2004)	-	-	AC > A/AC > VF	-	//	-	AC > VF/A > VF
Gerlach et al. (2006)	//	//	//	//	//	//	//
Gerlach (Appendix A)	//	//	//	//	//	M > N	M > N
Gorno-Tempini et al. (2000)	//	//	//	//	//	//	//
Mechelli et al. (2006)	//	//	//	M > A	M > A	//	//
Moore & Price (1999)	N > M	//	//	//	//	//	//
Moss et al. (2005)	//	//	//	//	//	//	//
Smith et al. (2001)	//	//	N > M	//	//	//	N > M
Tyler et al. (2003)	//	//	//	//	//	//	//
Total	1/17: 1N	5/18: 4N/1M	8/19: 7N/1M	4/18: 4M	4/19: 4M	4/18: 2N/2M	5/19: 3N/2M

Table 1. (continued)

	<i>L. Medial Occipital (BA 17/18)</i>	<i>R. Medial Occipital (BA 17/18)</i>	<i>L. Inferior Occipital (BA 18/19)</i>	<i>R. Inferior Occipital (BA 18/19)</i>	<i>L. Calcarine (BA 17)</i>	<i>R. Calcarine (BA 17)</i>	<i>L. Cerebellum</i>	<i>R. Cerebellum</i>
	<i>x = -10 (-20/-5), y = -91 (-88/-97), z = -1 (14/-14)</i>	<i>x = 16 (21/12), y = -86 (-68/-92), z = -1 (1/-4)</i>	<i>x = -39 (-46/-30), y = -80 (-78/-82), z = -13 (-1/-32)</i>	<i>x = 41 (29/50), y = -80 (-73/-84), z = -7 (-1/-11)</i>	<i>x = -9 (-13/-4), y = -86 (-83/-88), z = 4</i>	<i>x = 19, y = -87, z = 5</i>	<i>x = -48, y = -64, z = -36</i>	<i>x = 25 (7/40), y = -54 (-42/-69), z = -22 (-16/-30)</i>
Chao et al. (1999)	A > T	A > T	A > T	A > T	//	//	-	-
Chao & Martin (2000)	-	-	-	-	-	-	-	-
Chao et al. (2002)	//	//	//	//	A > T	A > T	//	//
Damasio et al. (2004)	A > T	A > T	//	A > T	//	//	//	A > T
Martin et al. (1996)	//	//	//	//	A > T	//	-	-
Okada et al. (2000)	A > T	A > T	//	//	//	//	//	//
Perani et al. (1999)	//	//	A > T	//	//	//	-	-
Whatmough et al. (2002)	A > T	A > T	A > T	A > T	//	//	//	//
Gerlach et al. (1999)	//	//	//	//	//	//	//	//
Gerlach et al. (2000)	//	//	//	//	//	//	//	//
Gerlach et al. (2002a)	//	//	//	//	//	//	//	//
Gerlach et al. (2004)	-	-	-	-	-	-	-	-
Gerlach et al. (2006)	//	//	//	//	-	-	-	-
Gerlach (Appendix A)	//	//	//	//	//	//	N > M	//
Gorno-Tempini et al. (2000)	//	//	//	//	//	//	//	//
Mechelli et al. (2006)	//	//	//	//	//	//	//	M > A
Moore & Price (1999)	M > N	//	//	//	//	//	//	N > M
Moss et al. (2005)	//	//	//	//	//	//	//	//
Smith et al. (2001)	//	//	//	//	//	//	//	//
Tyler et al. (2003)	//	//	//	A > VF/A > V/A > T	//	//	//	A > V/VF/T
Total	5/18: 4N/1M	4/18: 4N	3/18: 3N	4/18: 4N	2/17: 2N	1/17: 1N	1/14: 1N	4/14: 3N/1M

A = animals; AC = articles of clothing; BA = Brodmann area; M = manmade objects; N = natural objects; V = vehicles; VF = vegetables/fruit; // = a region covered in the statistical analysis that failed to be significantly activated in the particular study; - = a region not covered in the statistical analysis in the particular study; ? = a region for which it is uncertain whether it was covered in the statistical analysis in the particular study. The 'Total' cell for each of the 29 regions summarizes the findings of the 20 studies for that particular region. As an example, the 'Total' cell for the Left Anterior Cingulate says: "4/17: 3M/1N" which should be read as: category-effects were found in four out of the 17 studies where this region was covered in the statistical analysis; in three studies activation was found to be greater for manmade objects than for natural objects whereas one study found the reverse effect. The first eight studies listed compared Animals and Tools whereas the others compared either broader or more specific categories of objects.

applied (ranging from $p_{\text{uncorrected}} < .01$ to $p_{\text{corrected}} < .05$) and the size of the kernel used (4–16 mm) in imaging preprocessing to accommodate residual variability in morphological and topographical anatomy that was not accounted for by the stereotactic normalization process. Large kernel sizes and liberal statistical thresholds will generally yield large activations, whereas smaller kernel sizes and more conservative statistical thresholds will tend to break such activations into several distinct activation foci.

For studies where the activations reported are based on main effects and/or interactions, only peaks associated with these effects were considered in the present review. This procedure was chosen because not all studies report the activations associated with the simple main effects (e.g., Whatmough et al., 2002). For the sake of simplicity, two of the studies by Chao and Martin (2000) and Chao et al. (1999) were treated as single studies even though they were based on several individual experiments (passive viewing, visual matching, and basic level naming) for which data are reported separately. This decision is also in keeping with the spirit of these papers, which focused on commonalities across conditions (passive viewing, visual matching, and basic level naming); conditions that were not formally compared.

RESULTS

There is a clear lack of consistency across the 20 studies. Not a single region is consistently found activated for any given category. In fact, quite a few regions, 11 out of 29 to be specific, are reported to be activated by both natural objects and artifacts (albeit in different studies). This is the case for the left and right anterior cingulate cortex (Brodmann's area [BA] 24/32), the left inferior frontal cortex (BA 45/46/47), the right superior temporal cortex (BA 22), the right middle temporal cortex (BA 21), the right and left lateral fusiform cortex (BA 37/20), the right and left lateral occipital cortex (BA 19), the left medial occipital cortex (BA 17/18), and the right cerebellum. Of the remaining 18 areas that are "selectively" activated by one category, 6 are reported in one study only [the left middle frontal cortex (BA 11), the left superior temporal cortex (BA 22), the left inferior tem-

poral cortex (BA 20), the right anteromedial temporal cortex (BA 28/34/38), the right calcarine sulcus (BA 17), and the left cerebellum], whereas 4 areas are reported in two studies [the right inferior frontal cortex (BA 45/46/47), the right parietal cortex (BA 40), the left anteromedial temporal cortex (BA 28/34/38), and the left calcarine sulcus (BA 17)]. The left inferior occipital cortex (BA 18/19) is found activated in three studies during the processing of natural objects (but only for contrasts between animals and tools). The left middle temporal cortex (BA 21) and the left parietal cortex (BA 40) are also found activated in three studies; all during processing of artifacts (but again only for contrasts involving tools and animals).

