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Differences in the perceptual processing of living and non-living things: The role of configural processing

by

Christopher Hope

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ABSTRACT

Three experiments were conducted on normal functioning undergraduate university students to examine the role of configural processing in a set of living and non-living items. In Experiment 1 the participants were required to indicate whether a line drawing matched a word that preceded it. Half of the pictures depicted animals and half depicted clothing. Each picture was presented once in the upright position and once in the inverted position. The results indicated that inversion of the pictures of animals increased reaction times (RTs) more than inversion of the pictures of clothing, compared to pictures presented in the upright orientation. In Experiment 2 participants were required to categorize the same set of pictures used in Experiment 1. The pictures were again presented in upright and inverted orientations. In contrast to Experiment 1 inversion of the pictures increased RTs equally for the animals and the clothing. In Experiment 3 participants performed the same task as in Experiment 1. However, instead of clothing, pictures of non-living items that were hypothesized to encourage configural processing were used. Inversion of the pictures increased RTs equally for the animals and the set of non-living items.

The results are conceptualized as supporting the hypothesis that living things are processed more configurally than are non-living artefacts because of visual crowding (Humphreys & Riddoch, 1987) within the category of living things. The relevance of these findings to semantic category deficits for living things is discussed. It is hypothesized that damage to a part of the brain necessary for processing the configural relationships of objects can account for some of the instances of category specific deficits for living things.

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INTRODUCTION

A fundamental subject of inquiry, not just for psychology but for all social and biological science, involves the organization of information in the brain. Perhaps some of the most informative neuropsychological findings concerning this issue come from patients who can recognize some categories of objects but not others. Warrington and Shallice (1984) described a patient who sustained temporal lobe damage following herpes simplex encephalitis and was able to name and give accurate descriptions of nonliving artefacts, but had very limited knowledge for living things. For example, the patient was able to describe a compass as “tools for telling the direction you are going” and a briefcase as “a small case used by students to carry papers.” However, when asked to describe a parrot he said, “don’t know,” and for a snail he responded “an insect animal.”

The above examples are used to illustrate the presence of an overall pattern of impaired semantic knowledge for living things with preserved knowledge for nonliving things. Other patients present with the opposite pattern of results, specifically intact knowledge for living things and impaired knowledge for nonliving artefacts. This double dissociation has been observed for a number of different categories of knowledge. The symptoms of the first group of patients dissociate knowledge for living things from knowledge of other objects, and symptoms of the second group dissociate knowledge for nonliving artefacts from that of living things.

Other neuropsychological double dissociations that have been observed include ones for common vs. proper names, nouns vs. verbs, and abstract vs. concrete words. The presence of these double dissociations has been taken as evidence that different neural substrates underlie the processing of each. However, as Van Orden, Pennington, and

Stone (2001) state, the hypothesis that double dissociations indicate that different neural substrates are responsible for performing different cognitive processes is predicated on the assumption of modularity of brain functions. In contrast, many researchers have made the logical mistake of accepting the occurrence of double dissociations as proof of modularity. Van Orden et al. (2001) critique not only the application of double dissociations to theories of modularity, but the pursuit of defining neuropsychological modules at all. Firstly, modularity theories fail to explicate criteria necessary for the definition of pure case dissociations. Thus, the characteristics that define pure lesions of any module are not clear since the existence of the module is based on the presentation of cases. This results in the constant pursuit of a pure case and an inevitable expansion of exclusionary criteria. Secondly, because modularity places no limit on the number of fractionations, dissociations translate into increasingly more fine-grained modules. For example, an initial dissociation observed between nouns and verbs led to an observed fractionation between living and non-living things, which has now been further fractionated within the living things category to distinguish among animals, plants, and body parts.

Van Orden et al's (2001) compelling arguments notwithstanding, the investigation into double dissociations has had some practical utility in providing direction for understanding the organization of the mind and brain. Furthermore, investigating the dissociation observed between living and non-living artefacts does not require the acceptance of the modularity hypothesis. Quite the contrary, studies conducted in this area have been aimed at distinguishing between predictions made by several modular theories, connectionist theories, and theories that argue that the dissociation occurs as a function of stimulus properties and not of brain organization. Thus, the modular hypothesis of living and non-living artefacts is being tested rather than assumed.

The distinction between living and non-living things has encouraged a great deal of research involving the theoretical underpinnings of category specific deficits for a number of reasons. Firstly, results initially presented by Warrington and Shallice (1984) and subsequently corroborated by numerous studies (Basso, Capitani, & Laiacona, 1988; Caramazza & Shelton, 1998; De Renzi & Lucchelli, 1994; Farah & Wallace, 1992; Humphreys & Riddoch, 1988; Kolinsky et al. 2001; Laiacona, Capitani, & Barbarotto, 1997; Silveri & Gainotti, 1988) were very persuasive and consistent across different testing conditions. Secondly, these results inspired the development of a very influential theory by Warrington and Shallice (1984) that suggested that the living/non-living dissociation was actually a product of the differential weightings of visual-perceptual and functional attributes between living and non-living items. For instance, the identification of a living thing will depend primarily on its visual features, whereas identification of a non-living artefact such as a tool will rely less on visual and more on functional attributes. Finally, researchers took particular note of the living/non-living dichotomy presented by Warrington and Shallice (1984) because it was reported in 4 patients recovering from Herpes Simplex Encephalitis (HSE). This suggests that HSE results in a particular pattern of brain pathology that can be associated with a specific pattern of deficits. Such a link was seen to hold promise for establishing specific neuro-anatomical correlates to well defined cognitive processes.

Warrington and Shallice's (1984) theory also prompted a great deal of research activity aimed at challenging its predictions which in turn gave rise to the development of alternative explanations of the living/non-living dichotomy. Caramazza and Shelton (1998) argued that the dissociation between living and non-living artefacts occurs because they are represented in the brain by distinct neurological structures. They suggested that evolutionary pressures resulted in neural structures that are dedicated strictly to the processing of information from living items. Gonnerman, Anderson, and Devlin (1997), on the other hand, suggested that the dissociation between living and non-living artefacts occurs because of a different number of interconnections between sensory and functional attributes in these categories, rather than a differential weighting of sensory and functional attributes. Humphreys and Forde (2001) proposed the hierarchical interactive theory (HIT) in which categorical deficits arise because of greater visual and semantic similarity between categories of living items than between categories of nonliving things. Each of the above theories will be discussed in greater detail following a brief overview of the literature regarding the nature of semantic information in the human brain. Most relevant to this dissertation is a consideration of whether semantic information is represented in separate stores related to the modality of input (a separate store for visual, auditory, tactile, gustatory, motor, and verbal inputs) or in a single unitary semantic system that is amodal.

Unitary Versus Multiple Semantic Systems

Patients with category-specific deficits such as those described above do not appear to have difficulties that are confined to problems within a specific sensory modality, but are instead found for particular categories on questioning across multiple sensory modalities. Such generality suggests that the deficits relate to semantic memory and findings from these patients have been used to inform theories of the nature of semantic memory.

Semantic memory has traditionally been defined as the system responsible for storing information about the meanings of objects, concepts, and facts. For example, our semantic memory system contains the knowledge that a dog has fur, ears, eyes, a snout, and that it barks, is often walked with a leash, and can be used as a seeing-eye-dog. Some of this knowledge represents visual features, auditory features, motor features, and associations to other objects. A rudimentary analysis of the "contents" of what we refer to as semantic memory suggests that this is not a unitary system, but an interaction of systems that involve aspects of visual memory, auditory memory, motor memory, and verbal memory. However, the existence of category-specific deficits has led researchers to reconsider the possibility of a unitary semantic store.

Supporters of the single semantic system models suggest that information within semantic memory is amodal and that memory for sensorial features is accomplished by pre-semantic systems that hold modality specific information. Caramazza, Hillis, Rapp, and Romani (1990) argue that evidence that has been cited in favour of the multiple semantics hypothesis is equally compatible with variants of the single semantic system model. For instance, Shallice (1988) described three lines of evidence in support of a multiple semantic system model: 1) the existence of patients who show poor naming abilities that are restricted to one modality of input, despite evidence to suggest that access to semantic information through that modality is intact; 2) disproportionate memory impairments in one modality over another; and 3) the fact that individual's response times are helped more by priming within one modality than priming within another. In the multiple semantic system model it is hypothesized, based on the above findings, that different parts (modalities) of the semantic system can be accessed, without necessarily accessing the other parts; a phenomenon that Caramazza et al. (1990) termed "privileged access".

Caramazza et al. (1990) suggest, however, that a unitary semantic system model can also account for privileged access. A unitary semantic system hypothesis makes the assumption that the word "spoon" activates the full semantic representation of this concept in the same way that seeing a picture of a "spoon" does. However, Caramazza et al. (1990) state that it is also possible that the perceptual features of the presentation of the "spoon" will activate other semantic representations, such as those concerning the metallic colour or the representation of a handle. Thus, it is possible through the presentation of objects, that specific perceptual features will be given this "privileged access" without making the assumption of multiple separate semantic systems.

In contrast to the single, amodal semantic system model, Damasio (1990) proposed a multi-modal model in which semantic memory consists of different types of sensory and sensorimotor information. Any given item activates a pattern of activation across the different sensory and sensorimotor cortices. This results in a highly distributed semantic system in which various "feature fragments" are stored in the cortex that corresponds to each particular sensory modality and motor cortex. Thus, the representation for an apple would consist of distributed activation for the smell in the olfactory cortex, the visual features in the visual cortex, auditory associations in the auditory cortex, and motor associations in the motor cortex. There is also research suggesting that the emotional connections of an item are an important component of the semantic representation (Brousseau & Buchanan, 2004). Information from different sensory modalities is integrated at convergence zones in higher level association cortex. Recognition of an object can only occur once a sufficient number of "feature fragments" are activated.

Each of the theories of category specific deficits described in this paper could be categorized very broadly as a hypothesis based on an amodal semantic system or a multi-modal system. The categorical hypothesis (Caramazza and Shelton, 1998) and the interconnections hypothesis (Gonnerman et al., 1997) are examples of the former while the sensory/functional hypothesis (Warrington and Shallice, 1984) and the HIT model (Humphreys and Forde, 2001) are examples of the latter. Like these multi-modal perspectives, the model of categorical deficits described in this dissertation emphasizes visual processing and de-emphasizes a "core" semantic processor.

Sensory/Functional Hypothesis

The sensory/functional account of category-specific deficits assumes that knowledge in semantic memory is organized such that damage to a specific area of the brain will result in categorical dissociations even though memory may not be organized by semantic category. The sensory/functional hypothesis proposed by Warrington and Shallice (1984) was based on findings from a series of eight controlled experiments conducted on four patients who had partially recovered from HSE[1].

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[1] Because of verbal limitations two of the four patients were only able to participate in one of the eight experiments.

As a measure of overall visual and verbal agnosia, in the first experiment the two patients were required to name and describe 40 clear line drawings of mostly inanimate objects. Following a short interval they were then required to provide definitions to the object names presented auditorily. The researchers identified a moderately severe visual and verbal agnosia in both patients. In subsequent experiments both patients presented with a significant discrepancy in their ability to identify living versus non-living artefacts. Although they were usually able to name the superordinate category for both categories their ability to name and define living things was severely impaired compared to a significantly more preserved ability to identify non-living artefacts. Both patients also showed significant impairment in their ability to identify food items and one of the patients showed a preserved ability to define abstract words, but a moderately severe deficit in defining concrete words. The two patients presenting with more severe verbal impairments were administered a spoken word/picture matching task, requiring them to identify animals, foods, and inanimate objects. These two patients also demonstrated poorer performance on the animal and food categories than on the inanimate objects category.

