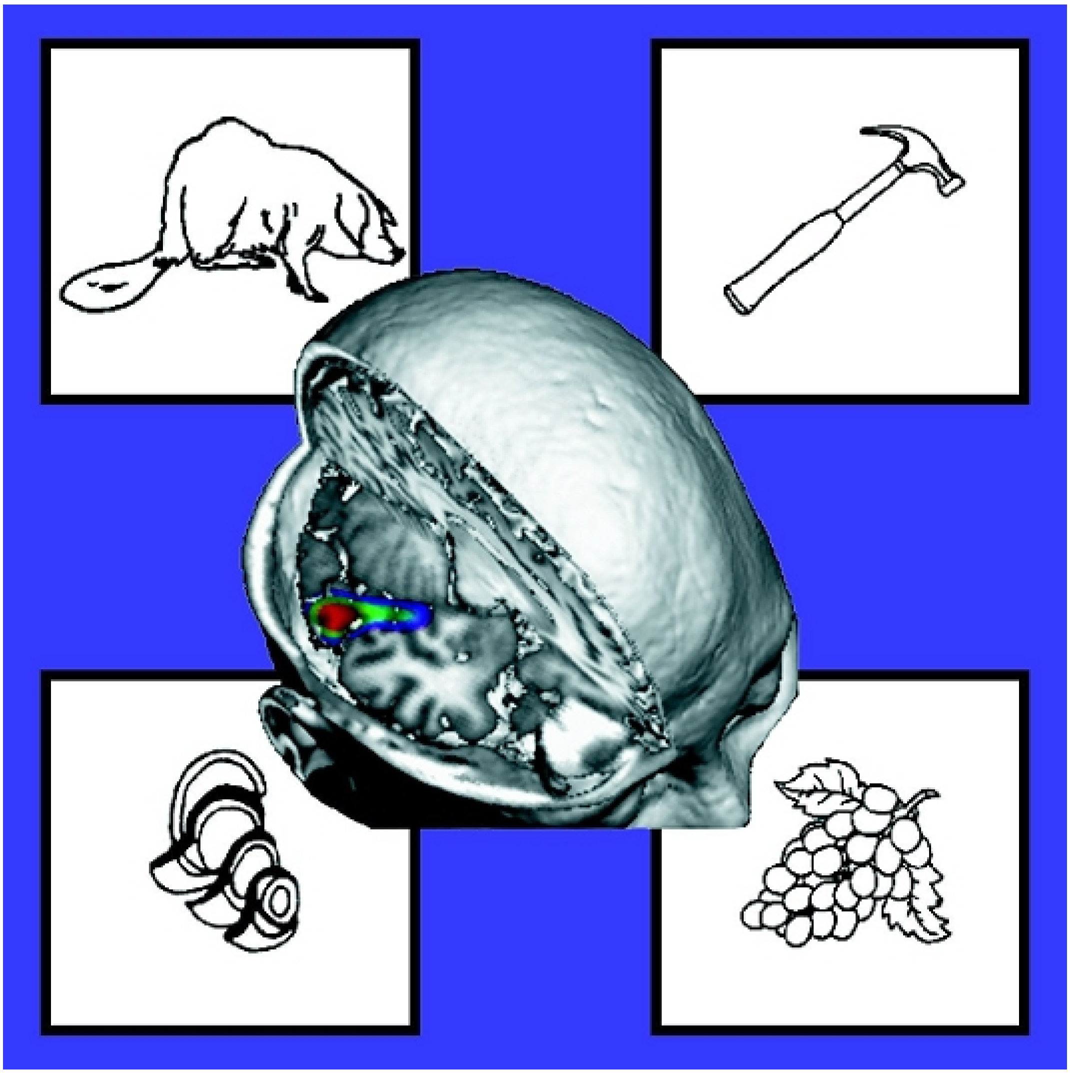
The functional organization of knowledge and its implementation in the brain



Christian Gerlach

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Cover figure

Stimuli used during object decision tasks. The level of difficulty was graded by using chimeric images of nonobjects, composed from single parts of known objects, and completely unknown novel nonobjects. The main activation effect of increased task difficulty was located in the posterior section of the right inferior temporal gyrus shown rendered on a structural MRI scan.

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All the people who for a day turned their body and mind into an object for science.

Abstract

This dissertation is an overview of the major findings presented in three articles. The topic of these articles is the functional organization of knowledge and its implementation in the brain studied by the use of imaging techniques (positron emission tomography, PET). As the results have been described in detail in the articles, this overview provides a broader theoretical framework in which the findings are brought together.

The first part of the dissertation presents a short historical introduction to the sub-field of neuropsychology concerned with the significance of different types of knowledge in visual object recognition. The primary evidence to this area has been cases with category-specific recognition impairments. Consequently, the largest part of the overview consists of an evaluation of the predominant accounts advanced in an attempt to explain these disorders. Although the explanatory power of these accounts is often limited to specific types of category-specific impairments, many of them offer valuable explanatory principles. It is argued that some of these principles are complementary and that they can be merged into a coherent framework. This framework, termed the eclectic model, can accommodate many of the cases reported although there are exceptions.

The latter part of the dissertation describes the PET-experiments performed by me. The findings from these experiments suggest: (i) that at least three types of knowledge (visual, semantic, and action knowledge) contribute to different stages in visual object recognition and that they are anatomically dissociable, and (ii) that natural objects and artifacts generally are subjected to the same kind of processing (engage the same brain structures) although natural objects, relative to artifacts, cause greater activation of areas involved in structural processing, whereas artifacts, relative to natural objects, cause greater activation of areas involved in the mediation of action knowledge.

1.0 Introduction

When we cannot categorize what we see our mind is blind. Indeed *associative mindblindness* was the term originally coined by Lissauer (1890) over a century ago to describe visual agnosic patients who apparently had normal vision, but could not make sense of what they saw. Lissauer noted that these patients were able to draw complex figures which they could not recognize. This observation led him to the conclusion that the process of visual object recognition was twofold. The first process involved the conscious reception of visual impressions, the latter the connection of these receptions to conceptual knowledge. According to Lissauer it was the first process that was functioning normally in visual agnosic patients, allowing them to copy drawings, and the second that was damaged and responsible for the failure of comprehension.

Although Lissauer published his theory in 1890 the distinction he drew between a perceptual and a semantic stage in visual object recognition did not receive much attention within the field of neuropsychology until the nineteen seventies. The reason for this was probably a reluctance to accept visual agnosia as other than an obscure neurological syndrome or a misconception (Benson, 1989). Accordingly, when Elizabeth Warrington in 1975 published what were to become a seminal paper on object recognition and semantics, she had to take pains in justifying the reality of visual agnosia. In this paper Warrington described three patients who were impaired in recognizing common objects. These impairments could not be accounted for by sensory or generalized cognitive deficits. Instead it appeared that the impairments were caused by damage to semantic memory itself. An interesting finding in this study was that the patient E.M. was often able to recognize the visual representation of a concept (a picture) but not its verbal representation (a word) whereas the reverse was true for the patient A.B. This observation of item-inconsistency between modalities led Warrington to suggest that there might exist two modality-specific semantic systems that could be selectively damaged, one visual and one verbal (see figure 1). How else could one explain that a patient could answer the question *is it an animal?* when shown a picture of a cat but not when shown the word cat? Whether or not Warrington's account was correct, it questioned the prevailing assumption of semantic memory as a unitary system serving all modalities. It also brought the organization of semantic memory within the scope of neuropsychological investigation.

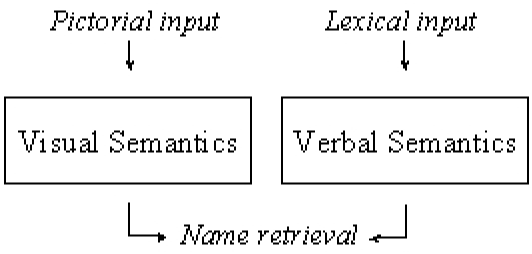

Figure 1. Warrington's 1975 account

In 1984 Warrington and Shallice described four patients, two of which exhibited the same pattern of inconsistent recognition success or failure across modalities as did the patients A.B. and E.M. In addition, Warrington and Shallice noted that these four patients were significantly more impaired in recognizing natural objects than artifacts. This was an intriguing observation. What was it that made a person able to define a briefcase as *a small case used by students to carry papers* but left him unable to define a parrot or made him define a snail as *an insect animal*? One explanation might be that natural objects for some reason are more difficult to recognize than artifacts and therefore more sensitive to disturbance following brain damage. This explanation, however, was dismissed by Warrington and Shallice because a patient with the opposite category-specific recognition impairment had been described (Warrington & McCarthy, 1983). Instead they favoured the explanation that semantic memory was categorically organized or, at the very least, that different categories were not processed in the same way.

Since the initial reports by Warrington and colleagues several cases with category-specific recognition impairments have been described, the majority exhibiting problems with natural objects. However, category effects do not seem confined to patients with brain damage but can also be observed in normal subjects (Lloyd-Jones & Humphreys, 1997) or even monkeys (Gaffan & Heywood, 1993). This opens the possibility that category-specific recognition impairments may reflect differences between categories that exist prior to neurological damage but become exacerbated due to this damage. To test this hypothesis, and a few others that will be discussed later, Ian Law, Anders Gade, Olaf B. Paulson and I conducted a series of experiments in which we measured the regional cerebral blood flow (rCBF) while normal subjects performed different tasks involving the processing of natural objects and artifacts. Although these experiments form the core of the present dissertation they will not be described in great detail as this has been done elsewhere (Gerlach et al., 1999, 2000a, 2000b). Instead I would like to bring the results of these investigations into a broader theoretical framework.