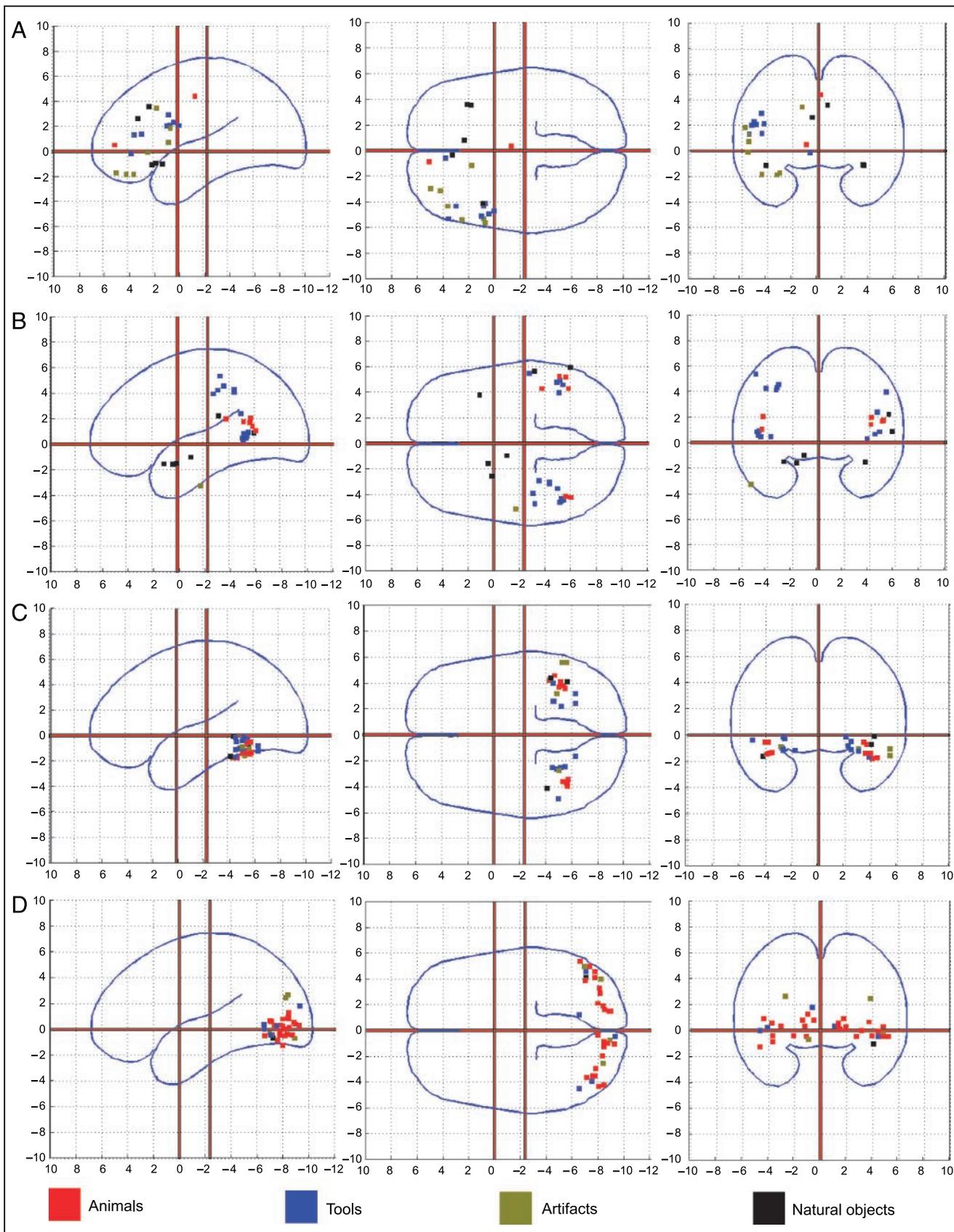
The most commonly activated regions are: (i) the right medial occipital cortex (BA 17/18); (ii) the right inferior occipital cortex (BA 18/19), which are found more activated by natural objects than by artifacts; (iii) the right and left medial fusiform cortex (BA 37/19); and (iv) the left dorsolateral frontal cortex (BA 6/44/45), which are found more activated by artifacts than by natural objects. The right medial occipital cortex, the right and left medial fusiform cortex, and the right inferior occipital cortex were found activated in four studies, whereas the left dorsolateral frontal cortex was found activated in five studies. However, even for these regions, the consistency is not overwhelming as the effects were only found in a minority of the studies that could, in principle, have identified them, that is, studies where the regions were covered in the statistical analysis (5/17 for the left dorsolateral region; 4/18 for the right inferior occipital region, the right medial occipital region, and the left medial fusiform cortex; and 4/19 for the right medial fusiform cortex).

DISCUSSION

Reasons for the Observed Inconsistency

Before addressing likely causes for the observed inconsistency, it should be noted that the studies included in this review were selected with the aim of being comparable. Consequently, the inconsistency does not result from gross differences between studies in stimulus modality (all studies used pictures as stimuli) or the

Figure 1. The figure shows the distribution of the 119 individual peak activations reported in the 20 studies selected for this review (four peaks in the cerebellum are not included). The peaks are displayed in Talairach space (Talairach & Tournoux, 1988) and grouped into four sections: (A) Peaks in the frontal cortex; (B) Peaks in the parietal and anterior/middle temporal cortex; (C) Peaks in the occipito-temporal cortex [lateral and medial fusiform cortex (BA 37/19)]; (D) Peaks in the occipital cortex. The peaks are color-coded representing the different types of contrasts they were identified with: red = animals vs. tools, blue = tools vs. animals, green = artifacts vs. natural objects, and black = natural objects vs. artifacts. It should be noted that not all contrasts given in black and green involved comparisons between the broad categories of natural objects vs. artifacts: Gerlach et al. (2004) compared the more specific categories of articles of clothing, animals, and vegetables/fruit; Mechelli et al. (2006) compared the specific category of animals with the broad category of artifacts; and Tyler et al. (2003) compared animals, vegetables/fruit, vehicles, and tools. Hence, for these studies, the green color signifies that activation in a particular area was significantly larger for a subcategory of artifacts compared with a subcategory of natural objects with similar complexity (e.g., vehicles vs. animals or vegetables/fruit vs. tools). The black color represents the reverse type of contrast. The figure was made with the Brede neuroinformatics toolbox (Nielsen & Hansen, 2000).



type of contrast made (all studies were based on direct contrasts between natural objects and artifacts).

Task Differences

One obvious reason for the inconsistency could be that the studies differ in the type of task used. The most common task is naming at the basic level, which was used in 12 studies (Mechelli et al., 2006; Moss et al., 2005; Damasio et al., 2004; Chao et al., 2002; Whatmough et al., 2002; Smith et al., 2001; Chao & Martin, 2000; Gorno-Tempini et al., 2000; Okada et al., 2000; Chao et al., 1999; Moore & Price, 1999; Martin et al., 1996), followed by object decision (deciding whether stimuli represent real objects or nonobjects), which was used in three studies (Gerlach et al., 1999, 2004, 2006) [excluding the study by Gerlach (Appendix A), which was based on a large-scale analysis of the three other studies by Gerlach et al. using object decision]. The remaining tasks included: passive viewing (Chao & Martin, 2000; Chao et al., 1999), matching to sample (Chao et al., 1999), superordinate classification (subjects decided whether pictures represented natural objects or artifacts) (Gerlach et al., 2000),⁵ global shape matching (subjects decided whether the global shape of objects were best described as round or oval) (Gerlach, Aaside, et al., 2002), picture matching (subjects decided whether simultaneously presented pictures corresponded to the same concept or not) (Perani et al., 1999), and semantic categorization (subjects were presented with three sequentially presented cue pictures and had to decide whether a fourth target picture belonged to the same subcategory) (Tyler et al., 2003).

Even when the comparison is confined to studies on the basis of basic level naming, the inconsistency remains: Five areas are now consistently activated by one category only (instead of both as in the comparison based on all 20 studies), namely, the right and left anterior cingulate cortex (BA 24/32), the right superior temporal cortex (BA 22), the right lateral fusiform cortex (BA 37/20), and the right lateral occipital cortex (BA 19). Yet, six regions are still found activated by both natural objects and artifacts [the right cerebellum, the right middle temporal cortex (BA 21), the left lateral fusiform gyrus (BA 37/20), the left lateral occipital cortex (BA 19), the left medial occipital cortex (BA 17/18), and the left inferior frontal cortex (BA 45/46/47)]. Perhaps the most interesting effect of confining the comparison to object naming is that the left middle temporal cortex (BA 21) is now found in 3 out of 11 studies (instead of 3/18). Given that five of the excluded studies used tasks likely to require shape processing only (Gerlach, Appendix A; Gerlach et al., 1999, 2004, 2006; Gerlach, Aaside, et al., 2002), this could suggest that activation in BA 21 is driven by semantically related operations (for additional evidence for this proposition, see Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005). This, of course,

does not explain why activation of this area is not found in all tasks requiring semantic processing (including the eight object-naming experiments which covered this region and where it failed to show up). In conclusion, although task differences are likely to produce different category effects, this factor alone cannot account for the discrepancy between the reviewed studies.