The above results clearly show categorical deficits for both living things and foods, in comparison to a well-preserved ability to identify non-living artefacts in all four patients. The performance differences between categories was present across tasks (verbal description, naming, mimed responses, and picture/word matching) and thus across input modalities.

In developing a convincing argument for the sensory/functional hypothesis alternative explanations first had to be discounted. Although all four patients had a relatively severe amnesic syndrome, the authors rejected the hypothesis that this was entirely responsible for the deficits observed in these patients. If this hypothesis were accurate, it would be necessary for all reported cases of category specific deficits to occur in conjunction with a severe amnesic syndrome, which is not the case (Warrington, 1975). The category specificity of the deficits also makes an explanation involving a visual processing deficit untenable (although this claim will be challenged in the present paper). More importantly, the fact that the deficit persists across testing in different sensory modalities implicates a semantic deficit. Likewise, because the deficit persisted on the word/picture matching tasks any argument that the results occurred because of an impoverished expressive vocabulary is discredited. In sum, it appears as though the dichotomy observed in these four patients was the result of a semantic processing deficit.

As further support for the hypothesis that these patients are presenting with a specific pattern of impairment and preservation of different semantic categories, Warrington and McCarthy (1987) documented a patient with a reversed pattern of category-specific deficit. While the four patients studied by Warrington and Shallice (1984) presented with an impairment in their knowledge of living things and foods and a preservation of knowledge of non-living artefacts, Warrington and McCarthy (1987) investigated a patient with semantic deficits for non-living artefacts with preserved knowledge of foods and living things.

To explain the categorical dissociation observed in their initial four patients Warrington and Shallice (1984) proposed that knowledge of non-living artefacts is different from that of living things and foods. More specifically, when distinguishing between different living things and foods one must rely on knowledge of sensory features such as size, colour, shape, and texture. For instance, to distinguish between a leopard and a tiger, precise visual information (e.g., stripes versus spots) must be accessed. In contrast, non-living artefacts are more typically defined by their function. Thus, the distinction between a screw and a nail is related primarily to how they are used (i.e. a nail is inserted using a hammer and a screw is inserted using a screwdriver). The sensory features of a screw can vary considerably, but the functional definition remains constant. Food and living things, on the other hand, have very few identifiable, unique functional features. Although the identification of non-living artefacts will require the accessing of some sensory features and the identification of some foods and living things will consist of some functional features, the weighting of these feature types within each category differs. Therefore, any damage that occurs to the system underlying the identification of sensory features will differentially affect foods and living things, whereas damage that occurs to the system sub-serving functional features will have a greater impact on the processing of non-living artefacts.

Warrington and McCarthy (1987) also found a distinction within the category of non-living artefacts, with their patient showing a deficit for small manipulable objects and preserved knowledge for large man-made objects. Gem stones and musical instruments tended to be impaired to the same extent as living things, whereas body parts patterned with non-living artefacts (Warrington & McCarthy, 1987; Warrington & Shallice, 1984). To account for this, Warrington and colleagues suggested that gem stones differ from other non-living artefacts in that they are differentiated primarily by visual features in much the same way that living things are. Likewise, body parts are differentiated based on their functional attributes as are most non-living artefacts.

However, some researchers argue that the sensory/functional hypothesis is not adequate to account for more fine-grained distinctions (Caramazza & Shelton, 1998) reported in the literature including a dissociation between the processing of plants and animals (Farah & Wallace, 1992; Forde, Francis, Riddoch, Rumiati, & Humphreys, 1997).

Pre-empting this argument, Warrington and McCarthy (1987) proposed an extension to the sensory/functional theory that still maintained the hypothesis that semantic information is organized by modality-specific information. They suggested that in addition to a differential weighting between the number of sensory features (visual, auditory, and sensorimotor features) in a category, there can also be a more fine-grained differentiation within modalities of knowledge. For instance, within the visual modality, knowledge of any object may consist of colour, shape, location, and motion. In the same way that different types of objects will have different weightings of features between modalities, different objects may have different weightings of colour, shape, location, and motion features. Thus, the process of differentiating between an apple and an orange may be more dependent on colour than the process of differentiating between species of animal, even though both distinctions are heavily reliant on visual features.

Each of these different types of visual features has been shown to be separable physiologically, anatomically, and psychologically (Warrington & McCarthy, 1987). Therefore, damage to one of these systems with the sparing of the others may lead to more fine-grained categorical deficits. It follows from this argument that these types of categorical deficit would be less likely to occur because of the anatomical proximity of the systems responsible for processing different features within a single modality. Hence, although these fine-grained deficits are possible they are less likely to occur than deficits to those categories of knowledge that differ in the weightings of features between modalities, such as the dissociation that occurs between living and non-living things.

Warrington and McCarthy (1987) proposed a further parsing of the semantic system based on the finding that deficits are consistent within modalities, but not across modalities. Because there were differences in consistency between modalities, they concluded that semantic knowledge is not only separated into sensory and functional stores, but also into independent stores based on the input modality. Therefore, there may be a sensory semantic store for visual objects and a sensory store for verbal input. Because there are separate sensory stores for both visual and auditory inputs there may be duplication of information within the semantic system. For instance, the fact that tigers have stripes may be represented in the visual input store as well as the auditory input store. This more fine-grained specialization of knowledge within the semantic system would lead to a quasi-categorically organized knowledge base for each modality of input. In fact, as Caramazza and Shelton (1998) point out, the more fine-grained the sensory/functional hypothesis becomes, the closer it is to being functionally identical to a purely categorical separation of living and non-living things within the semantic system. As more minute sensory details are hypothesized to compose one category and not the other the more the system is functionally separated into semantic categories.

Based on the arguments discussed above the validity of the sensory/functional hypothesis is dependent on the suggestion that sensory and functional features are differentially represented in living things versus non-living artefacts. Although Warrington and Shallice (1984) made the assumption that this was the case, they provided no formal test of the hypothesis. Farah and McClelland (1991) devised a test to quantify the number of functional and visual features associated with a list of living and nonliving artefacts. Forty-two undergraduate students were required to read the dictionary definitions of living and nonliving artefacts and underline all of the occurrences of functional and visual features. The results showed an average of 2.68 visual features for all living things and 1.57 for the nonliving artefacts. For functional features, there was an average of .35 for the living things and 1.11 for the nonliving artefacts. The ratios of visual to functional features are 7.7:1 for living things and 1.4:1 for nonliving artefacts. Thus, the data confirmed the hypothesis that visual features are more prevalent in the definitions for living things than nonliving artefacts.

To further test the predictions of the sensory/functional hypothesis, Farah and McClelland (1991) developed a parallel distributed processing model in which semantic knowledge was divided into visual and functional features. In accord with the sensory/functional hypothesis the assumption was made that semantic knowledge is composed of information from these two separate but interconnected stores and that the ratio of visual to functional features is much larger for living than for nonliving artefacts. When the visual component of the semantic store was "lesioned", the result proved to be a deficit for living things with the reverse dissociation occurring following lesions to the functional component of the semantic store. The results of this study indicate that category specific deficits can arise from a semantic system that is not categorically organized, but is instead organized by visual and functional features.

However, as Caramazza and Shelton (1998) point out, the results of the modeling experiment performed by Farah and McClelland (1991) are not surprising considering the ratio of visual to functional features was set at 16.1:2.1 for living things and 9.4:6.7 for nonliving artefacts. Given these ratios, it is not difficult to predict that damage to the visual semantic network would result in a more severe deficit for living than for nonliving things. Thus, the finding of major importance in the study conducted by Farah and McClelland (1991) is the discrepancy in the ratios of visual and functional features between living and nonliving artefacts.

Even this finding has been refuted, however (Caramazza & Shelton, 1998; Tyler, Moss, Durrant-Peatfield, & Levy, 2000). Caramazza and Shelton (1998) argued that Farah and McClelland encouraged their participants to exclude functional properties of living things by the instructions that were given. The participants examining definitions of words for functional features were instructed to consider only what the item "is for", which is principally a property of artefacts. Potentially, the participants could have found many more nonsensory features of living things such as, ferocious, carnivore, omnivore, etc., had the instructions been altered. Thus, the differences in the ratios of sensory to nonsensory information for living and nonliving things could have been much smaller.

To test this, Caramazza and Shelton (1998) instructed two groups of participants to underline either all sensory features or all nonsensory features in the definitions of the living and nonliving artefacts used by Farah and McClelland. They found that the ratios of sensory to nonsensory features for living things and nonliving artefacts to be 2.9:2.5 and 2.2:2.3, respectively. These results are difficult for the sensory/functional hypothesis to accommodate and call into question the hypothesis that living things are defined by more sensory than nonsensory features.

Humphreys and Riddoch (1999) found results that they interpreted as supporting the hypothesis that non-living artefacts are better represented by functional definitions than sensory definitions. They examined the ability of a learning disabled child to learn lists of non-living artefacts under two different presentation conditions. In one condition the child was presented with the target object and another relational object. These were accompanied by a statement that related the objects spatially. For example, she was shown a picture of a glass and a table and was told, “this is a glass and you find it on a table.” This condition was believed to encourage the child to process sensorial features. In the other condition the child was shown a picture of the object, which was accompanied by the experimenter miming the action that is typically associated with using the object. If the object was a glass, for example, the experimenter would mime taking a drink from the glass. Following each trial the child was required to repeat the name of the object before moving on to the next trial. Subsequently, she was presented with all of the pictures from the lists and asked to give the name of the object and her performance was better for words learned in the actions condition than in the spatial condition. Humphries and Riddoch viewed these results as support for the sensory/functional hypothesis.

Variable and vague usage of the term “functional” has been another criticism of the sensory/functional hypothesis. Functional knowledge of an object has been interpreted as how one would act on an object as well as how the object itself operates. An example of the former interpretation is how one swings a hammer to hit a nail; an example of the latter is how a horse pulls a carriage. It has also been interpreted as purely motor knowledge for manipulating an object. Importantly, if not defined as motor knowledge, "functional" knowledge must be based in sensory or verbal knowledge or some combination of the three (sensory, verbal, and motor), since these are the only forms of knowledge possible. The concept of "sensory knowledge" has also been used somewhat ambiguously in the literature with some researchers referring specifically to visual knowledge and others meaning all forms of sensory knowledge.

Processing of Perceptual and Functional Features in Patients with Categorical Deficits

The literature investigating whether patients with deficits for living things have deficits for the sensory features of all items offers conflicting results. Although a number of studies appear to confirm this prediction, others have not. Basso et al. (1988) were among the first to test for the presence of a sensory modality-specific deficit in a patient with a deficit for living things. They reported that the patient answered 25 out of 29 questions regarding the functional features of living things correctly. By contrast, the same patient responded correctly to only 10 out of 20 questions regarding the sensory features of living items.

Silveri and Gainotti (1988) reported results similar to Basso et al's (1988) from their examination of a patient with a deficit for living things. The patient was able to name 1 out of 11 animals correctly from definitions that were based primarily on visual descriptions, but was able to name 8 of 14 correctly from definitions that stressed the functional features of the animals. Similarly, De Renzi & Lucchelli (1994) reported that their subject could answer questions about the functional attributes of living things, but was unable to answer questions relating to their sensory features. This dissociation between functional and sensory attributes, however, was not found for non-living artefacts.

