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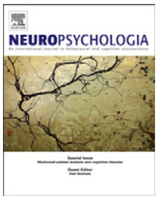

Shapes, scents and sounds: Quantifying the full multi-sensory basis of conceptual knowledge

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ABSTRACT

Contemporary neuroscience theories assume that concepts are formed through experience in multiple sensory-motor modalities. Quantifying the contribution of each modality to different object categories is critical to understanding the structure of the conceptual system and to explaining category-specific knowledge deficits. Verbal feature listing is typically used to elicit this information but has a number of drawbacks: sensory knowledge often cannot easily be translated into verbal features and many features are experienced in multiple modalities. Here, we employed a more direct approach in which subjects rated their knowledge of objects in each sensory-motor modality separately. Compared with these ratings, feature listing over-estimated the importance of visual form and functional knowledge and under-estimated the contributions of other sensory channels. An item's sensory rating proved to be a better predictor of lexical-semantic processing speed than the number of features it possessed, suggesting that ratings better capture the overall quantity of sensory information associated with a concept. Finally, the richer, multi-modal rating data not only replicated the sensory-functional distinction between animals and non-living things but also revealed novel distinctions between different types of artefact. Hierarchical cluster analyses indicated that mechanical devices (e.g., vehicles) were distinct from other non-living objects because they had strong sound and motion characteristics, making them more similar to animals in this respect. Taken together, the ratings align with neuroscience evidence in suggesting that a number of distinct sensory processing channels make important contributions to object knowledge. Multi-modal ratings for 160 objects are provided as supplementary materials.

1. Introduction

Semantic memory is our store of conceptual knowledge about the world, including the characteristics of objects, places and people and the meanings of words. Understanding the computational and neural structure of this information store is a key goal for cognitive neuroscience. Almost all contemporary theorists agree that the semantic system is at least partly distributed, with features specific to particular sensory modalities represented in areas close to those that perform the corresponding perceptual processing (Barsalou, 2008; Binder & Desai, 2011; Martin, 2007; Patterson, Nestor, & Rogers, 2007; Pulvermuller, 2001). This distributed knowledge theory can potentially account for the various patterns of category-specific knowledge deficits found in neuropsychological patients (e.g., Capitani, Laiacona, Mahon, & Caramazza, 2003; Caramazza & Shelton, 1998; Warrington & Shallice, 1984) and induced in healthy subjects following repetitive TMS (Pobric, Jefferies, & Lambon Ralph, 2010) by assuming that different categories of object are associated with different types of perceptual experience and therefore depend on each modality-specific region to differing extents (Cree & McRae, 2003; Farah & McClelland, 1991; Mahon & Caramazza, 2009). This idea was first advanced by Warrington and Shallice (1984), who proposed that sensory characteristics were particularly important for distinguishing between living things, while functional information was central to the representation of artefacts (termed the sensory-functional theory).

The sensory-functional dichotomy proved a popular framework for interpreting category-specific deficits but as it was investigated in more detail, it became clear that the explanatory power of the theory depended on precisely which types of information were classed as sensory and which as functional. Some researchers were concerned specifically with *visual* sensory information (Farah & McClelland, 1991), while others included tactile, auditory and gustatory modalities under the "sensory" umbrella (Devlin, Gonnerman, Andersen, & Seidenberg, 1998; Garrard, Lambon Ralph, Hodges, & Patterson, 2001). The definition of functional features proved equally pliable, with some restricting this to what

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an object is used for (Devlin et al., 1998; Farah & McClelland, 1991), while others included behaviours an entity performed independently (e.g., owls can fly; Garrard et al., 2001) or defined all non-sensory information as functional (Caramazza & Shelton, 1998). Others have argued that the key factor is not the function of an object but the motor acts involved in manipulating it (Martin, Ungerleider, & Haxby, 2000). These difficulties were compounded by problems in how multisensory features should be classified (discussed below).

Going beyond the issue of feature classification, a number of authors have argued that a simple dichotomy of knowledge types is insufficient to account for the various patterns of category-specific impairment reported in the literature, and that a more fine-grained taxonomy of knowledge types is necessary to elucidate fully the structure of conceptual knowledge (Allport, 1985; Cree & McRae, 2003; Crutch & Warrington, 2003; Martin & Caramazza, 2003; Warrington & McCarthy, 1987). This assertion is supported by an ever-growing neuroimaging literature, which indicates functional specialisation for processing object properties in different sensory channels. Processing an object's visual characteristics activates ventral occipitotemporal cortex, even when subjects are presented with the object's name rather a picture (Chao, Haxby, & Martin, 1999; Thompson-Schill, Aguirre, D'Esposito, & Farah, 1999). In contrast, auditory properties of objects are linked to activation in posterior superior temporal gyrus (Kiefer, Sim, Herrnberger, Grothe, & Hoenig, 2008; Lewis et al., 2004), while somatosensory properties activate the post-central gyrus and gustatory information activates medial orbitofrontal cortex (Goldberg, Perfetti, & Schneider, 2006). Within the visual modality, there is evidence for further functional specialisation, with motion processing associated with the middle and superior temporal gyri (Beauchamp, Lee, Haxby, & Martin, 2002) while visual form and colour rely on the posterior fusiform (Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995). Finally, knowledge of object manipulation is thought to be represented in the inferior parietal lobule, but appears to be neurally distinct from information about the object's function (Buxbaum & Saffran, 2002; Ishibashi, Lambon Ralph, Saito, & Pobric, 2011; Kellenbach, Brett, & Patterson, 2003). Taken together, these findings indicate a complex pattern of neuroanatomical specialisation in object representation, which cannot be accounted for by a simple sensory-functional dichotomy.

To develop a comprehensive theory of conceptual knowledge representation and to reconcile the emerging neuroanatomical picture with the various forms of category-specific knowledge deficit, it is necessary to move beyond the broad sensory-functional distinction and towards a fine-grained understanding of which sensory-motor channels contribute to object knowledge, how they relate to one another, and how they differentially contribute to each category of object we encounter. Cree and McRae (2003) took an important first step in this direction by analysing the features of a large set of objects, using a taxonomy that distinguished between different types of visual and other sensory characteristics, as well as function knowledge. As with many other studies (Devlin et al., 1998; Garrard et al., 2001; Tyler, Moss, Durrant-Peatfield, & Levy, 2000; Vinson, Vigliocco, Cappa, & Siri, 2003; Zannino, Perri, Pasqualetti, Caltagirone, & Carlesimo, 2006), they used verbal features generated by participants as the basis for their classification. Feature generation has proved to be a powerful tool in the study of object knowledge, with one of its key advantages being the ability to explore the degree to which objects share features with their category neighbours (Devlin et al., 1998; Garrard et al., 2001; Tyler et al., 2000). While feature lists are ideally suited for some purposes, they may not give a complete picture of how knowledge is distributed amongst the various sensory-motor modalities available from our experience of the environment. There are three particular ways in which verbal feature lists may distort the true breadth of sensory-motor experience.