Stimulus Material

Although the studies selected for this review were all based on direct contrasts between natural objects and artifacts, they differ in the exact categories compared: Eight studies compared the subcategories of animals and tools (Damasio et al., 2004; Whatmough et al., 2002; Chao et al., 2002; Chao & Martin, 2000; Okada et al., 2000; Chao et al., 1999; Perani et al., 1999; Martin et al., 1996), eight studies compared a broader selection of stimuli drawn from the categories of natural objects and artifacts (Gerlach, Appendix A; Gerlach et al., 1999, 2000, 2006; Mechelli et al., 2006; Gerlach, Aaside, et al., 2002; Smith et al., 2001; Gorno-Tempini et al., 2000), and four studies compared additional subcategories including articles of clothing, vegetables/fruit, and vehicles (Moss et al., 2005; Gerlach et al., 2004; Tyler et al., 2003; Moore & Price, 1999). There is good reason to believe that differences in the exact (sub)categories compared can explain at least some of the inconsistency. Consider the activations reported in the posterior and ventral regions of the brain [the lateral occipital cortex (BA 19), the medial occipital cortex (BA 17/18/19), the calcarine sulcus (BA 17), and the lateral fusiform cortex (BA 37/20)]. Most of these activations are reported in studies that contrasted animals with tools. Given that animals are rated as more visually complex than tools (Snodgrass & Vanderwart, 1980), and in general consist of more components than tools, it is likely that these activations reflect structural (shape based) rather than semantic or lexical differences between categories. Evidence in favor of this suggestion comes from the studies by Tyler et al. (2003) and Moore and Price (1999). They found direct effects of visual complexity in some of these regions, with animals causing greater activation compared with tools, but not necessarily compared with more complex artifacts such as vehicles. Likewise, Gerlach et al. (2004) found greater activation of the right lateral occipital cortex (BA 19) for both animals and articles of clothing compared with vegetables/fruit. In addition, the right lateral fusiform cortex (BA 37/20) was also found more activated by articles of clothing compared with both animals and vegetables/fruit.

The findings considered above seem to highlight a point that has been clear in patient studies for some time: Spurious category effects may arise if the stimulus material is not matched across categories on parameters such as visual complexity and familiarity (Funnell & Sheridan, 1992; Stewart, Parkin, & Hunkin, 1992). Less

than half of the studies considered in this review fulfill this requirement (Gerlach, Appendix A; Gerlach et al., 1999, 2000; 2004, 2006; Moss et al., 2005; Tyler et al., 2003; Whatmough et al., 2002; Smith et al., 2001) and the majority of these studies fail to find category effects in the posterior and ventral regions.⁶ The exceptions are: (i) Gerlach et al. (2004), who found greater activation for both articles of clothing and animals compared with vegetables/fruit in the right lateral occipital cortex (BA 19), and for articles of clothing compared with both animals and vegetables/fruit in the right lateral fusiform cortex (BA 37/20); (ii) Tyler et al. (2003), who found greater activation in the right inferior occipital cortex for animals compared with both vegetables/fruit, vehicles and tools; (iii) Smith et al. (2001) who found greater activation of the right lateral occipital cortex (BA 19) for natural objects compared with artifacts; and (iv) Whatmough et al. (2002), who found increased activation for animals compared with tools in several posterior and ventral regions (see Table 1). Considering the findings obtained by Gerlach et al. and Tyler et al., it is likely that the activations reported by Whatmough et al. would not have been found had animals been compared with a “many-component” class of artifacts such as vehicles instead of the “few-component” class of tools (see also Moore & Price, 1999). Activations in the ventral regions, therefore, might not reflect semantic or lexical differences between categories but rather structural differences. The only finding that could be problematic for this hypothesis is the right lateral occipital activation (BA 19) found by Smith et al. (2001) for natural objects with a stimulus material matched for visual complexity. However, if natural objects are more structurally similar than artifacts and therefore harder to differentiate perceptually, which is likely to be the case (Gerlach et al., 2004; Tranel, Logan, Frank, & Damasio, 1997; Humphreys, Riddoch, & Quinlan, 1988), natural objects may still cause greater activation of this area compared with artifacts even when the two categories are matched for visual complexity.

Based on these observations, it seems likely that differences in the stimulus material (the exact categories compared) can account for some of the inconsistency across studies. This leads to the question of whether a more consistent picture would emerge if only studies examining animals and tools, or the broader categories of natural objects and artifacts, were included in the comparison. Examination of Table 1 suggests that this is not the case. There are only five areas where the inconsistency is caused by differences in contrasts involving tools and animals on the one hand and natural objects and artifacts on the other [the right anterior cingulate (BA 24/32), the right superior temporal cortex (BA 22), the right middle temporal cortex (BA 21), the right lateral fusiform cortex (BA 37/20), and the left medial occipital cortex (BA 17/18)]. Of these areas, the right anterior cingulate and the right middle temporal

cortex are only found activated in two studies, whereas the right superior temporal cortex is only found activated in three studies. Constraining the comparison to one type of contrast might therefore, in principle, heighten the consistency in relation to these areas, but it would do little to heighten the reliability, as these areas were found activated in very few studies to begin with. The same is not true of the activations in the right lateral fusiform cortex and the left medial occipital cortex. For these areas, a comparison confined to contrasts involving animals and tools would suggest a relatively high degree of consistency with the right lateral fusiform cortex being reported in five out of eight studies and the left medial occipital cortex being reported in four out of eight studies. However, and as argued above, activations in these areas are more likely to reflect differences in visual complexity between animals and tools than true categorical differences. For this reason, limiting the comparison to this type of contrast would yield a misleading picture. Moreover, if the comparison was limited to contrasts involving animals and tools, the findings would have little direct bearing on category-specific deficits as these rarely are confined to animals and, probably, never to tools.

Statistics and Power

As argued by Devlin, Moore, et al. (2002), differences in the regional cerebral blood flow (rCBF) associated with the processing of different categories are often small (less than 3%). Consequently, studies with a small number of observations may fail to find activations that survive correction for the multiple comparisons typically made in the statistical analysis. There are three ways to address this problem: (1) One can “ignore” it and report the findings at an uncorrected level of significance; (2) One can limit the search volume to a region or set of regions based on a priori hypotheses and argue that this justifies that the statistical threshold be lowered. Although a number of studies adopt this procedure, they often still fail to correct for the number of comparisons made within the region(s) of interest (ROI) or provide any formal estimation of the likelihood of false positives given the adopted threshold and the number of comparisons made; or (3) One can try to increase the sensitivity of the study, for example, by having many observations. Whereas Options 1 and 2 are not uncommon (Whatmough et al., 2002; Smith et al., 2001; Chao & Martin, 2000; Okada et al., 2000; Chao et al., 1999; Moore & Price, 1999; Perani et al., 1999; Martin et al., 1996), only a few studies have apparently been sensitive enough to detect category effects *at the level of whole-brain analysis* that survive correction for multiple comparisons (Mechelli et al., 2006; Tyler et al., 2003; Gerlach, Aaside, et al., 2002; Gerlach et al., 2000; Gerlach, Appendix A). One likely reason for this is that most imaging studies are based on (too) few subjects. If

we exclude the studies by Gerlach (Appendix A) and Damasio et al. (2004), which pooled subjects from several studies, the average number of subjects in the remaining studies is 10.5 (range 4–18).