Although these results appear to support the predictions of the sensory/functional hypothesis, Caramazza and Shelton (1998) argue that these studies should be viewed with caution because of the presence of uncontrolled confounds. Specifically, the above studies failed to control for the relative difficulty of questions about sensory and functional features. For instance, in the study by Silveri and Gainotti (1988) the patient was tested on the functional attributes of domesticated animals and the visual attributes of wild animals, which may well differ in difficulty level. Also, research has shown that judgments regarding the visual features of items are more difficult than questions about the functional features (Stewart, Parkin, & Hunkin, 1992). Stewart et al. reported that the dissociation between visual and functional features disappeared when the difficulty of items was controlled for in a patient with a category-specific deficit for living things. Caramazza and Shelton (1998) state that it has yet to be shown that there is a discrepancy between the processing of visual and functional features in a patient with a category-specific deficit for living things.

Keeping these potential confounds in mind, Gainotti and Silveri (1996) retested their patient with a category-specific deficit for living things. They controlled for the effects of word frequency and stimulus familiarity, examined whether the dissociation between the patient's ability to identify visual and functional features was an artefact of stimulus selection, and tested whether the patient's deficit was limited to visual features, or included other sensory features as well. The patient again presented with deficits for animals, plants and flowers, food, and musical instruments, with a relative preservation of knowledge for non-living objects and body parts. This effect was observed when the words were matched for frequency and when they were not. Also, although familiarity of the items accounted for a large portion of the variance the difference between the categories persisted after it was controlled.

The most important experiment of Gainotti and Silveri's (1996) study for the present discussion tested for deficits for visual-perceptual information and for functional-encyclopedic information. To control for any stimulus frequency or familiarity effects two descriptions of each item were presented to the patient. One of the descriptions was based on visual features and the other was based on functional features. The patient was required to name the item based on the descriptions given. For example, for the word "horse" the functional description was "domestic animal that neighs, trots, and gallops" and the visual description was "domestic animal with a flowing mane and tail." To select items for which both the functional and visual descriptions were unambiguous and relatively easy, 150 sentences were given in random order to 5 independent judges matched to the patient in age and education. The patient had a greater impairment for identifying the animals from their visual descriptions than from their functional descriptions (6% and 43% correct, respectively). By contrast, both the visual and the functional descriptions of non-living artefacts resulted in identical performance of 58 percent correct. However, these results are somewhat compromised by the finding that the control subjects also performed slightly better when identifying animals from their functional descriptions than from their visual descriptions (95% and 82% correct, respectively).

In contrast to the results reported by Gainotti and Silveri (1996), Laiacona et al. (1997) described two patients with category-specific deficits for living things that showed equal impairment on visual and functional features of items. When these two patients were tested on a forced-choice task with questions about visual or functional features that were matched for difficulty, there was no difference between performance on visual and functional questions for living things (73% and 69% correct, respectively for one patient; 55% and 58% correct, respectively for the other) or nonliving artefacts (96% correct for both visual and functional features for one patient; 91% and 84% correct for the other). Similarly, Funnell and De Mornay Davies (1997) found that the patient previously examined by Warrington and Shallice (1984) had an equal amount of impairment for the visual and the functional features of a list of living things.

Consistent with these findings, Caramazza and Shelton (1998) had their patient respond “true” or “false” to an attribute statement about an object. The patient had an impaired ability to make judgments about the attributes of animals and food items regardless of whether the statement related to visual or functional features. This was contrasted to her performance on the questions about non-living artefacts, which was within normal limits for both visual and functional features. The impairment with which this patient presented did not appear to be specific to visual knowledge as hypothesized by the sensory/functional hypothesis.

As a further test of the predictions of the sensory/functional hypothesis, Caramazza and Shelton (1998) had their patient view a set of pictures and determine whether each one was a real animal or a real artefact. Half of the pictures represented a real item with the other half being a combination of two different items. For example, one false animal picture was a bear with a horse’s head and a false artefact was a hammer with the handle of a screw-driver. The patient had difficulty determining which pictures represented real animals, with a tendency to respond “yes” (70% hit rate and 50% correct rejection). On the other hand, the patient had little difficulty distinguishing real from unreal artefacts (similar results were reported by Kolinsky et al., 2002). In another task, the patient was required to select which of two heads went with a headless body, or which of two parts went with a non-living artefact that was missing something. Again, the patient was severely impaired at selecting the correct animal head, but had no trouble identifying the correct part for the artefact.

Two conclusions can be reached from the above results. Firstly, performance on the real and unreal pictures task rules out the possibility that the patient's impairment was simply a name retrieval deficit. Secondly, it is difficult for the sensory/functional hypothesis to account for the finding that the patient's visual knowledge for living things was impaired, but his visual knowledge for non-living artefacts was intact. If patients with deficits for living things have a specific impairment for the processing of visual/sensory features of items then one would predict that their knowledge for the visual features of both animals and artefacts would be impaired, while their knowledge for the functional features of both animals and artefacts would be spared. The present results, however, indicate impaired knowledge for the visual and functional attributes of animals with spared visual and functional knowledge of non-living artefacts.

Kolinsky et al. (2002) also showed that a patient with a category-specific deficit for living things had impaired knowledge for the structural attributes of living things but not non-living artefacts. Their patient displayed poor memory drawing and drawing completion of living things despite an intact ability to copy the figures. Furthermore, they observed a significant impairment in the patient's colour knowledge for living things. For example, in one of the tasks the patient was required to select the correctly coloured object from a set of four. Although he performed within the average range on pictures of non-living artefacts his performance on pictures of animals was very poor (71% correct and 5% correct, respectively). This was the case even on items that he recognized (e.g. he selected the red mouse, yet he correctly named and described it).

The sensory/functional hypothesis has difficulty accounting for the results of studies presenting patients with deficits for both the sensory and functional features of living things with a sparing of knowledge for the sensory and functional features of non-living artefacts. However, Humpreys and Forde (2001) pointed out that there are flaws in both the methodology used and the conclusions reached by the researchers reporting these results.

Firstly, as mentioned previously the term "functional features" is not well defined with variability in its use arising not only between studies, but also within them. The most problematic methodological error is a difference in the definition used for functional features for living and non-living artefacts. Functional knowledge for nonliving things has generally referred to how the item is used, which is in many cases dependent on the motor activity involved in its usage. Functional knowledge for living things, on the other hand, has included the behaviour of the organism, the environment in which certain plants and animals are found, and even the sounds that animals make.

In addition to the methodological problems associated with the definition of functional features the conclusions reached by those who have found deficits for both sensory and functional features of living things are flawed. Humphreys and Forde (2001) argue that hypotheses that stress the differential damage of types of knowledge (such as the sensory/functional hypothesis) can account for category-specific deficits that include all types of information (i.e. deficits for both sensory and functional knowledge for living things). If patients represent living things primarily in terms of visual/sensory information, then damage to this visual/sensory store may render the knowledge for any particular living thing inaccessible. Thus, the patients may not be able to access enough information to distinguish one member of a living category from another. For instance, if a patient does not know that a camel has two humps, or is brown, or has four legs, then that patient does not really know what a camel is and will not be able to answer typical "functional" questions such as "Does a camel live in the desert." It is possible that in order to answer any questions about living things, one must first access a visual representation of that living thing.

The hypothesis that accessing any information about living things is highly dependent on first accessing a visual representation of that item has been supported by a number of neuro-imaging studies which showed that areas of the brain responsible for processing form were activated when participants answered questions about visual features and functional features of living things (Chao, Haxby, & Martin, 1999; Thompson-Schill, Aguirre, D'Esposito, & Farah, 1999). Thus, one's ability to "know" what a living thing is and answer questions both about what it looks like and how it functions appears to be dependent on one's ability to access the visual features of the item. This is contrasted with the finding that the same area of the brain responsible for the processing of form features is not activated when participants are retrieving functional information about non-living items. These neuro-imaging data are consistent with an explanation for category-specific deficits for both sensory and functional knowledge of living things that is in keeping with the sensory/functional hypothesis.

In summary, a great deal of research activity has been devoted to falsifying the sensory/functional model. The model has been defended from these attacks by claims of methodological problems associated with the definition of functional knowledge in living things and non-living artefacts. However, the sensory/functional hypothesis has more difficulty accounting for patients with deficits for living things who have difficulty performing object decision tasks with living things, but not with non-living artefacts. If there is damage to visual information processing systems such damage should also impair the visual processing of non-living artefacts. This inconsistency is addressed in the HIT model, the visual crowding hypothesis, and in the model being proposed in this paper, each of which will be discussed later in the introduction.

Categorical Hypothesis

The categorical hypotheses states that living things and non-living artefacts are represented in separate stores within semantic memory. For instance, Caramazza and Shelton (1998) proposed that separate stores for living and non-living things have developed as a result of evolutionary pressures. Initially, evolutionary pressures would have encouraged the development of neurological structures devoted to living things. More specifically, neurological structures would have developed to represent animals because they are important for food and as potential predators. Separate structures would have developed to represent plant-life also as a source of food and for medicinal purposes. Non-living artefacts would not be of such importance until later in human evolution when tool usage developed. The evolutionary gains that accompanied an ability to distinguish between living and non-living things led to the development of distinct neurological structures which now form the organizational basis for conceptual knowledge.

Proponents of the categorical hypothesis argue that the idea that conceptual knowledge is organized into these three basic categories can account for some of the research findings that cannot be easily accommodated within a sensory/functional framework. For instance, a number of studies described above have reported that patients with category-specific deficits have an equal impairment for their knowledge of the functional and sensorial attributes of living things. This is accompanied by an intact knowledge for both the sensorial and the functional attributes of nonliving things (Caramazza and Shelton, 1998; Funnell & De Mornay Davies, 1997; Laiacona et al. 1997). Of course, the sensory/functional hypothesis makes the prediction that if a patient has a deficit for living things they should have a deficit for the sensorial attributes of both living and nonliving items but intact functional knowledge for both. The categorical hypothesis, on the other hand, predicts that categorical deficits should be associated with deficient knowledge for both sensorial and functional features of the affected category, with intact sensory and functional knowledge for the unaffected category.

The categorical hypothesis can also account for the reports involving some of the finer-grained dissociations that have been found in patients with category-specific impairments. For instance, although a number of patients have been found to have deficits for both plants and animals, some studies have reported on patients presenting with deficits for one but not the other (Caramazza & Shelton, 1998; Farah & Wallace, 1992; Forde et al. 1997). If knowledge of plants and animals was maintained by functionally separate systems, results such as these would be expected to occur.

The sensory/functional hypothesis explains such deficits as occurring because of different types of sensory knowledge being more important for certain items (Warrington & McCarthy, 1987). For example, intact colour knowledge may be of greater importance for distinguishing between different types of plants and fruits, whereas shape may be of greater importance for differentiating between different animals. Therefore, loss of either colour or shape knowledge will differentially affect these two categories.

One problem with this explanation, however, is that differential weightings of colour and shape features between categories is currently only assumed and has yet to be empirically validated or quantified. A second problem with this explanation is similar to the problem with the broader differentiation of sensory and functional features. Category-specific deficits for plants or animals have not been shown to be consistently associated with deficient colour knowledge. For instance, as described earlier Kolinsky et al. (2002) presented a patient with a category-specific deficit for living things. This patient was unable to select correctly coloured animals, but performed within the average range when required to select the correctly coloured non-living artefact. If this patient's deficit for animals was related to deficient colour knowledge, he would not have been able to select the correctly coloured non-living artefacts.

