ACADEMIC PRESS

Available online at www.sciencedirect.com

SCIENCE DIRECT®

NeuroImage

NeuroImage 18 (2003) 542–557

www.elsevier.com/locate/ynimg

Rapid Communication

Objects and their actions: evidence for a neurally distributed semantic system

L.K. Tyler,[a,b,*] E.A. Stamatakis,[a] E. Dick,[a] P. Bright,[a] P. Fletcher,[c] and H. Moss[a]

[a] *Department of Experimental Psychology, University of Cambridge, Cambridge CB2 3EB, UK*
[b] *Wolfson Brain Imaging Centre, University of Cambridge, Cambridge CB2 3EB, UK*
[c] *Department of Psychiatry, University of Cambridge, Cambridge CB2 3EB, UK*

Received 21 March 2002; revised 6 June 2002; accepted 26 August 2002

Abstract

An influential model of conceptual knowledge claims that objects are represented in a distributed network of cortical areas that store information about different types of attributes, such as form, colour, and motion (A. Martin et al., 2000, in: The Cognitive Neurosciences, 2nd ed., MIT Press, Cambridge). Two specific claims of this account are that (a) the motions and actions associated with objects (along with other attributes) are automatically activated whenever the object concept is evoked and (b) topographically distinct neural regions are responsible for motion/action attributes pertaining to objects in the categories of tools and animals. We used fMRI to examine the neural activation associated with conceptual processing of nouns referring to animals and tools and for verbs referring to tool-associated actions (e.g., drilling, painting) and biological actions (e.g., walking, jumping). We found that object names and their associated actions activated the same set of neural regions (left fusiform gyrus, superior and middle temporal cortex) consistent with the claim that word tool and animal concepts implicitly activate the actions associated with them. However, there was no evidence of category specificity for either objects or actions, with essentially the same activations for the form and motion attributes of both living and nonliving categories.

A central issue in cognitive neuroscience concerns the way in which conceptual knowledge is represented and processed in the brain. There are currently two opposing classes of account. One claims that there are distinct neural stores for different types of knowledge (sensory/motor; category/domain), while the other argues that conceptual knowledge is represented in an undifferentiated neural network. Studies of brain-damaged patients who show category-specific semantic deficits have been taken as compelling evidence in favour of the former account—that conceptual knowledge is organised into distinct stores in the brain, organised according to either content domain (e.g., Caramazza and Shelton, 1998; Goodglass et al., 1966) or type of property (e.g., Warrington and McCarthy, 1987; Warrington and Shallice, 1984). However, recent computational work has challenged this interpretation of the neuropsychological data by showing how an undifferentiated distributed semantic system can exhibit category-specific deficits when it is "lesioned" to simulate the effects of brain damage (Devlin et al., 1998; Durrant-Peatfield et al., 1997; Greer et al., 2001; Tyler et al., 2000). Moreover, category-specific deficits are not always associated with selective damage to a specific cortical region, as would be predicted by a model in which domain-specific neural systems have developed to process evolutionarily salient stimuli such as animals and plant life (Caramazza and Shelton, 1998). For example, although deficits for living things are usually associated with bilateral temporal damage (Gainotti, 2000), they have been reported in patients who have damage elsewhere (e.g., Patient EW Caramazza and Shelton, 1998), and recent analyses using voxel-based morphometry suggest that there is considerable variation in the extent to which the damage is bilateral (Gitelman et al., 2001). Given the lack of clear lesion–deficit correlations, functional neuroimaging studies, in which we can more directly relate brain activation to the

* Corresponding author. Department of Experimental Psychology, University of Cambridge, Cambridge CB2 3EB, UK. Fax: +44-0-1223-766458.

E-mail address: lktyler@csl.psychol.cam.ac.uk (L.K. Tyler).

1053-8119/03/$ – see front matter © 2003 Elsevier Science (USA). All rights reserved.
doi:10.1016/S1053-8119(02)00047-2

processing of specific types of stimuli in the undamaged brain, have an important role to play in this debate.

A number of neuroimaging studies have been carried out over the past few years to investigate the neural representation of conceptual knowledge, although little consensus has emerged from this work (for reviews, see Martin et al., 2000; Price and Friston, 2002; Tyler and Moss, 2001). Studies have focussed on three major distinctions in the conceptual system—between the domains of living and nonliving things, between nouns and verbs, and between abstract and concrete words. We will restrict the discussion here to the domains of living and nonliving things since these are most relevant to the present research.

In exploring the cortical representation of living and nonliving things, several neuroimaging studies have reported either domain-specific (living vs. nonliving) or category-specific (animals, tools) activations (Cappa et al., 1998; Martin et al., 1996; Moore and Price, 1999; Mummery et al., 1996; Perani et al., 1995). However, there is little consistency in the cortical regions that are activated for these different domains or categories in the various studies, undermining the claim that specific regions of cortex are preferentially involved in the representation and/or processing of concepts in different domains and categories (Tyler and Moss, 2001). Moreover, some studies have reported no significant differences in activation as a function of category or domain when materials are appropriately controlled for relevant variables, such as familiarity, frequency, and imageability (Devlin et al., 2002a; Pilgrim et al., 2002; Tyler et al., 2002), supporting our proposal that conceptual knowledge is represented in a distributed neural system that is not differentiated as a function of category or domain (Tyler and Moss, 2001). The claim here is that neural activation will vary as a function of task and stimulus characteristics rather than category or domain.

Other studies have argued against the category/domain account on other grounds, claiming instead that semantic knowledge is neurally represented according to type of semantic property. For example, Martin and colleagues have claimed that object knowledge is represented in a distributed system involving a variety of neural regions that store information about object attributes, such as form and motion, with the topography of these regions paralleling the organisation of sensory and motor systems (Beauchamp et al., 2002; Chao and Martin, 1999; Martin et al., 1995, 1996, 2000; see also Pulvermuller et al., 2001, for a related view). Attributes relevant to the visual form of an object are represented in the fusiform gyrus, and they are topographically organised such that those that are associated with objects in different categories are represented close together. Pictures of animals and their written names activate (relative to tools) regions of lateral fusiform gyrus bilaterally, whereas tools (both pictures and words) produce significantly greater bilateral activation in the medial portion of the fusiform gyrus (Chao et al., 1999). Martin and colleagues also claim that different regions of temporal cortex are activated by the actions associated with different types of objects, with biological motion typically activating left superior temporal sulcus (L STS) (Bonda et al., 1996) and motion associated with the use of man-made objects generating activation in the left medial temporal gyrus (L MTG) and ventral premotor cortex (Martin et al., 2000).

There are two crucial components to "The Sensory/Motor Account" of Martin et al.: (a) their claims concern the central conceptual representations of objects and entities rather than modality-specific processes of visual object recognition. Thus, it is argued that the same semantic network is activated for both pictures and words (Chao et al., 1999; Martin et al., 1996); and (b) evoking the conceptual representation of an object (via a picture or word) involves automatic and implicit access to information about both its form and the patterns of visual motion with which it is associated (Martin et al., 2000). Thus, pictures of living things (or the words that denote them) should always activate lateral fusiform regions (form attributes) and the STS (biological motion), whereas tools should activate more medial fusiform regions (form attributes) and the L MTG and premotor cortex (actions associated with the use of tools).

However, an alternative interpretation of the data is possible. Perhaps topographically distributed, domain-specific networks of attributes are *not* implicitly activated whenever an object or entity is identified. Rather, the selective activations may be a function of the task in which the subject is engaged. As an example, consider the association between activation of the L MTG and the representation of the actions/motions associated with tools, which is probably the most consistently reported selective activation across published studies (e.g., Devlin et al., 2002b). By far the majority of the evidence for this effect comes from studies in which subjects are presented with an object (either a picture or a word) and they are asked to generate an action word related to that object (Fiez et al., 1996; Martin et al., 1995; Warburton et al., 1996; Wise et al., 1991). In this paradigm, subjects do not only need to activate the conceptual representation of the object, but also to explicitly pair it with a relevant action and to activate the conceptual representation corresponding to the appropriate verb to express that action. For example, when subjects are presented with a picture of a pair of scissors, and they generate the verb *cut* in response, they have activated the conceptual representation for the verb *cut* as well as the noun *scissors*. Perhaps L MTG activation in these studies reflects the conceptual representations of action verbs rather than the implicit activation of tool attributes. This is plausible, especially since in some word generation studies, simple naming of the same objects has been used as the baseline (e.g., Martin et al., 1995). Thus the L MTG activation for action word generation (and similarly fusiform activation for colour word generation) is specific to the generation task *over* and *above* any implicit activation of that region when naming the same object. While there are a few studies that report L MTG activation

for tools in tasks that do not involve explicit generation of an action verb (Chao et al., 1999; Martin et al., 1996; Mummery et al., 1996), these are offset by studies in which no L MTG activation was found for tools (Devlin et al., 2002a; Perani et al., 1995; Pilgrim et al., 2002; Tyler et al., 2002).

The evidence for regional activation of motions/action attributes associated with living thing concepts is somewhat weaker. There is little *direct* evidence that a picture of a living thing (or the word for a living thing) activates the STS. Most evidence for activation of the STS in response to biological actions comes from studies of the perception of biological motion (hand movements) in monkeys (Oram and Perrett, 1994) and of human subjects viewing point-light displays or moving eyes and mouths in human faces (Bonda et al., 1996; Puce et al., 1998; Vaina et al., 2001). Moreover, other researchers have interpreted the findings from the animal literature as evidence that the STS is part of a visuomotor action network involved in the processing of concepts for graspable objects such as tools and fruit, rather than an area specialised for the biological motion attributes of living things (Devlin et al., 2002b). A recent study, published since the inception of the current research, provides more direct evidence of selective STS activation when subjects were presented with either static or moving images of humans versus tools (Beauchamp et al., 2002), Nevertheless, questions still remain about the implicit activation of biological motion information in the STS, since (a) STS activation was significantly greater for the humans that were actually moving than the static pictures of humans and (b) all stimuli were pictures, so we cannot conclude that words would necessarily produce the same activations.