The combination of liberal statistical thresholds and few observations is likely to produce false-positive activations which, by definition, are not reproducible.⁷ Although it is not possible to tell which activations reflect Type 1 errors, some qualified guesses can be made. A starting point for this could be the study by Tyler et al. (2003), in which care was taken to examine rCBF in some of the regions that had previously been reported to exhibit effects of category. The regions examined were those reported by Chao and Martin (2000) and Chao et al. (1999) and included: (a) the left ventral premotor cortex (BA 6; $x, y, z = -47, 5, 24$), (b) the left posterior parietal cortex (BA 40; $x, y, z = -31, -34, 45$), (c) the left middle temporal gyrus (BA 21; $x, y, z = -47, -51, 7$), (d) the left lateral fusiform gyrus (BA 37/20; $x, y, z = -38, -57, -16$), (e) the right lateral fusiform gyrus (BA 37/20; $x, y, z = 39, -54, -17$), (f) the left medial fusiform gyrus (BA 37/19; $x, y, z = -29, -50, -11$), and (g) the right medial fusiform gyrus (BA 37/19; $x, y, z = 28, -56, -14$). In none of these regions were Tyler et al. able to detect any effect of category, although the threshold was very liberal ($p < .6$, using small volume correction based on 5–9 mm spheres centered on the peak coordinates reported by Chao and colleagues). Before jumping to the conclusion that all activations reported for these regions reflect Type 1 errors, it should be noted that several studies have found activation in some of these areas that survived correction for multiple comparisons: Gerlach et al. (2000) found activation in the premotor area; Damasio et al. (2004), Gerlach et al., (2000, 2004), and Gerlach, Aaside, et al. (2002) found activation in the left and right lateral fusiform cortex; and Mechelli et al. (2006) found activation in the left and right medial fusiform cortex. These findings could suggest that the study by Tyler et al. might have lacked sensitivity. A cautious conclusion is, therefore, that the activations reported for the left ventral premotor cortex and the left and right lateral fusiform cortex may be reliable, whereas the category-specific activations reported for the left posterior parietal cortex and the left middle temporal cortex need further support to be considered reliable. With respect to the left and right medial fusiform cortex, these areas have only been found activated at a corrected level of significance when the stimulus material was not matched. When the material was matched for “semantic relevance,” these activations were no longer significant (Mechelli et al., 2006).

Summary

Given that the present studies were selected with the aim of being comparable, the lack of consistency across

studies is striking. This would not have been alarming had the discrepancy been accountable for in terms of task differences (e.g., object decision vs. object naming). Unfortunately, it is not. Even when one limits the comparison to studies which examined object naming—the task most commonly employed—the discrepancy remains. Clearly then, other factors must contribute to the diversity. One of these is likely to be low sensitivity in terms of design, statistical power, or both. Very few studies have reported category effects that survive correction for multiple comparisons, at least at the level of whole-brain analysis. This raises the concern that many of the category effects reported could reflect Type 1 errors (for similar conclusions, see Devlin, Russell, et al. 2002; Price & Friston, 2002). Another factor likely to contribute to the inconsistency is the specific categories compared. Typically, the studies that report category effects for natural objects in ventral and posterior parts of the brain obtain these findings by comparing complex natural objects (animals) with less complex artifactual objects (tools). When the stimulus categories compared are more similar in terms of visual complexity, these activations are not reproduced. This is the case for the category-specific activations claimed for the calcarine sulcus, the inferior occipital cortex, and the medial occipital cortex. In other words, a consistent finding is that visually complex objects, typically natural objects, cause increased activation of posterior and ventral regions—but this has little to do with category specificity per se. To count as category-specific, activation associated with processing of simple natural objects (vegetables/fruit) should exceed that associated with processing of simple artifactual objects (tools), whereas activation associated with complex natural objects (animals) should exceed that associated with complex artifacts (e.g., articles of clothing and vehicles), or vice versa, and this appears not to be the case.

Do the Reliable Activations Reflect Category-specific Processing?

Having discussed plausible reasons for the lack of consistency for the majority of the category-specific activations reported, let us examine six areas that do exhibit some consistency across studies, namely: (i) the right medial occipital cortex (BA 17/18), (ii) the right inferior occipital cortex (BA 18/19), (iii) the right and left medial fusiform cortex (BA 37/19), all of which are found activated in four studies, (iv) the left dorsolateral frontal cortex (BA6/44/45), which is found activated in five studies, and (v) the left middle temporal cortex (BA 21), which is found activated in three studies. Are these regions involved in category-specific processing?

As mentioned, the activations in the right and left medial fusiform cortex are modulated by “semantic relevance” rather than category per se (Mechelli et al.,

2006). Also, it cannot be excluded that factors other than category may explain the activations reported for natural objects in the right medial and right inferior occipital cortex. These activations could reflect that natural objects in general are more visually complex than artifacts. Indeed, the right medial occipital cortex (BA 17/18) is only associated with natural objects when animals are compared with tools. When animals are compared with more complex artifacts such as articles of clothing or vehicles, this area fails to show up in the analyses. The same is true when less complex natural objects such as vegetables/fruits are compared with tools. Although this is not the case for the right inferior occipital cortex (BA 18/19) and the right lateral occipital cortex (BA 18), which do exhibit increased activation for natural objects compared with complex artifacts (Tyler et al., 2003; Smith et al., 2001), noncategorical explanations may still apply. As mentioned, natural objects are harder to differentiate perceptually than artifacts because they are more structurally similar. Hence, natural objects may still cause greater activation of posterior and ventral regions than artifacts even when the two categories are matched for visual complexity.

There is also reason to believe that a noncategorical explanation may apply to the activations reported for artifacts in the left dorsolateral frontal cortex (BA 6/44/45). Typically, activations in this region have included the premotor cortex (Chao et al., 2002; Chao & Martin, 2000; Gerlach et al., 2000; Martin et al., 1996), which has led to the suggestion that recognition/comprehension of artifacts may rely on access to action knowledge (for more detailed and critical discussions of this proposition, see Gerlach, Law, Gade, & Paulson, 2002; Gerlach, Law, & Paulson, 2002). Although this hypothesis is plausible, activation of the premotor region is not specific to artifacts because it is also found with manipulable natural objects (vegetables/fruit) (Gerlach, Law, & Paulson, 2002).

The last area to be considered here is the left middle temporal cortex (BA 21), which has been associated with processing of artifacts. This region is chosen for discussion because it has been identified as a consistent finding in the review by Devlin, Russell, et al. (2002). In the present review, the area is only found activated in 3 out of the 18 studies that covered this region. If the focus is limited to studies based on object naming, in which this region was covered, the statistics looks somewhat better (3 out of 11) as all studies which reported activation of this area used object naming. This could suggest that the area is involved in semantic processing (see also Kable et al., 2005). Nevertheless, it must be noted that activation of this area has never been reported at a corrected level of significance in studies which used pictures as stimuli and that it is not found by the remaining eight studies that used object naming (of which three also contrasted tools and animals). Moreover, even if it had been found activated in all studies that compared processing of tools and processing of animals during

object naming, it is not clear that this would justify calling it a category-specific area. It may be that this area is activated by other categories besides tools. Some evidence for this proposition comes from a study by Downing, Chan, Peelen, Dodds, and Kanwisher (2005). They found very similar activations for tools and vegetables/fruit in this area. Likewise, Moore and Price (1999) found that activation of this region was as high for tools as it was for nonobjects. Hence, category-specific activation of the left posterior middle temporal region may not be reliable in the context of visual object processing.

DISCUSSION

As mentioned in the introduction, the explanations advanced to account for category-specific disorders can be grouped into three general classes (Caramazza & Mahon, 2003): the sensory/functional account, the correlated-feature account, and the domain-specific account. These accounts will be briefly described and their compatibility with the findings of the present review will be evaluated in the subsequent subsections.

General Accounts of Category Specificity

The Domain-specific Account

The domain-specific account (Caramazza & Shelton, 1998) is based on the assumption that evolutionary pressure has resulted in specialized and functionally dissociable neural circuits dedicated to processing different categories of objects (both perceptually and conceptually). Plausible candidate categories are claimed to be animals, fruit/vegetables, conspecifics, and possibly tools (Caramazza & Mahon, 2003). Given that this account does not entail any principles of organization besides specialization, only two predictions can be derived from this account regarding category effects in functional imaging: (i) activation in some areas should be category-specific (for animals, fruit/vegetables, conspecifics, and perhaps tools), and (ii) (specialized) areas subserving processing of, for example, animals and vegetables/fruit, should not overlap to great extents.