2.0 The distinction between sensory and functional knowledge

In their 1984 study, Warrington and Shallice noted that though their patients had difficulties in recognizing natural objects, the recognition of artifacts being relatively spared, there were violations of this pattern. The patient J.B.R. for example was very impaired at defining items from the categories of musical instruments and precious stones while performing at the same level as a control subject on items from the categories of body parts and weather. It therefore seemed that the distinction between natural objects and artifacts was a useful approximation only to some other underlying factor of division. Thus, instead of arguing for a truly categorical partitioning of semantic memory, Warrington and Shallice proposed that the category-specific impairments for natural objects reflected the loss a particular kind of knowledge pertinent to the category of natural objects but also to specific subcategories of artifacts. In keeping with a suggestion previously advanced by Warrington and McCarthy (1983), Warrington and Shalllice proposed that retrieval of fine-grained sensory information was necessary for the recognition of natural objects. As an example they argued that the distinction between a raspberry and a strawberry drew on detailed information about size, colour, texture and shape whereas the recognition of an artifact depended critically on determination of its functional significanse. Based on these speculations Warrington and Shallice proposed that two functionally independent semantic systems may have evolved: one containing functional information important for the identification of artifacts, and another containing sensory information important for the identification of natural objects. Given this model, category-specific impairments for natural objects would arise following damage to the sensory semantic system whereas category-specific impairments for artifacts would arise following damage to the functional semantic system. However, since the category-specific impairments for natural objects would be caused by damage to a store containing sensory rather than category-specific knowledge the deficit might generalise to artifacts that also depend on the retrieval of sensory knowledge for their recognition, for example precious stones and musical instruments.

To the suggestion of two functionally independent semantic systems divided by knowledge type we have to ad the division by modality suggested by Warrington in 1975. Thus, based on the suggestions of Warrington and colleagues semantic memory is partitioned into four compartments as a function of knowledge type and input modality (see figure 2). Consequently, it should be possible for a recognition impairment to be *both* category- and modality-specific. Indeed such a case has been described by McCarthy and Warrington (1988). This patient, T.O.B., was impaired in the comprehension of natural objects compared with artifacts and more so when items from this category were presented verbally than pictorially.

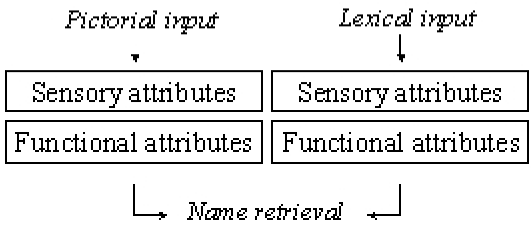

Figure 1. Warrington & Shallice's 1984 account

Although this multiple semantic systems account might seem reasonable it cannot account for cases of category-specificity where retrieval of sensory and functional knowledge is equally impaired (see Caramazza & Shelton, 1998; Funnell & De Mornay Davies, 1996; Laiacona et al., 1997) or for cases with category-specific recognition impairments for natural objects where sensory knowledge appears intact (Laiacona et al., 1997; Sacchett & Humphreys, 1992). In fact there is even reason to be critical with respect to one of the cornerstones in the model, namely the suggestion of modality-specificity. The argument for modality-specificity rests on the observation of item-consistency within modalities but item-inconsistency between modalities. However, item-consistency may not necessarily reflect degraded knowledge but may instead reflect impaired access mechanisms (Forde & Humphreys, 1995; Forde et al., 1997). Accordingly, it cannot be argued that knowledge of a particular concept has been lost just because it can be accessed from one modality but not another. Moreover, many patients do show item-consistency between modalities suggesting that it is the same semantic system that serves different modalities[1] (Forde & Humphreys, 1997; Forde et al., 1997; Sheridan & Humphreys, 1993).

A third problem for the multiple semantic systems account is that it cannot explain dissociations observed within the very categories of natural objects and artifacts. This problem led Warrington and McCarthy (1987) to propose a refined version of the sensory/functional hypothesis, based on a framework originally developed by Lissauer (1890). Inspired by the associationist philosophy of his time Lissauer suggested that objects could only be recognized if their image invoked associations previously established through experience. Thus, the recognition of a car will depend on whether associations concerning its sound, its name, or its handling are brought to life. In this way various modalities take part in the formation of concepts based on linkages between different types of knowledge. Warrington and McCarthy (1987) developed this idea further by proposing that the modality-specific recollections that formed these concepts were stored in separate channels and that these channels could be very fine-grained so that visual information for example might be stored in several functionally independent channels, say a colour channel, a size channel, a shape channel, and so on. Drawing upon an earlier idea they further imagined that different types of knowledge were important for the comprehension of different (sub)categories. As initially suggested by Warrington and McCarthy (1983), sensory/visual knowledge might be of special importance for the recognition of many natural objects whereas functional knowledge or action knowledge might be more important for the recognition of artifacts. Accordingly, this differential weighting of knowledge types across categories would produce a quasi-categorically organized system of knowledge. If damaged, such a system might produce recognition impairments for subcategories of natural objects and artifacts. Thus, an impaired shape channel might cause particular recognition problems for the category of animals, whereas an impaired colour channel might affect the categories of fruits and vegetables more than the category of animals[2]. Similarly, if the action channel was damaged this might primarily affect the recognition of tools and other manipulable artifacts. Although there is practically no limit to which kind of category-specific impairment one could imagine it should be noted that some of the more subtle category-specific recognition impairments just mentioned have actually been reported (Warrington & McCarthy, 1987, for a deficit with small manipulable artifacts; Hart et al., 1985, for a category-specific recognition impairment with fruit and vegetables; Hart & Gordon, 1992, and Caramazza & Shelton, 1998, for a deficit with animals only).

Despite this refinement of the sensory/functional model, that allows it to accommodate more subtle category-specific impairments, it still cannot account for patients with category-specific impairments for natural objects who seemingly have intact visual knowledge (Laiacona

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[1] In fact in a reexamination of Warrington and Shallice's patient J.B.R. it was found that he showed item-consistency between modalities (Funnell & De Mornay Davies, 1996). Moreover, he was also found equally impaired in the retrieval of sensory and functional knowledge.

[2] Granted of course, that colour is diagnostic for members of these categories.

et al., 1997; Sheridan & Humphreys, 1993) or for cases where retrieval of sensory knowledge and functional knowledge is equally impaired (Caramazza & Shelton, 1998; Funnell & De Mornay Davies, 1996).

2.1 The relationship between sensory and functional knowledge

The fact that patients with category-specific impairments for natural objects may have (i) *impaired visual knowledge* and impaired retrieval of both visual and functional knowledge (Caramazza & Shelton, 1998; Funnell & De Mornay Davies, 1996), (ii) *intact visual knowledge* but impaired retrieval of visual and functional knowledge (Laiacona et al., 1997; Sheridan & Humphreys, 1993), or (iii) impaired retrieval of visual knowledge but normal retrieval of functional knowledge (Hart & Gordon, 1992; Humphreys et al., 1997) seems two imply to things: (i) that visual and functional knowledge are functionally dissociable, and (ii) that visual knowledge per se may not be more important than functional knowledge per se for the recognition of natural objects. Evidence for the latter point also comes from a study by Tyler and Moss (1997) in which they compared the effects of priming for functional and perceptual attributes for natural objects and artifacts in normal subjects. If functional attributes are more salient in the representations of artifacts compared with natural objects and if perceptual attributes are more salient in the representations of natural objects compared with artifacts, then priming effects should be greater for artifacts than for natural objects when primes involve functional attributes whereas the reverse should be true when primes involve perceptual attributes. Contrary to what the sensory/functional account would predict, there was no significant difference between the two categories as a function of prime type.

Although the evidence considered here does not support the sensory/functional account it cannot be precluded that the relationship between sensory and functional properties may differ between natural objects and artifacts. Thus, it has been suggested by De Renzi and Lucchelli (1994) that because artifacts are produced with a special purpose, the relationship between their form and their function is not arbitrary[3]. This is not true for natural objects as their shape bears no relation to the use humans make of them. Accordingly, if there are stronger bonds between visual and functional attributes for artifacts than for natural objects, a general loss of visual knowledge would be more harmful for natural objects than for artifacts because the visual attributes of artifacts might be recovered by inferences and cross-references from intact functional attributes.

The suggestion by De Renzi and Lucchelli seems plausible for words, because words directly[4] activate semantic knowledge, including functional attributes, that could be used to

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[3]As an example De Renzi and Lucchelli (1994) argue that: ‘The fact that a hammer consists of a solid head set crosswise on the handle is not arbitrary, but the direct consequence of the aim that prompted its construction, driving nails and beating metals’ (p.20).

[4]To be more precise, written words do need to be recognized visually to gain access to semantics. However, this visual knowledge (the word-form) bears no relation to the concept it represents. Thus, the visual word-form does not

specify hypotheses on the nature of the visual attributes of concepts. For pictures the proposal is more complicated because evidence suggests that pictures cannot activate semantic knowledge unless they are first matched with stored representations specifying visual attributes (Schacter et al., 1991; Carr et al., 1982; Humphreys et al., 1988). Accordingly, to retrieve functional knowledge about pictures that could assist in the recovery of the visual attributes of the depicted objects, integrity of the very same visual attributes appears necessary. In De Renzi and Lucchelli's own words it therefore *remains to be explained how the function of an object can be inferred from its visual appearance, if this has not been recognized or retrieved from memory* (p.19). One possibility might be that semantic knowledge can be accessed through action knowledge rather than visual knowledge. Evidence for such a proposal comes from Sirigu et al. (1991). They described an agnosic patient who could determine how to manipulate certain objects in spite of his incapacity to define their function or their context of utilization. Of special interest was the fact that the patient could perform object decisions[5] to artifacts and artifactual nonobjects despite his marked problems in visual object recognition. However, the patient could only perform object decisions when the nonobjects were functionally *im*plausible. When the object decision task was changed so that the nonobjects were functionally plausible, performance deteriorated because the patient now accepted the nonobjects as real. Apparently the patient's performance was affected by whether the nonobjects afforded a plausible way of handling, implying that action knowledge did contribute to the patient's performance.

