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Top-down processes in object identification: evidence from experimental psychology, neuropsychology and functional anatomy

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SUMMARY

Many models of object identification are bottom-up and serial in nature; processing at a first stage needs to be complete before it is passed on to a subsequent stage, and there is no top-down feedback from the later to the earlier stages. However, data on picture identification in normal observers contradict a strict serial account of processing, since effects of variables on early and late stages of object identification combine in an interactive rather than an additive manner. Recent neuropsychological and functional anatomical data also indicate that object identification involves top-down activation of earlier stages of visual processing. In neuropsychological patients, subtle perceptual deficits can produce naming problems, even when there is good access to associated semantic knowledge; in functional activation studies, there is increased activity in visual processing areas when conditions require object naming relative to object recognition. These studies provide evidence that increased visual processing occurs in identification tasks, suggesting that there is re-current feedback during the identification process.

1. INTRODUCTION

In everyday circumstances, object identification is impressively efficient. However, this efficiency masks the complexity of the processes involved. Initially, early visual processes must encode the properties of the object, its shape, and perhaps also its surface details. Subsequently, different forms of stored knowledge must be contacted so that the object can be recognized and perhaps eventually assigned an individual name. Neuropsychological studies (cited below) indicate that several forms of stored knowledge must be accessed before an object's name can be retrieved, including knowledge about the form of the object (its stored structural description), about its functional and associative properties (its semantic description) and its name (its phonological description). We consider the evidence for each type of stored knowledge before discussing how such knowledge is activated during object identification.

Impairments in knowledge about the visual properties of objects can be demonstrated in several ways. For example, patients can be impaired at 'object decision' tasks, which require familiarity discriminations between pictures of real objects and non-objects made by combining parts of different real objects. The same patients show poor drawing from memory, and they are impaired at answering questions about the visual properties of objects and at giving names to definitions that stress such properties (e.g. Sartori & Job 1988; Gainotti & Silveri 1996). Nevertheless, early visual processing in such patients can be good (judged by perceptual matching and copying performance), as can their knowledge about the functional and associative properties of objects, and their general naming abilities (e.g. when given verbal questions and definitions). Problems in visual object recognition in such cases are not linked to deficient visual processing or to the loss of semantic or phonological representations, but to the impairment of visual knowledge about objects (e.g. to impaired stored structural descriptions).

In other patients, deficits seem due to impaired access to semantic representations after access to stored visual knowledge occurs. These patients can discriminate between real and plausible non-objects (Riddoch & Humphreys 1987*a*; Sheridan & Humphreys 1993; Hillis & Caramazza 1995), but they are deficient at associative matching tasks (e.g. matching a hammer to a nail or a screw) as well as at object naming. The same patients can perform associative matching to the names of objects, and they can name to verbal definition, so any problems are not due to generally poor semantic knowledge or to deficits in name retrieval. In such cases, there is impaired visual access to semantic knowledge following intact access to stored visual knowledge.

The above deficits can be classed as problems in object recognition rather than naming, since problems arise even when naming is not required. In some patients, however, the deficit is restricted to name retrieval. Such patients may have full access to semantic information about the visual, functional, and associative properties of objects (judged from object decision and associative matching tests; Kay & Ellis 1987), but they are impaired at retrieving phonological information.

These cases indicate that stored knowledge about the visual properties of objects can be separated from semantic and phonological representations, and that semantic representations can be separated from phonological representations. Many theories of object identification assume that these different types of stored representation are accessed sequentially, based on bottom-up, serial processes (e.g. Levelt 1989). On such accounts, processing at a first stage needs to be complete before information is passed on to a subsequent stage, and there is no top-down feedback from the later to the earlier stages. In contrast to this, we will present evidence that object identification does not proceed serially but rather in a cascade, so that information processing at later stages can begin prior to processing at earlier stages being completed. Also, identification can involve top-down as well as bottom-up processes. In particular, there can be further recurrent activation of perceptual representations when we retrieve an object's name, relative to when we retrieve semantic information from the object. Evidence comes from experimental studies with normal observers, from neuropsychological studies, and from functional anatomical studies. We first review evidence against a strict serial account of object identification, before proceeding to discuss evidence for top-down processes.