The Correlated-feature Accounts

On these accounts, conceptual features (representing object properties) that often co-occur are assumed to be stored close together in semantic space. Hence, brain damage may give rise to category-specific semantic deficits either because the conceptual knowledge corresponding to objects with similar properties is stored in adjacent neural areas, or because damage to a given property will propagate damage to highly correlated properties. One of the more articulated versions of a correlated-feature account has been proposed by Moss

and Tyler (2000) and Tyler, Moss, Durrant-Peatfield, and Levy (2000). Their conceptual-structure theory is based on three assumptions: (1) natural objects have more shared features than artifacts, that is, artifacts have more distinctive features than natural objects; (2) information on biological function is highly correlated with shared perceptual properties (e.g., can see → has eyes) for natural objects, whereas functional information is highly correlated with distinctive perceptual properties (e.g., used for spearing → has tines) for artifacts; and (3) features that are highly correlated with other features will be more resistant to damage than features that are not highly correlated. On this specific account, a disproportionate deficit for natural objects will be observed when damage is relatively mild, whereas a disproportionate deficit for artifacts will arise when damage is so severe that only highly correlated shared perceptual and functional features remain.

Given that correlated-feature accounts assume a widely distributed conceptual system that is not organized by category, these accounts do not generally anticipate that category effects should be found with functional imaging.

The Sensory/Functional Accounts

On the sensory/functional account, which was initially proposed by Warrington and Shallice (1984) and Warrington and McCarthy (1983), and later modified by others (e.g., Humphreys & Forde, 2001; Martin, Ungerleider, & Haxby, 2000), category-specific disorders are held to arise because the ability to recognize natural objects, in general, depends more critically on visual information than the ability to recognize artifacts. In comparison, the ability to recognize artifacts is assumed to depend more critically on functional/associative information than the recognition of natural objects. Central to the sensory/functional account is also the assumption that semantic knowledge is organized in two separable systems that are modality-specific so that visual semantic knowledge is stored in one system and functional/associative in another (note though that this assumption was loosened in Warrington & McCarthy's, 1987 account). Following this, damage to visual semantic knowledge should have more devastating effects on the comprehension of natural objects, whereas damage to functional/associative knowledge should have more devastating effects on the comprehension of artifacts.

The assumptions underlying the sensory/functional accounts lead to the predictions: (i) that processing of natural objects should yield greater activation than processing of artifacts in areas associated with visual processing, and (ii) that artifacts should cause greater activation of areas mediating functional/associative knowledge (e.g., the inferolateral temporal lobes) or action knowledge, that is, knowledge of how things are manipulated (fronto-parietal regions).

Are the Present Findings Compatible with Theories of Category Specificity?

Based on the 20 imaging studies considered here, there is little evidence for brain regions selective to processing of either natural objects or artifacts. The majority of the “category-specific” activations reported are only found in one or two studies and the few activations that have been replicated by more than three studies, and which are reported for one category only instead of for both, do not seem to reflect categorical differences between natural objects and artifacts but rather differences in visual complexity, structural similarity, semantic relevance, or manipulability between the (sub)categories compared.

The Domain-specific Account

The failure to find consistent category-specific activations is problematic for the domain-specific account. If evolutionary pressure had resulted in specialized and functionally dissociable neural circuits dedicated to processing different categories of objects, these circuits should be engaged whenever a given category is processed. Moreover, on the domain-specific account, the same areas of the brain should not be engaged in the processing of both natural objects and artifacts, and very many areas are. It can, of course, be argued that many regions will behave nonspecifically because they are not part of a specialized circuitry. Although this is certainly a valid argument, the great overlap in activation for natural objects and artifacts remains problematic as long as no category-specific circuit has yet been identified. Caramazza and Mahon (2003, 2006) and Mahon and Caramazza (2003) have suggested that such circuits do exist. They point to the observation by Chao et al. (1999, 2002) that tools tend to activate the medial parts of the fusiform gyri, whereas animals tend to activate more lateral parts. However, as is evident from the present review, this pattern is not a reliable finding. First of all, it is not reproduced in studies where the stimulus material is matched for visual complexity and where the statistical analysis is corrected for multiple comparisons. Secondly, some studies have found the lateral fusiform region to be more activated by artifacts than by natural objects (Gerlach et al., 2004; Okada et al., 2000). Thirdly, in the only study which found activations of the right and left medial fusiform cortex for artifacts at a corrected level of significance, these activations were shown to reflect semantic relevance rather than category per se (Mechelli et al., 2006).

The Correlated-feature Accounts

Although the lack of true category-specific activations is not compatible with the domain-specific account, it is compatible with the correlated-feature accounts. A null finding is easily accommodated by these accounts given

their assumption of a widely distributed conceptual system that is not organized by category. Nevertheless, in one of the more articulated versions of a correlated-feature account, the conceptual-structure theory proposed by Moss and Tyler (2000) and Tyler et al. (2000), some effects of category are anticipated. On this specific account, it is held that processing of natural objects should be associated with greater activation than artifacts in tasks that necessitate fine-grained differentiation between concepts. This follows from the assumption that natural objects share more common features than artifacts, and therefore, should be harder to differentiate. Evidence in favor of this hypothesis can be found in three studies. Moss et al. (2005) and Moore and Price (1999) have found greater activation of the left anteromedial parts of the temporal cortex during processing of natural objects. This is compatible with the conceptual-structure theory in so far as this region is believed to be involved in the integration of information from different modalities (Moss et al., 2005);⁸ a property which may be needed when similar concepts are to be differentiated. Likewise, Gerlach (Appendix A) found that natural objects caused greater activation than artifacts in areas which are recruited when discriminations become difficult (the anterior cingulate gyri and the right inferior frontal gyrus; Cabeza & Nyberg, 2000). This is compatible with the notion that processing of natural objects should lead to greater activation than artifacts in tasks that necessitate fine-grained differentiation between objects.

Perhaps the most consistent finding in this review, namely, that artifacts tend to activate the left premotor cortex in tasks requiring decisions on the basis of semantics, might also be compatible with the correlated-feature accounts if artifacts share more common features than natural objects in terms of manipulability. Given their assumption of a widely distributed conceptual system that is not organized by category but by similarity in features, these accounts are even compatible with observation of premotor activation during processing of vegetables/fruit (Gerlach, Law, & Paulson, 2002).

The Sensory/Functional Accounts

The finding that artifacts tend to activate the left premotor cortex is also compatible with the sensory/functional accounts. However, the additional finding that the premotor region is also activated by manipulable natural objects (vegetables/fruit) (Gerlach, Law, & Paulson, 2002) is not. At least not with the early version suggested by Warrington and Shallice (1984), where category-specific deficits for natural objects were thought to reflect impaired visual knowledge only. It is also not the case that natural objects tend to cause greater activation than artifacts in regions involved in visual processing as the sensory/functional accounts predict. If such a tendency is apparent at all, it can be accounted for in terms of differences in visual complexity or

structural similarity between the categories compared. In studies where visual complexity is matched across category, artifacts may even be associated with greater activation than natural objects in visual object processing areas (Gerlach, Appendix A; Gerlach et al., 2004).