The suggestion that semantics may be accessed by means of action knowledge in cases where visual knowledge is impaired seems to raise a question similar to that which it was supposed to answer. It remains to be explained how actions appropriate for an object can be inferred from its visual appearance, if this has not been recognized or retrieved from memory. Although visual object recognition is associated with ventral structures in the brain (Mishkin et al., 1983; Kohler et al., 1995), evidence suggests that dorsal structures have some capacity for object recognition and that these structures are particularly involved in the computations underlying action towards objects (Milner & Goodale, 1995). Information concerning the nature of an object might be mediated by these structures even if the object's visual identity cannot be retrieved. Accordingly, occasionally it may be that semantic representations are not activated directly from a stage of perceptual recognition, but indirectly through the representations of actions that a particular object affords. This proposal seems to fit with the patient described by Sirigu et al. (1991). They reported that their patient often used spontaneous gestures that could serve as self-cueing kinaesthetic strategies helping the patient to form hypotheses about the

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specify that a CAR has four wheels, it only specifies the characters C, A, and R. Accordingly, the semantic knowledge associated with a word can be accessed as soon as the word-form is recognized -no access to the visual attributes of the concept is needed. It is in this sense that access is direct.

[5]In an object decision task the subject has to decide whether pictures represent real objects or nonobjects. On the assumption that object decision tasks can be performed without accessing semantic knowledge (see Gerlach et al., 1999, 2000a for evidence of this) this task is thought to assess the integrity of stored visual knowledge.

function of objects. Such a strategy of course would be more useful for objects that affords certain ways of handling (ie., most artifacts) than for objects that do not (ie., most natural objects). It should be noted though, that even if it is possible that knowledge of functional attributes can be retrieved through action knowledge and that this knowledge in turn can be used to recover knowledge of the perceptual attributes of objects such a process will be time consuming and probably not very efficient. As an illustration of this one can consider the response given by Sirigu et al.'s (1991) patient when shown a safety pin: "You open on one side, stick something on it, close it, and it stays in. I can tell you how it works, but I don't see its exact use. I don't think I have seen one like this before, it is not a very common object" (p.2555). Consequently, items from the category of artifacts might also be affected by loss of visual knowledge although less so than natural objects.

Common for the form-function hypothesis advanced by De Renzi and Lucchelli (1994) and Sirigu et al. (1991) is that category-specific disorders for natural objects are thought to be caused by a general loss of visual knowledge that compromise natural objects more than artifacts because: (i) the tight bonds between form and function for artifacts can be used to form hypotheses on the nature of the object left undefined by visual processing (De Renzi & Lucchelli, 1994), or (ii) artifacts afford certain ways of handling that can be used to form hypotheses about the function of objects (Sirigu et al., 1991). It is worth noting that both accounts imply that artifacts should be less vulnerable to damage than natural objects. This in fact seems the case as the majority of cases reported have concerned category-specific disorders for natural objects. One the other hand both accounts also seem to imply that the recognition of artifacts should be far from perfect as the recognition of these items is performed in an indirect manner that is time-consuming and prone to errors. That this is not always the case is witnessed by a study by Moss et al. (1997). They presented the patient SE who had a category-specific recognition impairment for natural objects. However, contrary to what might be predicted from the accounts proposed by De Renzi and Lucchelli (1994) and Sirigu et al. (1991) SE did not appear to experience any problems with the recognition of artifacts. In addition, SE showed normal priming for the visual properties of artifacts but not for natural objects. This finding appears to be problematic for the explanations proposed by De Renzi and Lucchelli (1994) and Sirigu et al. (1991) because they imply that recovery of the visual attributes of artifacts is time-consuming and effortful. The operation of such a mechanism simply does not seem likely under the rapid and automatic access conditions of a priming task. According to Moss et al. (1997) the finding of intact priming for visual attributes of artifacts does not rule out all versions of form-function hypothesis, but only versions in which the form-function links are computed as time-consuming inferences. As an alternative they propose that form-function correspondences are encoded within the semantic representation of an object, rather than being inferred by consciously effort. They also suggest (Tyler & Moss, 1997) that common perceptual attributes for natural objects (e.g., animals that have four legs) are associated with functional properties (e.g., land animals) while distinctive visual attributes are not (e.g., a leopard's spots), whereas for artifacts, functional attributes are associated with distinctive visual attributes (e.g., used for cutting has a blade). In terms of a connectionist model, these suggestions may be implemented as excitatory links between certain functional properties and corresponding visual properties, where these activation links may exist to a larger extent for artifacts than for natural objects. In such a model category-specific impairments for natural objects may be caused by a general deficit for visual attributes (consisting of significant underactivation of visual attribute nodes by the input), which for artifacts is compensated for by activation from the intact functional attributes. For natural objects, however, there are only a few activation links between visual attribute nodes and functional attribute nodes, and although these links may support the recovery of some general visual attributes (land animal has legs) it will not be possible to compensate for the loss of more distinctive visual attributes.

Before accepting the conclusion reached by Moss et al. (1997) it should be noted that De Renzi and Lucchelli (1994) and Sirigu et al. (1991) based their proposals on performance within the visual modality whereas the findings in Moss et al.'s (1997) study are based on performance in the verbal modality. This difference is not trivial if it is correct that pictures, as opposed to words, cannot access semantic knowledge unless some activation of stored visual knowledge has occurred. In this case, we would actually predict that recovery of visual knowledge would be more accurate and fast for words than for pictures. We would expect this because the semantic attributes, from which the visual attributes are recovered, can be accessed directly[6] for words but has to be derived from faulty visual knowledge (De Renzi & Lucchelli, 1994) or from indirect access to semantics by means of action knowledge (Sirigu et al., 1991) for pictures. Accordingly, the findings by Moss et al. (1997) and De Renzi and Lucchelli (1994) and Sirigu et al. (1991) are not incompatible, and they do leave room for the possibility that category-specific impairments for natural objects may be caused by a general loss of visual knowledge. With respect to the account proposed by Moss et al. (1997), this might even explain why information about biological function can be preserved in patients with poor recognition of natural objects (Hart & Gordon, 1992; Humphreys et al., 1997) However, the models need to be elaborated if they are to account for cases with poor comprehension of natural objects despite intact visual knowledge or for the cases showing category-specific impairments for artifacts.

2.2 Stages of processing.

Common for many accounts reviewed thus far is that they do not really make a distinction between visual and semantic knowledge. As an example consider the account by Moss et al. (1997). In this account, the category-specific impairments for natural objects are thought to be caused by a general deficit for visual attributes, which for artifacts is compensated for by activation from intact functional attributes. However, both functional and visual attributes are supposed to be stored in a semantic system and it is not quite clear how they should be differentially affected by brain damage unless stored in different parts of the brain. Without making a functional (or anatomical) distinction between visual and functional knowledge it becomes difficult to account for the fact that visual knowledge for natural objects may be intact

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[6] Cf. note4.

in cases where retrieval of functional knowledge is impaired (Laiacona et al., 1997; Sheridan & Humphreys, 1993), or vice versa (Hart & Gordon, 1992; Humphreys et al., 1997).

One model that does distinguish explicitly between visual and functional (semantic) knowledge has been proposed by Humphreys et al. (1988). In this model object naming may be characterized by three general stages. In stage one, visual information activates associated structural representations specifying the object's form[7] (the structural description system). In stage two, activation of structural descriptions spreads to associated semantic representations specifying functional/associative knowledge (the semantic system). In stage three, activation of semantic representations spreads to phonological representations specifying object names. It is assumed that the representations of many stimuli can be activated in parallel within any given level (structural, semantic, or phonological). Moreover, the stages involved in picture naming are thought to operate in cascade, viz. information is transmitted from one stage to the next before completion of processing at preceding stages.

The relevance of this model stems from the hypothesis that natural objects tend to be globally more visually similar and share more common parts with other members of their categories than artifacts (Humphreys et al., 1988; Riddoch & Humphreys, 1987). If natural objects generally share more common parts than artifacts and if many representations can be activated in parallel, competition within the structural description system (and subsequent processing systems) will be larger for natural objects compared with artifacts. Accordingly, natural objects will be more difficult to differentiate than artifacts when matched to memory, yielding artifacts an advantage. Hence, damage at a level corresponding to the structural description system could lead to a category-specific deficit for natural objects.

The hypothesis that artifacts are differentiated more easily perceptually than natural objects has found support in a study by Lloyd-Jones and Humphreys (1997), where responses were found to be significantly slower to natural objects compared with artifacts on an object decision task[8]. Additional evidence in favour of the notion that artifacts are differentiated more easily than natural objects comes from Gaffan and Heywood (1993) who found that normal observers make more errors while identifying living as opposed to nonliving things under degraded viewing conditions (the stimuli were presented for only 20 msec). Moreover, Gaffan and Heywood found that the same was true for monkeys trained to discriminate between objects from the same set of items.

Although the model by Humphreys and colleagues predicts that category-specific impairments for natural objects can occur because of damage at both the structural and the semantic level (*see* Sheridan & Humphreys, 1993), it does not predict that natural objects are always disadvantaged. Whether they are depends on what kind of processing is needed for solving the particular task. In naming tasks and difficult object decision tasks, where the demand on differentiation (structural/semantic) is high because the selection of a representation corresponding to a particular object is needed, the model predicts that natural objects will be disadvantaged.