2. OBJECT IDENTIFICATION IN NORMAL OBSERVERS

If object identification involves discrete and serial stages, clear predictions can be made concerning the effects of variables influencing different stages of processing. For example, consider how identification may be affected by perceptual overlap between objects. If objects are perceptually similar, the time taken to access individual structural descriptions will be longer than if they are perceptually distinct. This is confirmed by studies using object decision latency as the measure of access to structural descriptions. Object decisions are slowed if an object is perceptually similar to other objects from the same category (Vitkovitch & Tyrrell 1995; Lloyd-Jones & Humphreys 1996). However, if tasks do not require differentiation between category members, but rather responses based on similarity within the category (e.g. judging that objects belong to the same superordinate category), then responses are faster to objects from categories with perceptually similar members (e.g. animals) than to objects from categories with dissimilar members (e.g. vehicles) (Riddoch & Humphreys 1987*b*). This does not simply reflect a general speeding of responses when categorization responses are required, but rather a differential facilitation for stimuli from categories with perceptually similar members; indeed, effects of perceptual overlap are reversed in superordinate classification relative to object decision responses. These reversed effects of perceptual overlap on tasks designed to tap first structural and then semantic knowledge should not occur if processing at a structural level had to be complete before semantic knowledge could be accessed. Slow access to structural knowledge should lead to slow access to semantic knowledge. Rather, the results fit with a cascade account in which semantic information is activated before processing at a structural level is completed. Objects from categories with similar members produce a spread of activation across the structural representations of perceptual neighbours. This slows the time to access individual structural descriptions for object decision. In contrast, activation of the representations of other category members is useful if passed forward (in cascade) for semantic categorization, since it provides additional evidence for the target's category. Slow object decision but fast categorization responses are the result.

Consider now the effects of a variable such as name frequency, which influences name retrieval (a late stage of object naming), but not access to stored structural or semantic information. For instance, the frequency of an object's name affects the time taken to name an object, but not the time to assign it to a semantic category (Wingfield 1968; Morrison *et al.* 1992). In a discrete model, the effects of name frequency should combine additively with the effects of a variable such as perceptual overlap, which influences an earlier stage (access to structural descriptions). For example, though the time to access stored structural descriptions will be faster for stimuli from categories with perceptual-distinct relative to perceptual-similar exemplars, the effects of name frequency on name retrieval should be equal since name retrieval will only begin after access to structural descriptions has taken place. The data contradict this. Humphreys *et al.* (1988; see also Snodgrass & Yuditsky 1996) found that name frequency interacts with the effects of perceptual overlap in naming; frequency effects are larger on objects from categories with perceptually dissimilar members. In categories with similar exemplars, frequency effects may be attenuated because of the increased time to differentiate a target's structural representation from those of its perceptual neighbours; in a system operating in cascade, the delay in accessing stored structural descriptions will allow some activation of name representations whilst processing at a structural level is being completed. This particularly benefits those low-frequency names that are otherwise difficult to retrieve.

Other data favouring a cascade account concern the errors that normal subjects make when naming objects. One class of naming error reflects both semantic and phonological similarity between the target and the (incorrect) name ('mixed' errors: carrot → cabbage). Interestingly, these mixed errors occur more frequently than would be expected from the independent occurrence of each error type alone (Dell & Reich 1991; Martin *et al.* 1989), suggesting that semantic and phonological information interacts in name retrieval.

Vitkovitch & Humphreys (1991) and Vitkovitch *et al.* (1993) noticed another type of error made when participants had to name to a deadline: a target object was given the name of a related (prime) object that was named earlier (a 'perseverative' error). Participants saw and responded to two separate blocks of stimuli; Vitkovitch *et al*. were interested in the effects of the first stimuli in priming responses to the second block (the targets). These perseverative errors occurred when the primes were pictures that participants named; however, perseverative errors did not occur if participants categorized the prime pictures, or if the primes were printed words that participants read aloud (even though the words corresponded to the names of the picture primes). Object naming requires mapping from a semantic representation of an object to its name. In contrast, word naming can operate non-semantically (Van Orden 1987), whilst object categorization demands access to semantic information but not to the names of objects (Potter & Faulconer 1975). Neither word naming nor picture categorization require mapping from a semantic representation to a name representation. Since perseverations only occur when object naming is the priming task, and not with either word naming or picture categorization, these errors seem specifically to reflect a bias in mapping from semantic to name representations, favouring previously named objects. A target related to a previously named object may reactivate the original (biased) mappings, leading to a perseverative error (production of the prime's name). Vitkovitch *et al*. (1993) found that perseverations were always semantically and visually related to target objects; they were never purely semantically related. This indicates that mapping from a semantic to a name representation (the locus of perseverative errors) is constrained by a combination of visual and semantic similarity between objects. This would be expected if visual, and subsequently semantic activation, is transmitted continuously, to influence name retrieval.

These results contradict a strict serial, discrete account of object identification, suggesting instead that activation can be passed on in cascade between processing stages. The data can be simulated relatively easily within models that assume continuous transmission of activation in object identification (Humphreys *et al*. 1995).

3. NEUROPSYCHOLOGICAL IMPAIRMENTS OF OBJECT NAMING

As already noted, impairments in object naming can arise at different processing stages. This is consistent with a serial model of identification. However, as with normal subjects, the model is contradicted by patterns of errors produced by patients. Caramazza & Hillis (1990, 1991) report interesting dissociations between the errors generated when patients use different responses, such as speaking versus writing the names of objects. Some patients typically produce semantically related errors in naming (e.g. carrot → onion), but not in writing (when the correct response is made); others show the opposite pattern of performance. Since the same patient can produce the correct written response as well as a spoken semantic error (or vice versa), access to the appropriate semantic representation seemingly takes place. The semantic error arises in name retrieval for speaking or writing, but not in semantic access. This is consistent with there being activation of the names of sets of semantically related objects, reflecting partial activation from semantic information during object identification.