Thus, it remains an open question as to whether there is implicit and automatic activation of the form and motion attributes associated with a concept, whether presented pictorially or in verbal form, as Martin et al. (2000) claim, or whether certain attributes are activated only under specific task conditions. Second, if these attributes are automatically activated, to what extent can their representation be mapped onto topographically distinct neural regions for living and nonliving things? We addressed these questions in an event-related fMRI study by focussing on objects and their associated actions, comparing cortical activation for man-made tools and living entities (denoted by their written names) with activation for written words referring directly to the actions associated with tools (e.g., drilling, welding) and living things (e.g., walking, galloping). If, as Martin et al. (2000) claim, identification of a tool or animal involves the automatic activation of its associated motion attributes, then we should see common activations for tools, for the actions associated with them, and for animals and biological actions. If, in contrast, tool actions and biological motion are only activated in the context of an explicit pairing with the relevant object, then we would not expect to see overlap between the activation generated by objects and their actions in the present task where they are not explicitly paired. Second, if the motion attributes associated with tools and living things are represented in distinct neural regions, then we should see a different area of common activation for tool nouns and tool-action verbs (L MTG) and for living nouns and biological motion verbs (STS). On the other hand, we may find common activation for objects and actions that are not domain-specific. This would be more consistent with an account in which conceptual knowledge is represented in a unitary system that is not differentiated according to semantic domain (Tyler et al., 2000; Tyler and Moss, 2001).

Method

Subjects

We tested 12 right-handed, native English speakers whose mean age was 24 years (8 males, 4 females). Each gave informed consent and was paid for their participation.

Stimuli and design

We used the semantic categorisation task developed for our previous studies (Devlin et al., 2002a; Pilgrim et al., 2002; Tyler et al., 2001, 2002). In the test conditions, subjects saw three words presented sequentially, consisting of two cue words (in lowercase) followed by a target word (in uppercase). Stimuli were presented in the centre of a computer screen, and subjects made a speeded decision as to whether the target word was semantically related to the cue words. For example, on related trials subjects might see the cue words *spoons, forks* followed by the target *KNIVES* or *drilling* and *welding* followed by SOLDERING. On unrelated trials, they might see the cue words *pencils* and *pens* followed by the target *SHOVELS* or *fighting* and *attacking* followed by *SWIMMING*.

There were four test conditions: words denoting animals, tools, biological actions, and actions associated with tools. The words denoting animals and tools were plural nouns whereas the words denoting actions were all inflected verbs. In half the trials the cues and target were semantically related (as determined by pretests; see below) and in the other half they were semantically unrelated. The cues and targets in each category were matched as closely as possible on familiarity, frequency, letter length, and imageability (Baayen and Pipenbrook, 1995; Coltheart, 1981). Since action and object words could not be perfectly matched on length, and imageability, these variables were entered into all analyses (both behavioural and imaging) as covariates. There were no significant differences across the four test conditions on any of the other variables (all F's < 1).

We also constructed, as a baseline condition, a letter categorisation task that shared the same stimulus and response characteristics as the semantic categorisation task but had no lexical or semantic element. Subjects were presented with two sequences of letters, matched in length to

the word stimuli, and were asked whether a third sequence, in capital letters, contained the same letter. For example, "fffff, fffffffff, FFFFFF," "ttttt, tttt, HHHH." There were 80 trials in each of the four experimental conditions (40 same and 40 different) and 80 baseline trials.

Semantic relatedness pretest

We assessed the semantic relatedness of the triplets in each of the four experimental conditions by means of a pretest in which we presented a pair of cue words followed by its target to 11 subjects and asked them to decide how related they were, using a scale of 1–7, where 1 was very unrelated and 7 was very related. For the "same" sets we rejected any triplet with a mean relatedness score of less than 5.5. The mean relatedness score for the final "same" set of items in each of the four experimental conditions was: animals = 6.3; tools = 6.31; object actions = 6.39; biological actions = 6.10 (F[1,10] = 1.539, P = 0.209). The relatedness scores for the unrelated items were significantly lower (mean = 2.08).

Procedure

A trial consisted of two cue stimuli (words or letter strings) followed by a target stimulus. Each of the three words or letter strings was presented for 200 ms with a between-item delay of 400 ms. The target item was followed by a delay of 3 s. Each event (triplet of words/letter strings) lasted for 4.4 s. The same timing parameters were used for both the semantic and baseline tasks. Presentation and timing of stimuli was controlled by DMDX software (Forster and Forster, 1991). Cue words (and letter strings) were in lowercase and the target was in uppercase.

Test and baseline trials were pseudo-randomly organised into four sessions with 30 practise trials (10 baseline and 20 test items) preceding the first session. Each session comprised 100 test trials (20 for each condition plus 20 baseline) with 5 lead-in trials. Subjects made a semantic relatedness judgement on each of the test trials by pressing a left button if target and cues were related and a right button if they were not. In the baseline condition, they indicated whether the target letters were the same or different from the cue strings in the same manner. A word was repeated once in each session, either as a cue or as a target. In sessions 1 and 2, and in sessions 3 and 4, each word appeared once in a trial where the target was related to the cues and once where the target was unrelated. Four session orders were used that were counterbalanced across subjects. We recorded both reaction times and accuracy.

MRI acquisition

Scanning was carried out on a 3-T Bruker Medspec Avance S300 system at the Wolfson Brain Imaging Center, Cambridge, England, using a gradient-echo EPI sequence (TR = 3000 ms, TE = 30 ms, flip angle 90°, FOV 25 × 25 cm, 21 oblique slices, 4 mm thick (1-mm gap between slices, 128 × 128 in-plane resolution, 152 repetitions) with head coils, 200-kHz bandwidth, and spin-echo-guided reconstruction. T1-weighted scans were acquired for anatomical localisation.

Results

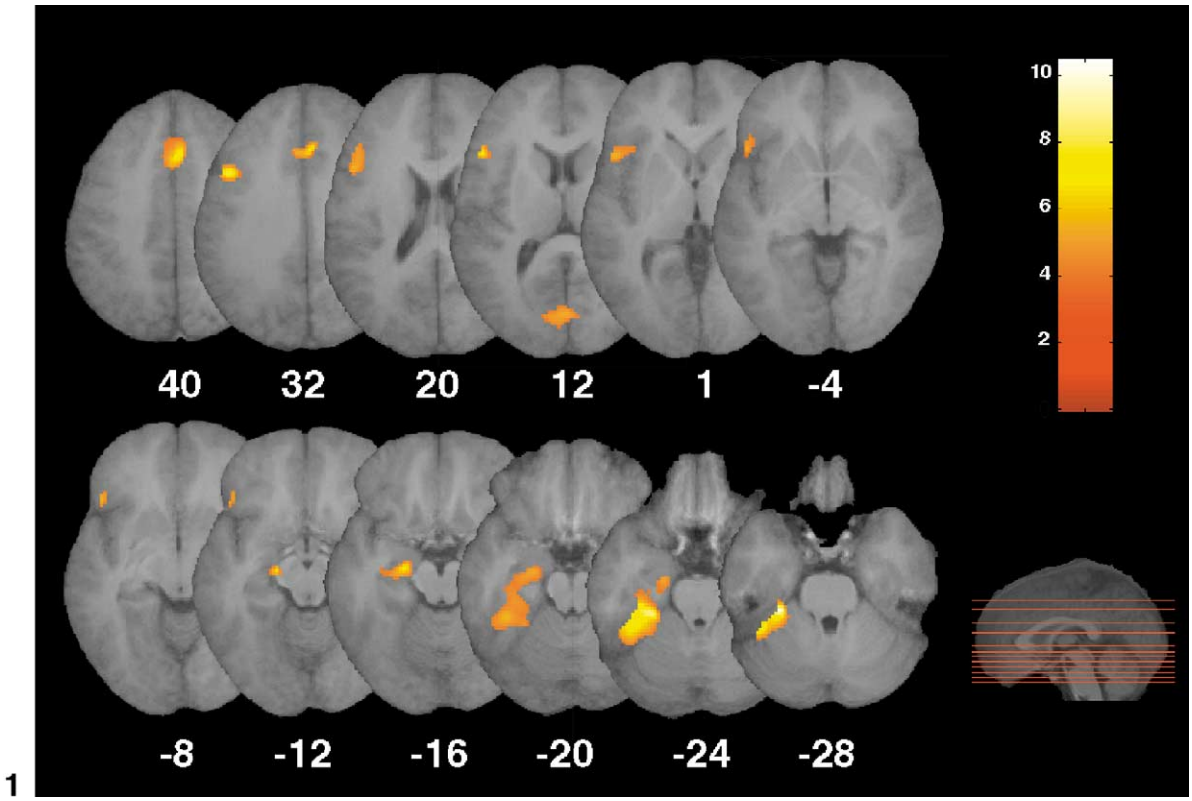
Behavioural data

Behavioural data collected during scanning showed no difference in reaction times from any of the four test conditions (F[1,291] = 1.16, P = 0.282) when letter length and word frequency were included in a covariate analysis.