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[7]It should be stressed that structural descriptions do not represent information about the object's function or its association with other objects.

[8]As mentioned, this task is believed to require access to structural descriptions but not necessarily to semantics (Chertkow et al., 1992; Sheridan & Humphreys, 1993).

However, in categorization tasks where objects are assigned to a super-ordinate category, natural objects may actually be categorized faster than artifacts (Riddoch & Humphreys, 1987). According to the model this happens because natural objects, due to their greater visual similarity, initially will activate a greater number of related representations at the structural level. These representations will in turn activate their corresponding semantic representations, including super-ordinate category representations. Because objects with similar physical form tend to belong to the same super-ordinate category (Carr et al., 1982), this means that evidence for super-ordinate category membership may accumulate faster for natural objects than for artifacts[9].

The proposal that structural similarity for natural objects causes rapid access to common semantic knowledge (e.g., shared biological functions) but slowed identification of the individual objects, resembles the suggestions by Moss et al. (1997) regarding shared and distinctive perceptual attributes. In Humphreys and colleagues' account, however, these effects are coupled to different levels in visual objects recognition. This allows the model to accommodate cases with category-specific impairments for natural objects where visual knowledge seems intact but where semantic information is compromised (Laiacona et al., 1997; Sheridan & Humphreys, 1993). According to the model this happens because of damage to semantic memory itself. Such damage would have more severe consequences for the comprehension of natural objects because natural objects are also harder to differentiate at the semantic level (they share both visual and semantic features) but it would not affect visual knowledge per se.

2.3 A case for a truly categorically organized brain

Although the model by Humphreys and colleagues can explain why category-specific disorders for natural objects may arise despite intact visual knowledge it does not readily explain cases where visual and functional knowledge seem equally impaired. In fact, Caramazza and Shelton (1998) have argued that such cases imply that semantic memory is actually categorically organized. In support of this claim they presented a patient with a category-specific deficit restricted to the category of animals, who was impaired in processing both visual and functional/associative attributes about animals but not artifacts. Given that this patient performed normally on tasks involving the visual processing of complex objects, Caramazza and Shelton argued that the impairment had to reflect an impairment of semantic memory selective for animals. As to why semantic memory should be categorically organized Caramazza and Shelton offers the explanation that this is a consequence of evolutionary pressure. They motivate this proposition with the speculation that:

[9]It also means that evidence for super-ordinate category membership may actually accumulate before activation has attained a stable state in which the representation corresponding to the particular object is strongly activated while other candidate representations are effectively inhibited. Consequently, it might be possible to know that a particular object is an animal before it is identified as a dog.

It is not impossible to assume that evolutionary pressures led to specific adaptions for recognizing and responding to animal and plant life.....The fitness value of these adaptions are obvious: Animals are potential predators but also a potential source of food; plants are a source of food and medicine. The ability to recognize and respond quickly to types of animals has clear survival and reproductive value, as does the ability to accurately distinguish among different plants for their alimentary and medicinal value (p.20).

However, there are several problems with Caramazza and Shelton's arguments: (i) If evolutionary pressure should have led to efficient recognition of natural objects, Mother Nature has done a lousy job because it takes normal subjects longer to recognize natural objects (Lloyd-Jones & Humphreys, 1997) than artifacts and because both humans and monkeys make more errors when recognizing natural objects as opposed to artifacts (Gaffan & Heywood, 1993; Lloyd-Jones & Humphreys, 1997); (ii) The fact that the patient performed successfully on a visual matching task, an item match task, two variants of the unusual views task, and Boston Famous Faces task does not exclude the possibility that the patient has a visual recognition problem (in addition to a semantic problem). It does not exclude this possibility because the visual matching task, the item match task and the unusual views tasks do not require that the identity of the stimuli has been visually recognized. With respect to the Famous Faces tasks, this task can hardly be used to assess the capacity for visual object recognition in general as face and object recognition dissociate (Moscovitch et al., 1997). In fact on tasks that do require access to stored visual knowledge, (object decision tasks and associative tasks) the patient performed rather poorly with animals. (iii) On an attribute processing task the patient was impaired in evaluating both specific visual attributes (does it have feathers) and specific functional/associative attributes (can it fly). However, the patient performed equally well on general visual attributes (does it have eyes) and general functional/associative attributes (does it breathe) for both animals and artifacts. Thus, although the patient's performance with specific visual attributes mirrored the performance with specific functional/associative attributes it is not entirely correct to conclude that the patient suffered from loss of both visual and functional/associative knowledge. Rather it would appear that the patient suffered from loss of a particular sort of visual and functional/associative knowledge, namely loss of knowledge about attributes of individual objects as opposed to knowledge about common attributes. The finding that the loss of knowledge for animals is not clear cut, as it does not involve knowledge of both specific and common attributes, appears problematic for Caramazza and Shelton's model in which all knowledge about animals presumably is stored separately. Nevertheless, the finding that functional and visual knowledge about specific attributes of natural objects can be equally impaired, regardless of the modality tested, remains problematic for accounts in which category-specific disorders for natural objects are thought to arise from general damage to visual knowledge. In order for these accounts to accommodate such results the additional assumption must be made that visual knowledge is also required to answer questions regarding functional attributes[10]. Two accounts employing such an assumption will be reviewed below.

2.3.1 The primacy of visual knowledge in the comprehension of natural objects

On one account, suggested by Farah and McClelland (1991), knowledge representations are assumed to be distributed and interactive, with each part of an object's representation providing collateral activation to the other parts. As a consequence of this architecture, the activation of one part may depend on the activation of other parts. This will affect natural objects and artifacts in different ways if natural objects, as opposed to artifacts, are primarily represented in terms of visual attributes. In this case activation of nodes representing functional attributes of natural objects may depend on some degree of activation of nodes representing visual attributes. The validity of this account of course depends on whether it is possible empirically to demonstrate that the proportion of visual knowledge is greater in the representations of natural objects than in the representations of artifacts. Although Farah and McClelland (1991) provide some evidence for this proposal, this evidence has been called into question by Caramazza and Shelton (1998)[11]. In addition, the proposal is incompatible with the results obtained by Tyler and Moss (1997), mentioned in section 2.1, who found no significant difference in priming between natural objects and artifacts as a function of prime type (perceptual vs. functional). Despite these problems, some evidence in favour Farah and McClelland's account has come from a recent fMRI-study by Thompson-Schill et al. (1999). In this study activation of the left fusiform gyrus (an area believed to be involved in retrieval of visual knowledge) was examined during four conditions in which subjects answered yes/no questions regarding: (i) visual attributes of animals, (ii) visual attributes of artifacts, (iii) functional attributes of animals, and (iv) functional attributes of artifacts. Compared with a baseline task (listening to the questions being played backwards) all conditions, except the one concerning functional attributes of artifacts, caused increased activation in the left fusiform gyrus. In addition, a significant interaction between category and question type was observed in a region of interest in the left fusiform gyrus. In this region there was no significant difference for animals as a function of question type, whereas for artifacts, activation was only observed during evaluation of visual attributes. Although these findings are presented in support of Farah and McClelland's account, there are two problems with this interpretation: (a) the interaction between question type and category did not arise simply because the evaluation of functional attributes for natural objects caused greater activation in the left fusiform gyrus than

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[10] As an example of this Humphreys and Forde (In press) argue that: "if a patient does not know that a giraffe has a long neck, he/she does not really know what a giraffe is, and therefore could not answer question tapping 'functional' knowledge, such as 'does a giraffe eat meat or leaves?".

[11] Farah and McClelland asked subjects to mark the functional attributes of objects in dictionary definitions by asking: *What does the item do or what is it used for?* Caramazza and Shelton argue that this procedure biases artifacts and leads to an underestimate of the functional properties of natural objects. When all sensory properties are noted in dictionary definitions then the bias for more sensory properties for natural objects is greatly reduced.

did the evaluation of functional attributes for artifacts. Part of the interaction can probably be ascribed to the fact that the left fusiform gyrus actually deactivated during the evaluation of functional attributes for artifacts, as evidenced by the fact that activation in this area was significantly reduced during this condition compared with the baseline task. Accordingly, instead of arguing that visual knowledge is important for the evaluation of functional attributes about natural objects one might as well argue that visual knowledge disturbs the evaluation of the functional attributes of artifacts, and hence is suppressed. A more plausible explanation, however, would be that the subjects also retrieve visual knowledge (engage visual imagery) during the baseline task, but that the amount or degree of visual retrieval is greater for natural objects than for artifacts during evaluation of functional properties compared with the baseline task. Although this explanation saves the interpretation offered by Thompson-Schill et al., it also means that one cannot exclude the possibility that the subjects actually retrieved visual knowledge even in the conditions where the functional aspects of artifacts were evaluated, albeit less so than in the baseline condition; (b) the most critical aspect of the study seems to be that the functional questions asked for the categories of natural objects and artifacts were not equivalent. Consider the following questions: *are snails edible*, *are pandas found in China*, *does a toaster use more electricity than a radio*, and *can headphones play stereo music*. While the knowledge requested for artifacts seems to relate to their core concepts, the knowledge requested for the natural objects seems tangential to the understanding of what these objects are. To evaluate properly the possibility that visual knowledge must be retrieved for natural objects, but not for artifacts, when functional knowledge has to be accessed, we must compare functional attributes that are equally salient in the respective categories[12]. Since this has not been done, it cannot be excluded that the activation difference, observed in the left fusiform gyrus between natural objects and artifacts, is in fact an artifact.