Other recent studies not only go against a serial account of object identification, but also favour a more top-down approach in which perceptual knowledge is recurrently activated during naming. These studies link deficits in object naming to problems with stored perceptual knowledge. Patients may demonstrate access to relatively detailed semantic knowledge about an object, but the loss of perceptual knowledge prevents access to the object's name.

We have worked with two patients, S.R.B. and D.M., in whom object naming could be linked to impaired perceptual knowledge. S.R.B., a 38-year-old man, suffered an intracerebral haemorrhage from an arteriovenous malformation (AVM). D.M., a 44-year-old woman, had multiple AVMs in her lungs due to hereditary telangiectasia. An infection from an AVM tracked to her brain and caused an abscess that was evacuated. MRI scans revealed damage to the left medial and inferior occipitotemporal regions of both patients (figure 1); both had right homonymous hemianopias and were alexic. A detailed case report of S.R.B. is given in Forde *et al*. (1997).

Both S.R.B. and D.M. presented with a clinical problem in naming animate objects; in contrast, they maintained a relatively preserved ability to name artefacts. Initial testing took place within three months of their lesions developing. Given standardized line drawings of animate and artefactual objects, matched for their name frequencies (taken from Humphreys *et al*. 1988), S.R.B. named 37 out of 38 of the artefacts (95%), but only 28 out of 38 (71%) animate objects. Given the same items on two different test occasions D.M. named 57 out of 76 (75%) of the artefacts but only 35 of 76 (46%) animate objects. Neither patient was affected by the frequency of the object names. When unable to name an object, each patient quite often produced a detailed circumlocution, suggesting the activation of associated semantic information. For example, when asked to name a drawing of some celery, S.R.B. said 'it is green and you have it as a main course. I dip it in salt'; for a lemon he said 'bitter . . . an orange . . . no'. When given a lemon, D.M. said 'sour and you have it with . . . you make them in a pan, put milk and eggs and whisk them with this other stuff in a frying pan. Pancakes!' (lemons are traditionally used with pancakes in the UK). Access to semantic information from objects was tested more formally using the associative matching task from the Birmingham Object Recognition Battery (Riddoch & Humphreys 1993) and the 'pyramids and palm trees' task (Howard & Orchard-Lisle 1984). Associative matching requires the patient to decide which of two reference pictures (e.g. a screw and a nail) is most associated with a target picture (a screwdriver). In the pyramids and palm trees test, a similar decision is made concerning which of two reference pictures (e.g. palm tree and a fir tree) is most related to a target