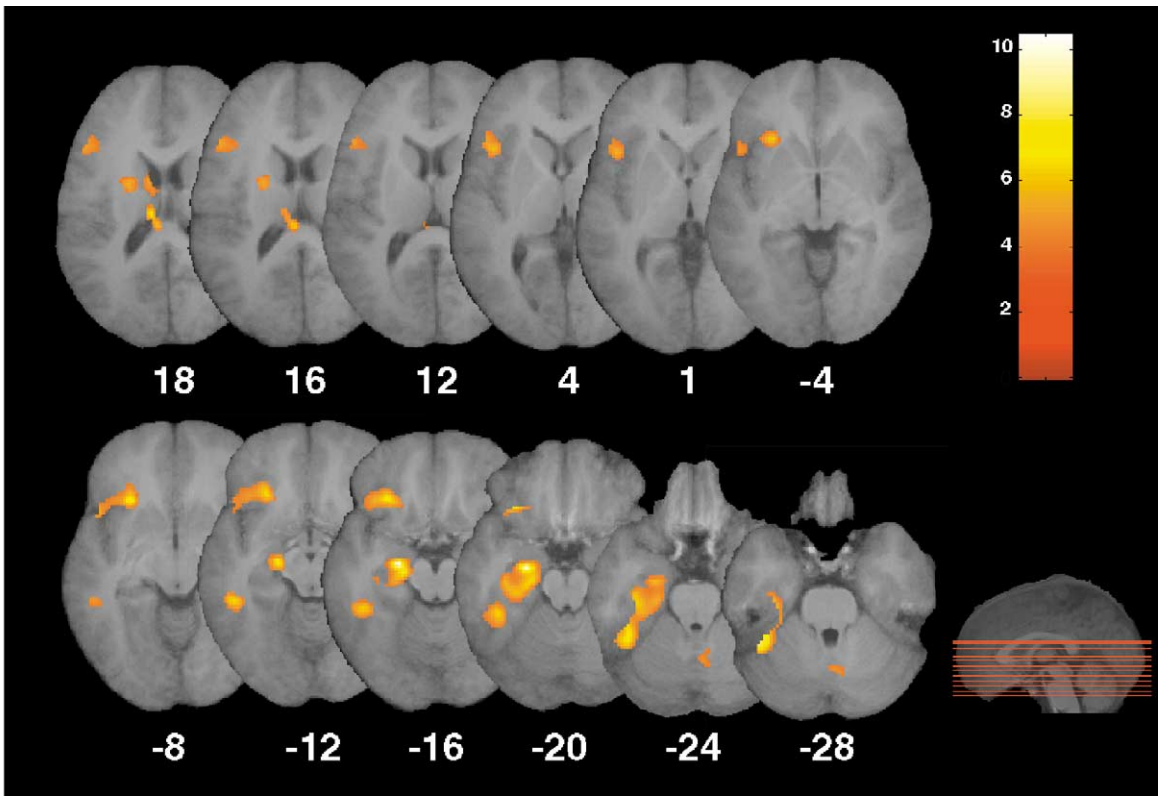
Imaging data

Preprocessing (slice timing correction, image realignment into standard stereotactic space, and smoothing) and statistical analysis of the data were performed using SPM99 software (Wellcome Institute of Cognitive Neurology, www.fil.ion.ucl.ac.uk), implemented in Matlab (Mathworks Inc., Sherborn, MA, USA). The first six scans of each time series were discarded to allow for T1 equilibrium before the test trials started. Slice timing correction was followed by image realignment to account, respectively, for different slice acquisition times and head motion. The images were then spatially normalised to a standard EPI template based on the Montreal Neurological Institute (MNI) reference brain, using 7 × 8 × 7 nonlinear basis functions. The spatially normalised images were smoothed with an isotropic 12-mm full-width half-maximal Gaussian kernel. The data were analysed using the general linear model as implemented in Statistical Parametric Mapping (SPM99b, Wellcome Institute of Cognitive Neurology, www.fil.ion.ucl.ac.uk). The BOLD response for each event was modelled with the canonical haemodynamic response function (HRF). The time series in each voxel were highpass filtered to remove low-frequency noise and scaled to a grand mean of 100 over voxels and scans within each session.

Four sessions and five event types were entered into the model (animals, tools, biological actions, artefact actions, and baseline). Since the sets could not be perfectly matched on imageability and letter length, these variables were entered as parametric modulators (with linear expansion). Trials were entered as events and modelled using a canonical HRF. This analysis was performed for each subject, and contrast images were combined into a group random effects analysis. Brain regions that were activated for each condition compared to baseline, and for the direct contrasts among the four test conditions were identified by examining a height threshold of 0.001. Within this threshold we looked only at clusters that were significant after correcting for multiple comparisons across the whole brain volume at the 0.05 level. We subsequently looked at corrected clusters



1



2

Fig. 1. Clusters activated for the contrast of tools minus baseline at a threshold of $P < 0.05$ corrected for multiple comparisons (height threshold of 0.001). The activations are superimposed on the mean T1 image obtained from the 12 subjects. The colour bar indicates z scores and the red lines on the sagittal section (bottom right) indicate the location of the horizontal sections shown. The Talairach z coordinates are given below each horizontal section. The activated areas are described in detail in Table 1.

Fig. 2. Clusters activated for the contrast of animals minus baseline at a threshold of $P < 0.05$ corrected for multiple comparisons (height threshold of 0.001). The activations are superimposed on the mean T1 image obtained from the 12 subjects. The colour bar indicates z scores and the red lines on the sagittal section (bottom right) indicate the location of the horizontal sections shown. The Talairach z coordinates are given below each horizontal section. The activated areas are described in detail in Table 2.

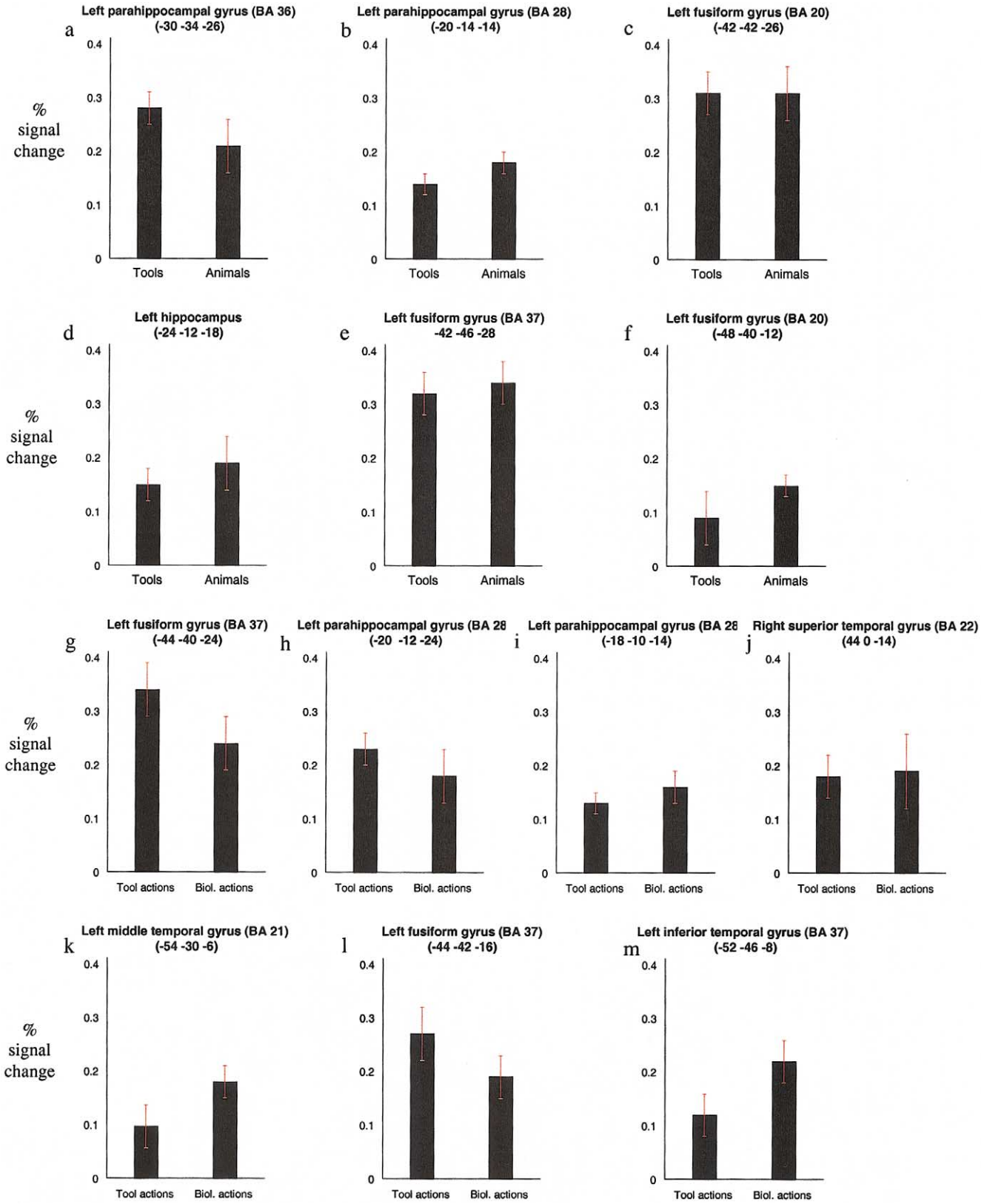


Fig. 3. Plots of percentage of signal change (with standard error bars) at each of the local maxima in temporal cortex for the contrast tools minus baseline (a–c), animals minus baseline (d–f), tool actions minus baseline (g–j), and biological actions minus baseline (k–m). Coordinates presented in MNI space.

Table 1
Brain areas of activity for the contrast of tools minus baseline

Regions	Coordinates			Voxel level		Cluster level	
	x	*y*	*z*	$P_{corrected}$	*t*	$P_{corrected}$	Extent
L inf. frontal gyrus							
BA 44	−46	12	32	0.214	7.73	0.000	534
BA 45	−50	20	12	0.436	6.74	(*0.000*)	(*4248*)[a]
BA 47	−48	28	−10	0.784	5.70		
L parahip. gyrus							
BA 36	−30	−34	−26	0.035	10.24	0.000	746
BA 28	−20	−14	−14	0.117	8.54		(*4248*)[a]
L fusiform gyrus (BA 20)	−42	−42	−26	0.246	7.54		
R ant. cingulate gyrus (BA 32)	4	24	36	0.056	9.55	0.000	473
	0	14	48	0.450	6.70	(*0.003*)	(*1074*)
L medial frontal gyrus (BA 32/8)	*−6*	*28*	*54*	*0.999*	*4.26*		
Cuneus (BA 17)	0	−80	8	0.505	6.52	0.008	230
R. cuneus (BA 17)	16	−82	10	0.999	4.12	(*0.000*)	(*2365*)
R. lingual gyrus (BA 19)	*10*	*−58*	*−2*	*0.511*	*6.50*		

Note. Peaks shown for all clusters significant at $P < 0.05$. Coordinates presented in MNI space. Cluster extents are presented at height threshold of 0.001 and 0.01 (italics). Peaks significant only at the lower threshold are shown in italics. Multiple peaks within an extent are shown on subsequent lines. L, left; R, right; inf., inferior; ant., anterior; parahip., parahippocampal.