2.3.2 The form-function hypothesis revisited

Based on the evidence considered above there appears to be little evidence for the suggestion that visual knowledge is retrieved only when we evaluate functional questions concerning natural objects. This, however, does not mean that visual knowledge might not be necessary for answering functional questions about objects in general. It might be that visual knowledge is retrieved regardless of which class of objects we evaluate. Now, to sustain the hypothesis that visual knowledge might be retrieved when answering certain verbal questions about objects in general, we must explain why damage to visual knowledge impairs the comprehension of natural objects more than the comprehension of artifacts. We can do this by assuming: (i) that functional properties for natural objects are associated with shared rather than distinctive visual attributes whereas for artifacts, functional attributes *are* associated with distinctive visual attributes (Moss et al., 1997), and (ii) that following brain damage, the visual attributes strongly connected to the

[12] In the case of natural objets these functional attributes could be related to body functions (e.g., can it see?, does it breathe? etc.) (cf. Tyler and Moss, 1997).

functional attributes of objects may be better recovered than those with weak connections. If these assumptions are correct, damage to visual knowledge will have different consequences for artifacts and natural objects. For natural objects, knowledge of common visual attributes might be recovered from the linked functional attributes. However, because the identification of individual natural objects depends on distinctive visual attributes this information will be of little help in the identification of these items. For artifacts, functional knowledge is correlated with distinctive visual attributes for which reason the recovery of distinctive visual attributes of individual artifacts might be better. Accordingly, to the extent that visual knowledge needs to be retrieved for answering functional questions, artifacts will be better off[13].

The account suggested above has the neatness of not postulating different proportions of visual and functional attributes in the representations of different categories. Nevertheless it can explain the equal impairment of visual and functional knowledge seen in some cases with category-specific disorders for natural objects, and it can account for the finding of preserved visual and functional knowledge concerning general attributes about natural objects.

3.0 The eclectic model

In what follows, I will selectively merge the results from the studies reviewed above (and below) into a lager framework. I term this framework *the eclectic model* because it basically represents ideas I have taken from other people.

I will start by noting that the evidence considered so far offers little support for the sensory/functional hypothesis in which the representations of natural objects and artifacts are thought to have different weighting of visual and functional attributes. Alternatively, damage to visual knowledge may affect natural objects and artifacts differentially because natural objects are more structurally similar than artifacts and therefore more difficult to differentiate perceptually. This effect of similarity, however, does not seem confined to a structural level because the functional attributes of natural objects tend to be correlated with shared visual attributes whereas the functional attributes of artifacts tend to be correlated with distinctive attributes. Accordingly, the differentiation of natural objects may also be harder at the semantic level. Consequently, category-specific disorders for natural objects may arise due to damage of both visual and semantic knowledge. If these differences are tied to a model in which structural and functional knowledge is functionally (and perhaps anatomically) dissociable, we can account for cases with category-specific disorders for natural objects in which visual knowledge is compromised but also for cases where visual knowledge appears intact (cf. section 2.2).

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[13] On the hypothesis I'm developing here, I do not wish to commit my self to the view that visual knowledge is always retrieved/necessary for answering functional questions. Whether it is depends on the extent to which the functional knowledge relates to the core of the concept in question. So, for answering the questions *are chairs for sitting* and *do snails reproduce*, I would not presume that visual information is important. However, visual knowledge might be important for answering questions like *do umbrellas protect from the rain if held upside down* or *are snails edible*.

The eclectic model outlined here most easily accommodates results obtained from tasks using pictures as input. But what about results obtained from verbal tasks like *attribute verification* and *naming to definition* where effects of structural similarity do not apply ? Let me give an example. Imagine a task in which a person is shown pictures of both artifacts and animals and where he cannot recognize the animals. This impairment may be accounted for in terms of damage to visual knowledge and structural similarity. However, imagine that the same happens when the person is shown words denoting artifacts and animals. Here, we may still argue that the impairment arises form faulty visual knowledge[14], but we cannot argue that the category-specific nature arises from structural similarity, because the structural similarity between the words DOG and HORSE is not greater than between the words TABLE and CHAIR. Nevertheless, to the extent that specific visual knowledge is needed for comprehending stimuli used in verbal tasks, we may assume that visual knowledge is recovered more easily for artifacts than for natural objects if the functional attributes of these objects are associated with distinctive visual features (cf. section 2.3.2).

Although the eclectic model can explain the patterns of impairment exhibited in many of the cases reviewed above, it is virtually silent with respect to the category-specific disorders reported for artifacts (Warrington & McCarthy, 1983; Warrington & McCarthy, 1987; Sacchett & Humphreys, 1992; Hillis & Caramazza, 1991; Warrington & McCarthy, 1994). Before considering how these impairments may be accounted for, let me first point out that they cannot arise from damage to semantic memory alone. As mentioned, this sort of damage would lead to a category-specific impairment for natural objects -at least in the eclectic model. Nevertheless, nearly all cases with category-specific disorders for artifacts seem to suffer from semantic impairments[15]. This is interesting since most of these patients had lesions in left fronto-parietal areas rather than the in the temporal lobes[16] (Warrington & McCarthy, 1983; Warrington & McCarthy, 1987; Sacchett & Humphreys, 1992). While it may not be surprising that these patients suffered from right-sided hemiplegia it is noteworthy that these frontal lesions affected their motor system. This is interesting because activation of left premotor structures has been found in imaging studies during the processing of artifacts (Grabowski et al., 1998; Gerlach et al., 2000a; Grafton et al., 1997; Martin et al., 1996). Accordingly, category-specific disorders for artifacts may arise in part because of damage to action knowledge, a suggestion initially advanced by Warrington and McCarthy (1987). This suggestion does not seem unreasonable given that most artifacts, as opposed to natural objects, are made with human handling in mind.

The evidence presented above suggests that action knowledge may play some role in visual object recognition, at least for artifacts. Accordingly, the notion of action knowledge must

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[14]Provided of course that visual attributes are important for comprehending artifacts and natural objects. Cf. the discussion in sections 2.3.1 and 2.3.2.

[15]See Silveri et al. (1997) for an exception.

[16]Usually it is temporal lobe damage rather than fronto-parietal damage that is associated with semantic deficits.

be incorporated into the eclectic model if it is to account for cases with category-specific disorders for artifacts. This can be done by adding a new component to the model, termed action knowledge (see figure 3).

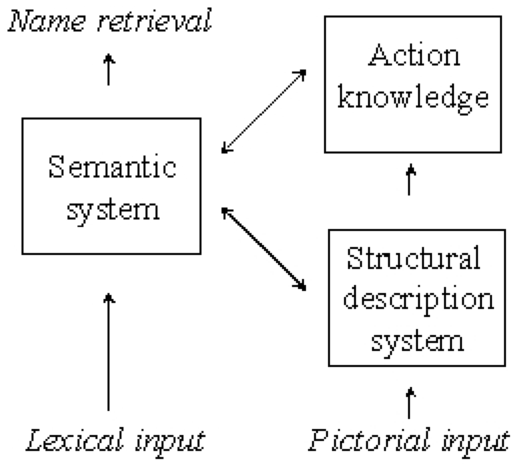

Figure 3. The eclectic model

Like Rothi et al. (1991) I will suggest that action knowledge comprises conceptual knowledge related to object use and actions, and that this knowledge is distinct from associative knowledge, thought to be stored in the semantic system (e.g., associations like *hammer nail*), and from the praxis production system (comprising structural knowledge contained in motor programs). The suggestion that action knowledge dissociate from semantic knowledge seems secure and dates back to 1902 when Pick reported a few patients who often misused objects they could both recognize and name (De Renzi, 1989). Accordingly, semantic knowledge does not seem sufficient for correct object utilization. More surprising perhaps, is the finding that intact semantic knowledge may not even be necessary for correct object utilization. This suggestion comes from a study by Buxbaum et al. (1997) in which the performance of two patients on naturalistic action tasks was compared. The patient DM was found moderately or severely impaired on all tasks tapping semantics but nevertheless showed good object utilization whereas the reverse was true for the patient HB.

Though action knowlege may dissociate from semantic knowledge, normal object utilization is probably not mediated entirely by a non-semantic route from the structural description system to action knowlegde bypassing the semantic system. Consider for example the patients described by Sirigu et al. (1991) or Magnie et al. (1999). Although these patients demonstrated some capacity for object utilization it most often pertained to the objects' mechanics rather than to their function that was often not appreciated. Accordingly, normal object utilization is most likely mediated by both a semantic and a non-semantic route[17].

Returning to the eclectic model I suggest that even though action knowledge may support visual object naming it does not play a necessary part. This is a departure from the model suggested by Warrington and McCarthy (1987) in which action knowledge appears to play a mandatory role in visual object naming. Part of this discrepancy arises from the fact that Warrington and McCarthy's model does not operate with distinct stages in visual object recognition whereas the present model does, placing the system of action knowledge after the stage of matching objects to visual memory (the structural description system) and apart from the semantic system (see figure 3). While this appears to be an advantage in the explanation of some cases with category-specific disorders, it makes the role of action knowledge in visual object recognition less clear. Thus, in Warrington and McCarthy's model, category-specific disorders for artifacts may arise directly from damage to action knowledge whereas they cannot do this in the eclectic model. However, if knowledge representations are distributed and interactive, with each part of an object's representation providing collateral activation to the other parts, damage of one part may affect the activation of other parts. Accordingly, to the degree that action knowledge provides input to the semantic system, the activation-level of the representations in this system may not be significantly increased to support recognition. This will affect artifacts more than natural objects, because the link between function and action is presumed to be tighter for these objects than for natural objects. Thus, if the semantic system is impaired in cases with category-specific disorders for artifacts, as evidence suggests that it is, this semantic processing deficit will be exacerbated for artifacts following damage to action knowledge. In this way damage to action knowledge may impair the comprehension of artifacts although action knowledge per se is not necessary for the comprehension of these objects.