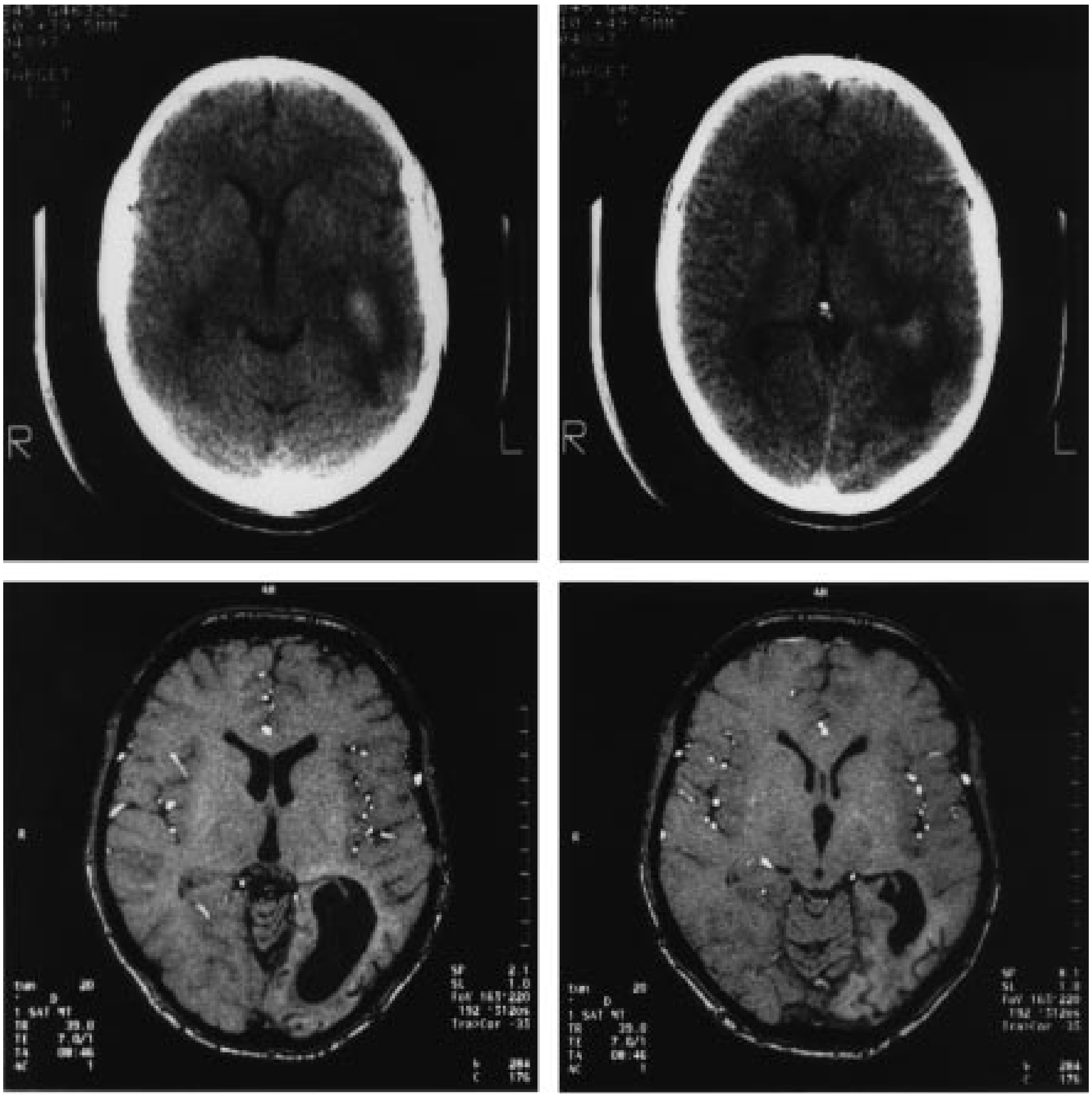

Figure 1. MRI scans for patients S.R.B. (top) and D.M. (bottom). In each case there is a lesion affecting the left inferior medial occipito-temporal region.

picture (e.g. a pyramid). In each test, the items to be matched are not visually related. S.R.B. scored 29 out of 30 (97%) and 48 out of 50 (96%) correct on the associative match and pyramids and palm trees tests; D.M. scored 27 out of 30 (90%) and 45 out of 50 (90%) respectively. A control score on each task is, respectively, around 96%. S.R.B. scored at a control level. D.M. scored just below the control level, but at most revealed a mild impairment.

The associative match and the pyramids and palm trees tests both involve a minority of animate stimuli, and so may not stress a deficit in accessing semantic knowledge for animate objects. This was tested further by having the patients categorize sets of fruits and vegetables (items that they found difficult to name), and carry out associative matching with living things (matching a wine bottle or milk bottle to grapes). S.R.B. categorized 18 out of 20 (90%) of the fruits and vegetables (naming only 13 correctly), and he scored 37 out of 40 (93%) correct on the associative test. D.M. categorized 20 out of 20 of the fruits and vegetables (naming only 13 correctly), and scored 40 out of 40 on the associative task. S.R.B. also made two errors on fruit/vegetable categorization when given the object names; he did not show an impairment specific to vision in this task. S.R.B.'s score on the associative matching task was slightly below the control level (mean 39 out of 40, s.d. = 0.84), but still quite impressive. D.M. performed at ceiling level. The results suggest that, despite their difficulties in naming, both patients could access semantic information from objects. It is tempting to conclude that their deficits are solely in name retrieval (see Hart *et al*. 1985; Farah & Wallace 1992).

However, other evidence indicates that, for these patients, this conclusion is incorrect. For instance, both patients had lesions in brain areas associated with high-level visual processing rather than name retrieval (cf.

Frackowiak 1994; Ungerleider 1995). In addition, both had deficits in stored perceptual knowledge, particularly for animate objects. When asked to draw from memory, both S.R.B. and D.M. generated poor representations of animate objects, whereas their drawings of artefacts were good. The animate objects that the patients were poor at drawing tended also to be the ones that they failed to name, suggesting a link between their degraded perceptual knowledge and the naming defect.

Other tests confirmed that stored perceptual knowledge about objects was degraded. On object decision both patients scored 27 out of 32, which is above chance but more than two standard deviations below control subjects. In addition, the patients were required to produce a name to definitions, stressing either the perceptual properties of objects (e.g. what is the name for an orange, cone-shaped vegetable?) or functional and associative properties (e.g. what is the root vegetable said to help you see in the dark?). The definitions were to the same objects that had been used in the picture-naming task. With functional definitions, the patients scored 70 out of 76 (92%) (S.R.B.) and 68 out of 76 (89%) (D.M.); the control mean was 71 (s.d. = 2.1). With perceptual definitions, S.R.B. scored 39 out of 76 (51%) and D.M. 32 out of 76 (42%); the control score was 56 out of 76 (74%) (s.d. = 4). S.R.B. and D.M. answered functional definitions at the control level, but both performed considerably below the control level on the perceptual definitions. This matches the performance of other patients with reported deficits in stored perceptual memory (Gainotti & Silveri 1996). On the perceptual definitions the patients were worse with animate objects than with artefacts; for S.R.B., 16 versus 23 out of 38; for D.M. 13 versus 19 out of 38. This was in the opposite direction to the effect for controls: means of 25 out of 38 with artefacts and 31 out of 38 with animate objects, consistent with perceptual information being more useful for the definition of animate objects than for artefacts (Farah & McClelland 1991). The poorer performance of the patients with animate objects counters the argument that they did worse with perceptual definitions just because these were the more difficult, and suggests instead a specific deficit in using perceptual information to derive the names of animate objects.