1. *Some features are not specific to a single modality*. The features generated by subjects are classified post-hoc by researchers as being experienced in a particular sensory modality, yet many features are experienced in more than one. For example, subjects often say that objects are "made of metal". This gives both visual and somatosensory information but such features are usually classed as visual features (Cree & McRae, 2003). In another instance, suppose that a subject reports that a cat "has legs". They may assume that, by giving this feature, they have implied that cats move by walking around and will fail to give this information explicitly. It would be an interpretive leap on the part of the investigator to assume that "having legs" is a motion feature (after all, tables have legs but rarely use them to move), so having legs is classified as visual form information and the motion knowledge that is part of the subject's representation is not captured in their feature list.
2. *Feature listing is a verbal act*. The task is biased towards modalities in which information can be easily expressed verbally. Detailed visual form information can be given, for example, by listing an object's constituent parts. However, we have more limited vocabulary for describing tastes, sounds and so on, restricting the amount of information that can be expressed for these modalities. In particular, fine discriminations in modalities other than vision are often hard to describe (e.g., most people can distinguish between car and a truck on the basis of sound, but might have difficulty describing the difference verbally). This bias might distort the true nature of object knowledge in two ways. First, sensory modalities that are hard to verbalise may be under-represented in the database as a whole. Second, objects that are rich in verbalisable features may appear to be more strongly represented in the semantic system, relative to those that depend on other, less verbally-oriented modalities.
3. *Feature listing is a time-limited activity*. Subjects are typically asked to produce up to 10 features for each concept (e.g., McRae, Cree, Seidenberg, & McNorgan, 2005) or are given a time-limit. This restricted window is not sufficient for subjects to express their sum total of knowledge for most items, so they are likely to focus on the most salient and distinctive information. This strategy could disadvantage particular sensory modalities because they are less salient. In addition, participants are likely to focus on information that distinguishes between, and are less likely to produce attributes that are shared across broad domains of item (Rogers et al., 2004). For example, nearly all animals have necks but this information is rarely listed, except for animals for which the neck is a particularly distinguishing feature (e.g., giraffe; Garrard et al., 2001). The restriction in output also limits the usefulness of feature data for distinguishing between knowledge-rich items and those about which we know less. It is likely that more familiar items have richer and more detailed sensory-motor representations than more unusual items but, when faced with a limited response window, subjects are likely to produce similar numbers of features for all items.

In the Cree and McRae (2003) feature listing study, visual form and function information dominated the feature database. Although some other modalities were moderately important for narrow categories (e.g., colour features were often reported for fruits and vegetables), no other modalities were strongly represented across a broad range of items.[1] Cree and McRae also noted

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[1] Encyclopaedic knowledge was also strongly represented in the feature data, but this is not discussed here as it is not clear whether this information can be mapped to a particular sensory-motor modality.

that few features referred to motor acts and that their function features were mostly of the "what it's for" variety. This might also have arisen from difficulty in expressing verbally how an object is manipulated, or an assumption that such information is conveyed implicitly when its function is described, rather than a dearth of such knowledge. So, while Cree and McRae's (2003) study was an important advance in recognising the need for a more fine-grained taxonomy of sensory-motor knowledge, the range of knowledge expressed was limited by the verbal feature response format.

Two previous studies have explored an alternative approach to studying the sensory-motor composition of object knowledge. Tranel, Logan, Frank, and Damasio (1997) and Gainotti, Ciaraffa, Silveri, and Marra (2009) asked participants to rate how strongly they associate items with information in each of a variety of sensory-motor modalities. This strategy avoids some of the pitfalls of feature listing. Because subjects express their knowledge in each domain directly, there is no need for post-hoc interpretation of what type of information is conveyed in each response. This also avoids the problem of ambiguous features that are experienced in multiple modalities. Ratings also allow subjects to express their level of knowledge without recourse to verbal features, thus removing the inherent bias towards visual information that can be verbalised easily. These previous studies suggested that a rich tapestry of sensory knowledge contributed to the representation of familiar objects, supporting a more fractionated view than the traditional sensory-functional dichotomy. However, neither study directly compared the information gleaned from ratings with verbal feature data. This is critical because all of the current incarnations of the sensory-functional theory depend heavily on results from feature generation, so a mismatch would motivate reconsideration of these theories. In the present study, we performed this direct comparison by collecting ratings of experience in various sensory-motor modalities for 160 items and comparing these with verbal features for the same items, as reported by McRae et al. (2005). Our goals were:

1. to ascertain the extent to which ratings and feature lists provided convergent information about the relative importance of each sensory-motor modality for object knowledge.
2. to determine whether ratings and features provided the same distribution of knowledge across modalities for living vs. non-living things.
3. to assess how categories grouped together in terms of their dependence on particular modalities, and whether this similarity structure differed for features vs. ratings.
4. to compare the information given by ratings and feature lists about the overall quantity of sensory-motor information available for individual objects, by comparing their ability to predict latencies in word recognition and picture naming tasks.

Previous studies have indicated that verbal feature listing emphasises the importance of an object's visual form and function, because these qualities are easy to verbalise. In contrast, when rating sensory experiences directly, we expected relatively greater weight to be given to other sensory modalities, consistent with the neuroanatomical evidence for specialised regions for representing sound, motion, somatosensory and gustatory knowledge. As a result, we expected ratings to capture more accurately the full breadth of sensory-motor knowledge available for particular object concepts, making the ratings a better predictor of performance in visual word and picture recognition than the feature database. We explored the distribution of knowledge in different object categories to ascertain the extent to which our data supported the expected sensory-functional distinction between animals and manmade artefacts.

Although this is not the first study to probe conceptual knowledge through ratings of experience in particular modalities, this is the first time that the ratings method has been compared with the dominant feature generation paradigm directly. In addition, we made one important deviation from the method used in previous rating studies (Gainotti et al., 2009; Tranel et al., 1997). In these studies, stimuli were presented in pictorial form, potentially biasing subjects towards giving higher ratings for visual qualities. In contrast, we presented items as written words. We provide the ratings for all 160 concepts in Supplementary materials and hope that these will be useful for researchers in their own studies.

2. Method

2.1. Participants

One hundred-one undergraduate students took part (mean age = 19.4 years). Data from one subject was excluded due to failure to follow task instructions.

2.2. Stimuli

One hundred-sixty living and non-living objects were selected for rating. One hundred-fifty-two items were taken from the McRae et al. (2005) feature listing norms (the remaining eight items were used to ensure overlap with our clinical testing materials and are not discussed further here). Items were selected to ensure a broad range of animals, plants, manipulable objects and other non-living items were included (see the Appendix A for a full list). Items were presented as written words for rating. Where words were judged to be potentially ambiguous, they were presented with a disambiguating cue (e.g., *orange* (*fruit*)).

2.3. Procedure

Each item was rated for its overall familiarity and for its strength of association with eight sensory-motor modalities. The modalities were those identified by Cree and McRae (2003) based on the neuroscientific literature. Three referred to different aspects of visual experience (*colour*, *visual form* and *observed motion*), four to other sensory experiences (*sound, taste, smell* and *tactile sensation*) and the final one to *performed actions*. The action category differed slightly from Cree and McRae's taxonomy, whose final category was *function*. We chose to ask about actions rather than functions because actions are closely tied to physical experience while functions are a broader class that can include verbally-mediated encyclopaedic knowledge. However, when re-analysing McRae et al.'s (2005) feature norms, we retained their original classification of functions because there were few features that referred specifically to actions.