The eclectic model, as presented here, cannot account for all cases of category-specific disorders. In particular it cannot explain why category-specific impairments may be confined to fruit and vegetables (Hart et al., 1985) or animals only (Hart & Gordon, 1992; Caramazza & Shelton, 1998), nor can it account for disorders where the category-specific impairments are more pronounced on name retrieval than on tests of semantic knowledge (Hillis & Caramazza, 1991; Silveri et al., 1997). Nevertheless, the model is sufficiently articulated to account for the results obtained by Ian Law, Anders Gade, Olaf B. Paulson and me in the series of PET experiments that will be described below. Before I present these results I will review other imaging studies concerning category-specificity[18].

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[17] A similar conclusion was reached by Buxbaum et al. (1997), who argued that DM's semantic knowledge of objects, which was found impaired on normal semantic tasks, was actually enhanced in tasks using naturalistic object manipulation by a non-semantic route from structural knowledge to action semantics.

[18] Although imaging studies of category effects have been reported using words as stimuli (e.g., Mummery et al., 1996) I will restrict my review to studies using pictorial stimuli.

4.0 Brain areas associated with processing of natural objects

Martin et al. (1996) compared brain regions activated when subjects silently named natural objects (animals) and artifacts (tools). They found that naming animals compared with tools caused increased rCBF in the left calcarine sulcus. According to Martin et al., this finding could reflect 'top-down' reactivation necessary for identifying animals because animals compared with tools are more visually similar. Whether or not this interpretation is correct, the finding remains obscure as there are no reports of category-specific impairments following lesions in this area. However, it should be noted that Martin et al. did not match items from the respective categories for visual complexity[19], a factor that if not controlled for can lead to spurious category-effects (Funnell & Sheridan, 1992; Stewart et al., 1992). It is therefore likely that the calcarine activation reflects visual complexity rather than categor[20,21].

In a study by Perani et al. (1995; 1999) subjects were requested to judge whether a pair of pictures represented the same concept or not. The picture pairs either represented two artifacts or two natural objects. The direct comparison between natural objects and artifacts was associated with increased rCBF in the left fusiform gyrus and the left lingual gyrus. Although these activations may be compatible with the patient studies reviewed above in that category-specific disorders for natural objects are associated with bilateral lesions of the inferior temporal lobes, this study suffers from the same weaknesses as the Martin et al. (1996) study[22].

Damasio et al. (1996) like Martin et al. (1996) compared lexical retrieval of words denoting animals or tools, but only studied activation in the temporal lobe. They found that naming of animals was associated with increased rCBF in left inferior temporal lobe.

Common for the studies by Martin et al. (1996), Perani et al. (1995) and Damasio et al. (1996) appears to be that natural objects activate posterior and ventral parts of the left hemisphere more than artifacts. However, the location of the category-specific activations ranges from the calcarine sulcus to the inferior temporal gyrus. Rather different findings come from a study by Moore and Price (1999). They found that natural objects compared with artifacts caused increased

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[19]Though Martin et al. did try to compensate for this by displaying the objects as silhouettes, this really does not ensure that the objects are equally visually complex, because complexity may also relate to the global shape of objects which is left unchanged by presenting them as silhouettes.

[20]See Moore and Price (1999) for evidence for this explanation.

[21]Another problem with this study relates to the statistical aspect of comparing different conditions. Because quite a few false positive activations can be expected when thousands voxels are compared on a voxel by voxel basis, it is usually recommended that some kind of correction needs to be performed on the data set (Poline et al., 1997). The Z-scores for the activations reported by Martin et al. are modest and would probably not survive a correction for multiple non-independent comparisons. Accordingly, these activations may not be reliable.

[22]It should be noted that Perani et al. (1995) made a region-of-interest analysis in the direct comparison of natural objects and artifacts, thereby affording a less stringent thresholding. Such an approach may be warranted if one has an a priori hypothesis. However, in Perani et al.'s study, this hypothesis was based on contrasting both conditions with a baseline condition. One may therefore question whether the direct comparison was really as independent as it should have been.

rCBF in the posterior part of the right middle temporal gyrus and the anterior temporal lobes. The areas of activation in the right hemisphere were nevertheless eliminated when the stimuli were coloured, as opposed to black and white, line drawings. Because colour facilitates object recognition, especially for fruits and vegetables (Price & Humphreys, 1989), this finding was interpreted by Moore and Price as reflecting areas in which activation increased as a function of task difficulty. Thus, the right hemisphere activations observed in this study are probably not related to effects of category per se, but rather to increased demands on perceptual differentiation which happens to affect natural objects more than artifacts. As such, this finding appears to support models that argue that category-specific disorders for natural objects may arise because these objects are more visually (or semantically) similar than artifacts. According to Moore and Price the only area that did show a genuine effect of category was the left anterior temporal cortex. In this area rCBF was greater during the processing of fruits and vegetables compared with the processing of animals. To the extent that the anterior temporal cortices are specialized for perceptual knowledge (Breedin et al., 1994), and they may not be (Biederman et al., 1997; Sergent et al., 1992), this finding seems to support models that argue that visual attributes are more important for the recognition of natural objects than artifacts.

4.1 Brain areas associated with processing of artifacts

In Perani et al.'s (1995) study, artifacts were associated with increased activation in the left inferior frontal gyrus. A somewhat similar activation was found by Martin et al. (1996) who reported increased activation in the lateral part of the left inferior frontal cortex, especially in the left premotor area, for artifacts. In addition, Martin et al. also found increased rCBF in the left middle temporal gyrus as did Moore and Price (1999). The left premotor was also found to be more activated during the naming of artifacts than during the naming of natural objects in a study by Grabowski et al. (1998). That these left premotor activations do not just reflect object naming is evidenced by a study by (Grafton et al., 1997) in which rCBF was found to increase in the left premotor area during the naming of tool use compared with just naming the tools.

As mentioned in section 3.0 the activations observed in the left premotor cortex are compatible with the proposition that category-specific disorders may arise because of impaired action knowledge (Warrington & McCarthy, 1987). Because the posterior part of the left middle temporal gyrus has previously been associated with the generation of action words relative to object naming (Martin et al., 1995) and with the recognition of meaningful vs. meaningless actions (Decety et al., 1997), this structure may also be involved in the processing of action knowledge.

5.0 Looking at stages of processing

Although the studies reviewed above takes us some way in understanding the neural correlates of category effects, there are two major obstacles in relating findings from these studies to models of category-specificity: (i) the stimulus material used has usually not been adequately matched across categories, and (ii) the brain regions found activated cannot be linked to particular stages in visual object processing because of the tasks used. Thus, there is really no way of knowing whether the activations observed arose at a structural, a semantic, or a phonological stage in visual object recognition. In the three studies I conducted in collaboration with Ian Law, Anders Gade and Olaf B. Paulson (Gerlach et al. 1999, 2000a, 2000b) we tried to overcome these weaknesses by having the stimulus material adequately matched and by using tasks intended to tap particular stages in visual object recognition.

In the first study (Gerlach et al., 1999) we contrasted object decision tasks (see note 5) that differed in task type (easy vs. difficult) and in the category of the real objects used (natural objects vs. artifacts). In accord with previous studies (Lloyd-Jones & Humphreys, 1997) a significant interaction was found in the behavioural data between task type and category, with the increase in reaction time between the easy and the difficult task being largest for natural objects. In the PET data there was no interaction between task type and category and no main effect of category. There was, however, a significant main effect of task type associated with increased rCBF in the posterior part of the right inferior temporal gyrus during difficult compared with easy object decision tasks. Although an interaction between task type and category was not evident in the PET data a trend in this direction was found by comparing the size of the activated areas for natural objects and artifacts respectively as a function of task type. In this comparison the region associated with increased task difficulty for natural objects was approximately four times larger than the region associated with increased task difficulty for artifacts. In addition, increased task difficulty for natural objects seemed to cause increased rCBF in both the left and the right inferior temporal gyri. Given that the areas associated with increased task difficulty are usually believed to reflect structural rather than semantic processing (Sergent et al., 1992; Schacter et al., 1995), these findings suggest that natural objects are more difficult to differentiate perceptually than artifacts. Accordingly, these results are most readily accommodated in models where effects of category are thought to arise because of differences in structural similarity between categories of objects. In fact, the lack of clear category effects across task type appears troublesome for models that assume that knowledge of natural objects and artifacts are stored in functionally distinct areas of the brain (e.g., the account proposed by Caramazza & Shelton, 1998). Had this been so, we would have expected the processing of artifacts and natural objects to be associated with different areas of the brain. This was clearly not the case.

In the second study (Gerlach et al., 2000a) we compared the rCBF associated with difficult object decision tasks and categorization tasks[23]. There were two versions of each task. In one of the object decision tasks the real objects were natural objects whereas they were artifacts in the other. In one of the categorization tasks the majority of objects presented in the critical scan window were natural objects whereas they were artifacts in the other. As in the previous study this design allowed us to test for interactions between task type (object decision vs. categorization) and category (natural objects vs. artifacts).

[23]In this task the subjects had to decide whether the displayed objects represented natural objects or artifacts.

As would be expected from models where structural knowledge and semantic knowledge are thought to be stored in functionally independent systems, there were clear effects of task type. The categorization tasks generally caused increased activation in areas believed to be involved in semantic processing (the left inferior temporal gyrus) (Vandenberghe et al., 1996) whereas the object decision tasks generally caused increased activation in areas believed to be involved in structural processing (the right inferior temporal gyrus and both fusiform gyri) (Kohler et al., 1995).