Conclusion

The present article provides a review of 20 functional imaging studies which have examined category specificity. The studies included fulfilled three criteria: (i) they used pictures as stimuli, (ii) they were based on direct contrasts between categories (e.g., natural objects and artifacts), and (iii) they reported findings in Talairach space. In order to make the 123 individual peak activations from the 20 studies comparable, the peak coordinates were grouped into 29 rather broad anatomical regions. Although this procedure should increase the likelihood of finding commonalities across studies, there is a striking lack of consistency. Not a single area is consistently activated across all studies. In contrast, 11 out of the 29 regions are reported activated by both artifacts and natural objects (albeit in different studies). The observed inconsistency could reflect that category effects are context-specific, appearing in some but not all task types. Although category effects are undoubtedly context-specific, differences in task requirements alone cannot account for the diversity observed. If the comparison is restricted to studies examining object naming at the basic level, the inconsistency remains. The most likely causes of the inconsistency are: (i) adoption of liberal statistical thresholds, which are likely to yield false-positive activations (9 out of the 20 studies did not correct for the multiple comparisons made during the statistical analysis); (ii) limited sensitivity due to low number of observations (the average functional imaging study is based on 10.5 subjects [range 4–18]) and perhaps inefficient designs; and (iii) failure to match categories on confounding variables such as familiarity and especially visual complexity (less than half of the studies used matched stimulus material). To this we may add a fourth factor, which concerns the limitations of the hemodynamic techniques: The level of spatial and temporal resolution provided by hemodynamic imaging means that these techniques cannot reveal category-specific effects present in the temporal dynamics of brain activation but also that they may potentially obscure category effects, should these effects be present at finer spatial scales than the level of resolution presently offered. Whether this will turn out to be the case is an open question. It must be noted, however, that the category-specific deficits observed in patients are probably not likely to be explained by a patchy organization as the lesions causing these deficits are often vast.

If effects of visual complexity can be considered as a category-specific finding, this is perhaps the most robust

one in that natural objects, which are generally more visually complex than artifacts, tend to cause greater activation than artifacts in posterior and ventral parts of the brain (e.g., the calcarine sulcus, the inferior occipital cortex, the medial occipital cortex, and the lateral parts of the fusiform gyri). When the categories are matched for visual complexity, these activations are not reproduced.

The most consistent activation found in the present review is that the left dorsolateral prefrontal cortex (the premotor area) tends to be activated during (semantic) processing of artifacts. It is found in 5 out of 14 studies that used tasks requiring semantic processing, and which covered this region in the statistical analysis. Moreover, in at least one study, this region was found activated at a corrected level and with matched stimulus material. This region, however, is not specifically activated by artifacts but rather by manipulable objects in general, be they natural (vegetables/fruit) or artificial (Gerlach, Law, & Paulson, 2002). This lack of “true” category-specific activations is problematic for theories of category specificity that argue that knowledge is categorically organized, but is readily accounted for by theories that assume a widely distributed conceptual system that is not organized by category. In this respect, the conceptual-structure theory proposed by Moss and Tyler (2000) and Tyler et al. (2000) seems to be the theory most in line with the findings of this review. This theory can account for: (i) the general lack of “true” category-specific activations, (ii) the finding that manipulable objects tend to be associated with activation of the left premotor cortex, and (iii) that natural objects tend to be associated with greater activation than artifacts in regions supporting fine-grained discriminations (the left anteromedial temporal cortex, the anterior cingulate gyri, and the right inferior frontal gyrus).

The lack of consistency found here across studies on category specificity echoes the conclusions of previous reviews (Devlin, Russell, et al., 2002; Price & Friston, 2002; Joseph, 2001). This is so even though the present review had a narrower scope, in that only studies examining picture processing were included and that 12 of these studies were not part of the previous reviews. Hence, the inconsistency observed across all four reviews is unlikely to reflect the particular studies included.

If future studies using functional imaging are to produce more consistent findings than the existing ones, more attention must be paid to methodological issues such as sensitivity, stimulus matching, and statistics. Moreover, studies which examine object naming without manipulating variables other than category, to give an example, are unlikely to be very informative because they do not address any particular cognitive operation but rather a whole range. Hence, if functional imaging studies are to make (more sophisticated) contributions to theories of category specificity—besides showing that some areas might be more active than

others when a particular category is displayed—more specific experimental designs are called for. Fortunately, such studies are increasing in number.

APPENDIX A

	Region Coordinates			BA	Z Score
	x	y	z		
<i>Artifacts > natural objects</i>					
R. Middle occipital gyrus	40	-86	22	19	6.28
L. Middle occipital gyrus	-26	-88	24	19	5.13
<i>Natural objects > Artifacts</i>					
L. Anterior cingulate gyrus	-4	32	30	32	5.14
L. Cerebellum	-48	-64	-36		4.96
R. Anterior cingulate gyrus	8	22	40	32	4.82
R. Inferior frontal gyrus	36	22	-12	47	4.57

Coordinates are in millimeters in the MNI version of the Talairach atlas (Talairach & Tournoux, 1988), relative to the anterior commissure. L = left; R = Right; BA = Brodmann’s area. Threshold was set at $p_{\text{corrected}} < .05$.

The results were obtained by performing a large-scale analysis on the data reported in the studies by Gerlach et al. (1999, 2004, 2006). In all three studies, the subjects performed object decision tasks in which they were required to decide whether stimuli depicted real objects or nonobjects. The tasks differed in that the stimuli were either natural objects (or “natural” nonobjects) or artifacts (or “artificial” nonobjects). In two of the studies (Gerlach et al., 1999, 2006), the categories of artifacts and natural objects were rather broad, as the category of artifacts included items from such diverse subcategories as furniture and tools, whereas the category of natural objects included both animals, insects, and vegetables/fruit. In these studies, only two object decision tasks were performed, one with natural objects and one with artifacts. In the third study (Gerlach et al., 2004), the subjects performed four different object decision tasks on the basis of the more constrained categories of animals, fruit/vegetables, articles of clothing, and nonmanipulate artifacts. In summary, a total of 102 [(15 subjects × 2 conditions) + (12 subjects × 2 conditions) + (12 subjects × 4 conditions)] scans involving object decision were entered into the large-scale analysis. For all subjects, the complete brain volume was sampled. Standard image analysis was performed using Statistical Parametric Mapping software (SPM2, Wellcome Department of Cognitive Neurology, London, UK).

APPENDIX B

	<i>Task</i>	<i>Region(s) Covered in the Statistical Analysis</i>	<i>Corrected Statistics</i>	<i>Stimulus Material Matched For:</i>	<i>No. of Subjects</i>
Chao et al. (1999)	Passive viewing	18 contiguous, 5-mm-thick coronal images of posterior cortex	No	Not matched	8
	Shape matching				4
	Basic level naming				6
Chao & Martin (2000)	Passive viewing	22 contiguous, 5-mm axial slices covering frontal and parietal regions	No	Not matched	5
	Basic level naming				5
Chao et al. (2002)	Basic level naming	Whole brain	No	Not matched	7
Damasio et al. (2004)	Basic level naming	Whole brain (and ROI covering the bilateral temporal poles and left inferior temporal cortex)	Yes	Not matched	51
Gerlach et al. (1999)	Object decision	Whole brain	Yes	Familiarity	15
				Visual complexity	
Gerlach et al. (2000)	Object decision/ categorization	Whole brain	Yes	Familiarity	15
				Visual complexity	
				Image agreement	
Gerlach et al. (2002)	Global shape matching	Whole brain	Yes	Not matched	10
Gerlach et al. (2004)	Object decision	Right posterior temporal gyrus extending into the middle fusiform gyrus	Yes	Familiarity	12
				Visual complexity	
				Image agreement	
Gerlach et al. (2006)	Object decision	The ventral parts of the brain bilaterally, extending from the inferior occipital gyri over the fusiform gyri and into the inferior temporal gyri. The right inferior frontal gyrus	Yes	Familiarity	12
				Visual complexity	
				Image agreement	
Gerlach (Appendix A)	Object decision	Whole brain	Yes	Familiarity	39
				Visual complexity	
				Image agreement	
Gorno-Tempini et al. (2000)	Basic level naming	Whole brain	Yes	Not matched	8
Martin et al. (1996)	Basic level naming	Whole brain	No	Not matched	16
Mechelli et al. (2006)	Basic level naming	Whole Brain	Yes	Semantic relevance	12
Moore and Price (1999)	Basic level naming	Whole brain	No	Not matched	8
Moss et al. (2005)	Basic level naming	Whole brain (and ROI covering the antereomedial temporal cortex bilaterally)	Yes	Concept agreement	12
				Exemplarity	
				Familiarity	
				Age of acquisition	
				Visual complexity	
Okada et al. (2000)	Basic level naming	Whole brain	No	Name frequency	12
Perani et al. (1999)	Object matching	Whole brain	No	Not matched	11
Smith et al. (2001)	Basic level naming	Whole brain	No	Familiarity	18
				Visual complexity	
Tyler et al. (2003)	Categorization	Whole brain	Yes	Familiarity	9
				Visual complexity	
Whatmough et al. (2002)	Basic level naming	Whole brain	No	Familiarity	15
				Visual complexity	

Acknowledgments

I thank Randi Starrfelt and two anonymous reviewers for valuable comments. I would also like to thank Finn Årup Nielsen for assistance with the Brede neuroinformatics toolbox.