Ratings were collected through an online questionnaire which subjects completed at their convenience. Before beginning, they were given descriptions of each sensory modality with examples of objects displaying qualities in that modality. They were then presented with a worked example of how they might rate the item *door* (for full task instructions see Supplementary materials). Subjects were asked "How much do you associate this item with a particular colour?" (and visual form, motion and so on). We asked about strength of association because we wanted to capture not just whether a particular modality is experienced for an item, but also the degree of consistency in this experience across exemplars. For example, whenever one walks through a door its colour is experienced, but since this experience varies greatly with each exemplar (i.e., different doors can be painted in different colours), colour is unlikely to play an important part in the general concept. In contrast, strawberries are always associated with the same colour experience, so colour is likely to be central to their conceptual representation. Between these extremes, there are cases for which there is a degree of variability in the experience but a clear central tendency (e.g., horses can be white, grey or black, but are most often brown). We assumed that by asking about the strength of association with each modality, subjects would consider where each concept fell on this continuum. All ratings were completed on a seven-point scale, with 1 indicating "not at all" and 7 "very strongly". The nine ratings for each item were completed on a single webpage, with the item's name shown at the top of the page.

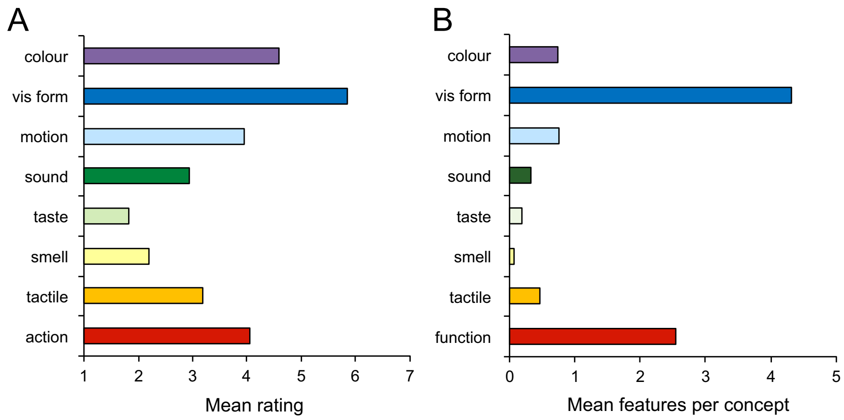

Fig. 1. Mean ratings and number of features produced in each modality.

2.4. Design

Each item was rated by 20 subjects in total. Each item was assigned to four of 20 unique sets of 32 items and each subject received one of these sets of 32 items to rate. This procedure ensured that no two items were rated by the same 20 individuals. The full set of ratings is available as Supplementary materials.

3. Results

3.1. What is the overall distribution of knowledge across different modalities?

We began by averaging results across all objects and comparing the mean ratings for each modality with the number of features assigned to each modality in the McRae et al. (2005) feature norms (see Fig. 1). There was some similarity between the two datasets in the general pattern of information across modalities. Visual form was the dominant modality in both datasets, followed by function/action. In contrast, smell and taste were given low ratings and were associated with few features because these modalities are only relevant for a minority of items. Though this basic pattern was present for both datasets, there was clear divergence in terms of the relative contribution of each modality. Feature lists were strongly dominated by visual form (and, to a lesser extent, function) knowledge, with fewer than one feature per concept being produced in the other modalities. In contrast, there was a more balanced distribution across modalities in the ratings data, suggesting a richer multimodal distribution of knowledge. This interpretation was supported by a 2×8 within-items ANOVA, which revealed an interaction between dataset and modality ($F(7,1057)=56.5$, $p<0.001$). The discrepancy was largest for motion and colour information.

Fig. 2 provides a more detailed picture of each modality in the form of histograms. Ratings and feature lists give similar distributions in some modalities. For example, no taste or smell features were present for most concepts in the feature norms and the ratings also indicated that these modalities were usually unimportant, with the majority of concepts receiving ratings between 1 and 2. In other cases there were conflicting results, illustrated most clearly in the colour modality. In the feature norms, no colour information was present for over half of the concepts tested. The absence of colour features for so many items suggests that colour may not play a major part in the representation of many familiar items. However, when asked to rate colour knowledge specifically, subjects indicated that most items were quite strongly associated with particular colours, with the median rating between 4 and 5 and very few concepts in the lowest 1–2 range. A similar discrepancy was present for motion and, to a lesser extent, sound and tactile information. Thus, while the feature norms provide no evidence for the role of these modalities in the representation of many common objects, people often report having such knowledge when asked to rate it specifically. There were some striking examples of this problem at the level of individual concepts. For example, in the McRae et al. norms there are no motion features associated with the concept *bus*, indicating that of the 30 subjects presented with this concept, fewer than five reported explicitly that it could move. In contrast, when we asked subjects how much they associated *bus* with a particular kind of motion, they rated it very highly (6.25 out of 7). Clearly, subjects were aware that buses move in a particular way when providing their features, but may have felt they expressed this information implicitly when describing its visual appearance (“has wheels”) or function (“used for transportation”). In general, these findings support the notion that the feature listing biases subjects towards giving visual form and function knowledge and misses other sensory information that is available when probed more directly.

3.2. How does each modality contribute to knowledge of living and non-living things?

Next we investigated the contribution of different types of knowledge to different classes of objects. To compare ratings with feature data directly, we needed to take into account the fact that they were measured on different scales and that the bias towards visual form information was much stronger in the feature data. Accordingly, we expressed each concept’s mean rating/number of features in each modality as a *z*-score relative to all concepts. Fig. 3 shows the mean *z*-scores for creatures and artefacts.[2] Having accounted for the general bias towards visual form information in the feature data, ratings and feature listing demonstrated both important similarities and differences with regard to the relative importance of different sensory modalities to the two types of concept. Both agreed that artefacts were associated with greater function/action knowledge and that creatures were more likely to be associated with particular colours and types of motion. In the ratings data, smells and tastes were also more strongly associated with creatures but this was not observed in the feature data, perhaps because smell and taste features were produced for very few items. We compared the distributions for each measure with a $2\times2\times8$ ANOVA that

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[2] Following Cree and McRae (2003), we use the term “creatures” to refer to all animate living things and “artefacts” to refer to manmade objects. However, we excluded musical instruments, foods and fruit/plants from this analysis as they were identified by Cree and McRae (2003) as “salient exceptions” to the usual living/non-living distinction.