[a] Single cluster at threshold 0.01 encompassing >1 clusters at threshold 0.001.

after lowering the height threshold to 0.01 to take a less conservative approach to the data. Since SPM coordinates are given in MNI space the results reported here were converted to Talairach space with a nonlinear transform.

Objects

Comparing tool activation against the baseline, we found four large clusters of activation, primarily in LH, at a height threshold of 0.001. The largest cluster (746 voxels) centered around the L parahippocampal gyrus (BA 28, 36) and extended into the fusiform (BA 37). The fusiform activation was maximal around the middle and anterior portions (BA 20, 37, and 38). A second cluster was located in the right (R) anterior cingulate gyrus extending into the medial frontal gyrus (BA 8,9), while a third centred around the L IFG extending into the medial frontal gyrus. Finally, there was a cluster of activation in the R cuneus extending into the L. When we lowered the height threshold to $P = 0.01$, the same LH regions were activated but with greater extent. In particular, the parahippocampal cluster spread into the STG and the MTG, and the occipital activation now extended into the RH peaking in the R lingual gyrus (see Table 1 and Fig. 1).

Comparing animals against baseline we found a very similar set of activations, including a cluster (766 voxels) in the L IFG (BA 45, 47) extending into the STG (BA 38,22) and a second large cluster (1046) with a peak in the L hippocampus and parahippocampal gyrus (BA 28,36,35), spreading into the ITG (BA 37) and fusiform gyrus (BA 20). A third cluster was located in the corpus callosum extending into the L anterior cingulate gyrus (BA 24).

When we lowered the height threshold to $P = 0.01$, the L IFG cluster merged with the corpus callosum/cingulate gyrus activation, extending into the L MTG and RH. Three new RH clusters were found involving IFG, fusiform gyrus, parahippocampal, and anterior cingulate regions (see Table 2 and Fig. 2).

To determine whether there were any regions significantly activated for tools more than animals, we compared them directly and found no significant differences at a corrected level or when we lowered the threshold to 0.01. Finally, we plotted the percentage of signal change at each of the local maxima in temporal cortex for the tools–baseline contrast (Fig. 3a–c) and the animals–baseline contrast (Fig. 3d–f). None of the differences were significant. Thus, contrary to the claims made by Martin et al. (2000), we did not find that MTG was more active for tools and STS was more active for animals.

The degree to which the activation for tools and animals overlap can be seen in Fig. 4 where we overlay the animals–baseline activation (at a height threshold of 0.01) and tools–baseline activation (also at 0.01). Fig. 4 clearly shows the considerable overlap in activation for tools and animals. In general, animals activate the same LH regions as tools although to a slightly greater extent. The only other notable difference is that there is slightly more activation for tools in the L STS, although this was not significant.

Actions

We compared tool actions against the baseline and found a similar set of regions activated as for the tools themselves. A large region of L IFG was activated (1919 voxels), in-

Table 2
Brain areas of activity for the contrast of animals minus baseline

Region	Coordinates			Voxel level		Cluster level	
	x	*y*	*z*	$P_{corrected}$	*t*	$P_{corrected}$	Extent
L hippocampus	−24	−12	−18	0.034	10.41	0.000	1046
L fusiform gyrus							
BA 37	−42	−46	−28	0.201	7.94	(*0.000*)	(*2781*)
BA 20	−48	−40	−12	0.603	6.34		
L inf. frontal gyrus (BA 47)	−28	24	−8	0.336	7.23	0.000	766
BA 47, 45	−30	28	−18	0.341	7.21	(*0.000*)	(*4757*)[a]
	−44	18	4	0.782	5.81		
L corpus callosum	−8	−20	20	0.114	8.70	0.000	387
	−6	4	24	0.663	6.16		(*4757*)[a]
	−4	−28	16	0.779	5.82		
R cerebellum	10	−72	−34	0.481	6.71	0.038	146
	8	−64	−26	0.991	4.66	(*0.019*)	(*693*)
R inf. frontal gyrus (BA 47)	*34*	*28*	*−10*	*0.792*	*5.78*	*0.002*	*1019*
	42	*18*	*6*	*0.956*	*5.08*		
R ant. cingulate gyrus (BA32)	*18*	*26*	*24*	*0.991*	*4.66*		
R parahippocampal gyrus							
BA 35	*16*	*−26*	*−22*	*0.908*	*5.35*	*0.022*	*667*
BA 28	*10*	*−20*	*−20*	*0.937*	*5.20*		
R fusiform gyrus (BA 20)	*38*	*−28*	*−22*	*0.958*	*5.07*		
R ant. cingulate gyrus (BA 32)	*4*	*20*	*44*	*0.908*	*5.35*	*0.021*	*675*

Note. Peaks shown for all clusters significant at $P < 0.05$. Coordinates presented in MNI space. Cluster extents are presented at height threshold of 0.001 and 0.01 (italics). Peaks significant only at the lower threshold are shown in italics. Multiple peaks within an extent are shown on subsequent lines. L, left; R, right; inf., inferior; ant., anterior.

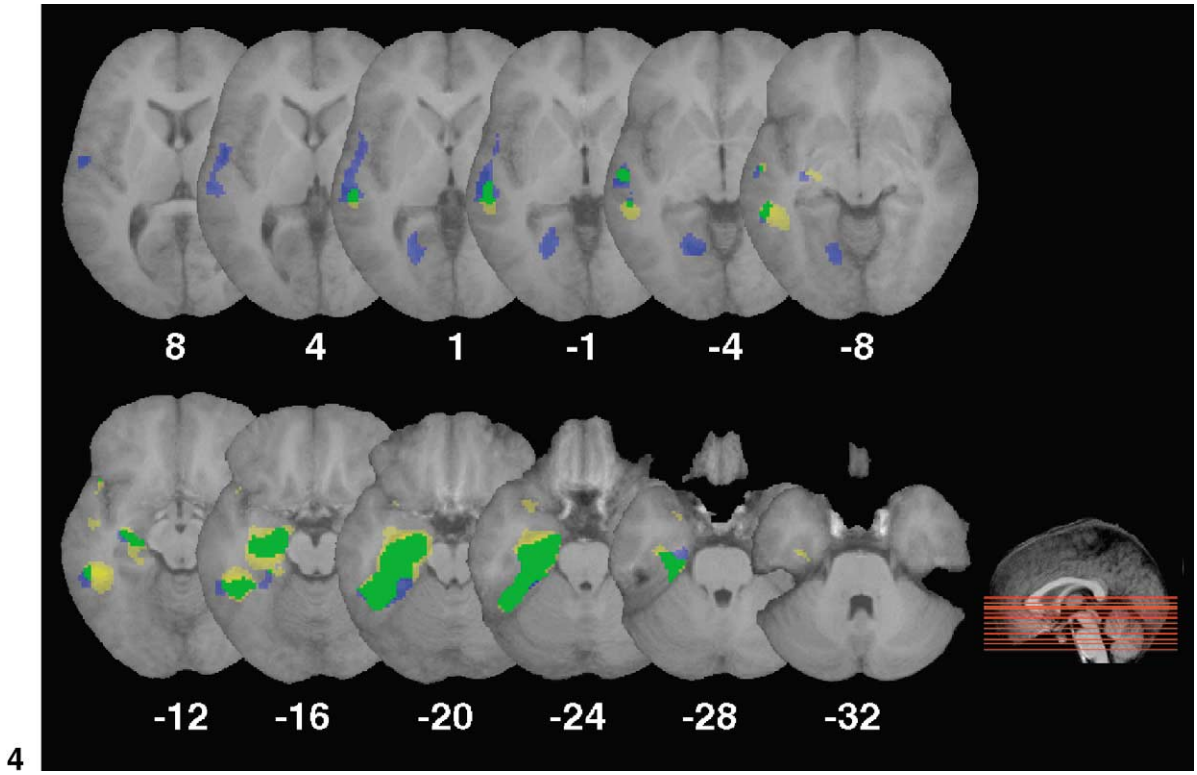
[a] Single cluster at threshold 0.01 encompassing >1 clusters at threshold 0.001.

cluding the insula and extending into the middle frontal gyrus and inferiorly into the STS (BA 38), a second cluster (672) peaked in the R anterior cingulate and extended into the L MFG (BA 6,8) a third cluster (986) focussed on the L parahippocampal gyrus and the fusiform, a fourth cluster of 227 voxels in the L lingual gyrus, and a fifth (178 voxels) in the R IFG (Table 3 and Fig. 5). When the height threshold was lowered, a very large cluster (12,391 voxels) was activated, encompassing the IFG, MFG, STS, and the cingulate gyrus bilaterally.