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Notes

1. It is not clear how the contrast between words and pictures was computed in this study. The analysis is reported to be based on seven different experiments published separately. One of these experiments is Experiment 2 in Moore and Price (1999), where words and pictures were presented simultaneously. The inclusion of this experiment in the analysis makes the contrast between words and pictures less than clear-cut. For this reason, the study is not included in the present review.
2. It should be noted that other studies by the Iowa group, such as Damasio, Grabowski, Tranel, Hichwa, and Damasio (1996), were not included as separate studies in the present comparison because they form part of the multistudy analysis presented by Damasio et al. (2004), which is included.
3. This criterion also excludes studies on the basis of electro-physiology even though several such studies focusing on category specificity exist.
4. The results described in Appendix A were obtained by doing a large-scale analysis on the data reported in the studies by Gerlach et al. (1999, 2004, 2006), which were all based on object decision (deciding whether stimuli represent real objects or nonobjects). This large-scale analysis is included in the present review because it illustrates that robust category effects can be found at the level of whole-brain analysis if the number of observations is increased; none of the studies, considered in isolation, revealed significant effects of category at a corrected level of significance during whole-brain analysis.
5. It should be noted that Moss et al. (2005) employed a similar condition in which they compared naming at the domain level (subjects had to name the pictures as either living or manmade). In this condition, no significant activation differences were found between: animals and vehicles, vegetables/fruit and tools, animals and tools, vegetables/fruit and vehicles.
6. The activations in the right and left medial fusiform cortex reported by Mechelli et al. (2006) were found with unmatched stimulus material. When animals and artifacts were matched for “semantic relevance” (the degree to which features of a given concept are diagnostic for the particular concept), these activations were no longer significant at a corrected level of significance.
7. The disadvantage of only accepting activations that survive correction for multiple comparisons is that this may result in Type 2 errors because the correction is perhaps too conservative. Nevertheless, it may be easier to avoid Type 1 errors, by conducting sensitive studies, than to dismiss results as Type 2 errors once they have been reported.
8. It should be noted though that this area is probably only important when objects must be differentiated at a conceptual level. In the dataset present in Appendix A, no activation of this area was observed for processing of natural objects during difficult object decision tasks, where objects are to be discriminated based primarily on their shape properties. This held true even when the analysis was based on ROIs limited to the left and right anteromedial temporal cortex (small volume correction based on a 15-mm sphere centered at $x, y, z = -22, 2, -16$ and $x, y, z = 22, 2, -16$).

REFERENCES

- Cabeza, R., & Nyberg, L. (2000). Imaging cognition: II. An empirical review of 275 PET and fMRI studies. *Journal of Cognitive Neuroscience*, *12*, 1–47.
- Capitani, E., Laiacona, M., Mahon, B., & Caramazza, A. (2003). What are the facts of semantic category-specific deficits? A critical review of the clinical evidence. *Cognitive Neuropsychology*, *20*, 213–261.
- Caramazza, A., & Mahon, B. Z. (2003). The organization of conceptual knowledge: The evidence from category-specific semantic deficits. *Trends in Cognitive Sciences*, *7*, 354–361.
- Caramazza, A., & Mahon, B. Z. (2006). The organisation of conceptual knowledge in the brain: The future's past and some future directions. *Cognitive Neuropsychology*, *23*, 13–38.
- Caramazza, A., & Shelton, J. R. (1998). Domain-specific knowledge systems in the brain: the animate-inanimate distinction. *Journal of Cognitive Neuroscience*, *10*, 1–34.
- Chao, L. L., Haxby, J. V., & Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nature Neuroscience*, *2*, 913–919.
- Chao, L. L., & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *Neuroimage*, *12*, 478–484.
- Chao, L. L., Weisberg, J., & Martin, A. (2002). Experience-dependent modulation of category-related cortical activity. *Cerebral Cortex*, *12*, 545–551.
- Damasio, H., Grabowski, T. J., Tranel, D., Hichwa, R. D., & Damasio, A. R. (1996). A neural basis for lexical retrieval [see comments]. *Nature*, *380*, 499–505.
- Damasio, H., Tranel, D., Grabowski, T., Adolphs, R., & Damasio, A. (2004). Neural systems behind word and concept retrieval. *Cognition*, *92*, 179–229.
- Devlin, J. T., Moore, C. J., Mummery, C. J., Gorno-Tempini, M. L., Phillips, J. A., & Noppeney, U. (2002). Anatomic constraints on cognitive theories of category specificity. *Neuroimage*, *15*, 675–685.
- Devlin, J. T., Russell, R. P., Davis, M. H., Price, C. J., Moss, H. E., & Fadili, M. J. (2002). Is there an anatomical basis for category-specificity? Semantic memory studies in PET and fMRI. *Neuropsychologia*, *40*, 54–75.
- Downing, P. E., Chan, A. W.-Y., Peelen, M. V., Doods, C. M., & Kanwisher, N. (2005). Domain specificity in visual cortex. *Cerebral Cortex*, *16*, 1453–1461.
- Friston, K. J., Ashburner, J., Frith, C. D., Poline, J. B., Heather, J. D., & Frackowiak, R. S. (1995). Spatial registration and normalization of images. *Human Brain Mapping*, *3*, 165–189.
- Funnell, E., & Sheridan, J. (1992). Categories of knowledge? Unfamiliar aspects of living and nonliving things. *Cognitive Neuropsychology*, *9*, 135–153.
- Gainotti, G. (2000). What the locus of brain lesion tells us about the nature of the cognitive defect underlying category-specific disorders: A review. *Cortex*, *36*, 539–559.
- Gainotti, G. (2002). The relationships between anatomical and cognitive locus of lesion in category-specific disorders. In G. W. Humphreys & E. M. E. Forde (Eds.), *Category-specificity in brain and mind* (pp. 403–426). Hove: Psychology Press.
- Gerlach, C., Aaside, C. T., Humphreys, G. W., Gade, A., Paulson, O. B., & Law, I. (2002). Brain activity related to integrative processes in visual object recognition: Bottom-up integration and the modulatory influence of stored knowledge. *Neuropsychologia*, *40*, 1254–1267.
- Gerlach, C., Law, I., Gade, A., & Paulson, O. B. (1999).