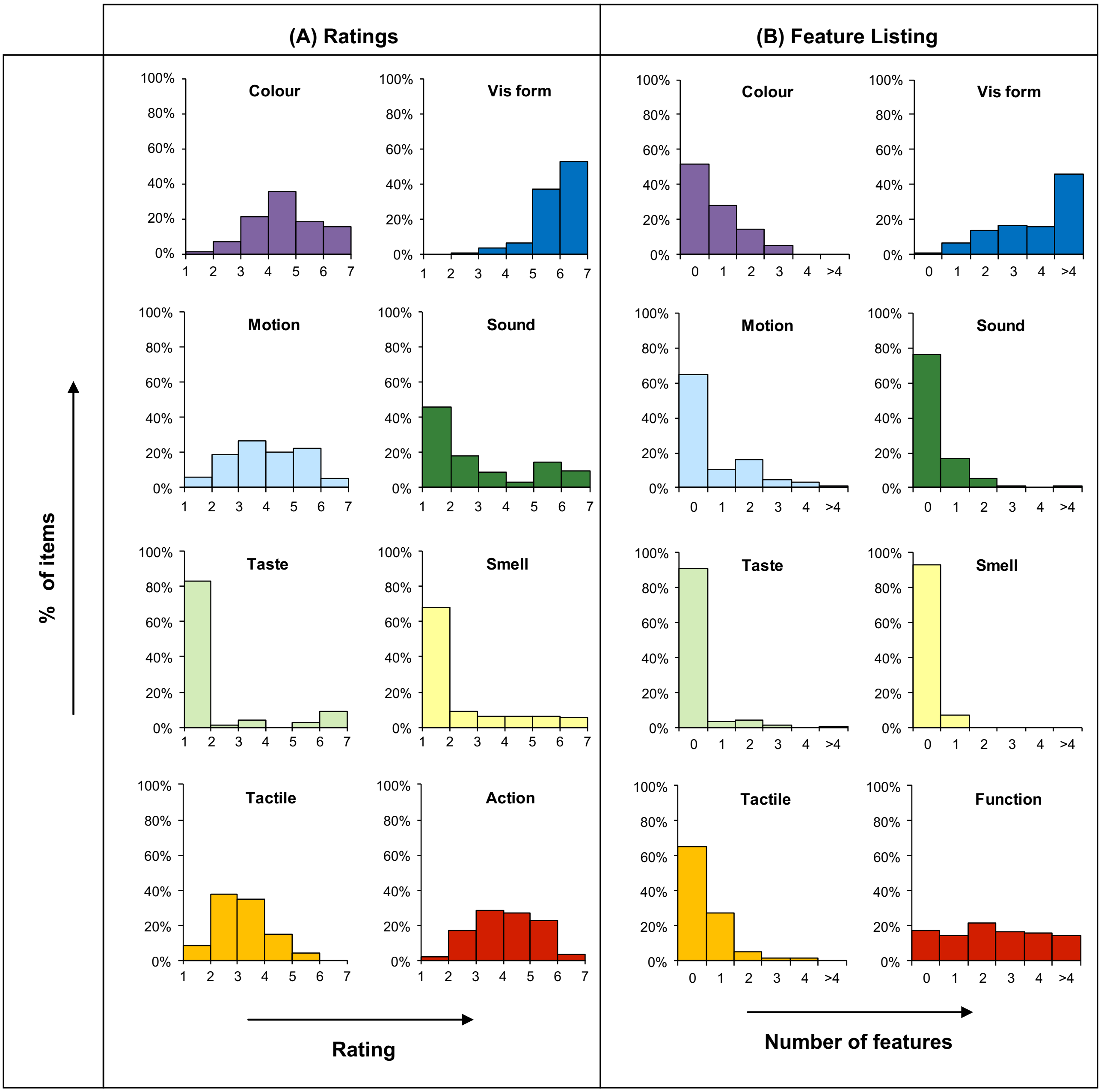

Fig. 2. Distribution of ratings and number of features in each modality.

included dataset, concept domain (creatures vs. artefacts) and modality as factors. This revealed main effects of modality ($F(7,847)=7.34$, $p<0.001$) and domain ($F(1,121)=4.64$, $p<0.05$) and an interaction between them ($F(7,847)=31.8$, $p<0.001$). Most importantly, there was a three-way interaction between these two factors and dataset ($F(7,847)=7.53$, $p<0.001$), indicating that the ratings and feature listing gave different conclusions regarding the relationship between modality and concept domain. Post-hoc tests revealed that the two datasets gave different results in the modalities of motion and taste (motion: $F(1,121)=32.0$, $p<0.001$; taste: $F(1,121)=8.89$, $p<0.01$). Taste information did not discriminate between creatures and artefacts in the feature data while it did in the ratings (because subjects reported having taste information about edible creatures in the ratings but did not provide this information in feature listing). Feature lists highlighted a larger discrepancy for motion information than did the ratings, perhaps indicating that feature lists underestimate the relevance of motion information for artefacts.

3.3. How do categories group together based on ratings vs. feature data?

Feature listing studies often employ hierarchical cluster analyses in order to elucidate the structure of semantic knowledge (Cree & McRae, 2003; Garrard et al., 2001; Rogers et al., 2004). Such analyses typically reveal a tri-partite organisation of knowledge, with three major clusters emerging that distinguish between creatures, artefacts and fruits and vegetables. This corresponds to the three major forms of category-specific semantic impairment found in the neuropsychological literature (Capitani et al., 2003). Here, we performed a hierarchical cluster

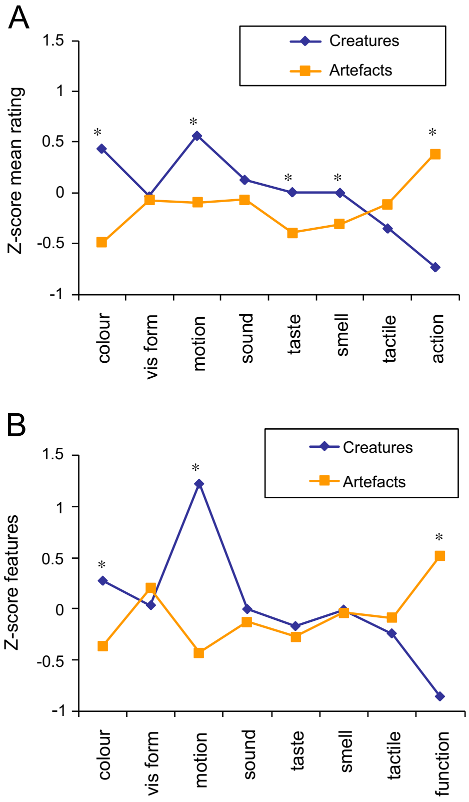

Fig. 3. Levels of knowledge across modalities for creatures and non-living things. *Indicates a significant difference between creatures and non-living things ($p < 0.05$). (A) Ratings and (B) Feature listing.

analysis on our modality ratings, following the method used by Cree and McRae (2003). These authors placed individual concepts into higher-level categories and performed the analysis on average data for each category. We followed this approach, using Cree and McRae's classification to assign concepts to categories.[3] We then performed a hierarchical cluster analysis of the categories, based on the mean ratings for each modality and using the average-linkage between-groups method and cosine distance measure.

The dendrogram in Fig. 4A indicates that there were four major clusters. The earliest split produced a cluster of four categories, which all contained edible items. Another cluster contained all of the remaining creature categories. Non-living things appeared in two distinct clusters. One was entirely separate from the creatures and edible items while the other patterned at a late stage with the creatures. We refer to this second non-living cluster as "mechanical devices" (it also includes musical instruments). This division amongst non-living things was not expected on the basis of the tri-partite distinction discussed above. For comparison, we performed a cluster analysis on the feature listing data for categories derived from the same 152 concepts (see Fig. 4B). These data *did* yield a tri-partite structure, with all of the non-living items in a single cluster, indicating that the fractionation of non-living things generated by the ratings method is a novel observation. It should also be noted that in the feature data the fruits and plants did not cluster with the foods, presumably because taste and smell information is less salient in the feature database. Musical instruments are also distinct from all other non-living items in the feature data, while they appear in a larger cluster in the ratings-based dendrogram. One possibility for this difference is that sound information is only rarely produced in feature listing, and at a much higher rate for musical instruments than for any other category. Therefore musical instruments are highly distinctive in the feature database.