Although many proponents of the categorical hypothesis state that this theory offers a better explanation of the more fine-grained dissociations that occur, there are some patterns that do not fit with the predictions of the theory. The categorical hypothesis provides no explanation for the patterns of deficits reported by Warrington and McCarthy (1987) which led to the development of the sensory/functional hypothesis. Although this patient had deficits for nonliving things, a more fine-grained examination of the deficits revealed difficulties with small manipulable objects and body parts, but preserved knowledge for large man-made objects, gem stones, and musical instruments. This pattern of impairments is difficult to explain in terms of the categorical hypothesis, but is actually predicted by the sensory/functional hypothesis.

Much of the research supporting the argument that living and nonliving things are represented in functionally distinct areas of the brain comes from developmental studies and research involving semantic knowledge in children. S. Gelman (1988), for example, reported that four-year-olds could state whether something was made by people, thus indicating that they had the ability to identify man-made artefacts.

Other studies have shown that preschoolers have an understanding of the basic differences between living and non-living things. R. Gelman (1990) asked a group of preschool children to describe what was on the inside and outside of both living and non-living things. The children described the inside of living things in different ways than they described the outside. The inside of non-living things, on the other hand, was described in the same way as the outside. Gelman argued that children had learned at an early age about the biological structure of a particular living thing and had generalized to other living things without crossing the boundary between living and non-living things. From this Gelman argued that knowledge of living and non-living things was domain-specific and based on a contrasting set of principles.

Massey and R. Gelman (1988) conducted a similar study on the three- and four-year-olds' knowledge of living and non-living things. The children were presented with novel pictures of mammals, non-mammalian animals, rigid complex artefacts, wheeled objects, and statues composed of animal-like parts, and asked to determine which of the items was capable of going up a hill unassisted. The children selected both the mammals and non-mammals, rejecting all other categories including the statues with animal-like parts. This indicates that the children had the ability to identify those visual-perceptual characteristics that were reflective of things capable of self-initiated movement. R. Gelman (1990) later concluded that this ability to distinguish between items that can and cannot move on their own was the basis of the conceptual distinction between animate and inanimate objects.

Other researchers have investigated this ability to differentiate animate from inanimate objects at an even younger age. Mandler, Bauer, and McDonough (1991) examined the ability of 18-month-old infants to make even more fine-grained distinctions, separating animals, plants, and non-living items. The infants were able to make these distinctions as well as distinctions within the categories, such as separating furniture from kitchen utensils. These results led the authors to hypothesize that the infants were grouping items not based on visual similarities, but were relying instead on the movement patterns and the origin of the movement associated with each category. This hypothesis has implications for the dissociations that occur in category-specific deficits, possibly illustrating a mechanism by which evolution could select for the functional separation of the representations of living and non-living things. Furthermore, elements of the sensory/functional hypothesis are also incorporated. If infants are selected to distinguish and group objects based on the sensory feature of movement patterns, then this would provide a mechanism by which the representations of animate and inanimate objects are functionally separated within the semantic system.

Caramzza and Shelton (1998) elaborated on their proposal that semantic information is organized categorically in The Organized Unitary Content Hypothesis (OUCH). In OUCH the idea of modality specific semantic organization and the notion that category-specific deficits arise from differential weightings of sensorial and non-sensorial features between categories is rejected. In OUCH, although there are no categorical boundaries within the semantic system, a categorical structure emerges because of clustering of like features within a category.

Caramazza and Shelton (1998) elaborate on two fundamental characteristics of categories on which the OUCH is based. First of all, the properties of an object are highly intercorrelated. Second, members of a superordinate category share a number of features in common. Thus, a certain group of animals is going to consist of particular shapes, textures, colours, and scents, whereas a non-living artefact is going to have different types of features. In other words, certain properties tend to occur with one another or are intercorrelated. In addition, these intercorrelated features are going to be differentially distributed in the categories of living and nonliving things. Therefore, the multidimensional space of semantic features is not organized homogeneously, but instead consists of some regions that are densely packed and others that are more diffuse (lumpy). The dense regions consist of features that are highly correlated and are likely to represent concepts relating to living things. This is because living items tend to have more highly correlated features than do nonliving things.

From this hypothesized inhomogeneous organization of the semantic system it follows that focal damage is likely to result in category-specific deficits. Furthermore, those semantic categories that contain highly correlated features (living things) are densely packed and more likely to be damaged than those categories with less correlated features. The other prediction arising from this theory is that various patterns of category-specific deficits can occur as a result of the differences in the patterns of brain damage from case to case. Because the semantic system is hypothesized to be unitary but lumpy, the exact pattern of deficits will depend on the exact areas of the brain that have been damaged. Therefore, although it is more likely that a patient will present with a category-specific deficit for living things because the features of this category are densely packed, in the OUCH the possibility that a patient may present with a deficit for large non-living objects and gem-stones in addition to living things is allowed.

Another major prediction made by OUCH is that category-specific deficits should not be associated with a disproportionate deficit for visual over functional attributes. This is because focal damage to the semantic system should affect highly correlated features regardless of whether those features are visual or functional. This prediction clearly distinguishes the OUCH hypothesis from the sensory/functional hypothesis which predicts a discrepancy in the knowledge for sensory versus functional features.

The discrepancy between the processing of perceptual and functional features in living and non-living things was discussed in the previous section. There is evidence that patients with deficits for living things have greater difficulty processing the visual attributes of this category compared to their ability to process the visual attributes of non-living artefacts (Caramazza & Shelton, 1998; Kolinsky et al., 2002).

Alzheimer's Disease and the Intercorrelations Hypothesis

Alzheimer's Disease and Category-Specific Deficits

Recently, many of the hypotheses about the representation and storage of categorical knowledge has also been examined in patients with Alzheimer's Disease (AD) that present with category-specific deficits. The fact that a number of researchers previously believed that category-specific deficits were the result of localized lesions and AD resulted in damage that was more diffuse led to the AD population being largely ignored until recently (Gonnerman et al. 1997).

However, Silveri et al. (1991) hypothesized that because AD patients present initially with damage to temporolimbic structures they would be likely to experience such impairments, much like HSE patients. As predicted, AD patients demonstrated a pattern of impairment similar to that of HSE patients, showing greater impairments for living things than for non-living things. Based on these results and those from earlier studies of stroke patients the authors hypothesized that damage to temporolimbic structures results in a selective semantic impairment for living things, and damage to frontoparietal areas results in a category-specific impairment for non-living artefacts.

A later paper by Guistolisi, Bartolomeo, Daniele, Marra, and Gainotti (1993) reported similar results to those of Silveri et al. (1991) for patients in the early stages of the disease. When the patients were tested six months later, two of three no longer showed an effect of category. As one would expect, this was not the result of an improvement in their performance with living things, but a deterioration in their performance with non-living artefacts. The authors concluded that as the disease progresses the damage becomes so pervasive that deficits become apparent in all forms of knowledge. This illustrates one of the difficulties with studies involving AD patients: the pattern of deficits is extremely heterogeneous, meaning that much larger sample sizes are necessary than those used in the above studies in order to make any conclusions about the group as a whole.

The finding that AD patients present with category-specific deficits suggested to some researchers the possibility that they can emerge as a result of non-selective damage to a unitary semantic system. This depends, however, on the assumption that concepts are represented as different patterns of activation over multiple semantic features. It is the patterns of connections that differentiate one category from another with some categories being represented by more or fewer connections than others. Random damage to connections will then result in a pattern of deficits that appears to be category-specific.

The Intercorrelations Hypotheses

The idea that category-specific deficits can arise from diffuse damage to a connectionist system has received some empirical support from studies of patients with AD and from patients with other forms of pathology. Moss and Tyler (1997, 2000) examined a patient with generalized cerebral atrophy who presented with a disproportionate deficit for non-living artefacts that became more pronounced as her condition worsened. Likewise, Tyler et al. (2000) reported the same pattern of deficits in a patient with generalized cerebral atrophy, thus indicating that focal lesions are not necessary for the development of category-specific semantic impairments.

Gonnerman et al. (1997) tested a group of 15 patients with probable AD in the mild to moderate stages. In contrast to the results reported by Silveri et al. (1991), as a group the patients did not show greater impairment in their knowledge for living things than for non-living things. Based on the discrepant findings of the two studies and the argument that the neuropathology present in AD is actually less localized than Silveri et al. suggested, Gonnerman et al. rejected the hypothesis that patients with AD present with category-specific deficits for living things because of damage to temporolimbic structures.

However, closer inspection of the data of individual subjects revealed that one of the patients had a category-specific deficit for living things and another had a selective deficit for non-living things. Furthermore, in contrast to the findings reported by Silveri et al., data from these two patients revealed that these category-specific deficits remained fairly stable over the course of two to four years. Although the authors acknowledged that the results could be explained simply by assuming that the patient with deficits for living things had damage to temporolimbic structures and the patient with deficits for non-living things had frontoparietal damage, they stated that neither MRI scans nor neuropsychological testing supported this hypothesis.

In a second experiment involving 15 patients with mild to moderate AD Gonnerman et al. (1997) found that those patients who were less impaired tended to show slight deficits for non-living artefacts, whereas those who were more severely impaired tended to have a greater deficit for living things. Although this trend was not statistically verified it motivated the development of a theory to explain the pattern of deficits in AD patients. In this theory, living things are less affected by small amounts of generalized brain atrophy than non-living things because living things tend to have a greater number of intercorrelated features than non-living things. Intercorrelated features are those features that occur together for multiple items within a semantic category. For instance, “has fur” and “has teeth” are features that occur together for a number of different animals and are therefore considered intercorrelated features. Moreover, according to this view, those features that distinguish one item in a category from another item are different for living and non-living things. Similar to the sensory/functional hypothesis (Warrington & McCarthy, 1987) and the visual crowding hypothesis (Humpreys and Riddoch, 1987; described in the following section) Gonnerman et al. suggest that distinguishing features tend to be sensorial for living things and functional for non-living things.

Thus, the main tenets of the theory are that living things tend to have a higher ratio of sensory to functional features than non-living things; living things have a greater number of intercorrelations between features than non-living things; and those features that distinguish one living thing from another tend to be sensorial, while functional features distinguish non-living things from one another. The effect of the numerous intercorrelations among living things will be protective when the damage is minimal because the information from individual features is supported by the intercorrelations with other features. However, as the disease progresses and more connections are lost a critical point will be reached when the remaining connections can no longer compensate for the loss and activation of the remaining features will no longer reach the threshold of comprehension. Once this stage is reached all of those items that relied on the connections among a damaged set of features are left unavailable. Similar to the categorical hypothesis (Caramazza and Shelton, 1998) this theory allows for a unitary semantic system.

A similar theory has been proposed by McRae and Seidenberg (1997). McRae and Seidenberg had normal participants generate lists of the important features of exemplars from living items and non-living artefacts. The results indicated that living items tend to have more intercorrelated features than non-living items. This is protective for living items when there is a small amount of damage, but results in the loss of entire categories with larger amounts of damage. As an illustration of this process imagine the features "has four legs", "has fur", "has teeth", and "has claws". These features are all intercorrelated and represent a large number of mammals. If the connections between one of the features is damaged the remaining connections will be able to compensate, thereby allowing comprehension of all of the mammals that are represented by these features. However, once a critical point is reached all of those mammals that are represented by the features will no longer be available in semantic memory. The result of this process is a non-linear deterioration in the representations of living things as AD progresses.