- Perceptual differentiation and category effects in normal object recognition: A PET study. *Brain*, *122*, 2159–2170.
- Gerlach, C., Law, I., Gade, A., & Paulson, O. B. (2000). Categorization and category effects in normal object recognition: A PET study. *Neuropsychologia*, *38*, 1693–1703.
- Gerlach, C., Law, I., Gade, A., & Paulson, O. B. (2002). The role of action knowledge in the comprehension of artefacts—A PET study. *Neuroimage*, *15*, 143–152.
- Gerlach, C., Law, I., & Paulson, O. B. (2002). When action turns into words. Activation of motor-based knowledge during categorization of manipulable objects. *Journal of Cognitive Neuroscience*, *14*, 1230–1239.
- Gerlach, C., Law, I., & Paulson, O. B. (2004). Structural similarity and category-specificity: A refined account. *Neuropsychologia*, *42*, 1543–1553.
- Gerlach, C., Law, I., & Paulson, O. B. (2006). Shape configuration and category-specificity. *Neuropsychologia*, *44*, 1247–1260.
- Gorno-Tempini, M. L., Ciolotti, L., & Price, C. J. (2000). Category differences in brain activation studies: Where do they come from? *Proceedings of the Royal Society of London, Series B, Biological Sciences*, *267*, 1253–1258.
- Grabowski, T. J., Damasio, H., & Damasio, A. R. (1998). Premotor and prefrontal correlates of category-related lexical retrieval. *Neuroimage*, *7*, 232–243.
- Kiefer, M. (2001). Perceptual and semantic sources of category-specific effects: Event-related potentials during picture and word categorization. *Memory & Cognition*, *29*, 100–116.
- Humphreys, G. W., & Forde, E. M. (2001). Hierarchies, similarity, and interactivity in object recognition: “Category-specific” neuropsychological deficits. *Behavioral and Brain Sciences*, *24*, 453–476.
- Humphreys, G. W., Riddoch, M. J., & Quinlan, P. T. (1988). Cascade processes in picture identification. *Cognitive Neuropsychology*, *5*, 67–104.
- Joseph, J. E. (2001). Functional neuroimaging studies of category specificity in object recognition: A critical review and meta-analysis. *Cognitive, Affective, & Behavioral Neuroscience*, *1*, 119–136.
- Kable, J. W., Kan, I. P., Wilson, A., Thompson-Schill, S. L., & Chatterjee, A. (2005). Conceptual representations of action in the lateral temporal cortex. *Journal of Cognitive Neuroscience*, *17*, 1856–1870.
- Låg, T. (2005). Category-specific effects in object identification: What is “normal”. *Cortex*, *41*, 833–841.
- Laws, K. R. (2005). “Illusions of normality”: A methodological critique of category-specific naming. *Cortex*, *41*, 842–851.
- Mahon, B. Z., & Caramazza, A. (2003). Constraining questions about the organisation and representation of conceptual knowledge. *Cognitive Neuropsychology*, *20*, 433–450.
- Martin, A., Ungerleider, L. G., & Haxby, J. V. (2000). Category specificity and the brain: The sensory/motor model of semantic representations of objects. In M. S. Gazzaniga (Ed.), *The new cognitive neurosciences* (2nd ed., pp. 1023–1036). Cambridge: MIT Press.
- Martin, A., Wiggs, C. L., Ungerleider, L. G., & Haxby, J. V. (1996). Neural correlates of category-specific knowledge. *Nature*, *379*, 649–652.
- Mechelli, A., Sartori, G., Orlandi, P., & Price, C. J. (2006). Semantic relevance explains category effects in medial fusiform gyri. *Neuroimage*, *30*, 992–1002.
- Moore, C. J., & Price, C. J. (1999). A functional neuroimaging study of the variables that generate category-specific object processing differences. *Brain*, *122*, 943–962.
- Moss, H. E., Rodd, J. M., Stamatakis, E. A., Bright, P., & Tyler, L. K. (2005). Anteromedial temporal cortex supports fine-grained differentiation among objects. *Cerebral Cortex*, *15*, 616–627.
- Moss, H. E., & Tyler, L. K. (2000). A progressive category-specific semantic deficit for non-living things. *Neuropsychologia*, *38*, 60–82.
- Nielsen, F. Å., & Hansen, L. K. (2000). Experiences with Matlab and VRML in functional neuroimaging visualizations. *Visualization Development Environments*, Princeton, New Jersey, April 27–28.
- Noppeney, U., Price, C. J., Penny, W. D., & Friston, K. J. (2006). Two distinct neural mechanisms for category-selective responses. *Cerebral Cortex*, *16*, 437–445.
- Okada, T., Tanaka, S., Nakai, T., Nishizawa, S., Inui, T., & Sadato, N. (2000). Naming of animals and tools: A functional magnetic resonance imaging study of categorical differences in the human brain areas commonly used for naming visually presented objects. *Neuroscience Letters*, *296*, 33–36.
- Perani, D., Schnur, T., Tettamanti, M., Gorno Tempini, M., Cappa, S. F., & Fazio, F. (1999). Word and picture matching: A PET study of semantic category effects. *Neuropsychologia*, *37*, 293–306.
- Price, C. J., & Friston, K. J. (2002). Functional imaging studies of category specificity. In G. W. Humphreys & E. M. E. Forde (Eds.), *Category specificity in brain and mind* (pp. 427–447). Hove: Psychology Press.
- Price, C. J., & Humphreys, G. W. (1989). The effects of surface detail on object categorization and naming. *Quarterly Journal of Experimental Psychology A: Human Experimental Psychology*, *41*, 797–827.
- Price, C. J., Noppeney, U., Phillips, J., & Devlin, J. T. (2003). How is the fusiform gyrus related to category-specificity? *Cognitive Neuropsychology*, *20*, 561–574.
- Riddoch, M. J., & Humphreys, G. W. (1987). Picture naming. In G. W. Humphreys & M. J. Riddoch (Eds.), *Visual object processing: A cognitive neuropsychological approach* (1st ed., pp. 107–143). Hove: Erlbaum.
- Rogers, T. T., Hocking, J., Mechelli, A., Patterson, K., & Price, C. (2005). Fusiform activation to animals is driven by the process, not the stimulus. *Journal of Cognitive Neuroscience*, *17*, 434–445.
- Rosazza, C., Imbornone, E., Zorzi, M., Farina, E., Chiavari, L., & Cappa, S. F. (2003). The heterogeneity of category-specific semantic disorders: Evidence from a new case. *Neurocase*, *9*, 189–202.
- Smith, C. D., Andersen, A. H., Kryscio, R. J., Schmitt, F. A., Kindy, M. S., Blonder, L. X., et al. (2001). Differences in functional magnetic resonance imaging activation by category in a visual confrontation naming task. *Journal of Neuroimaging*, *11*, 165–170.
- Snodgrass, J. G., & Vanderwart, M. (1980). A standardized set of 260 pictures: Norms for name agreement, image agreement, familiarity, and visual complexity. *Journal of Experimental Psychology: Human Learning and Memory*, *6*, 174–215.
- Spitzer, M., Kwong, K. K., Kennedy, W., Rosen, B. R., & Belliveau, J. W. (1995). Category-specific brain activation in fMRI during picture naming. *NeuroReport*, *6*, 2109–2112.
- Stewart, F., Parkin, A. J., & Hunkin, N. M. (1992). Naming impairments following recovery from herpes simplex encephalitis: Category-specific? *Quarterly Journal of Experimental Psychology A: Human Experimental Psychology*, *44*, 261–284.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain. 3-Dimensional proportional system: An approach to cerebral imaging* (1st ed.). Stuttgart: Thieme.
- Tranel, D., Logan, C. G., Frank, R. J., & Damasio, A. R. (1997). Explaining category-related effects in the retrieval of

- conceptual and lexical knowledge for concrete entities: Operationalization and analysis of factors. *Neuropsychologia*, *35*, 1329–1339.
- Tyler, L. K., Bright, P., Dick, P., Tavares, P., Pilgrim, L., & Fletcher, P. (2003). Do semantic categories activate distinct cortical regions? Evidence for a distributed neural semantic system. *Cognitive Neuropsychology*, *20*, 541–559.
- Tyler, L. K., Moss, H. E., Durrant-Peatfield, M. R., & Levy, J. P. (2000). Conceptual structure and the structure of concepts: a distributed account of category-specific deficits. *Brain and Language*, *75*, 195–231.
- Warrington, E. K., & McCarthy, R. (1983). Category specific access dysphasia. *Brain*, *106*, 859–878.
- Warrington, E. K., & McCarthy, R. A. (1987). Categories of knowledge. Further fractionations and an attempted integration. *Brain*, *110*, 1273–1296.
- Warrington, E. K., & Shallice, T. (1984). Category specific semantic impairments. *Brain*, *107*, 829–854.
- Whatmough, C., Chertkow, H., Murtha, S., & Hanratty, K. (2002). Dissociable brain regions process object meaning and object structure during picture naming. *Neuropsychologia*, *40*, 174–186.