To investigate the basis of the four clusters and, in particular, the reason for the separation of mechanical devices from the other artefacts, we performed a principal components analysis on the ratings for all categories. A four-factor solution accounted for 93% of the variance. The varimax-rotated solution is shown in Table 1 and reveals patterns of co-occurrence between modalities. Factor 1 loads heavily on both taste and smell, as expected because these two modalities are often experienced together. Factor 2 is associated principally with sound and motion, presumably because items that move are also likely to make sounds. Factor 3 combines two key aspects of visual experience: colour and visual form. Factor 4 is associated with action and tactile information, which are jointly experienced through object manipulation.

For each cluster of concepts in Fig. 4A, we calculated its loading on the four factors by averaging values from the individual categories that comprised the cluster (see Table 2). The edible cluster loaded heavily on Factor 1 only, reflecting the importance of taste and smell to these items. The main artefact cluster loaded most heavily on Factor 4 (praxis), supporting the notion that action/function knowledge is critical for non-living things. Creatures loaded equally on two factors: sound/motion and vision. This indicates that creatures are associated with a variety of sensory characteristics. Finally, the mechanical devices did not fit neatly with either the creatures or the other artefacts: they loaded with the creatures on Factor 2 (sound/motion) but, like the other non-living items, also loaded heavily on the praxis factor. This suggests that these items depend on a wide range of sensory-motor information. Examination of the categories in this cluster supports this idea. Like other non-living objects they can be manipulated but critically the cluster includes objects that move (e.g., machinery), make distinctive sounds (e.g., appliances like radio, telephone; and musical instruments) or both (vehicles). Since most other artefact categories do not move or make sounds but creatures often do, mechanical devices clustered loosely with the creatures in the dendrogram. It is important to note that this clustering does *not* imply that creatures and mechanical devices move in similar ways or make similar sounds, because we did not collect data on the specific content of the information in each modality. It merely indicates that the modalities of sound and motion, and potentially the neural regions associated with them, are of similar importance to both types of concept. This novel result was not present in the feature listing data because feature listing underestimates the importance of sound and motion knowledge in conceptual representation (see Fig. 2) and, in particular, underestimates the amount of motion information we have about non-living things (Fig. 3).

3.4. *Can the amount of sensory-motor knowledge associated with an item predict how quickly its name is recognised or produced?*

One way of testing the validity of information gleaned from feature listing and ratings is to test their ability to predict speed of processing in lexical-semantic tasks. It is well-established that concepts with richer semantic representations benefit from a processing advantage (e.g., concrete relative to abstract words; Degroot, 1989; James, 1975; Plaut & Shallice, 1993). Therefore, if feature listings and ratings data accurately reflect the total amount of sensory-motor knowledge we have about particular items, we would expect these measures to successfully predict

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[3] Our set of concepts included no exemplars of the category "roots/tubers". We also omitted six categories for which we had fewer than three exemplars, though similar results were obtained when these categories were included.

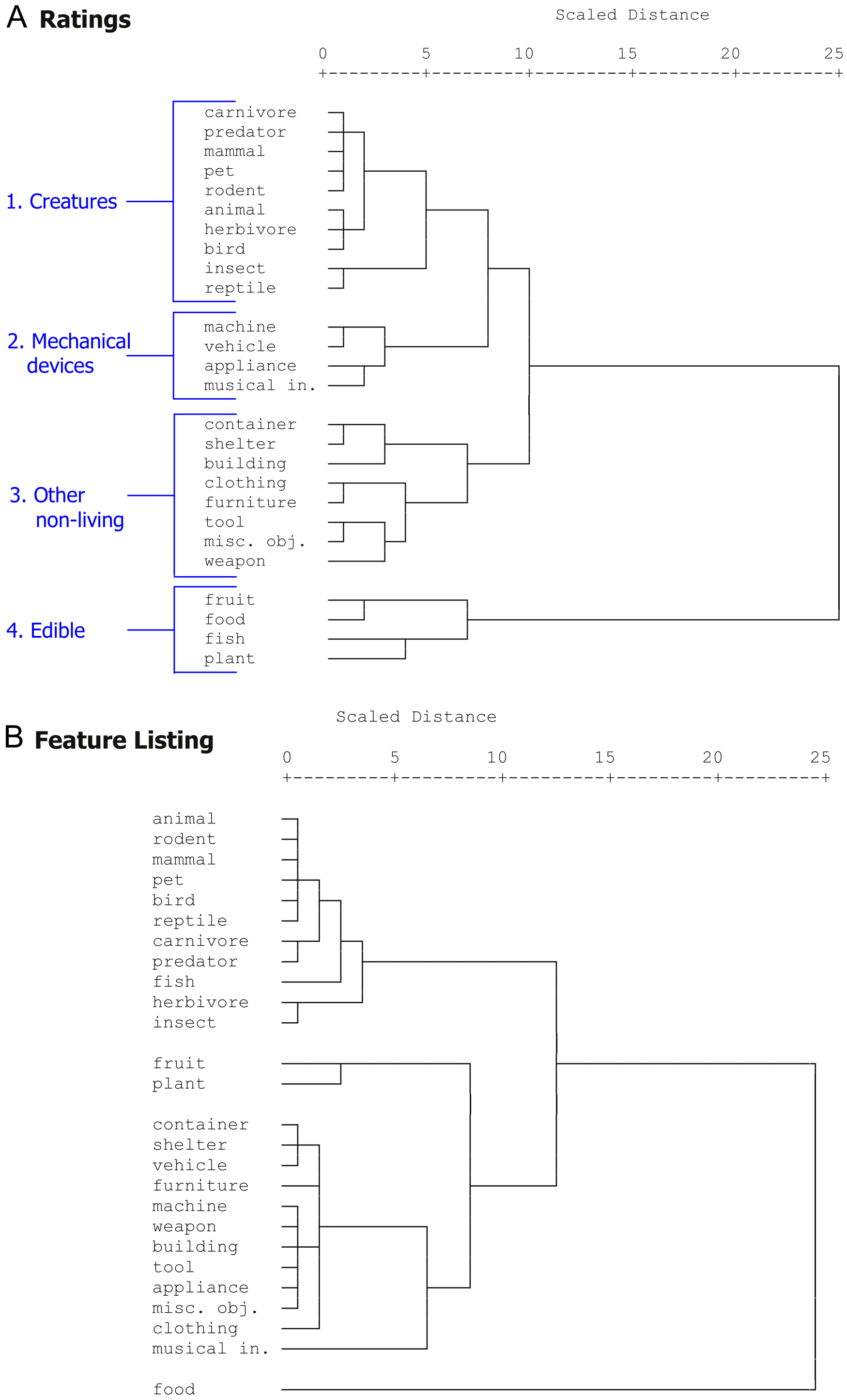

Fig. 4. Dendrograms produced by hierarchical cluster analysis of each dataset.

speed of lexical access in semantic processing tasks. Indeed, Pexman, Hargreaves, Siakaluk, Bodner, and Pope (2008) found that the number of features in the McRae et al. (2005) database was a significant predictor of latencies in visual lexical decision and semantic categorisation tasks. The names of objects associated with a greater number of features were recognised and categorised more quickly than those with fewer features. Here, we tested whether our sensory ratings could predict lexical-semantic processing efficiency in a similar way, and how its predictive power compared with that of McRae et al.'s feature database. We explored these factors using data from two standard behavioural tasks: visual lexical decision data from the English Lexicon project (Balota et al., 2007) and picture naming data collected in our lab.