A particularly interesting finding from this study was that the ventral part of the left premotor cortex was associated with the categorization tasks regardless of category, and with the processing of artifacts regardless of task type, with rCBF reaching its highest value during the categorization of artifacts compared with any other task. If the ventral part of the left premotor cortex does indeed subserve action knowledge this finding suggests that action knowledge may be more important for artifacts in general than for natural objects, but that it also contributes to the categorization of natural objects. Why should this be so? One explanation might be that the act of categorizing an object is based in part on what kind of action applies to it (Lakoff, 1987), but that the link between action and category membership is stronger for artifacts than for natural objects. A similar conclusion was reached by Miller and Johnson-Laird (1976). In their view an artifact, as opposed to a natural object, is assigned to a category not because of any intrinsic aspect of its three-dimensional shape, but because its form is perceived as appropriate for a particular function.

The interpretation given above for the activation of the left premotor cortex seems compatible with the models suggested by Farah and McClelland (1991) and Warrington and McCarthy (1987), in which category-specific disorders for artifacts are thought to arise because of impaired functional knowledge[24]. However, neither of these models can easily account for the finding that action knowledge is more important during the categorization of artifacts than during object decisions to artifacts. There may be two reasons for this, of which neither is exclusive. (i) These models do not distinguish between different stages in visual object recognition, and therefore cannot accommodate effects that affect such stages differentially. (ii) The implicit assumption in these models regarding a mandatory role for action knowledge in the processing of artifacts may be wrong[25]. While the present results do suggest that different stages in visual object processing can and should be dissociated, they do not allow us to reach any firm conclusion regarding the potential mandatory role for action knowledge in the processing of artifacts[26]. In an attempt to settle this matter, we performed a third analysis (Gerlach et al.,

[24] Granted of course, that function is somehow related to aspects of action.

[25] Cf. the discussion in section 3.0 p.16.

[26] In fact, the data presented so far seem inconsistent because no association was found between artifacts and premotor structures in the first study (contrasting easy and difficult object decision tasks) whereas an association was found in the second study (contrasting difficult object decision tasks and categorization tasks).

2000b) in which we contrasted the rCBF associated with two types of semantic tasks: a categorization task and a semantic probe task[27], both of which were divided by category (natural objects vs. artifacts). The rationale behind this study was the following. If the comprehension of artifacts is always based on action knowledge mediated by the left premotor cortex, we should expect to see activation of this area in both kinds of semantic tasks. Alternatively, if action knowledge is 'only' important for the categorization of artifacts we should not. Much like in the second study, activation of the left premotor cortex was found during the categorization task for artifacts compared with both the categorization task for natural objects and the semantic probe task for artifacts. However, the left premotor cortex was *not* associated with the contrast between the semantic probe task for artifacts and the semantic probe task for natural objects nor with the main effect of artifacts. This result strongly suggests that action knowledge does not play a mandatory role in the comprehension of artifacts but is only called upon when objects are to be categorized.

Given that the results of the third study seem to refute models in which action knowledge is thought to play a necessary part in the comprehension of artifacts, how are we to account for the association between left prefrontal damage and category-specific disorders for artifacts ? As argued in the eclectic model, considered in section 3.0, one possibility might be that even though action knowledge play no necessary part in the comprehension of artifacts, the link between action knowledge and artifacts may be stronger than the link between action knowledge and natural objects (as evidenced by study two and three). Accordingly, if knowledge representations are distributed and interactive, damage to action knowlegde may lead to a lower activation level for nodes in the semantic system that represents artifacts. Because this system is presumably malfunctioning in patients with category-specific disorders for artifacts, such damage would primarily affect the comprehension of artifacts.

6.0 Conclusion

The evidence considered here suggests that at least two stages can and should be distinguished in visual object recognition. The first stage concerns the matching of objects to visual memory, the second the retrieval of functional knowledge from semantic memory. Category-specific disorders for natural objects may arise following damage to each of these stages because members of this category generally share more visual and semantic features than members from the category of artifacts and therefore are more difficult to differentiate. Category-specific disorders for artifacts, however, may also arise from damage to semantic memory provided that their representations are further underspecified by additional damage to action knowledge.

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[27] In the semantic probe task the subjects were asked to decide whether the displayed pictures represented objects that could be bought in a major warehouse.

Note that while this task can be accused of being artificial, it introduces no bias between categories because the aspect probed for was equally peripheral for objects belonging to the respective categories. That is, for neither category does the probe question relate to the object's core concept (cf. the discussion in the last part of section 2.3.1).

In the three PET-studies described, natural objects and artifacts often caused increased activation in the same areas of the brain. Thus, for both categories rCBF increased in the posterior part of the right inferior temporal gyrus during object decision tasks and in the left inferior temporal gyrus and left premotor cortex during the categorization tasks. Nevertheless, despite the overlap in the areas activated by the respective categories, there was a tendency for natural objects to be more coupled to structures involved in structural processing and artifacts to be more coupled to structures involved in the mediation of action knowledge (Gerlach et al., 2000a). Accordingly, the processing of these categories seems to lead to differences in degree rather than in kind of activation. At first hand this observation is more compatible with models which assume that visual and functional knowledge contribute differentially to the comprehension of natural objects and artifacts (i.e. Farah & McClelland, 1991; Warrington & McCarthy, 1987) than with models that assume that knowledge is categorically organized in the brain (i.e., Caramazza & Shelton, 1998). However, there is very little evidence for the assumption that visual attributes dominate in the representations of natural objects whereas functional attributes dominate in the representations of artifacts (Farah & McClelland, 1991). Thus, although some evidence was obtained for the suggestion that artifacts may be more closely linked to action knowledge than are natural objects, this sort of knowledge does not seem very important for their comprehension. Similarly, although natural objects did cause greater activation in areas believed to store visual knowledge, this provides no evidence that this sort of knowledge should dominate in the representations of natural objects compared with the representations of artifacts. Rather, the findings obtained in the first study seem to imply that activation increased in these areas because natural objects are more difficult to differentiate.

7.0 References

Benson DF (1989) Disorders of visual gnosis. In: Neuropsychology of visual perception (Brown JW ed), pp 59-78. Hillsdale,NJ: Erlbaum.

Biederman I, Gerhardstein PC, Cooper EE & Nelson CA (1997) High level object recognition without an anterior inferior temporal lobe. Neuropsychologia 35:271-287.

Breedin SD, Saffran EM & Coslett HB (1994) Reversal of the concreteness effect in a patient with semantic dementia. Cognitive Neuropsychology 11:617-660.

Buxbaum LJ, Schwartz MF& Carew TG (1997) The role of semantic memory in object use. Cognitive Neuropsychology 14:219-254.

Caramazza A & Shelton JR (1998) Domain-specific knowledge systems in the brain the animate-inanimate distinction. Journal of Cognitive Neuroscience 10:1-34.

Carr TH, McCauley C, Sperber RD & Parmalee CM (1982) Words, pictures and priming: On semantic activation, conscious identification and the automaticity of information processing. Journal of Experimental Psychology. Human Perception and Performance 8:757-777.

Chertkow H., Bub D & Caplan D. (1992) Constraining theories of semantic memory processing: Evidence from dementia. Cognitive Neuropsychology. 9:327-365.

Damasio H, Grabowski TJ, Tranel D, Hichwa RD & Damasio AR (1996) A neural basis for lexical retrieval. Nature 380:499-505.

De Renzi E (1989) Apraxia. In: Handbook of neuropsychology, Vol.2 (Boller F, Grafman J eds), pp 245-263. Amsterdam: Elsevier.

De Renzi E & Lucchelli F (1994) Are semantic systems separately represented in the brain? The case of living category impairment. Cortex 30:3-25.

Decety J, Grezes J, Costes N, Perani D, Jeannerod M, Procyk E, Grassi F & Fazio F (1997) Brain activity during observation of actions. Influence of action content and subject's strategy. Brain 120:1763-1777.

Farah MJ & McClelland JL (1991) A computational model of semantic memory impairment: modality specificity and emergent category specificity. Journal of Expimental Psychology. General 120:339-357.

Forde EME & Humphreys GW (1995) Refractory semantics in global aphasia: on semantic organisation and the access-storage distinction in neuropsychology. Memory 3:265-307.

Forde EME, Francis D, Riddoch MJ, Rumiati RI & Humphreys GW (1997) On the links between visual knowledge and naming: A single case study of a patient with a category-specific impairment for living things. Cognitive Neuropsychology 14:403-458.

Forde EME & Humphreys GW (1997) A semantic locus for refractory behaviour: Implications for access-storage distinctions and the nature of semantic memory. Cognitive Neuropsychology 14:367-402.

Funnell E & De Mornay Davies P (1996) JBR: A reassessment of concept familiarity and a category-specific disorder for living things. Neurocase 2:461-474.

Funnell E & Sheridan J (1992) Categories of knowledge? Unfamiliar aspects of living and nonliving things. Cognitive Neuropsychology 9:135-153.

Gaffan D & Heywood CA (1993) A spurious category-specific visual agnosia for living things in normal human and nonhuman primates. Journal of Cognitive Neuroscience 5:118-128.

Gerlach C, Law I, Gade A & Paulson OB (1999) Perceptual differentiation and category effects in normal object recognition -a PET study. Brain 122:2159-2170.

Gerlach C, Law I, Gade A & Paulson OB (2000a) Categorization and category effects in normal object recognition -a PET study. Neuropsychologia 38: 1693-1703.

Gerlach C, Gade A, Paulson OB & Law I (2000b) The role of action knowledge in the comprehension of artifacts -a PET study. Submitted.