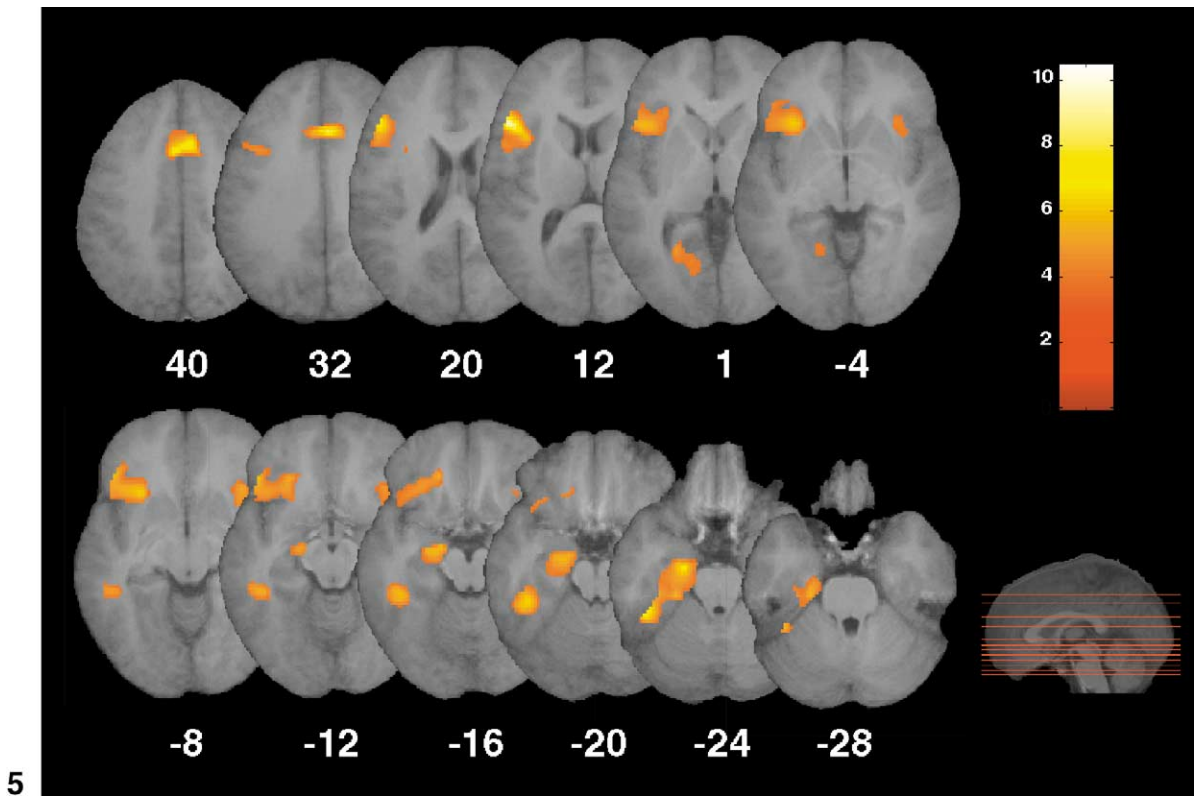
Biological actions compared against the baseline produced a very similar set of activations as for the tools actions−baseline. At a height threshold of 0.001, we found five large clusters of significant activation. One large cluster (1824 voxels) in the L IFG (BA 44,45, 47), extended inferiorly into the STG (BA 38,22) and included the insula (BA 13) and precentral gyrus; a second cluster (603 voxels), in the L parahippocampal gyrus (BA 35,34,28) and fusiform gyrus; and third cluster of 424 voxels, in the L fusiform, ITG, and MTG (BA 21). Finally, there was a cluster of 210 voxels in the L posterior parahippocampal gyrus (BA 27,30) extending into the L lingual gyrus. At a lower threshold, activation spread into L MTG, R anterior cingulate, and L medial frontal gyrus (Table 4 and Fig. 6). When we compared biological and tool actions, we found no significant differences at a height threshold of 0.01. We also plotted the percentage of signal change at each of the local maxima in temporal cortex for the tool actions−baseline contrast (Fig. 3g–j) and the animal actions−baseline contrast (Fig. 3k–m). Biological actions generated greater signal change compared to tool actions in two regions, L MTG and L ITG (Fig. 3k and m), and tool actions showed greater activation than biological actions in two regions in the left fusiform (Fig. 3g and l). However, only one of these differences was significant (Fig. 3g) when we controlled for the number of comparisons using Bonferroni correction, and this is not a region that has been claimed to be more involved in tool-related activity.

Comparing objects and actions

Comparing tools against tool actions, we found no significant differences at either the $P = 0.01$ or the $P = 0.001$ level of significance. The reverse contrast also showed no significant differences at a threshold of 0.001. However, when we lowered the height threshold to 0.01, we found that tool actions generated much larger activation in the L IFG and the insula than the tools themselves (Table 5). We attribute this to differences in lexical processing in that the words denoting tools are plural nouns, whereas the words denoting actions are inflected verbs (*hammering*). The L IFG is specifically involved in processing regular verb mor-



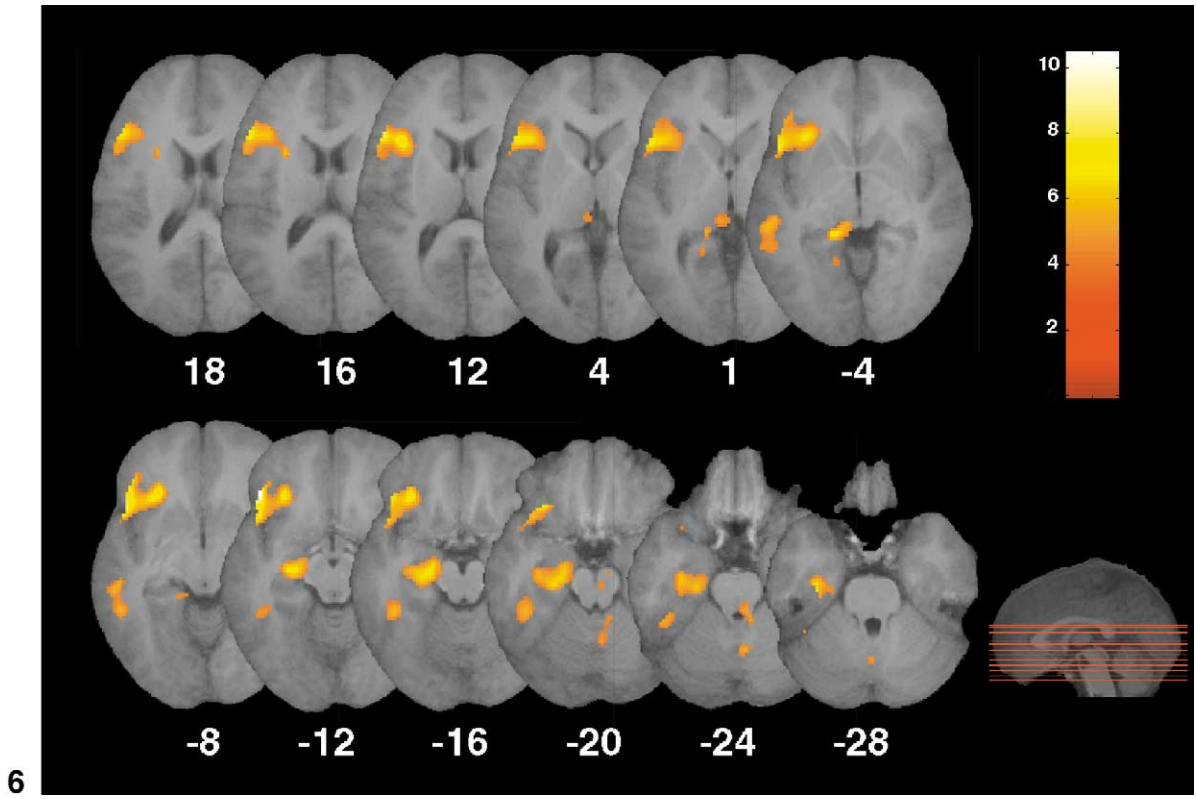
4



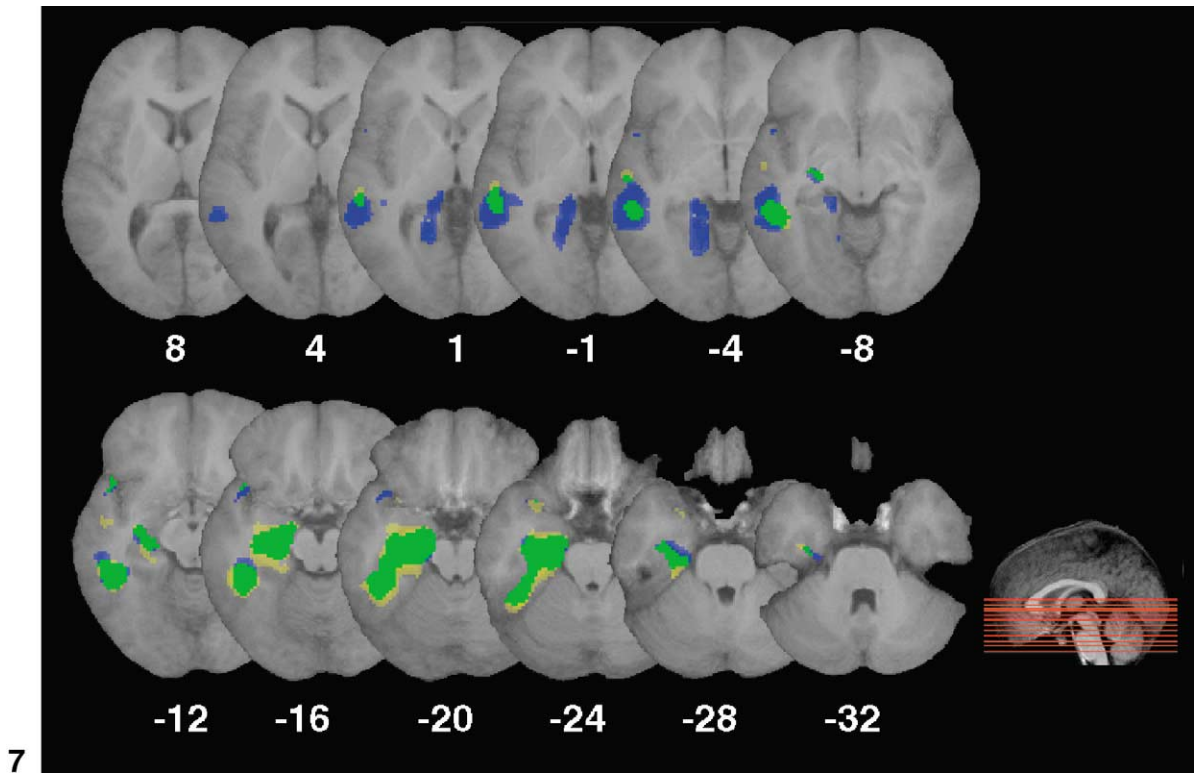
5

Fig. 4. Clusters of activation in left temporal cortex for the contrast animals−baseline (yellow) and tools−baseline (blue) and their overlap (green). Both contrasts were obtained at a threshold of $P < 0.05$ corrected for multiple comparisons (height threshold of 0.01). Clusters are superimposed on the mean T1 image obtained from the 12 subjects. The red lines on the sagittal section (bottom right) indicate the location of the horizontal sections shown. The Talairach *z* coordinates are given below each horizontal section.