3.4.1. *Measures of sensory richness*

For the ratings data, we simply took an object's mean rating across all eight modalities as a measure of the overall strength of its sensory-motor representation. This is of course not the only way in which one could calculate an average. It could be argued that modalities that receive consistently high ratings (e.g., visual form) contribute more strongly to the representations and should be weighted more strongly when averaging, but in the absence of a strong theoretical motivation to do this, we opted instead for a simple average. From the feature database, we used the total number of features listed for each item to represent the amount of information associated with it. Following Pexman et al. (2008), we excluded taxonomic features from the total.

3.4.2. *Visual word recognition*

Reaction times for visual lexical decision (*z*-scores) were available for 150 items in the English Lexicon Project database (Balota et al., 2007). These were analysed using a hierarchical multiple regression model. In the first step of the regression, we entered a number of variables known to influence lexical decision: word length, log word frequency (from the CELEX database; Baayen, Piepenbrock, & van Rijn, 1993), item familiarity (from our ratings) and orthographic Levenshtein distance, a measure of the density of a word's orthographic neighbourhood (Yarkoni, Balota, & Yap, 2008). In the second step, we added number of features to determine whether this variable could account for any additional variance in latencies. In a final third step, we added the mean sensory ratings to determine whether these had any additional predictive power beyond that provided by the number of features.

Table 1
Principal components analysis of ratings data.

	Factor 1: taste/ smell	Factor 2: sound/ motion	Factor 3: vision	Factor 4: praxis
Colour	**.478**	.127	**.718**	−.433
Visual form	.074	.090	**.950**	.060
Motion	−.315	**.836**	.290	−.025
Sound	−.168	**.910**	−.089	.242
Taste	**.943**	−.209	.186	−.035
Smell	**.931**	−.276	.111	−.056
Tactile	**.470**	−.358	**.517**	**.525**
Action	−.096	.252	−.057	**.934**

Factor loadings are shown in **bold** if greater than 0.4.

Table 2
Mean factor scores for each cluster of concepts.

Clusters	Factor 1: taste/ smell	Factor 2: sound/ motion	Factor 3: vision	Factor 4: praxis
Creatures	−0.27	0.58	0.54	−0.66
Mechanical devices	−0.02	1.30	−0.64	1.17
Other non-living	−0.64	−1.04	−0.45	0.34
Edible	1.99	−0.67	0.19	−0.20

3.4.3. *Picture naming*

Reaction times in picture naming were collected from 17 students at the University of Manchester (mean age=22) as part of a separate study. Participants named 131 of the items. Pictures were obtained from the International Picture Naming Project (Szekely et al., 2004) and presented on 15-inch computer monitor. No time limit was placed on responses, though participants were asked to respond as quickly as possible. Reaction times were recorded with an electronic voice-key, with responses scored online and recorded for later verification. A three-step hierarchical regression model was computed from the data. The first step included number of syllables, number of phonemes, log word frequency and item familiarity. Number of features was entered in the second step and mean sensory rating in the third step.

3.4.4. *Results*

The correlation matrix for lexical decision variables is given in Table 3. Note that both the mean sensory ratings and the number of features were strongly correlated with familiarity, consistent with the idea that we have more detailed representations of items we encounter regularly in our environment. The regression results are presented in Table 4. The initial psycholinguistic variables were able to account for more than 50% of the variance in lexical decision latencies; however, both sensory measures made an additional, independent contribution beyond this. In line with Pexman et al.'s (2008) results, including number of features significantly improved the fit of the model. The inclusion of sensory ratings improved the model still further and the beta values indicated that this variable, rather than number of features, was the stronger predictor. This conclusion was supported by a second regression model in which sensory ratings were entered in the second step and number of features in the third. In this model, sensory ratings boosted the R^2 of the model significantly ($\Delta R^2 = .024$; $F(1,143) = 8.46$, $p = 0.004$), but the

Table 4
Results of hierarchical regression analysis on lexical decision RTs.

Predictor	*B*	Standard error	β	R^2	ΔR^2
Initial step				.572***	.572***
Second step (number of features)				.586***	.013*
Third step (sensory rating)				.603***	.017*
Number of syllables	.018	.034	.049		
Word length	.020	.017	.140		
Levenshtein distance	.091	.040	.286*		
Word frequency (log)	−.171	.042	−.302***		
Familiarity	−.020	.020	−.082		
Number of features	−.009	.006	−.091		
Sensory rating	−.077	.032	−.166*		

$^{**} = p < 0.01$.
$^{*} = p < 0.05$.
$^{***} = p < 0.001$.

Table 3
Correlations between lexical decision variables.

Variable	2.	3.	4.	5.	6.	7.	8.
1. Reaction time	.52***	.57***	.64***	−.63***	−.45***	−.37***	−.33***
2. Number of syllables	–	.78***	.80***	.39***	−.11	−.11	.03
3. Word length		–	.88***	−.40***	−.08	−.12	.01
4. Levenshtein distance			–	−.48***	−.20*	−.19*	−.10
5. Word frequency (log)				–	.57**	.35***	.20*
6. Familiarity					–	.38***	.55***
7. Number of features						–	.38***
8. Sensory rating							–

$^{*} = p < 0.05$.
$^{**} = p < 0.01$.
$^{***} = p < 0.001$.

Table 5
Correlations between picture naming predictors.

Predictor	2.	3.	4.	5.	6.	7.
1. Reaction time	.15	.24**	−.28**	−.32***	−.26**	−.35***
2. Number of syllables	–	.83***	−.38***	−.09	−.09	.07
3. Number of phonemes		–	.45**	−.17	−.18*	−.08
4. Word frequency (log)			–	.55***	.31***	.13
5. Familiarity				–	.29**	.47***
6. Number of features					–	.33***
7. Sensory rating						–

* $=p<0.05$.
** $=p<0.01$.
*** $=p<0.001$.

Table 6
Results of hierarchical regression analysis on naming RTs.

Predictor	B	Standard error	β	R^2	ΔR^2
Initial step				.147***	.147***
Second step (number of features)				.167***	.019
Third step (sensory rating)				.205***	.038*
Number of syllables	−10.0	35.5	−.042		
Number of phonemes	20.9	18.1	.177		
Word frequency (log)	−40.3	41.3	−.107		
Familiarity	−17.6	20.2	−.095		
Number of features	−6.6	6.3	−.093		
Sensory rating	−78.4	32.1	−.239*		

**$=p<0.01$.
* $=p<0.05$.
*** $=p<0.001$.

subsequent inclusion of number of features led to no significant improvement in the model ($\Delta R^2=.006$; $F(1,142)=2.29$, $p=0.13$).