This pattern of deficits is contrasted by those that occur for non-living artefacts. Because there are fewer intercorrelations between the features of non-living artefacts, there is a very limited ability of intact connections to compensate for damaged ones. This results in a slight deficit for artefacts even in the earlier stages of disease progression. As the disease progresses there will be a loss of knowledge of individual items across categories of artefacts. However, because there are relatively few intercorrelations among artefacts whole categories are not lost at advanced stages of the disease. Thus, the presentation of deficits for artefacts will proceed linearly with disease progression, in contrast to the pattern of deficits for living things.

Although the theory proposed by Gonnerman et al. (1997) seems to hold some explanatory power for the results of a number of the patients examined in their study, the results from the AD population as a whole are far from clear. In fact, a number of the patients studied by Gonnerman et al. (1997) did not fit the predicted pattern, with four showing greater non-living artefacts deficits than would be predicted. The authors suggest the possibility that in some cases damage that is more focal in nature may occur by chance resulting in patterns of deficits that do not fit with predictions.

As mentioned previously the results of Silveri et al. (1991) are at odds with those of Gonnerman et al. Silveri et al. reported that their subjects with moderate AD showed an overall deficit for living things, whereas the patients in Gonnerman et al.'s study did not. Giustolisi et al. (1993) reported results that were similar on initial testing to those reported by Silveri et al., with the group of AD patients showing an overall deficit for living things. They also reported that when the patients were examined six months later the category-specific deficit for living things disappeared. The authors argued that AD patients present initially with deficits for living things, but at later stages of the disease process damage becomes so pervasive that the category effect is lost. This pattern of results conflicts with the predictions of Gonnerman et al. (1997), who state that there should be an initial deficit for non-living things followed by a deficit for living things as the disease progresses.

Garrard, Patterson, Watson, and Hodges (1998) reported results that were similar to those of Silver et al. (1991) and Guistolisi et al. (1993), with their patients showing an overall deficit for living things. Garrard et al. also questioned whether intercorrelations between features would provide protection from decay. They disagree with Gonnerman et al. (1997) who state that the majority of patients with degenerative diseases present with neural pathology that is more diffuse than focal. Garrard et al. state that in the majority of cases patients will present with category-specific deficits for living things that are associated with an initial involvement of the transentorhinal cortex and the temporal neocortex. A minority of patients will show deficits for non-living things that is related to damage of bi-parietal regions. The authors incorporate the hypotheses developed in the sensory/functional hypothesis, stating that the double dissociation that occurs between the two groups of patients reflects the storage of perceptual features in the temporal lobes and the storage of functional features in the fronto-parietal regions.

Whatmough et al. (2003) also found an overall deficit for biological things in a group of 72 AD patients. To examine the relationship between the severity of the semantic deficit and the strength of the category effect the authors grouped the patients based on their scores on a picture naming task (the Categorical Picture Naming Task (CPNT) developed by Chertkow, Murtha, Frederickson, and Whitehead, 1999). Those patients that performed at the highest level on the CPNT did not show any category-specific deficit for living things. As the level of semantic impairment increased, however, so did the degree of separation between performance with living things and non-living artefacts, up to a category difference of 20% for those patients who were most severely impaired. In fact, 68 of the 72 AD patients presented with the categorical deficit for living things and only two presented with the opposite pattern of deficits. These results are not consistent with the intercorrelational model proposed by Gonnerman et al. (1997).

The potential for random damage in a unitary semantic system to create category-specific deficits has also been examined by lesioning distributed connectionist models.

Devlin, Gonnerman, Andersen, and Seidenberg (1998) were concerned with how such a model could account for category-specific deficits that occurred as a result of the random, patchy damage that is found in patients with AD. Similar to the model developed by Farah and McClelland (1991) concepts were represented as vectors distributed over perceptual and functional semantic features and living things were represented with a higher proportion of perceptual features than non-living things. These implementations also accounted for those characteristics described by Gonnerman et al. (1997) such as the differential representation of distinctive features between the categories, with living things having more shared features and fewer distinctive features than non-living things. The living things category was also given more strongly correlated features than non-living things as was demonstrated by McRae, de Sa, and Seidenberg (1997).

Similar to the pattern of results reported by Gonnerman et al. (1997) mild nonselective damage to the model caused a category-specific deficit for non-living things because there were fewer correlated features to compensate for the loss than there was for living things. With more severe lesions, however, whole categories of living things were lost resulting in a greater deficit for living things. This model predicts that with mild nonselective damage there will be a deficit for non-living things that will progress to a deficit for living things as damage becomes more extensive. However, the study by Gonnerman et al. (1997) is the only one to report anything that resembles this pattern of deficits in a patient population.

In a more recent investigation of the deficits associated with AD, Zannino, Perri, Carlesimo, Pasqualetti, and Caltagirone (2001) attempted to determine whether a true category-specific deficit exists for this population and whether the pattern of deficit was related to the overall severity of the impairment. This study improved upon previous ones by controlling confounding variables such as frequency, prototypicality, visual complexity, age of acquisition, and name and image agreement. The results showed an overall category-specific deficit for living things similar to those reported in previous studies (Garrard et al., 1998; Guistolisi et al., 1993; & Sliveri et al., 1991) and contrasted with the results reported by Gonnerman et al. (1997). Furthermore, although Gonnerman et al. hypothesized that AD patients may present with deficits for non-living things early in the disease process, Zannino et al. (2001) failed to find a single subject out of a total of fifty-three that presented with this pattern of deficits.

The relationship between disease progression and severity of category-specific deficit was also examined. The results reported differed from all other reports of this relationship. Gonnerman et al. (1997) reportedly found deficits for non-living artefacts early in the disease process followed by a switch to a more severe deficit for living things later in the progression of AD. In contrast, Guistolisi et al. (1993) reported an initial category-specific deficit for living things that later disappeared as performance with non-living artefacts also deteriorated. Zannino et al. (2001) reported that the initial category-specific deficit for living things was mild and actually became more pronounced in the latter stages of the disease.

Tyler et al. (2000) proposed a connectionist model similar to that of Gonnerman et al. (1997) hypothesizing that diffuse damage, as opposed to focal damage, was responsible for category-specific deficits for living things. This theory also allows for the possibility of a unitary semantic system that is not separated into different components for different types of semantic information. Central to this model is the hypothesis that functional features of concepts are of particular importance and are more resilient to brain damage than sensorial features. Furthermore, functional features play a different role in the representations of living and non-living things. For non-living things the function of an item is of utmost importance to the conceptual representation and is clearly associated with the physical form of the item. For instance, the shape of a shovel is strongly connected to its function and it is this function that differentiates it from other items. From this, Tyler et al. (2000) suggest that it is functional information that differentiates one non-living item from another.

Although previous theories have suggested that functional features are relatively limited for living things, Tyler et al. (2000) disagree. They propose that functional information (albeit a different type of functional information) is very important to the representation of living things. This was supported from property generation norms in which subjects listed the features for non-living artefacts and living things. A feature was scored as perceptual if it could be processed by the senses and functional if it indicated how the item interacted with the environment. Using this procedure and the revised definition for functional features subjects actually reported more functional features for living things than for non-living artefacts. This functional information, termed biological function, includes any range of activities including eating, sleeping, moving, flying, running, etc. In the same way that certain functional features of non-living things are associated with certain perceptual features, functional information about living things is connected to sensorial features. Thus, the function of flying is associated with the perceptual features of wings, walking with legs, and seeing with eyes.

It is the connections between functional and perceptual features that are emphasized in this theory. Those perceptual features shared within categories of living things are strongly connected to shared functions. That is, those perceptual features that are common to most members of a category are associated with the function that most members of the category also possess. This is not necessarily true for distinctive perceptual features, which are less likely to be associated with a function. In contrast, non-living artefacts are composed of distinctive perceptual features that are associated with equally distinctive functional features. Those perceptual features that a group of non-living artefacts share are not likely to be associated with a function.

If one assumes that strongly connected features are more resilient to damage than are weakly connected features, these differences in the connections that exist between the features of living and non-living things have implications for the patterns of deficits expected following damage. Because distinctive perceptual features of non-living things are connected to functional features and shared perceptual features of living things are connected to functional features it is these features that will be most resistant to damage. Following non-focal lesions, distinctive features of non-living things will remain, but only those features that are shared among groups of living things will be preserved.

Tyler et al. (2000) created a connectionist model that incorporated the features discussed above to test the following predictions: 1) strongly correlated features will be robust against lesioning because of mutual activation compensating for degraded features, 2) functional information for both living and non-living things will tend to be preserved because it is always associated with perceptual information; 3) functional information for living things should be more robust than for non-living artefacts because the functional features of living things are themselves highly intercorrelated, and 4) the preservation of perceptual features will depend on whether they are intercorrelated with each other and/or functional features. For the reasons discussed above, this should result in preserved distinctive information for non-living artefacts with degraded shared perceptual information and degraded distinctive perceptual information with intact shared perceptual information for living things.

The modeling data from this study supported the predictions. Random lesioning of both perceptual and functional feature connections produced an initial impairment for living things followed by impairment for non-living artefacts with more severe damage. At moderate levels of damage the model predicts difficulty discriminating between living things within a category, but preserved knowledge of shared information. For artefacts, on the other hand, there should be no difficulties distinguishing among items, but knowledge of category membership will be impaired.

Currently, there is little patient data to support the predictions of this model since the discrepancies in performance on tests of distinctive and shared features have not been examined. Since deficits for non-living artefacts and living things are predicted with different degrees of damage, the authors argue that the model is able to account for the double dissociation between living and non-living things. However, none of the studies on AD patients have shown a progression from deficits for living things to deficits for non-living artefacts at later stages of the disease.

To summarize, given the heterogeneity of the findings, the deficits that have been shown to occur in patients with AD could not be said to support or refute any of the current theories regarding category-specific deficits. The only observation that has been reported with some consistency is that some AD patients do present with a category-specific deficit for living things. Presently, the results of testing for category-specific deficits in patients with AD has not allowed for any solid conclusions about the presentation or progression of these deficits, due to the amount of variability in the results. Although this variability is likely an artefact of the nature of the disease itself (and its diagnosis), further research is necessary to clarify those experimental variables that are causing additional variability between different studies. In all studies of category specific deficits in AD, patient categorization based on disease severity and neuropsychological profiles may be helpful in determining the relationship between neuropathology and category specific deficits.

The Hierarchical Interactive Theory (HIT)

The HIT model is perhaps the most comprehensive conceptualization of object recognition and category-specific deficits for living and non-living artefacts. The model was developed from the cascade model and the concept of visually crowded categories as proposed by Humphreys and Riddoch (1987). The theory of visually crowded categories suggests that because living things such as mammals and fruits have such a high degree of visual similarity within categories that any impairment in visual processing is going to affect living things more than non-living things. Visual crowding occurs when the features extracted from an item are no longer sufficient to differentiate it from another similar item.