Fig. 5. Areas activated for the contrast of tool actions minus baseline at a threshold of $P < 0.05$ corrected for multiple comparisons (height threshold of 0.001). The activations are superimposed on the mean T1 image obtained from the 12 subjects. The colour bar indicates *z* scores and the red lines on the sagittal section (bottom right) indicate the location of the horizontal sections shown. The Talairach *z* coordinates are given below each horizontal section. The activated areas are described in detail in Table 3.



6



7

Fig. 6. Areas activated for the contrast of biological actions minus baseline at a threshold of $P < 0.05$ corrected for multiple comparisons (height threshold of 0.001). The activations are superimposed on the mean T1 image obtained from the 12 subjects. The colour bar indicates z scores and the red lines on the sagittal section (bottom right) indicate the location of the horizontal sections shown. The Talairach z coordinates are given below each horizontal section. The activated areas are described in detail in Table 4.

Fig. 7. Clusters of activation in the left temporal lobe for the contrast of animals–baseline (yellow), biological actions–baseline (blue), and their overlap (green). Both contrasts were obtained at a threshold of $P < 0.05$ corrected for multiple comparisons (height threshold of 0.01). The clusters are superimposed on the mean T1 image obtained from the 12 subjects. The red lines on the sagittal section (bottom right) indicate the location of the horizontal sections shown. The Talairach z coordinates are given below each horizontal section.

phology as has been shown in both neuropsychological and neuroimaging studies (Tyler et al., 2002; Ullman et al., 1997).

Comparing biological actions against animals, we find a large cluster in the L IFG, which, as with the words denoting biological actions, we attribute to this region's participation in processing the morphological structure of inflected verbs (Tyler et al., 2002). In addition, there was a cluster of activation in the L MTG (Table 6). When we lowered the threshold, we found that the L MTG activation extended more superiorly. In the reverse contrast, where we subtract the animal activation from the activation for biological actions, we found no significant activations at either $P = 0.01$ or $P = 0.001$. The degree to which the activation for animals and biological actions overlap in the L temporal lobe is shown in Fig. 7 where we overlay the animals–baseline activation and the biological actions–baseline activation (both at 0.01). Although there was more extensive activation for biological actions in superior regions, a high degree of overlap is observed across the sections.

Discussion

Two issues motivated the current research: first, whether objects and entities implicitly and automatically activate the actions with which they are associated, as claimed by Martin et al. (2000). The present results partially confirm this claim in that the same regions of the L fusiform gyrus and superior and middle temporal cortex were consistently activated both by the name of an object or entity and by the actions with which it is associated. The second issue was whether actions involved in the use of tools and biological actions are topographically represented in distinct neural regions. Since both types of action activated essentially the same cortical regions, the present results undermine claims for different neural networks responsible for processing different types of information that tend to be associated with different categories of knowledge (Chao and Martin, 1999; Martin et al., 2000).

With respect to the first issue, we found considerable overlap in the activation for tools and for their associated actions. The single exception to this was the L IFG activation generated by the tool-associated action words when we lowered the height threshold to 0.01. Since these words were also regularly inflected verbs (*hammering, hitting*), and the L IFG has been shown to be specifically involved in processing regularly inflected verbs (Marslen-Wilson and Tyler, 1997; Tyler et al., 2002; Ullman et al., 1997), the additional L IFG activation invoked by the verbs most plausibly resulted from the processing of their morphological structure. The activations for the names of animals and biological activities also largely overlapped, with the exception of additional activation for actions in the L IFG (verb processing) and in the L MTG. According to Martin et al., the L MTG should be activated for tool-associated actions and not for biological motion. However, these results support the claims of Martin et al. (2000) that processing the name of an object or entity involves the automatic activation of its motion-associated properties. However, it should be noted that an alternative interpretation is possible, in which the directionality of the argument is reversed such that action words automatically and implicitly activate the objects with which they are associated (e.g., when people hear the word *cut,* the *scissors* concept is activated.) In fact, we would suggest that *both* interpretations are correct; object nouns automatically activate their typical actions, and action verbs automatically evoke their typical agents and instruments. This is consistent with our findings of essentially overlapping neural activation for nouns and verbs in earlier study PET studies (Tyler et al., 2001).

The second issue motivating this research concerned the claim that the STS is the neural region for the selective processing and/or representation of biological motion and the MTG is a region where the movements associated with tool actions are stored and/or processed. Although both regions were consistently activated by objects and actions in our study, they were not preferentially activated by either tool-associated activity or biological actions, respectively. Perhaps it is not so surprising that words denoting biological movement do not selectively activate the STS, since almost all the studies which show activation in response to biological motion in this region have used a very different methodology. This has involved using point-light displays where movement is inferred from the trajectory of moving sets of lights (Bonda et al., 1996; Vaina et al., 2001) and where the focus is on the neural substrate involved in the perception of biological motion.

These studies show activation in the STS for biological movement. However, they rarely include a direct comparison between biological motion and the movements associated with the use of artefacts. Instead, most experiments contrast biological movement with various types of control conditions. For example, Vaina et al. (2001) used the point-light display methodology to investigate the neural regions associated with biological motion by comparing point-light displays depicting walking with those that depicted a "scrambled" walker in addition to other control conditions. They found that areas activated during the biological motion recognition task included both ventral and dorsal extrastriate cortical regions and their confluence in the STP in the STS.

These studies do not provide evidence that the movements associated with artefacts (such as tools) do not also activate the same regions as biological actions. In fact, the study by Bonda et al. (1996) suggests that the movements associated with the use of small artefacts activate the same regions of the STS as do biological movements. In this study, the perception of whole-body motion (dancing) and goal-directed hand actions (picking up a cup and moving it towards the mouth) were contrasted with a variety of different control conditions. These two types of motion were both considered to be examples of biological motion, even

Table 3
Brain areas of activity for the contrast of tool actions minus baseline

Regions	Coordinates			Voxel level		Cluster level	
	x	*y*	*z*	$P_{corrected}$	*t*	$P_{corrected}$	Extent
L inf. frontal gyrus							
BA 45	−50	22	10	0.021	10.91	0.000	1919
BA 47	−32	22	−6	0.474	6.56	(*0.000*)	(*12,391*)[a]
	−46	32	−10	0.497	6.49		
R ant. cingulate gyrus (BA 32)	6	22	34	0.025	10.65	0.000	672
	−4	14	46	0.059	9.40		(*12,391*)[a]
	−4	28	44	0.991	4.53		
L fusiform gyrus (BA 37)	−44	−40	−24	0.344	7.03	*0.000*	986
L parahip. gyrus (BA 28)	−20	−12	−24	0.349	7.01		(*12,391*)[a]
	−18	−10	−14	0.390	6.85		
L parahip./lingual gyrus (BA 19)	−24	−58	2	0.951	4.97	0.010	227
L lingual gyrus							
BA 17	−10	−78	6	0.989	4.58	(*0.002*)	(*1,175*)
BA 18	−14	−66	2	0.996	4.39		
R inf. frontal gyrus (BA 47)	*36*	*24*	*−8*	*0.851*	*5.43*	*0.007*	*943*
R sup. temporal gyrus (BA 22)	*44*	*0*	*−14*	*0.999*	*4.08*		
R inf. frontal gyrus (BA 47)	*46*	*20*	*6*	*1.000*	*3.55*		
R cerebellum	*10*	*−76*	*−34*	*0.940*	*5.04*	*0.018*	*783*
	6	*−60*	*−22*	*0.972*	*4.80*		
	10	*−50*	*−16*	*0.991*	*4.52*		

Note. Peaks shown for all clusters significant at $P < 0.05$. Coordinates presented in MNI space. Cluster extents are presented at height threshold of 0.001 and 0.01 (italics). Peaks significant only at the lower threshold are shown in italics. Multiple peaks within an extent are shown on subsequent lines. L, left; R, right; inf., inferior; sup., superior; ant., anterior; parahip., parahippocampal.

[a] Single cluster at threshold 0.01 encompassing >1 clusters at threshold 0.001

though the goal-directed movement involved actions associated with artefact use. Bonda et al. (1996) found that when the two biological motion conditions were directly compared, there was no difference in either L or R STS activations. Thus, there is no direct evidence from the point-light display experiments that the same cortical regions are not involved in the movements associated with the use of artefacts and with biological motion. Indeed, it would seem implausible that they would not be, since nonmechanical artefacts only move if an animate agent initiates their movement. Thus, most actions associated with the use of objects must, of necessity, include biological motion. Nevertheless, Beauchamp et al. (2002) have recently demonstrated that the STS may be selectively activated for biological motion, in a study where tool and human movements *are* directly contrasted. Significantly increased STS activation was found when subjects viewed video clips of natural articulated human movements, when compared both to moving tools and to humans moving in an artificial unarticulated way (e.g., whole-body rotation). This suggests that the STS may be sensitive to the complex movements of parts and wholes that are typical of humans and animals (although it was not possible to determine whether the STS would also respond to video clips of tools that are artificially animated to move in this complex articulated way, as this condition was not included).