These cases demonstrate that patients can be impaired at retrieving stored knowledge about the perceptual properties of objects, and yet have intact semantic knowledge of the functional characteristics of objects (judged from their naming of functional definitions) and still gain access to that semantic knowledge from vision (judged from their semantic matching and categorization performances). The patients are particularly impaired when tasks depend on stored perceptual knowledge to generate a unique response to an object (as in drawing from memory or naming a picture or a definition). We propose that bottom-up activation of semantic knowledge from vision may be insufficient to invoke a name; object naming requires recurrent activation of stored perceptual knowledge to differentiate activation from a target object from that present in other representations. Subtle impairments of stored perceptual knowledge produce naming deficits because recurrent activation operates less well with degraded perceptual representations. This argument, for recurrent top-down activation being impaired, fits with both our patients having relatively posterior lesions (in the medial occipitotemporal region). The deficits may be exacerbated with animate objects for a variety of reasons. Animate objects belong to categories with high perceptual overlap, while there tends to be lower perceptual overlap between artefacts. This increased perceptual overlap may place more demands on the process of differentiating the activation in target and other representations at a structural level (Humphreys *et al.* 1988, 1995). Additionally, animate objects may depend more than artefacts on the activation of stored perceptual knowledge for their identification (e.g. if they are distinguished more by perceptual than by functional features; Farah & McClelland 1991). In either case, impairments to stored perceptual knowledge will lead to problems that are more severe for animate objects.

4. THE FUNCTIONAL ANATOMY OF OBJECT NAMING

Our proposal for top-down processes in object identification receives support from recent studies of the functional anatomy of object naming, using positron emission tomography (PET) techniques.

PET can be used to measure changes in regional blood flow associated with different cognitive tasks, such as identifying objects. ^{15}O can be administered intravenously as radiolabelled water, and the total count per voxel (volumetric element) serves as an estimate of regional blood flow in the brain. Using this technique, a number of groups have investigated the neural areas involved in object identification. Martin *et al.* (1996) had subjects (i) silently name line drawings of animals or tools; (ii) view drawings of structurally plausible non-objects; or (iii) view random noise patterns. Subtraction of the images from each condition revealed the following. Viewing the non-objects relative to the noise patterns led to bilateral activation in the fusiform gyri and the inferior gyri of the occipital lobes, suggesting that these areas may be involved in encoding the structural properties of objects. Naming objects, relative to viewing the plausible non-objects, resulted in increased activation bilateral activity in the temporal lobes, overlapping but also anterior to the areas activated by the non-objects. Naming animals, relative to naming tools, gave rise to increased activation in the left medial occipital lobe, centred on the calcarine sulcus. Naming tools, relative to naming animals, produced increased activation in the left premotor area and in the left temporal lobe, but in an area more dorsal to that activated by animal naming. Quite similar results have been reported by Perani *et al.* (1995), using animals and a broader category of artefacts. Their experimental task required subjects to judge whether two pictures had the same name; the baseline task required matching of random shapes. Relative to this baseline, animals activated the inferior temporal lobes bilaterally; artefacts activated the left hemisphere primarily, including the lingual, the parahippocampal and the middle occipital gyri and the dorsolateral frontal cortex. Damasio *et al*. (1996) had subjects name animals and tools; in the baseline condition they said 'up' or 'down' to upright or inverted faces. Relative to the baseline, animal naming activated medial and inferior regions of the posterior temporal lobe (though somewhat anterior to the area suggested by Martin *et al*.); tool naming activated the middle and inferior temporal gyri. These results indicate that different regions of the brain mediate name retrieval with animals and artefacts, though there are some discrepancies in the areas highlighted by different studies. However, in all cases there is activation of relatively posterior neural regions when animals are named, regions usually thought to be involved with high-level visual processing. This suggests that the naming of these objects involves additional activation of perceptual representations.