This phenomenon may only occur when the stimulus set being learned exceeds some critical number (Gale, Done, & Frank, 2001). This is observed in the living world with certain biological categories (birds, fish, plants, flowers) for which expertise is required to distinguish between members of a super-ordinate category. Even when discriminating within categories for which expertise is not necessarily required (mammals), the members are much more similar than categories of non-living artefacts. When brain damage occurs category-specific deficits may emerge for visually crowded categories as a result of some restriction on the number of features available for each item (Gale et al., 2001). Although this explanation can account for specific deficits for living things with preserved visual recognition of non-living artefacts it offers no explanation for the reverse pattern of deficits.

The theory involving visually crowded categories received support from a study by Gaffan and Heywood (1993) who trained monkeys to discriminate between pairs of pictures from the Snodgrass and Vanderwart (1980) set. Error rates during training were three times higher when the monkeys were discriminating living things relative to non-living things. A similar pattern of performance was found with human participants as well. The authors argued that the concept of visually crowded categories offered the best explanation for their results.

Humphrys, Riddoch, and Quinlan (1988) elaborated on the concept of visually crowded categories in their "Cascade model" of object recognition and category specific deficits for living things. In this model object recognition occurs over three distinct stages; recognition of the object's structure, access to semantic information related to the object, and access to the object's name. Information regarding the object's structure is hypothesized to be separate from information regarding the object's use and its association to other objects (semantic information), and from the object's name. Semantic information refers to all other forms of non-perceptual knowledge. Selective damage can occur at any of the three stages such that a patient could have deficits for the semantic information regarding an object, but have intact structural knowledge.

The key to the cascade model is that activation can proceed to another stage before processing at the previous stage is complete. For "visually crowded" items activation of similar perceptual features across the category will result in semantic information regarding the category of an object to be derived quickly. The gains from this quick access are cancelled by slowed access to knowledge regarding the individual item due to increased competition within the category. The opposite pattern is assumed for structurally dissimilar objects, which will be relatively delayed on category decisions, but individual item identification will occur relatively quickly because of reduced perceptual competition among category members. Consistent with this prediction Humphreys et al. (1988) found that normal participants named living items more slowly than non-living artefacts. Furthermore, category decisions have been shown to be faster for living items than for non-living items (Humphreys & Forde, 2001).

Humphreys and Forde (2001) expanded on the Cascade model in the Hierarchical Interactive Theory (HIT) in which object naming requires the transmission of information through a series of interactive hierarchical stages. Thus, in addition to the hierarchical, three-stage process described in the Cascade Model, in the HIT a re-interrogation of structural knowledge is proposed. Object processing occurs as a "first pass" through the stored structural descriptions stage and then onto partial activation of an associative/functional (semantic) knowledge stage. However, individual identification of living things requires further interrogation of perceptual knowledge to allow the target to be differentiated from its closest neighbours. For example, processing of an apple would proceed from initial visual processing to access the semantic representation of fruit along with the word "fruit". This semantic information would then be fed back into the visual description system to distinguish among members of the category "fruit". Thus, for living items this means further processing of form via connections from the semantic system back to the visual system.

Patients with deficits for living items are hypothesized to have mild deficits in perceptual knowledge which prevents successful re-entrant activation from semantic memory. For non-living artefacts, interrogation of action-related information is necessary and patients with deficits for these items may have subtle deficits in action-related information.

Humphreys and Forde (2001) distinguish between two types of patients with category specific deficits for living things. One group of patients has difficulties performing object decisions for the affected category as described by Caramazza and Shelton (1998). This group is hypothesized to have deficits affecting their ability to access information for living things at the structural description level in addition to any deficits occurring at a latter stage in processing. A second group, however, has been shown to have intact object decision abilities for the affected category (Laiacona et al., 1997). Humphreys and Forde suggest that these patients do not have a deficit for the structural knowledge of the objects and that their deficit occurs at a later processing stage.

The HIT model is able to accommodate most, if not all, varieties of category-specific deficits observed clinically and the experimental findings associated with each. This includes all of those findings that support the sensory/functional hypothesis because a similar distinction is made between the importance of sensory and functional features in different categories of items. The advantage that the HIT account holds over the sensory/functional hypothesis is that the findings of Caramazza and Shelton (1998) involving poor object decision abilities for living things with intact object decision for non-living things can be explained. In the HIT model difficulties performing object decision tests specific to living things is predicted because such items are visually crowded and require re-entrant activation to distinguish among them.

Neuroanatomy of Category Specific Deficits

Each of the models discussed above makes a prediction as to what neuro-anatomical structures will be associated with a category-specific deficit. The sensory/functional hypothesis as proposed by Warrington and Shallice (1984) states that visual attributes are very important in constructing the semantic representation for living things suggesting that damage to those structures responsible for storing and processing visual features should be associated with this deficit. A similar prediction is made in the HIT account (Humphreys & Forde, 2001). Furthermore, deficits for non-living things should be associated with damage to those areas responsible for processing "functional" information.

Contrary to this prediction, those theories that emphasize the importance of the intercorrelations among semantic features hypothesize that it is not necessarily the location of the damage that accounts for these deficits, but the extent and severity of brain damage that will predict a category-specific deficit for living things (Gonnerman et al., 1997; Moss, Tyler, Durrant-Peatfield, & Bunn, 1998).

Finally, the predictions of the categorical hypothesis are based on the idea that separate semantic stores for animals, plants, and artefacts have developed through evolution. Because escape and feeding responses are associated with emotional reactivity it is hypothesized that limbic structures are responsible for representing the semantic features for plants and animals. Also, damage to the structures associated with these representations will result in deficits for all types of information related to these categories as opposed to deficits for just visual or functional features.

Gainotti (2000) performed a meta-analysis of the studies reporting on patients with category-specific deficits and the neuro-anatomical location of damage. The majority of the patients presenting with a semantic deficit for living things suffered from HSE, head trauma, and semantic dementia, which tended to result in bilateral damage to the anterior portions of the temporal lobes. This was contrasted by those patients that presented with just a lexical deficiency for living things which was usually caused by a stroke resulting in damage to the infero-mesial portions of the temporal and occipital lobes in only the left hemisphere. Although semantic deficits for living things were usually associated with bilateral damage, left hemisphere involvement was predominant in the majority of cases.

Closer inspection of the deficit for living things revealed some general differences in the neuro-anatomical damage associated with deficits for plants and those found with deficits for animals. Etiologically, diseases that tended to produce more focal damage also resulted in more focal deficits. Stroke tended to be the cause of category-specific deficits for plants, while HSE was equally represented in patients with deficits for plants, plants and animals, and animals. Semantic dementia, on the other hand, only resulted in deficits for both plants and animals. Also of interest is the finding that bi-temporal damage was reported in the majority of patients with deficits for both plants and animals, in half of the patients with deficits for animals, and in only a quarter of patients that had deficits for just plants.

Gainotti (2000) further examined twenty studies that reported a more fine-grained analysis of the structures involved in patients with category-specific deficits. The areas examined in the studies included the hippocampus (H), the parahippocampal gyrus (PHG), the temporal pole (TP), the inferior temporal lobe (IT), the antero-lateral temporal areas (AL), the postero-lateral temporal cortices (PL), and the medial temporo-occipital areas (TO). The results appeared to confirm that the usual neuro-anatomical correlate of category-specific semantic impairments for living things is bi-lateral temporal lobe lesions with a preference for the left temporal lobe. More specifically, damage was found to occur in the anterior portions of the temporal lobes including TP, H, PHG, IT, and AL, while the PL portions were spared. All patients showed damage to the inferior temporal lobe (IT), although the extension and symmetry of the damage was found to vary.

As expected, patients with deficits for non-living things tended to show a different pattern of neuro-anatomical damage than those patients with deficits for living things. Semantic deficits for non-living things were associated with damage to the left fronto-temporo-parietal area and were always accompanied by Broca's, Wernicke's, or global aphasia.

Broadly speaking, this neuroanatomical dissociation between deficits for living versus non-living things appears to reflect the separation between the ventral and dorsal pathways. This division is based on experiments showing that lesions of the parietal cortex in monkeys resulted in deficits in localizing an object with respect to a particular landmark, but not in the identification of the object. In contrast, lesions of the inferior temporal cortex resulted in an inability to recognize objects, but did not affect their ability to process the location of objects (Bullier, 2002). The observation of a similar dissociation in patient's with known lesions led to the distinction between the "what" pathway referring to the ventral stream and the inferior temporal cortex and the "where" pathway referring to the dorsal stream and the parietal cortex (Bullier, 2002). Currently, theories regarding the function of the dorsal pathway have been refined, suggesting that it is involved in visuomotor action networks, not only processing "where" an item is, but also "how" it might be used (Devlin et al., 2002).

Despite damage to these broad pathways and general areas being associated with different types of semantic impairment there is considerable variability in the effects of damage to specific areas. Based on the demonstrations of variability in the neuro-anatomical structures involved, Gainotti (2000) argued that the search for a structure that is critically involved in the representation of living things may not be fruitful. The results did, however, implicate some regions that are important for the processing of living things which he interpreted as supportive of the hypothesis that deficits for living things result from damage to visual knowledge and deficits for non-living things occur because of damage to functional knowledge.

Specifically, the network including the infero-temporal cortex, the mesial temporo-limbic structures, and the temporal pole appear to be involved in the representations of living things and have been found to be associated with sensory information. The inferior temporal lobe has been shown to receive projections from area V4 and is part of the extra-striate visual processing system which is believed to play a role in object recognition (Goodale, Milner, Jacobson, & Carey, 1991). The entorhinal cortex has been shown to receive integrated input from all of the sensory modalities receiving projections from unimodal association areas as well as polymodal association areas (Jones & Powell, 1970). Finally, Damasio (1990) has hypothesized that the temporal pole is a higher order convergence zone acting to bind together different components of an items representation. Thus, the above structures can be conceived of as components of a system that is involved in processing, storing, and retrieving sensory information.

In sum, the results of the meta-analysis performed by Gainotti (2000) have important implications for the theoretical basis of category-specific deficits. The sensory/functional hypothesis and the HIT are consistent with the results of this study which showed that deficits for living things are in fact associated with focal damage to areas of the brain believed to be involved in the storage and retrieval of sensory information. The results of cognitive testing were also consistent with this hypothesis showing that those categories that were more dependent on sensory features tended to pattern with living things, while categories that relied more on functional features did not. For instance, food and musical instruments tended to be deficient in those patients with specific deficits for living things, whereas knowledge for body parts was still intact along with all artefacts.

The categorical hypothesis,with its separate semantic categories for animals, plants, and artefacts, has difficulty explaining this pattern of deficits. The neuro-anatomical results are also problematic for the intercorrelations hypothesis. This theory states that the dissociation between living and non-living things is dependent more on the severity of damage to the semantic system than on the location of focal lesions. Thus, because living things have a greater number of intercorrelations among features they should be spared with limited diffuse damage to the semantic system, but show a dramatic decline with more severe brain damage. These data did not support this hypothesis.

Research with Non-Patient Populations

Gerlach and colleagues have performed a series of experiments using neuro-imaging techniques to examine what regions of the brain are activated during different types of object identification tasks in normals. For instance, Gerlach, Law, Gade, and Paulson (1999) examined the neural correlates of object recognition and whether these regions differed for living objects versus non-living artefacts. On an object decision task the authors reported peak activations in the fusiform gyri, the parahippocampal gyri, the limbic lobes, the right occipital gyrus, the right superior parietal lobe, the right inferior frontal gyrus, the left middle occipital gyrus, and the left inferior temporal gyrus for both living objects and non-living artefacts. Thus, compared to performance on a simple pattern discrimination task the object decision tasks activated more ventral and posterior parts of the brain. This is consistent with the hypothesis that the ventral stream is important for object identification.