We also found no selective activation for the actions associated with tool use in the L MTG, predicted by Martin et al. (2000). With the exception of the recent study by Beauchamp et al. (2002), there is no direct empirical evidence for this region's involvement in tool-associated movement. Instead, the evidence is rather indirect and relies upon the fact that naming and identifying tools activates the posterior L MTG, a region which is also activated when subjects generate action words (Martin et al., 2000) and which is close to motion areas in the extrastriate cortex (Corbetta et al., 1991). Indeed, the study by Martin et al. (1995) investigating the neural substrate for colour and motion (the latter was meant to be equivalent to function) for manufactured objects found that generating motion words for objects activated, amongst other regions, both the MTG and the STS. Again, more direct evidence for selective activation of the L MTG for tool-related actions has now been shown in the Beauchamp et al. (2002) study. A goal for future research will be to explore the bases of the contrasting results in this study and our own. One possibility is the difference between processing of pictures versus words. Although Martin et al. (2001) claim that the distributed network of regions specialised for different kinds of semantic properties should be recruited when subjects process verbally presented concepts as well as pictures/real objects (i.e., their claims are about conceptual representa-

Table 4
Brain areas of activity for the contrast of biological actions minus baseline

Regions	Coordinates			Voxel level		Cluster level	
	x	*y*	*z*	$P_{corrected}$	*t*	$P_{corrected}$	Extent
L inf. frontal gyrus (BA 47)	−46	30	−12	0.041	10.02	0.000	1824
	−32	32	−18	0.120	8.54	(*0.000*)	(*11,619*)[a]
L sup. temporal gyrus (BA 38)	−50	18	−6	0.126	8.46		
L parahip. gyrus							
BA 30	−14	−36	−2	0.236	7.62	0.011	210
	−8	−30	−2	0.840	5.54		(*11,619*)[a]
BA 19	−16	−48	0	0.970	4.88		
L parahip. gyrus (BA 28)	−26	−16	−12	0.363	7.03	0.000	603
L fusiform gyrus (BA 36)	−34	−16	−26	0.441	6.75		(*11,619*)[a]
L parahip. gyrus (BA 35/36)	−26	−22	−18	0.609	6.23		
L mid. temporal gyrus (BA 21)	−54	−30	−6	0.832	5.56	0.000	424
L fusiform gyrus (BA 37)	−44	−42	−16	0.850	5.50		(*11,619*)[a]
L inf. temporal gyrus (BA 37)	−52	−46	−8	0.885	5.37		
Cerebellum	−6	−68	−34	0.874	5.41	0.017	192
	6	−36	−26	0.907	5.27		(*11,619*)[a]
	6	−62	−24	0.954	5.01		
R ant. cingulate gyrus (BA 32)	*2*	*18*	*40*	*0.993*	*4.55*	*0.009*	852
L medial frontal gyrus (BA 8)	*−4*	*32*	*40*	*0.999*	*4.21*		

Note. Peaks shown for all clusters significant at $P < 0.05$. Coordinates presented in MNI space. Cluster extents are presented at height threshold of 0.001 and 0.01 (italics). Peaks significant only at the lower threshold are shown in italics. Multiple peaks within an extent are shown on subsequent lines. L, left; R, right; inf., inferior; mid., middle; sup., superior; ant., anterior; parahip., parahippocampal.

[a] Single cluster at threshold 0.01 encompassing >1 clusters at threshold 0.001.

tion rather than object recognition alone), it is possible that these activations are more robust when the task involves access to conceptual information via the object recognition system, rather than via visual or auditory word recognition processes. Further studies directly contrasting verbal and pictorial presentation of the same objects and actions will be needed to address this question.

Finally, this study also allowed us to test the claims for differential distribution of cortical regions involved in processing objects (tools) and entities (animals) themselves. Martin et al. (2000) claim that animal names activate regions of the lateral fusiform (associated with their visual properties) and the STS (associated with biological movements), whereas tools activate the medial fusiform and the MTG. Whether we assume a conservative or more lenient threshold, our results do not support these claims. In our study, animal and tool names robustly activated similar regions in the parahippocampal gyrus, fusiform, and middle and superior temporal cortex. This is clear from Fig. 4, which shows the overlap of activation at the low height threshold (to maximise any potential differences) and where animals and tools activate the same regions of fusiform and temporal cortex. The main difference between them consisted of a small amount of additional activation for tools in the L STS, a region that is predicted by Martin et al. (2000) to be preferentially activated for animals rather than tools.

Our results demonstrate that tools and animals and the actions with which they are associated activate essentially the same set of neural regions. This is a result that is consistent with our previous studies using PET and fMRI using written words (Devlin et al., 2002a; Pilgrim et al., 2002) and pictures as stimuli (Tavares and Tyler, 2001; Tyler and Moss, 2001; Tyler et al., submitted); and also with other studies (Moore and Price, 1999). Moreover, we also find that the activation generated by animals is generally more extensive, although in the same regions, as that generated by tools (Fig. 4). This is consistent with the conceptual structure account, a model of the representation of conceptual knowledge that we have recently developed (Tyler and Moss, 2001; Tyler et al., 2000). We have argued that conceptual knowledge is represented in a distributed system based upon semantic features (or some more abstract level of representation). Concepts vary in terms of the num-

Table 5
Brain areas of activity for the contrast of tool actions minus tools

Region	Coordinates			Voxel level		Cluster level	
	x	*y*	*z*	$P_{corrected}$	*t*	$P_{corrected}$	Extent
L inf. frontal gyrus							
BA 44	*−50*	*16*	*14*	*0.875*	*5.24*	*0.007*	*1026*
BA 47	*−44*	*32*	*−14*	*0.982*	*4.59*		
Insula (BA 13)	*−38*	*12*	*6*	*1.00*	*3.82*		

Note. Peaks shown for the only cluster significant at $P < 0.05$. Coordinates presented in MNI space. The cluster extent is presented at a height threshold of 0.01 (no clusters survived a height threshold of 0.001). L, left.

Table 6
Brain areas of activity for the contrast of biological actions minus animals

Region	Coordinates			Voxel level		Cluster level	
	x	*y*	*z*	$P_{corrected}$	*t*	$P_{corrected}$	Extent
L inf. frontal gyrus (BA 45)	−50	20	10	0.046	7.30	0.000	522
L inf. frontal gyrus (BA 47)	−36	28	−2	0.387	6.94	(*0.000*)	(*1574*)
L inf. frontal gyrus (BA 45)	−42	24	18	0.710	5.94		
L mid. temp. gyrus (BA 22)	−60	−50	2	0.320	7.21	0.003	273
L mid. temp. gyrus (BA 21)	*−52*	*−32*	*−4*	*0.999*	*4.20*	(*0.012*)	(*805*)

Note. Peaks shown for all clusters significant at $P < 0.05$. Coordinates presented in MNI space. Cluster extents are presented at height threshold of 0.001 and 0.01 (italics). Peaks significant only at the lower threshold are shown in italics. Multiple peaks within an extent are shown on subsequent lines. L, left; mid., middle; inf., inferior.

ber and types of features with which they are associated and the relationships between those features. These differences give rise to category effects without category structure being explicitly represented. For example, animals tend to have larger numbers of features than tools and many of these features are shared across many concepts. Moreover, the shared features of animals (e.g., eyes, move, legs) tend to be correlated with each other in that the presence of one presupposes the presence of another (e.g., has fur, has legs, has eyes, moves). Tools, on the other hand, have more distinctive features and fewer shared features (Greer et al., 2001; McRae et al., 1997; Tyler and Moss, 2001). Within this system, there is no explicit specialisation as a function of category or domain; rather, conceptual knowledge is represented and processed within a distributed system that involves a number of cortical regions including temporal, frontal, occipital, and parietal lobes. These different regions will be involved to a greater or lesser extent depending on a number of factors: the type of input (spoken words, written words, pictures), the nature of the task (e.g., naming words or pictures, reading words, matching), and the additional nonlinguistic cognitive demands required. Thus, for example, when the stimuli consist of pictures, the occipital cortex will be more involved than when they are spoken words, and the inferior prefrontal cortex will be more involved as the processing demands of the task and materials increase (Buckner et al., 2000). However, there are no specific regions specialised for the processing of concepts in any specific conceptual domain or category (Tyler and Moss, 2001).

This set of claims predicts that animals and tools should activate essentially the same neural networks in occipital, temporal, and frontal regions—a pattern that we observe in the present study. In addition, given the fact that animals tend to have more shared correlated properties than tools, the set of features which are activated upon presentation of a single animal name should activate many other animals that share the same features. This in turn predicts that the cortical regions activated by animals, while being the same as tools, should be larger in extent—a prediction that is supported in the present study.

Nevertheless, although our account is supported by the current results, we acknowledge that it requires further development to meet a range of important challenges. For example, Caramazza and Shelton (1998) claimed that this general class of reductionist models is vague about the organisation of semantic information, so allowing unconstrained flexibility in the patterns of deficit that are possible. We have tried to address this critique by specifying our representational assumptions in greater detail, but it remains the case that many degrees of freedom remain (Tyler et al., 2000). Second, while our account very naturally captures deficits for living things, in terms of loss of vulnerable weakly correlated distinctive features, the explanation of the rarer reverse pattern is less clear-cut. We suggest that artefact deficits arise when the semantic system in severely damaged such that only the most frequent, strongly intercorrelated properties are reliably activated, that is, the shared properties of living things. While we have some empirical evidence of the predicted domain by severity interaction (Moss and Tyler, 2000), other researchers have not replicated this effect (e.g., Garrard et al., 1998).

In sum, the results of this study support the claim that objects and entities automatically activate the set of motion properties with which they are associated. However, there is no evidence here that these different motion properties are represented in different regions of cortex. Instead, the results are more compatible with the claim that semantic knowledge is represented within a widespread distributed neural system. This does not, however, mean that we would never expect to find any differential activation for different kinds of concepts. On the contrary, we claim that patterns of activation will vary depending upon the interaction between the structure of individual concepts and the specific demands of different tasks. Both Martin and Chao (2001) and Grabowski et al. (2001) have argued that processing varies along different regions of temporal cortex. Martin and Chao (2001) claim that specificity of processing increases from posterior to anterior regions of temporal cortex, while Grabowski et al. (2001) have reported that regions of temporal cortex, specifically the left temporal pole, are involved when a task requires naming of a unique entity. We claim that differences in the internal structure of concepts will interact with task demands. In particular, living things concepts tend to have more shared correlated properties and are

thus generally more difficult to discriminate from each other, while artefact concepts have fewer shared, correlated properties and are thus easier to differentiate (McRae et al., 1997; Tyler et al., 2000). In a task such as the one used in this study—semantic relatedness—which subjects can perform on the basis of general properties of the stimuli and does not require fine-grained discrimination, we would expect to find minimal differences between concepts in different categories, which is what we find. However, when the task involves detailed differentiation (e.g., naming), we would predict differences with living things generating more activation in those regions of temporal cortex that are involved in detailed, fine-grained analyses. However, this does not imply different representations for different concepts, but rather that the type of analysis required by a task will interact with the properties of different concepts.