Price *et al*. (1996) and Moore & Price (1997) also examined object naming using PET methods. Price *et al*. presented subjects with coloured pictures of objects or non-objects (constructed from the same number of lines as the real objects). There were four conditions, leading to a factorial design in which subjects (i) named the real objects; (ii) said 'yes' to the occurrence of the real objects; (iii) named the colour of the non-objects; and (iv) said 'yes' to the occurrence of the non-objects. The two naming tasks (to objects and to colours, (i) and (iii)) both required the retrieval of learned phonological labels associated with visual stimuli; the 'say yes' tasks ((ii) and (iv)) required visual analysis and articulation without learned name retrieval. Subtraction of the 'say yes' conditions from the naming conditions reveals the neural areas associated with name retrieval. The neural areas associated with processing the shapes of objects are revealed by contrasting the conditions with objects ((i) and (ii)) and those with non-objects ((ii) and (iv)). In addition, the factorial design enables us to assess the interaction between naming and object recognition. This interaction concerns the differences between neural activation in the object naming condition ((i)) and its non-naming baseline ('say yes' to objects, (ii)), when compared to the differences between the colour naming condition ((iii)) and its non-naming baseline ('say yes' to non-objects, (iv)). From this interaction we reveal the neural areas specifically involved in name retrieval for objects relative to other visual name retrieval tasks (in this case colours).

Subtraction images are shown in figure 2. Object recognition (taking the two tasks with objects, relative to the non-object baselines) was associated with activation of the ventral and dorsal middle occipital cortex, the left mid inferior temporal lobe, the right anterior temporal lobe and the left cerebellum. Name retrieval (taking both the object and the colour naming tasks, relative to their baselines) activated the left inferior occipital gyrus, the left lingual and mid fusiform gyri, the left middle frontal lobe, the left thalamus, the left caudate and the right parahippocampus. More important for our present purposes, there was an interaction between object naming (relative to its baseline) and colour naming (relative to its baseline). The following

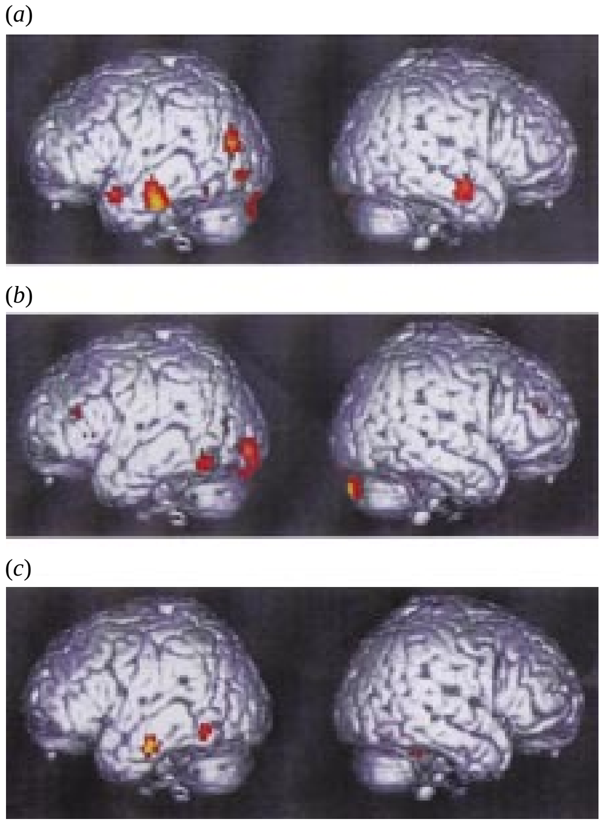

Figure 2. PET subtraction images (from the study of Price *et al*. 1996). (*a*) The main effect of object recognition reflects the differences between activation values when objects relative to non-objects were presented. (*b*) The main effect of naming reflects the differences in activation values when naming responses were required (to objects and colours) relative to the 'say yes' baselines. (*c*) The interaction of object recognition and naming reflects the increase in activation values in object naming relative to colour naming, relative to the respective 'say yes' baselines.

areas were more activated in name retrieval for objects: the medial anterior temporal lobes (bilaterally), the left superior temporal sulcus, the left posterior inferior temporal lobe, the left anterior insula and the right cerebellum.

Unlike prior studies using functional imaging to investigate object naming, we used the same visual stimuli in the naming and baseline conditions. Despite this, areas in the inferior occipital lobe and the lingual gyrus increased their activation in naming. These areas are linked to early visual processing of shape and colour (Humphreys & Riddoch 1993; Zeki *et al*. 1991). The data imply some modulation of early visual form and colour processing when object and colour naming is required. Object naming also generated larger activation increases than colour naming, particularly for areas in the left posterior inferior temporal lobe. Such areas seem to be strongly activated specifically in object identification tasks.

Moore & Price had similar object naming tasks to Price *et al*., but used either coloured or black and white line drawings for animate objects or artefacts, and these were either visually complex (animals and multi-component artefacts) or simple (fruits, vegetables, and artefacts with simple shapes). Coloured drawings are named faster than line drawings, particularly for animate objects (Price & Humphreys 1989), presumably because colour facilitates the process of differentiating between perceptually overlapping neighbours. Moore & Price's results matched this proposal. For animate objects, coloured drawings reduced activation levels in areas implicated in object recognition in the study of Price *et al*. (1996). Such a reduction in activation suggests that there is less top-down modulation of recognition processes for coloured drawings than for line drawings.