Correlations for picture naming variables are shown in Table 5 and the corresponding regression results in Table 6. The initial variables accounted for around 14% of the variance in this case. Addition of number of features did not improve the model significantly, though subsequent inclusion of the sensory ratings did. As with lexical decision, a second model was computed with the order of entry of the two semantic variables reversed. Including sensory ratings led to a significant improvement in the regression model ($\Delta R^2=.05$; $F(1,125)=7.85$, $p=0.006$), while the later addition of number of features had no effect ($\Delta R^2=.007$; $F(1,124)=1.10$, $p=0.3$).

It is important to note that although these two datasets originated on opposite sides of the Atlantic (our ratings were collected in the UK and McRae et al.'s (2005) feature data in North America), this difference is unlikely to account for these results. The danger is that there could be substantial cultural differences in experience with particular objects, which could potentially explain why our ratings were a better predictor of our UK-based picture naming data. However, ratings were also a better predictor of the American lexical decision data, arguing against this interpretation.

4. General discussion

It is widely accepted that a number of modality-specific neural processing regions contribute to semantic representation (Barsalou, 2008; Martin, 2007; Patterson et al., 2007; Pulvermuller, 2001; Warrington & Shallice, 1984). We investigated the relative contributions of each sensory-motor modality to different object concepts by collecting ratings of modality-specific knowledge; and we compared these data to those generated from verbal feature listing. The main findings can be summarised as follows:

1. Ratings and feature listing gave partly divergent information about the relative contributions of different sensory-motor modalities. Both highlighted the central role of visual form and function/action knowledge for object concepts, but ratings gave greater weight to other modalities, most notably motion and colour information, that were not strongly represented in the verbal feature database.
2. Both datasets supported established broad differences between creatures and artefacts, with function/action knowledge particularly central for artefacts and aspects of vision (colour and motion) key to creature knowledge.
3. At a more fine-grained level, the two datasets gave differing conclusions about which types of object rely on similar modalities. Hierarchical clustering based on the modalities of features revealed a tri-partite structure that neatly divided creatures, plants and artefacts. While a similar basic structure was present in the ratings data, there was one important deviation: mechanical devices did not cluster with other artefacts and instead shared greater similarity with creatures. Further investigation revealed that mechanical devices partially overlapped with both creatures and artefacts. In common with other artefacts, they were strongly associated with praxis but, like creatures, they relied heavily on sound and motion information. This novel observation was not present in the feature-based data because sound and motion features were under-represented in these data.
4. When used to predict latencies in picture naming and lexical decision, a concept's mean rating was a better predictor than the number of features it had. This suggests that the ratings technique better captures the overall quantity of sensory-motor knowledge available for each concept.

This work has implications for theories of conceptual representation and for understanding category-specific knowledge deficits. Category-specific deficits have traditionally been explained in terms of a dichotomous model that distinguishes between sensory and functional knowledge stores (Farah & McClelland, 1991; Martin et al., 2000; Warrington & Shallice, 1984). However, there has been growing acceptance that a dichotomy cannot easily explain the various patterns of spared and impaired categories reported in category-specific patients (Allport, 1985; Cree & McRae, 2003; Crutch & Warrington, 2003; Martin & Caramazza, 2003; Warrington & McCarthy, 1987). Moreover, rapidly accumulating neuroimaging evidence points to greater fractionation within the systems for representing sensory knowledge, with distinct activations for different aspects of visual experience, as well as for auditory, somatosensory, praxic and gustatory knowledge (Beauchamp et al., 2002; Goldberg et al., 2006; Kiefer et al., 2008; Lewis et al., 2004; Martin et al., 1995). However, while this evidence now indicates finer distinctions between the neural systems involved in storing different forms of sensory knowledge, investigations of the composition of object knowledge, predominately based on verbal feature listing, have mostly retained the original dichotomous division between sensory and functional knowledge (Devlin et al., 1998; Garrard et al., 2001; Tyler et al., 2000; Zannino, et al., 2006).

Although some attempts have been made to develop a more fine-grained approach, most notably by Cree and McRae (2003), the success of these endeavours has been limited because the feature listing paradigm does not lend itself to capturing the full range of sensory experience available to us. By dispensing with verbal features and probing each modality more directly, we have uncovered a richer pattern of sensory knowledge, in which a number of sensory-motor channels support conceptual knowledge of common objects. This provides further, convergent support for the idea that sensory knowledge is best understood as an amalgamation of a number of distinct processing channels, rather than a single homogeneous store of information.

One novel observation produced by the present study is the finding that mechanical devices (including vehicles, machines, electrical appliances and musical instruments) occupied a middle ground between artefacts and creatures. Like other artefacts, these items were associated with action knowledge, but in common with creatures, they were also linked with sound and motion knowledge. This suggests that concepts in the mechanical devices cluster have a widely distributed semantic representation involving regions important for representations of animals as well as for non-living items. Due to this distributed representation, we might expect relative preservation of these concepts, even when knowledge of other non-living things is impaired. Is there any evidence for this in the category-specific literature? We should note first of all that many studies have treated non-living things as a single category and in studies which have distinguished between more fine-grained categories, key confounding variables such as concept familiarity have often not been adequately controlled (see Capitani et al., 2003). Despite these caveats, there are some cases of patients with non-living deficits who showed relatively preserved knowledge of vehicles. Warrington and McCarthy's (1987) patient YOT showed poor comprehension of manipulable objects but more intact knowledge of large artefacts, many of which were vehicles, and similar results were observed in KE (Hillis, Rapp, Romani, & Caramazza, 1990) and GP (Cappa, Frugoni, Pasquali, Perani, & Zorat, 1998). It is also known that musical instruments sometimes pattern with living rather than non-living things (Dixon, Piskopos, & Schweizer, 2000; Gainotti & Silveri, 1996; Warrington & Shallice, 1984).[4] Based on the available evidence, it seems that mechanical devices and musical instruments are best treated as overlapping partially with creatures and partially with other non-living things. Our results suggest caution is warranted in treating manmade artefacts as a single homogeneous category and that the assertion that artefacts depend uniformly on action or function knowledge oversimplifies a complex situation.

The other main contribution of this study is to compare the predictive power of the rating vs. feature listing paradigms. The ratings data proved a better predictor of reaction times in two lexical-semantic tasks, suggesting that ratings give a more accurate indication of the overall quantity of sensory-motor information associated with a particular concept. This is consistent with our assertion that verbal features under-represent the amount of knowledge available in some modalities. In contrast, asking subjects to report their level of knowledge in each modality explicitly ensures that the full breadth of sensory-motor experience is sampled. We should note, however, that feature lists have a number of other advantages that ratings lack. The ratings method gives information about the strength of representation across modalities, but no information about the *content* of the representations. Conversely, feature lists give more detailed information about precisely what we know about objects, which can then be used to construct computational models (Devlin et al., 1998; Rogers et al., 2004; Tyler et al., 2000) and to design experiments that probe conceptual reasoning (Cree, McNorgan, & McRae, 2006; Mcrae, McNorgan, & Reid, 2011). Important insights regarding the ratio of shared to distinctive properties have also been derived from feature lists (Cree & McRae, 2003; Garrard et al., 2001), whereas our ratings method does not capture this aspect of conceptual representation. In sum, we see feature listing and ratings collection as complementary methods for elucidating the structure of conceptual knowledge. Ratings methods are suited to investigating how knowledge is distributed across sensory modalities, while feature lists provide deeper insights into the precise content of this knowledge.