Acknowledgments

This work was supported by an MRC program grant and McDonnell-Pew project grant to L.K.T.

References

Baayen, R., Pipenbrook, R., 1995. The Celex Lexical Database. Philadelphia Linguistic Data Consortium, University of Pennsylvania, Philadelphia.

Beauchamp, M.S., Lee, K.E., Haxby, J.V., Martin, A., 2002. Parallel visual motions processing streams for manipulable objects and human movements. Neuron 34, 149–159.

Bonda, E., Petrides, M., Ostry, D., Evans, A., 1996. Specific involvement of human parietal systems and the amygdala in the perception of biological motion. J. Neurosci. 16, 3737–3744.

Buckner, R.L., Koustall, W., Schacter, D.L., Rosen, B.R., 2000. Functional MRI evidence for a role of frontal and inferior temporal cortex in amodal components of priming. Brain 123, 620–640.

Cappa, S.F., Perani, D., Schnur, T., Tettamanti, M., Fazio, F., 1998. The effects of semantic category and knowledge type on lexical-semantic access: a PET study. NeuroImage 8, 350–359.

Caramazza, A., Shelton, J., 1998. Domain-specific knowledge systems in the brain: the animate–inanimate distinction. J. Cogn. Neurosci. 10, 1–34.

Chao, L., Haxby, J.V., Martin, M., 1999. Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. Nat. Neurosci. 2, 913–919.

Chao, L.L., Martin, A., 1999. Cortical regions associated with perceiving, naming, and knowing about colors. J. Cogn. Neurosci. 11, 25–35.

Coltheart, M., 1981. The MRC psycholinguistic database. Q. J. Exp. Psychol. 33A, 497–505.

Corbetta, M., Miezin, F.M., Dobmeyer, S., Shulman, G.L., Petersen, S.E., 1990. Attentional modulation of neural processing of shape, colour and velocity in humans. Science 248, 1556–1559.

Devlin, J.T., Gonnerman, L., Andersen, E., Seidenberg, M., 1998. Category specific semantic deficits in focal and widespread brain damage—a computational account. J. Cogn. Neurosci. 10, 77–94.

Devlin, J.T., Russell, R.P., Davis, M.H., Price, C.J., Moss, H.E., Fadili, M.J., Tyler, L.K., 2002a. Is there an anatomical basis for category-specificity? Semantic memory studies in PET and fMRI. Neuropsychologia 40, 54–75.

Devlin, J.T., Moore, C.J., Mummery, C.J., Gorno-Tempini, M.L., Phillips, J.A., Noppeney, U., Frackowiack, R.S.J., Friston, K.J., Price, C.J., 2002b. Anatomic constraints on cognitive theories of category specificity. NeuroImage 15(3), 675–685.

Durrant-Peatfield M., Tyler, L.K., Moss, H.E., Levy, J., 1997. The distinctiveness of form and function in category structure: a connectionist model, in: Shafto, M.G., Langley, P. (Eds.), Proceedings of the Nineteenth Annual Conference of the Cognitive Science Society, Erlbaum, Mahwah, NJ, pp. 193–198.

Fiez, J.A., Raichle, M.E., Balota, D., Tallal, P., Peterson, S.E., 1996. PET activation of posterior temporal regions during passive auditory word presentation and verb generation. Cereb. Cortex 6 (1), 1–10.

Forster, K.I., Forster, J.C., 1991. The DMASTR display system for mental chronometry. University of Arizona, Tucson.

Gainotti, G., 2000. What the locus of brain lesion tells us about the nature of the cognitive deficit underlying category-specific disorders: a review. Cereb. Cortex 36, 539–559.

Garrard, P., Patterson, K., Watson, P.C., Hodges, J.R., 1998. Category-specific semantic loss in dementia of Alzheimer's type: functional–anatomical correlations from cross-sectional analyses. Brain 211, 633–646.

Gitelman, D., Ashburner, J., Friston, K., Tyler, L.K., Price, C.J., 2000. Voxel-based morphometry of herpes simplex encephalitis. NeuroImage 13, 623–631.

Goodglass, H., Klein, B., Carey, P., Jones, K., 1966. Specific semantic word categories in aphasia. Cortex 2, 74–89.

Grabowski, T.J., Damasio, H., Tranel, D., Boles Ponto, L., Hichwa, R., Damasio, A., 2001. A role for left temporal pole in the retrieval of words for unique entities. Hum. Brain Mapp. 13, 199–212.

Greer, M.J., van Casteren, M., McLellan, S.A., Moss, H.E., Rodd, J., Rogers, T., Tyler, L.K., 2001. The emergence of semantic categories from distributed featural representations, in: Moore, J.D., Stenning, K. (Eds.), Proceedings of the Twenty-Third Annual Conference of the Cognitive Science Society, Erlbaum, Mahwah, NJ, pp. 386–391.

Marslen-Wilson, W.D., Tyler, L.K., 1997. Dissociating types of mental computation. Nature 387, 592–594.

Martin, A., Chao, L., 2001. Semantic memory and the brain: structure and processes. Curr. Opin. Biol. 11, 194–201.

Martin, A., Haxby, J.V., Lalonde, F.M., Wiggs, C.L., Ungerleider, L.G., 1995. Discrete cortical regions associated with knowledge of colour and knowledge of action. Science 270, 102–105.

Martin, A., Ungerleider, L.G., Haxby, J.V., 2000. Category-specificity and the brain: the sensory–motor model of semantic representations of objects, in: Gazzaniga, M.S. (Ed.), The Cognitive Neurosciences, second ed., MIT Press, Cambridge, pp. 1023–1036.

Martin, A., Wiggs, C., Ungerleider, L., Haxby, J., 1996. Neural correlates of category-specific knowledge. Nature 379, 649–652.

McRae, K., de Sa, V.R., Seidenberg, M.S., 1997. On the nature and scope of featural representations of word meaning. J. Exp. Psychol. Gen. 126, 99–130.

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., Tyler, L.K., 2000. A progressive category-specific deficit for non-living things. Neuropsychologia 38, 60–82.

Mummery, C.J., Patterson, K., Hodges, J.R., Wise, R.J., 1996. Generating 'tiger' as an animal name or a word beginning with T: differences in brain activation. Proc. R. Soc. Lond. B Biol. Sci. 263, 989–995.

Oram, M.W., Perrett, D.J., 1994. Responses of anterior superior temporal polysensory (STPa) neurons to "biological motion" stimuli. J. Cogn. Neurosci. 6, 99–116.

Perani, D., Cappa, S., Bettinardi, V., Bressi, S., Gorno-tempini, M.-L., Matarrese, M., Fazio, F., 1995. Different neural systems for the recognition of animals and man-made tools. NeuroReport 6, 1637–1641.

Perani, D., Cappa, S.F., Bettinardi, V., Bressi, S., Gornotempini, M., Mataresse, M., Fazio, F., 1995. Different neural systems for the recognition of animals and man-made tools. NeuroReport 6, 1637–1641.

Pilgrim, L.K., Fadili, J., Fletcher, P., Tyler, L.K., 2002. Overcoming confounds of stimulus blocking: an event-related fMRI design of semantic processing. NeuroImage 16(3), 713–723.

Price, C.J., Friston, K.J., 2002. Functional imaging studies of category specificity, in: Humphreys, G., Forde, E. (Eds.), Category Specificity in Mind and Brain, Psychology Press, East Sussex, pp. 427–447.

Puce, A., Allison, T., Bentin, S., Gore, J.C., McCarthy, G., 1998. Temporal cortex activation in humans viewing eye and mouth movements. J. Neurosci. 18, 2188–2199.

Pulvermuller, F., Haerle, M., Hummel, F., 2001. Walking or talking? Behavioral and electrophysiological correlates of action verb processing. Brain Lang. 78, 143–168.

Tyler, L.K., de Mornay Davies, P., Longworth, C., Randall, B., Marslen-Wilson, W.D., 2001. Dissociations in processing past tense morphology: neuropathology and behavioural studies. J. Cogn. Neurosci. 14 (1), 79–95.

Tyler, L.K., Tavares, L.K., 2001. Are there brain areas specialised for the processing of pictures of living and non-living things? An fMRI study. NeuroImage 13(6), S620.

Tyler, L.K., Moss, H.E., 2001. Towards a distributed account of conceptual knowledge. Trends Cogn. Sci. 5, 244–252.

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 Lang. 75, 195–231.

Tyler, L.K., Dick, E., Tavares, P., Pilgrim, L., Bright, P., Moss, H., Fletcher, P., 2002. Do semantic categories activate distinct cortical regions? Evidence for a distributed neural semantic system. Cogn. Neuropsych., in press.

Tyler, L.K., Russell, R., Fadili, J., Moss, H.E., 2001. The neural representation of nouns and verbs: PET studies. Brain 124, 1619–1634.

Ullman, M.T., Corkin, S., Coppola, M., Hickok, G., Growdon, J.H., Koroshetz, W.J., Pinker, S., 1997. A neural dissociation within language: evidence that the mental dictionary is part of declarative memory, and that grammatical rules are processed by the procedural system. J. Cogn. Neurosci. 9, 266–276.

Vaina, L.M., Solomon, J., Chowdhury, A., Sinha, P., Belliveau, J.W., 2001. Functional neuroanatomy of biological motion perception in humans. Proc. Natl. Acad. Sci. USA 98 (20), 11656–11661.

Warburton, E., Wise, R.J., Price, C.J., Weiller, C., Hadar, U., Ramsay, S., 1996. Noun and verb retrieval by normal subjects: studies with PET [review]. Brain 119, 159–179.

Warrington, E., McCarthy, R., 1987. Categories of knowledge: further fractionations and an attempted integration. Brain 110, 1273–1296.

Warrington, E., Shallice, T., 1984. Category specific semantic impairments. Brain 107, 829–853.

Wise, R., Chollet, F., Hadar, U., Friston, K., Hoffner, E., Frackowiak, R., 1991. Distribution of cortical neural networks involved in word comprehension and word retrieval. Brain 114, 1803–1817.