Moore & Price additionally found that activation in the left medial occipital lobe was increased for naming animate objects relative to artefacts. Interestingly, there were effects of both object category and visual complexity. Complex artefacts and animals had increased activation levels relative to the visually similar artefacts and fruits and vegetables. On top of this, animals and fruits or vegetables generated increased activation levels compared with their matched artefacts. It would appear that there is more protracted visual processing of complex relative to simple objects, and of animate objects relative to artefacts. In each case, the data fit with the argument for top-down processing in object identification, since increased activation occurs in naming compared with baseline tasks sensitive to object recognition (e.g. 'say yes' to objects relative to non-objects, in Price *et al*. 1996).

5. CONCLUSIONS

We have presented data from experimental studies with normal observers, neuropsychological studies with patients with naming deficits, and studies using functional imaging, which converge on the view that object identification involves top-down modulation of earlier visual processes.

The results from the experimental studies contradict the idea that object identification is based on discrete processing stages, and suggest instead that activation is transmitted in cascade between stages; therefore, later processing stages can be activated before earlier stages are completed. The neuropsychological data link impairments in name retrieval to deficits in stored knowledge for the perceptual properties of objects. Such deficits disrupt name retrieval whilst concurrently allowing semantic knowledge to be accessed from objects. This points to naming being dependent on the recurrent activation of stored perceptual knowledge even after semantic representations have been accessed. This recurrent activation process can be disrupted by lesions to brain areas where perceptual knowledge is stored (the posterior inferior occipito-temporal regions). Functional imaging studies are consistent with the argument for top-down processes in object naming. There is enhanced activation of visual processing areas associated with object naming in addition to object recognition. There is also enhanced activation of these areas when animate relative to inanimate objects are named; part of this last increase is linked to the visual complexity of the objects, but part also seems particular to animate objects. The additional enhancement for naming animals may be due to the greater visual differentiation required for categories with high perceptual overlap or to the discriminating role of perceptual features for animate objects.

There are alternative accounts for some of the results we have discussed. For example, the neuropsychological data could be attributed to a disconnection between right hemisphere recognition processes (intact in the patients) and processes in the left hemisphere concerned with object naming (cf. Geschwind 1965; Coslett & Saffran 1989). On this account, the data do not demonstrate top-down processes in object naming but rather separate routes, one to semantic knowledge (intact) and one to phonological retrieval (impaired). However, this fails to explain why the disorder was most pronounced for animate objects. Phonological retrieval for artefacts as well as animate objects is associated with left hemisphere activation (Perani *et al*. 1995; Martin *et al*. 1996). There seems little reason why a left hemisphere disconnection should affect one class of objects but not another. However, this result is consistent with animate objects being the more dependent on top-down activation of perceptual knowledge for identification. This top-down activation may be more pronounced in the left hemisphere due to its control of the naming process.

We conclude that serial models fail to account for human performance. Object identification involves processes that operate in cascade and that utilize recurrent top-down activation of knowledge sources.

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REFERENCES

Caramazza, A. & Hillis, A. E. 1990 Where do semantic errors come from? *Cortex* **26**, 95–122.

Caramazza, A. & Hillis, A. E. 1991 Lexical organization of nouns and verbs in the brain. *Nature* **349**, 788–790.

Coslett, H.B. & Saffran, E. M. 1989 Preserved object recognition and reading comprehension in optic aphasia. *Brain* **112**, 1091–1110.

Damasio, H., Grabowski, T. J., Tranel, D., Hichwa, R. D. & Damasio, A. R. 1996 A neural basis for lexical retrieval. *Nature* **380**, 499–505.

Dell, G. S. & Reich, P. A. 1981 Stages in sentence production: an analysis of speech error data. *J. Verb. Learn. Verb. Behav.* **20**, 611–629.

Farah, M. J. & McClelland, J. L. 1991 A computational model of semantic memory impairment: modality-specificity and emergent category-specificity. *J. Exp. Psychol.: Gen.* **120**, 339–357.

Farah, M. J. & Wallace, M. A. 1992 Categories of knowledge: unfamiliar aspects of living and non-living things. *Neuropsychologia* **30**, 609–621.

Forde, E. M. E., Francis, D., Riddock, M. J., Rumiati, R. I. & Humphreys, G. W. 1997 On the links between visual knowledge and naming: a singe case study of a patient with a category-specific impairment for living things. *Cog. Neuropsychol.* **14**, 403–458.

Frackowiak, R. S. J. 1994 Functional mapping of verbal memory and language. *Trends Neurosci.* **17**, 109–115.

Gainotti, G. & Silveri, M. C. 1996 Cognitive and anatomical locus of lesion in a patient with a category-specific semantic impairment for living things. *Cog. Neuropsychol.* **13**, 357–390.

Geschwind, N. 1965 Disconnexion syndromes in animals and man. *Brain* **88**, 237–294, 585–644.

Hart, J., Berndt, R. S. & Caramazza, A. 1985 Category-specific naming deficit following cerebral infarction. *Nature* **316**, 439–440.