The object decision tasks did not activate left dorsolateral prefrontal areas, which are generally associated with verbal/semantic knowledge suggesting that object decision tasks can be performed by accessing visual knowledge only. This type of task may be very useful when examining visual processing in isolation from semantics. As task difficulty increased larger parts of the right inferior temporal and anterior fusiform gyri were recruited for living objects compared to non-living artefacts. The authors suggest that this may support the idea that greater perceptual differentiation is required for living objects.

Similar results were reported by Whatmough, Chertkow, Murtha, and Hanratty (2002) and Moore and Price (1999). Whatmough et al. reported that naming of animals compared with the naming of tools was associated with increased regional Cerebral Blood Flow (rCBF) in the fusiform and inferior temporal gyri bilaterally. Moore and Price found that naming of living objects compared to naming of non-living artefacts resulted in increased rCBF in the posterior portion of the right middle temporal gyrus and the anterior temporal lobes. All of the above findings are consistent with the hypothesis that living objects are more visually similar.

Based on the above results obtained from tests on normal participants it appears as though some forms of category-specific deficits for living objects could result from damage to the visual processing system. This could be viewed as support for the visual crowding hypothesis (Humphreys & Riddoch, 1987) and the sensory/functional hypothesis (Warrington & McCarthy, 1987). However, the differences between living objects and non-living artefacts must extend beyond this visual processing differentiation because this alone cannot explain the presence of deficits for non-living artefacts in the absence of deficits for living objects.

A number of studies have implicated the left ventral premotor cortex (PMv) as playing a greater role in the processing of non-living artefacts than living objects (Chao & Martin, 2000; Gerlach et al., 2000). This area is believed to be the human homologue of the monkey F5 area which has been found to be involved in motor planning tasks such as grasping, holding, and manipulating objects (Binkofski et al., 1999). Furthermore, Gainotti, Silveri, Daniele, and Guistolisi (1995) observed that patients with category-specific deficits for non-living artefacts often have lesions in the area of the PMv. Based on these findings Chao and Martin (2000) have suggested that the comprehension of non-living artefacts may be dependent on motor-based knowledge of object utilization. Devlin et al. (2002) have since hypothesized that the left PMv along with the left posterior parietal lobe and the left posterior middle temporal region are an important part of the dorsal stream forming a visuomotor action network.

Gerlach et al. (2002) attempted to further illuminate the exact role that action knowledge may play in the comprehension of non-living artefacts. It does not appear as though deficient action knowledge as a whole can explain non-living artefact comprehension deficits since it has been shown that patients with apraxia resulting from left fronto-parietal lesions do not necessarily present with comprehension deficits. This has been illustrated in studies documenting patients that have preserved knowledge for the function of objects that they cannot utilize, or vice versa (Buxbaum, Schwartz, & Carew, 1997). This led Buxbaum et al. (1997) to distinguish between "what for" knowledge and "how" knowledge, neither of which is necessarily contingent on the other. Gerlach et. al (2002) have suggested that the left PMv may act as an interface between "what for" knowledge and "how" knowledge, damage to which would result in high-level praxis disorders such as ideational apraxia and conceptual apraxia (e.g. using a toothbrush like a comb).

Gerlach et. al (2002) reported on a PET study that they interpreted as supporting this hypothesis. The authors demonstrated that the left PMv was activated for non-living artefacts compared to living objects in a categorization task, but not in a comparison between naming of the same non-living artefacts and living objects. They suggest that the left PMv was activated during the categorization task and not the naming task because action knowledge is composed of information regarding the distinctive actions of objects and the act of categorization is based on an analysis of action equivalence.

This explains why the PMv is activated in the categorization but not the naming of non-living objects. However, an explanation of why the PMv is activated for non-living objects and not living objects is still required. This relates to the original sensory/functional hypothesis as proposed by Warrington and McCarthy (1983) which states that living objects are defined more by their sensory features and non-living objects are represented more by their functional (or in this case, motoric) features. Because non-living objects are more often manipulable they will be more likely to be partly defined by motoric features (i.e. how they are manipulated), resulting in activation of the left PMv during categorization tasks.

Gerlach, Law, and Paulson (2002) tested this latter hypothesis by examining differential left PMv activation between manipulable and non-manipulable objects. They found that the left PMv was activated during categorization of both fruits/vegetables and articles of clothing compared to categorization of animals and non-manipulable non-living objects. This supports the hypothesis that action knowledge is not necessarily required for the processing of non-living artefacts, but rather for the processing of manipulable objects. Left PMv activation is observed more during the categorization of non-living objects than living objects because non-living objects tend to be more manipulable.

All of the above evidence strongly implicates that the left PMv is activated during the categorization of non-living artefacts. However, this alone is not evidence that left PMv activation is necessary to successfully categorize non-living objects. Whether the PMv is necessary for comprehension is extremely important. If it is not necessary for the comprehension of non-living artefacts then activation of this area during a categorization task tells us very little about the presence of category-specific deficits or the organization of semantic information in the brain. It is entirely possible that the left PMv is activated simply as a result of a motor priming effect. As an attempt at controlling for this possibility Gerlach et. al (2002) had participants perform object decision tasks on the same fruit/vegetables and articles of clothing that were used in the categorization task. Only those areas that showed greater activation in the categorization task than in the object decision task were included in further analysis. Further research is necessary, however, to adequately control for the possibility of a motor priming effect.

Hope and Buchanan found results supporting the hypothesized role of the PMv in processing non-living things in an unpublished study in which normal participants were required to categorize a series of line drawings as living or non-living. The categorization task was done with and without a distraction task. The distraction task involved transferring marbles one at time from one bucket to another with the right hand in attempt to engage the left PMv. The distraction task increased reactions times significantly more for non-living artefacts than for living things.

The results of the neuroanatomical studies of category specific deficits for living and non-living things provide clear evidence for the importance of different structures for the processing of each category (Table 1). All of the studies reported in this review implicate the inferior, anterior, and mesial portions of the temporal lobe for the processing of living things and the left fronto-tempo-parietal area for the processing of non-living artefacts. These findings are most consistent with the sensory/functional hypothesis and the HIT.

Table 1: Depicts the neuroanatomical regions that are implicated for processing of living things and non-living things, as well as the studies reporting the findings.

Neuroanatomical location activated or injured	Study	Living	Non-Living	Theory Supported
Inferior Temporal Lobe, Fusiform Gyrus, and/or Anterior Temporal Lobe	Gainotti (2000)	X		HIT, Sensory/Functional
	Gerlach et al. (1999)	X		HIT, Sensory/Functional
	Whatmough et al. (2002)	X		HIT, Sensory/Functional
	Moore et al. (1999)	X		HIT, Sensory/Functional
Left Fronto-Temporo-Parietal Area/ PMv	Gainotti (2000)		X	HIT, Sensory/Functional
	Chao et al. (2000)		X	HIT, Sensory/Functional
	Gerlach et al. (2000)		X	HIT, Sensory/Functional
	Gainotti et al. (1995)		X	HIT, Sensory/Functional
	Gerlach et al. (2002)		X	HIT, Sensory/Functional

Summary of Theories of Semantic Category Deficits

The dissociation that has been found to occur between knowledge for living and knowledge for non-living things has generated a vast amount of research aimed at describing the organization of a semantic system that could accommodate such a pattern of deficits.

In the sensory/functional hypothesis the dissociation between living and non-living things occurs because the knowledge within these categories has differential weightings of sensory and functional features. It was initially hypothesized by Warrington and McCarthy (1984) and later supported by Farah and McClelleand (1991) that knowledge for living things is composed of a greater number of visual/sensory features than non-living things which are more reliant on functional information. Thus, damage to those parts of semantic memory responsible for sensory features will result in a deficit for living things, whereas damage to functional areas will result in a deficit for non-living things.

This theory was initially developed because of the finding that the living/non-living dissociation is not pure; that is, gem stones, musical instruments, and food tend to pattern with living things and body parts tend to pattern with non-living things, presumably because of the weighting of sensory and functional features of these items (Warrington & McCarthy, 1984; Warrington & Shallice, 1987). This hypothesis has received the most attention in the literature and arguably the most support. Neuro-anatomical data show that those areas believed to be responsible for the processing of sensory information are damaged in patients with categorical deficits for living things. Similarly, those areas believed to be responsible for the processing of motor/functional information have been found to be injured in patients with deficits for non-living things (Gainotti, 2000). The most damaging finding for the sensory/functional hypothesis is that patients with deficits for living things do not always present with deficient sensory knowledge of living and non-living things (Caramazza & Shelton, 1998).

Caramazza and colleagues have been the strongest advocates for a truly categorical organization of semantic memory. They hypothesize that semantic knowledge for living things and non-living things dissociates because each has a separate representation within the brain. More specifically, separate neurological structures have developed through the process of natural selection for knowledge about animals because they are either potential predators or a potential food source, and for knowledge about plants as another food source and for medicinal purposes. Later, a separate store for knowledge about non-living artefacts developed as tool usage became of increased importance.

This hypothesis is generally supported by the double dissociation between living and non-living things and the finding that plants and animals often dissociate as well (Caramazza & Shelton, 1998; Farah & Wallace, 1992; Forde et al., 1997). There are few other testable predictions for the categorical hypothesis and support is usually generated by reporting results that contradict the predictions of other hypotheses, particularly the sensory/functional hypothesis.

In the intercorrelations hypothesis the dissociation occurs because of a greater number of intercorrelated features for living things than for non-living things. Because of this, any minor damage to the semantic system will result in a deficit for non-living things because the large number of intercorrelations for living things is protective when the damage is minimal. As the damage progresses whole categories of biological items are lost, resulting in a category-specific deficit for living things.

In this theory category-specific deficits result from diffuse damage as opposed to more focal lesions. However, there has been very little empirical support for this theory. Although Gonnerman et al. (1997) reported that a group of AD patients presented with deficits for non-living things at early stages of the disease and deficits for living things as impairment progressed, a number of other studies have shown a pattern of impairment that does not fit with this model (Garrard et al., 1998; Silveri et al., 1991, Guistolisi et al., 1993; Whatmough et al., 2003; Zannino et al., 2001). Furthermore, the neuro-anatomical data do not fit with the predictions of the intercorrelational hypothesis which states that more extensive damage should result in a larger deficit for living things, while less severe damage should result in impairment for non-living things. Gainotti (2000) found no relationship between the severity of damage and the pattern of category-specific semantic deficit.

In the HIT proposed by Humphreys and Forde (2001) the dissociation between sensory and functional features of objects is included as well as an elaboration on the process of object identification. In the HIT account object recognition proceeds through three distinct stages including recognition of the objects structure, access to semantic information, and access to the name of the object. Processing can proceed through these stages in “cascade” meaning that processing can advance to another stage before processing at a prior stage is complete. This is the essence of the cascade model in which processing from a later stage can affect processing at an earlier stage through a feedback mechanism. Deficits can result from damage to any of the three stages.

The HIT is better able to accommodate that pattern of deficits that have been observed clinically than all other theories of category specific deficits. Unlike the sensory/functional hypothesis, the fact that patients with deficits for living things have difficulties processing the visual attributes of living things but not of non-living things is accounted for. Humphreys and Forde (2001) state that the individual identification of living things is more difficult than for non-living things because of greater visual crowding. Therefore, in a damaged visual recognition system living things may be unidentifiable even though the visual processing of non-living things is intact.