Although this is the first study to compare the ratings method with feature generation directly, two previous studies have reported sensory experience ratings of the type collected here. Tranel et al. (1997) collected ratings of experience in vision, sound and touch, as well as characteristic motion, as part of a broader study of the factors that differ between object categories. In line with our findings, vision ratings were higher than those in other modalities. There was also some overlap with our findings with respect to mechanical devices. Musical instruments and vehicles both received higher sound ratings than other artefacts. In addition, principal components analysis revealed a factor associated with high sound ratings and it appeared that some creatures loaded heavily on this factor, as well as musical instruments. Motion ratings were also collected but these are harder to interpret because Tranel et al. asked specifically about motion involved in using an item. This excluded the biological motion that our study revealed as integral to creature concepts.

Gainotti et al. (2009) collected ratings for a number of concepts that included the main sensory processing channels in addition to praxis knowledge and linguistic knowledge. They also found that visual experience was the dominant form of sensory information (though this was not sub-divided into colour, form and motion, as it was in the present study). Although their categories were only partially overlapping with ours, there were some striking similarities. The only mechanical devices included were vehicles and, as in the present study, these were the only class of artefacts for auditory information was considered important. Gainotti et al. also conducted a hierarchical clustering analysis. Direct comparison with our results is difficult because Gainotti et al. included a number of "unique entities" categories that we did not test. However, it is interesting to note that their cluster analysis placed vehicles in a different cluster to other artefact categories, in a cluster that also contained wild animals. There is convergent evidence, therefore, that vehicles are something of an oddity within the domain of artefacts.

This study has demonstrated that people are able to retrieve rich, multi-sensory information about objects when this information is probed directly. An important outstanding question is the degree to which this information is activated automatically whenever the concept is encountered, or whether activation of modality-specific knowledge only occurs when it is probed explicitly or is directly relevant to the task at hand. Functional imaging studies indicate that modality-specific brain regions can be activated even when they are not explicitly involved in the task. For example, objects with strong auditory properties selectively activate superior temporal regions involved in auditory perception, even when they were presented as written words in a lexical decision task (Kiefer et al., 2008). Similarly, passive reading of action words activates areas of premotor cortex in a somatotopic manner (Hauk, Johnsrude, & Pulvermuller, 2004). Other studies indicate that activity in these modality-specific regions actively contributes to processing. Recent studies have used transcranial magnetic stimulation to explore the function of the inferior parietal lobule, an area associated with object manipulation knowledge (Kellenbach et al., 2003). Stimulation to this region slows judgements of object manipulation in healthy participants (Ishibashi et al., 2011), but has also been shown to produce selective slowing of manipulable objects in a picture naming task for which manipulation knowledge was not probed directly (Pobric et al., 2010). Similarly, apraxic patients with parietal lobe lesions perform very poorly when questioned about how tools are manipulated, but they also show milder

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[4] To our knowledge, no studies have examined the status of appliances or machines as specific categories.

tool-specific deficits in other semantic tasks that do not directly require manipulation knowledge (Buxbaum & Saffran, 2002). In addition, Van Dam, van Dijk, Bekkering, and Rueschemeyer (in press) recently demonstrated that the degree of inferior parietal activation elicited by action-related objects is affected by task, being greatest when people made judgements about the action used to interact with the object. Taken together, these findings suggest that involvement of modality-specific brain regions in semantic processing is a graded phenomenon that depends on (a) the intrinsic relevance of the modality to the representation of the concept and (b) the importance of the modality to the current context or task.

Throughout this study, we have focused on sensory-motor knowledge gained through direct interaction with the environment. There is little doubt that language also plays a critical role in the formation of concepts (e.g., Landauer & Dumais, 1997) and that emotional states may be an important additional source of information, particularly for abstract concepts that have no direct physical referents (Barsalou, 2008). There also remains considerable debate over whether this network of specialised regions is sufficient by itself to represent conceptual knowledge or whether an additional integrative system is necessary to combine these different sources of information into modality-invariant concepts (Barsalou, 2008; Martin, 2007; Patterson et al., 2007; Rogers et al., 2004). The hub-and-spoke framework (Rogers et al., 2004) is an example of the latter view, inspired by studies of semantic dementia patients whose semantic deficit affects all categories of knowledge to a similar extent (Lambon Ralph, Lowe, & Rogers, 2007). If conceptual knowledge were simply the summation of activity in distributed modality-specific areas, these patients would need to have damage to a number of anatomically distinct regions in order to for all concepts to be affected. In fact, their pathology is homogenous and focussed on the inferior, anterior temporal lobes, which are not associated with any specific modality (Galton et al., 2001; Mion et al., 2010). The hub-and-spoke model instead attributes their pan-categorical, pan-modal deficit to damage to a central conceptual hub and indicates that the category-specific deficits of other patient groups arise from damage to one or more of the modality-specific “spokes” (Pobric et al., 2010). Understanding how these two elements of semantic representation interact is an important challenge for future research.

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Appendix A. List of 160 items presented for rating

Creatures: Alligator, ant, buzzard, camel, cat, caterpillar, catfish, chicken, cockroach, cod, cow, dog, duck, eagle, eel, elephant, flea, frog, goldfish, hornet, horse, hyena, kangaroo, mackerel, monkey, moth, mouse, octopus, ostrich, owl, peacock, penguin, platypus, rabbit, rhinoceros, salmon, sardine, spider, squid, squirrel, swan, tiger, trout, turtle, walrus, worm.

Non-living things: Aeroplane, axe, barn, barrel, basket, bazooka, bed, beehive, bike, bin_(waste), blender, bomb, bookcase, boots, bouquet, brick, bridge, brush, bus, cabinet, candle, cathedral, chandelier, clock, coat, comb, cottage, crane_(machine), crossbow, desk, dishwasher, earmuffs, emerald, envelope, escalator, glass_(drinking), gun, hammer, helicopter, house, kettle, key, lantern, machete, mirror, motorcycle, oven, paintbrush, pier, pliers, plug_(electric), pyramid, radio, rocket_(machine), saw_(tool), scissors, screwdriver, shawl, shelves, skirt, skyscraper, sledge, socks, sofa, spanner, spear, stool_(furniture), subway, suitcase, sword, table, tank_(army), telephone, tent, thermometer, toaster, toothbrush, train, trousers, truck, typewriter, unicycle, veil, wand, watering can.

Musical instruments: Bagpipe, clarinet, drum, guitar, harpsichord, piano, tuba, violin.

Plants and natural kinds: Banana, cherry, dandelion, oak, orange_(fruit), pear, pine_(tree), pineapple, seaweed, stick, stone, strawberry, tomato.

Food: Biscuit, bread, cake, cheese, pickle, pie.

Appendix B. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2012.11.009.

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