Grabowski TJ, Damasio H & Damasio AR (1998) Premotor and prefrontal correlates of category-related lexical retrieval. NeuroImage 7:232-243.

Grafton ST, Fadiga L, Arbib MA & Rizzolatti G (1997) Premotor cortex activation during observation and naming of familiar tools. NeuroImage 6:231-236.

Hart J, Berndt RS & Caramazza A (1985) Category-specific naming deficit following cerebral infarction. Nature 316:439-440.

Hart J & Gordon B (1992) Neural subsystems for object knowledge. Nature 359:60-64.

Hillis AE & Caramazza A (1991) Category-specific naming and comprehension impairment: a double dissociation. Brain 114:2081-2094.

Humphreys GW & Forde EME (In press) Category-specific deficits: A major review and presentation of the Hierarchical Interactive Theory (HIT). Behavioral and Brain Sciences.

Humphreys GW, Riddoch MJ & Quinlan PT (1988) Cascade processes in picture identification. Cognitive Neuropsychology 5:67-104.

Humphreys GW, Riddoch MJ & Price CJ (1997) Top-down processes in object identification: evidence from experimental psychology, neuropsychology and functional anatomy. Philosophical Transactions of the Royal Society.B: Biolological Sciences 352:1275-1282.

Kohler S, Kapur S, Moscovitch M, Winocur G & Houle S (1995) Dissociation of pathways for object and spatial vision: a PET study in humans. Neuroreport 6:1865-1868.

Laiacona M, Capitani E & Barbarotto R (1997) Semantic category dissociations: a longitudinal study of two cases. Cortex 33:441-461.

Lakoff G (1987) Women, fire, and dangerous things: What categories reveal about the mind. Chicago: The University of Chicago Press.

Lissauer H (1890) Ein Fall von Seelenblindheit nebst einem Beitrag zur Theorie derselben. Archiv für Psychiatrie 21:222-270.

Lloyd-Jones TJ & Humphreys GW (1997) Perceptual differentiation as a source of category effects in object processing: evidence from naming and object decision. Memory & Cognition 25:18-35.

Magnie MN, Ferreira CT, Giusiano B & Poncet M (1999) Category specificity in object agnosia: preservation of sensorimotor experiences related to objects. Neuropsychologia 37:67-74.

Martin A, Haxby JV, Lalonde FM, Wiggs CL & Ungerleider LG (1995) Discrete cortical regions associated with knowledge of color and knowledge of action. Science 270:102-105.

Martin A, Wiggs CL, Ungerleider LG & Haxby JV (1996) Neural correlates of category-specific knowledge. Nature 379:649-652.

McCarthy RA & Warrington EK (1988) Evidence for modality-specific meaning systems in the brain. Nature 334:428-430.

Miller GA & Johnson-Laird PN (1976) Language and perception. Cambridge,Mass. Harvard University Press.

Milner AD & Goodale MA (1995) The visual brain in action. Oxford: Oxford University Press.

Mishkin M, Ungerleider LG & Macko KA (1983) Object vision and spatial vision: two cortical pathways. Trends in Neuroscience 6:414-417.

Moore CJ & Price CJ (1999) A functional neuroimaging study of the variables that generate category-specific object processing differences. Brain 122:943-962.

Moscovitch M, Winocur G & Behrmann M (1997) What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. Journal of Cognitive Neuroscience 9:555-604.

Moss HE, Tyler LK & Jennings F (1997) When leopards lose their spots: Knowledge of visual properties in category-specific deficits for living things. Cognitive Neuropsychology 14:901-950.

Mummery CJ, Patterson K, Hodges JR & Wise RJ (1996) Generating 'tiger' as an animal name or a word beginning with T: differences in brain activation. Proceedings of the Royal Society of London, Series B: Biological Sciences 263:989-995.

Perani D, Cappa SF, 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.

Perani D, Schnur T, Tettamanti M, Tempini M, Cappa SF & Fazio F (1999) Word and picture matching: A PET study of semantic category effects. Neuropsychologia 7:293-306.

Poline JB, Holmes A, Worsley KJ & Friston KJ (1997) Making statistical inferences. In: Human brain function (Frackowiak RSJ, Friston KJ, Frith CD, Dolan RJ & Mazziotta JC eds.) San Diego,CA: Academic Press. pp. 85-106.

Price CJ & Humphreys GW (1989) The effects of surface detail on object categorization and naming. Quaterly Journal of Experimental Psychology A 41:797-827.

Riddoch MJ & Humphreys GW (1987) Picture naming. In: Visual object processing: A cognitive neuropsychological approach (Humphreys GW, Riddoch MJ eds), pp 107-143. Hove: Erlbaum.

Rothi LJ, Ochipa C & Heilman KM (1991) A cognitive neuropsychological model of limb praxis. Cognitive Neuropsychology 8:443-458.

Sacchett C & Humphreys GW (1992) Calling a squirrel a squirrel but a canoe a wigwam: A category-specific deficit for artefactual objects and body parts. Cognitive Neuropsychology 9:73-86.

Schacter DL, Cooper LA, Delaney SM, Peterson MA & Tharan M (1991) Implicit memory for possible and impossible objects: constraints on the construction of structural descriptions. Journal of Experimental Psychology. Learning, Memory & Cognition 17:3-19.

Schacter DL, Reiman E, Uecker A, Polster MR, Yun LS & Cooper LA (1995) Brain regions associated with retrieval of structurally coherent visual information. Nature 376:587-590.

Sergent J, Ohta S & MacDonald B (1992) Functional neuroanatomy of face and object processing. A positron emission tomography study. Brain 115 Pt 1:15-36.

Sheridan J & Humphreys GW (1993) A verbal-semantic category-specific recognition impairment. Cognitive Neuropsychology 10:143-184.

Silveri MC, Gainotti G, Perani D, Cappelletti JY, Carbone G & Fazio F (1997) Naming deficit for non-living items: neuropsychological and PET study. Neuropsychologia 35:359-367.

Sirigu A, Duhamel JR & Poncet M (1991) The role of sensorimotor experience in object recognition. A case of multimodal agnosia. Brain 114:2555-2573.

Stewart F, Parkin AJ & Hunkin NM (1992) Naming impairments following recovery from herpes simplex encephalitis: category-specific? Quaterly Journal of Experimental Psychology A 44:261-284.

Thompson-Schill SL, Aguirre GK, D'Esposito M & Farah MJ (1999) A neural basis for category and modality specificity of semantic knowledge. Neuropsychologia 37:671-676.

Tyler LK & Moss HE (1997) Functional properties of concepts: Studies of normal and brain-damaged patients. Cognitive Neuropsychology 14:511-545.

Vandenberghe R, Price C, Wise R, Josephs O & Frackowiak RS (1996) Functional anatomy of a common semantic system for words and pictures. Nature 383:254-256.

Warrington EK (1975) The selective impairment of semantic memory. Quaterly Journal of Experimental Psychology 27:635-657.

Warrington EK & McCarthy R (1983) Category specific access dysphasia. Brain 106:859-878.

Warrington EK & McCarthy RA (1987) Categories of knowledge. Further fractionations and an attempted integration. Brain 110:1273-1296.

Warrington EK & McCarthy RA (1994) Multiple meaning systems in the brain: a case for visual semantics. Neuropsychologia 32:1465-1473.

Warrington EK & Shallice T (1984) Category specific semantic impairments. Brain 107:829-854.

Danish summary

Denne afhandling udgør en oversigt over nogle af de hovedfund jeg har rapporteret i tre artikler. Artiklerne omhandler billeddannelses-studier (positron emission tomografi, PET) af hvorledes viden er organiseret i hjernen. Eftersom disse undersøgelser er detaljeret beskrevet i artiklerne er oversigten primært tænkt som en teoretisk ramme hvori resultaterne fra disse undersøgelser fremstilles samlet.

Første del af afhandlingen giver en kort historisk introduktion til det område af neuropsykologien der beskæftiger sig med betydningen af forskellige typer af viden i visuel objektgenkendelse. Det primære datagrundlag for dette område udgør undersøgelser af patienter med svækket evne til at genkende specifikke kategorier af objekter. Hovedparten af afhandlingens oversigt består derfor i en evaluering af de modeller der er fremsat i et forsøg på at redegøre for disse patienters forstyrrelser. På trods af at modellerne hver for sig ofte kun kan redegøre for enkelte typer af kategori-specifikke genkendelsesforstyrrelser, angiver hovedparten af dem værdifulde forklaringsprincipper. Det er en af afhandlingens teser at nogle af disse forklaringsprincipper er komplementære samt at de kan integreres i en overordnet teoretisk ramme. Omend der er undtagelser, så kan denne overordnede ramme, der i afhandlingen omtales som den eklektiske model, redegøre for hovedparten af de tilfælde af kategori-specifikke genkendelsesforstyrrelser der er beskrevet i litteraturen.

Den sidste del af afhandlingen beskriver de PET-studier jeg har foretaget. Resultaterne fra disse undersøgelser antyder: (i) at mindst tre forskellige typer af viden (visuel, semantisk og handlemæssig) indgår på forskellige niveauer i den visuelle genkendelse af objekter, samt at de kan dissocieres anatomisk og (ii), at naturlige objekter og menneskeskabte objekter underkastes samme type af behandlingsprocesser (behandles af de samme områder af hjernen), omend processeringen af naturlige objekter, sammenlignet med menneskeskabte objekter, medfører øget aktivering af de områder af hjernen der behandler visuel viden, hvorimod processeringen af menneskeskabte objekter, sammenlignet med naturlige objekter, medfører øget aktivering af de områder af hjernen der behandler handlemæssig viden.