Hillis, A. E. & Caramazza, A. 1995 Cognitive and neural mechanisms underlying visual and semantic processing: implications from 'optic aphasia'. *J. Cog. Neurosci.* **7**, 457–478.

Howard, D. & Orchard-Lisle, V. M. 1984 On the origin of semantic errors in naming: evidence from the case of a global aphasic. *Cog. Neuropsychol.* **1**, 163–190.

Humphreys, G. W. & Riddoch, M. J. 1993 Object agnosias. In *Baillière's clinical neurology* (ed. C. Kennard), pp. 339–360. London: Baillière Tindall.

Humphreys, G. W., Lamote, C. & Lloyd-Jones, T. J. 1995 An interactive activation–competition approach to object processing: effects of structural similarity, name frequency and task in normality and pathology. *Memory* **3**, 535–586.

Humphreys, G. W., Riddoch, M. J. & Quinlan, P. T. 1988 Cascade processes in picture identification. *Cog. Neuropsychol.* **5**, 67–103.

Kay, J. & Ellis, A. W. 1987 A cognitive neuropsychological case study of anomia: implications for psychological models of word retrieval. *Brain* **110**, 613–629.

Levelt, W. J. M. 1989 *Speaking: from intention to articulation.* Cambridge, MA: MIT Press.

Lloyd-Jones, T. J. & Humphreys, G. W. 1997 Perceptual differentiation as a source of category effects in object processing: evidence from naming and object decision. *Memory Cog.* **25**, 18–35.

Martin, N., Weisberg, R. W. & Saffran, E. 1989 Variables influencing the occurrence of naming errors: implications for a model of lexical retrieval. *J. Memory Lang.* **28**, 462–485.

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

Moore, C. & Price, C. J. 1997 Category-specific object naming differences: a controversy resolved? (In preparation.)

Morrison, C. M., Ellis, A. W. & Quinlan, P. T. 1992 Age of acquisition, not word frequency, affects object naming, not object recognition. *Memory Cog.* **20**, 705–714.

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

Potter, M. C. & Faulconer, B. A. 1975 Time to understand pictures and words. *Nature* **253**, 437–438.

Price, C. J. & Humphreys, G. W. 1989 The effects of surface detail on object categorisation and naming. *Q. Jl Exp. Psychol.* **41**A, 797–828.

Price, C. J., Moore, C. J., Humphreys, G. W., Frackowiak, R. S. J. & Friston, K. J. 1996 The neural regions sustaining object recognition and naming. *Proc. R. Soc. Lond.* B **263**, 1501–1507.

Riddoch, M. J. & Humphreys, G. W. 1987*a* Visual object processing in optic aphasia: a case of semantic access agnosia. *Cog. Neuropsychol.* **4**, 131–185.

Riddoch, M. J. & Humphreys, G. W. 1987*b* Picture naming. In *Visual object processing: a cognitive neuropsychological approach* (ed. G. W. Humphreys & M. J. Riddoch), pp. 107–143. London: Erlbaum UK.

Riddoch, M. J. & Humphreys, G. W. 1993 *BORB: the Birmingham Object Recognition Battery.* Hove: Erlbaum UK.

Sartori, G. & Job, R. 1988 The oyster with four legs: a neuropsychological study on the interaction of visual and semantic information. *Cog. Neuropsychol.* **5**, 130–152.

Sheridan, J. & Humphreys, G. W. 1993 A verbal-semantic category-specific recognition impairment. *Cog. Neuropsychol.* **10**, 143–184.

Snodgrass, J. G. & Yuditsky, T. 1996 Naming times for the Snodgrass and Vanderwart pictures. *Behav. Res. Meth. Instruments Comp.* **28**, 516–536.

Ungerleider, L. G. 1995 Functional brain imaging studies of cortical mechanisms for memory. *Science* **270**, 769–775.

Van Orden, G. C. 1987 A ROWS is a ROSE: spelling, sound and reading. *Memory Cog.* **15**, 181–198.

Vitkovitch, M. & Humphreys, G. W. 1991 Perseverative responding in speeded naming to pictures: its in the links. *J. Exp. Psychol.: Learn. Memory Cog.* **17**, 664–680.

Vitkovitch, M. & Tyrrell, L. 1995 Sources of disagreement in object naming. *Q. Jl Exp. Psychol.* **48**A, 822–848.

Vitkovitch, M., Humphreys, G. W. & Lloyd-Jones, T. J. 1993 On naming a giraffe a zebra: picture naming errors across different categories. *J. Exp. Psychol.: Learn. Memory Cog.* **19**, 243–259.

Wingfield, A. 1968 Effects of frequency on identification and naming of objects. *Am. J. Psychol.* **81**, 226–234.

Zeki, S., Watson, J. D. G., Lueck, C. J., Friston, K. J., Kennard, C. & Frackowiak, R. S. J. 1991 A direct demonstration of functional specialisation in human visual cortex. *J. Neurol.* **11**, 641–649.