In sum, the most widely researched and referenced theory appears to be the sensory/functional hypothesis which has also been supported by neuro-anatomical investigations. However, the application of this theory cannot account for all findings reported in the literature, indicating that the sensory/functional hypothesis may represent a simplification of the actual process that results in category-specific deficits. In the HIT account Humphreys and Forde (2001) build upon the distinction between sensory and functional features. By doing so they are better able to accommodate all of the available research findings. This includes the finding that some patients are able to perform object decision tasks for non-living things but not for living things. The HIT explanation for this dissociation is that individual identification of living things is more difficult because of visual crowding. The research reported in this dissertation examines a possible mechanism by which visual crowding affects object recognition.

Visual Object Recognition

In the proposed model of semantic category deficits for living things visual information is viewed as having particular relevance. Subcategories within the category of living things (as well as the category of musical instruments, foods, and large non-living objects) are visually crowded (they have a high degree of visual similarity between items within the category) and thus require a more holistic level of processing to distinguish among members within the subcategories. The processing of these items is hypothesized to be similar to that required for facial recognition and expert object recognition. This necessitates a brief discussion of the process of visual object recognition.

Tarr and Vuong (2002) categorized various theories of object recognition into two primary approaches: structural description and image-based theories. The structural description theories are based on the premise that objects are learned by decomposing them into a collection of three-dimensional parts and then are remembered by the basic configurations of those parts. Recognition occurs by recovering the three-dimensional parts from an image and comparing the basic configuration of the parts to those stored in object memory.

Biederman (1987) proposed a structural description theory called the recognition-by-components (RBC) theory of human image understanding. According to RBC theory, all objects are perceived by combining approximately 36 volumetric primitives called geons. These geons are perceived on the basis of highly stable non-accidental image properties. The term "non-accidental properties" refers to visual images that are unlikely to have occurred purely by chance. An example of a non-accidental property is three edges meeting at a single point as in an "arrow junction" or a "Y junction". Such a visual property is much more likely to represent the inside or outside edge of a rectangular object than to have occurred simply by the chance meeting of random disconnected lines.

Perception of objects occurs as the non-accidental primitives are translated into geons which are then combined into a complete configuration referred to as a geon-structural description. The spatial relationships between geons are hypothesized to be qualitative as opposed to quantitative. This is to satisfy the requirement that identification of any particular object can occur from multiple views. To identify an object from a collection of geons from multiple views, the relationships of the geons within a specific object must be flexible. Thus, the relative positions of the geons within an object are known, but the spatial relationships between those goens are not quantified. Such a method of object recognition would have difficulty accounting for expert object recognition (or the discrimination between the items within living categories), which is hypothesized to rely on differences in the relationships among features.

In contrast to the structural description models which state that an object is recognized in the same way from any view, proponents of image-based models hypothesize that object recognition is actually viewpoint dependent (Tarr and Vuong, 2002). This means that instead of geons that are detected invariably from any view objects are represented as a collection of views with each view representing the features of the object under different viewing conditions (Tarr & Vuong, 2002). Tarr, Williams, Hayward, and Gauthier (1998) argue that viewpoint dependency requires that as the input image of the object deviates from the image created when the object was learned, there are resultant decreases in recognition accuracy and speed, proportional to the amount of deviation. The authors were able to show that as images of geons were rotated from 0°, to 45°, to 90° participant's reaction times on a matching task were increased, supporting the hypothesis of the image-based model.

Tarr and Bulthoff (1998) propose a model of feature relationships that they describe as somewhere between completely disordered feature representations and rigid templates. In this model an object is represented by a local description of the positional certainty between various features. The relative positions of the features are probabilistic, meaning that variation within an image is tolerated, but recognition performance will degrade smoothly as the relative positions of the features deviate further from those in the originally learned image. The relationships between the features are organized hierarchically into multiple levels of increasing complexity. Thus, the relationship between highly associated features at the first level could then be related to other highly associated features at a second level.

It is difficult for image-based models to accommodate the recognition of exemplars of a given class or the act of classification within a category, which seems to require a great deal more flexibility in feature representation and feature relation (Hummel, 1998). What Tarr and Bultoff (1998) propose is that both image-based and structural description approaches to object recognition may be used by humans. Which method is used is dependent on the task characteristics. They suggest that a structural description may be used when discrimination between shapes only requires a simple ordering of the object features. An image-based description is more likely to be used when the relationships between the features are important for discrimination. Such relationships are likely necessary for facial recognition, expert object recognition, and as suggested in the present paper, the identification of certain living things.

Category Specific Deficits as a Type of Visual Agnosia

This dissertation tests an explanation of the semantic category specific deficit for living items that is based on the hypothesis that category specific deficits for living things occur because of a specific type of visual agnosia rather than a semantic memory deficit as is hypothesized in the majority of accounts of category specific deficits (Caramazza & Shelton, 1998; Gonnerman et al., 1997; Humphreys & Forde, 2001; Tyler et al., 2002; Warrington & Shallice, 1984).

Humphreys and Riddoch (1987a) described certain agnosic patients (referred to as integrative visual agnosics) who appear to be unable to integrate the features of objects. When the relationships are disrupted or are no longer quantifiable, objects that are dependent on these relationships can no longer be recognized. However, such patients are able to respond to verbal questions about such objects accurately. Humphreys and Riddoch (1987a) differentiated this type of agnosia from semantic agnosia and what is often referred to as associative agnosia. In their model of visual recognition integrative agnosia represents a disturbance of perception, whereas semantic agnosia occurs because of damage to the stored representations of objects. The dissociation between living and non-living things is hypothesized to occur in patients with semantic agnosia.

Humphreys and Riddoch (1987b) proposed that category specific deficits for living things can occur because living things tend to be more visually crowded than non-living things. Therefore, more detailed visual processing is required to access the stored representations of living things. What is proposed in the present paper is that some instances of category specific deficits for living things represent a type of semantic agnosia that is category specific because of visual crowding. The explanation for such an agnosia incorporates elements from the explanation offered for integrative visual agnosia.

The visual processing of living things is hypothesized to partially involve an analysis of the spatial relationships between the features of the items. The stored representations of such items are dependent on the quantification of these relationships. Therefore, an impaired ability to quantify spatial relationship knowledge will lead to impaired ability to access stored structural descriptions of living things. The focus is taken away from the visual features in semantic memory (as in the sensory/functional hypothesis of Warrington & Shallice, 1984) and is applied to the spatial relationships between those features in visual perception.

Viewing visual information as a single entity in perception is too simplistic. Visual information must be further subdivided into elements such as colour, movement, shape, line orientation, etc. The importance of this has not been lost on previous theories of semantic memory and has been incorporated into the sensory/functional hypothesis (Warrington & McCarthy, 1987). What has been largely ignored in the literature on category specific deficits, however, is the nature of the relationships between whole features during normal object recognition.

I hypothesize that perception of living and non-living artefacts differs with respect to the amount of configural processing that is required for members of each category. Living objects are identified more by holistic processing (an integration of all available features into a configural representation), whereas non-living artefacts can be more readily identified by single feature recognition. This configural representation of living things is represented in an image-based format (Tarr and Vuong, 2002) such that the spatial relationships between features are quantified. For example, to recognize an item as a dog you not only need to perceive that it has four legs, ears, fur, a tail, and a torso, but you have to quantify the relationships among those features in order to differentiate it from other similar items (i.e. a cat or a donkey). However, recognition of a shirt can be done simply by recognizing the presence of sleeves.

The integrative requirement of many living objects comes from the fact that these items tend to have more visual overlap than other non-living items, which is the basis of the visual crowding hypothesis (Humphreys & Riddoch, 1987b). Based on this, one would predict that an individual with a deficit for living things would not have difficulties identifying the super-ordinate category of "animal" because an integration of all visual features is not required. This has been repeatedly found (Riddoch & Humphreys, 2004). If a patient can identify a leg, then it must be an animal. This is also supported by studies of normal populations which show that subjects have greater difficulty naming living objects under time constraints, but show better performance naming super-ordinate categories under time constraints or degraded viewing conditions (Humphreys et al., 1998; Moore & Price, 1999).

Patients with deficits that are labelled as being specific to living objects have a tendency to have deficient knowledge for other specific non-living artefacts as well. For instance, numerous studies have reported on patients with a "living things" deficit that also have deficits for musical instruments, food, large non-living objects, and faces (Gainotti, 2000; Saumier, Arguin, & Lassonde, 2001; Warrington & McCarthy, 1983; 1987; 1994; Warrington & Shallice, 1984). What all of these categories appear to have in common is that the members are visually crowded. Therefore, to distinguish between those members one must rely on the relationships among the various features.

The super-ordinate category of musical instruments has many sub-categories with very visually similar items (i.e. members of the brass, woodwind, and reed instruments). The same can be said for food items (i.e. different cuts and types of meat and different vegetables) and for large man-made objects (i.e. different types of buildings, automobiles, and furniture). Thus, an inability to quantify the relationships between visual features would be expected to result in deficits for living items, foods, musical instruments, faces, and large man-made objects, as well as any other items that require a high degree of visual feature integration to distinguish between members of that category.

Non-living artefacts such as clothing, on the other hand, would seem to require less integration of visual elements to distinguish between members. Although a sweater is visually similar to other articles of clothing with sleeves and a hole for the head, such items are fairly limited (except for a clothing "expert"). A sweater is quite distinct from most articles of clothing, such as pants or a hat. Therefore, identification does not require a detailed analysis of the relationships between its features. Articles of clothing can instead be recognized from a single visual element such as the presence of a sleeve.

The following experiments were focussed on testing the hypothesis that animals are distinguished from one another based on the relationships among features (configural processing) because of increased visual crowding. Participant's reaction times (RT)'s on identification tasks were analyzed in response to images in which the relationships among features were disrupted by picture inversion. Picture inversion has been used extensively in the study of prosopagnosia as an indicator of configural processing (see discussion).

Comparisons were made between response time increases from inversion between animals and clothing.

EXPERIMENT 1

Participants were asked to quickly and accurately indicate whether a picture matched a printed word that preceded it. Half of the pictures were animal items and half were clothing items. Each participant responded to each picture once in an upright position and once in an inverted position. The pictures were presented in random order with “Direct RT” software.

The category of animals was selected because of the high degree of visual overlap between members of this category (Humphreys et al., 1988). Clothing items were used because this category is often differentiated from animals on clinical testing, they are less visually crowded, and they have a canonical orientation. The proposed model gives rise to the prediction of a main effect of inversion because of a combination of the disruption to feature identification and the disruption of the relationships between features. Further, this effect should interact with Category reflecting the fact that response times to the inverted animals would be increased to a greater extent than would response times to inverted clothing. This is based on the hypothesis that living items are identified by the relationships among features, whereas non-living objects can be identified by single features.

Method

Participants

Participants were 30 right-handed undergraduate students from the University of Windsor, ranging in age from 18 to 40 who volunteered for the study for course credit.

Materials and Procedure

Participants were asked to indicate whether a line drawing represented the same object as a word that immediately preceded it. The participants were then instructed that they were going to perform several practice trials before beginning the test trials. Thirty practice trials were conducted in which the participants were instructed to indicate whether the line drawing matched the word that preceded by pressing “1” for match and “2” for non-match on a standard computer keyboard. They were told that the pictures may be inverted or upright and to respond as quickly and as accurately as possible.

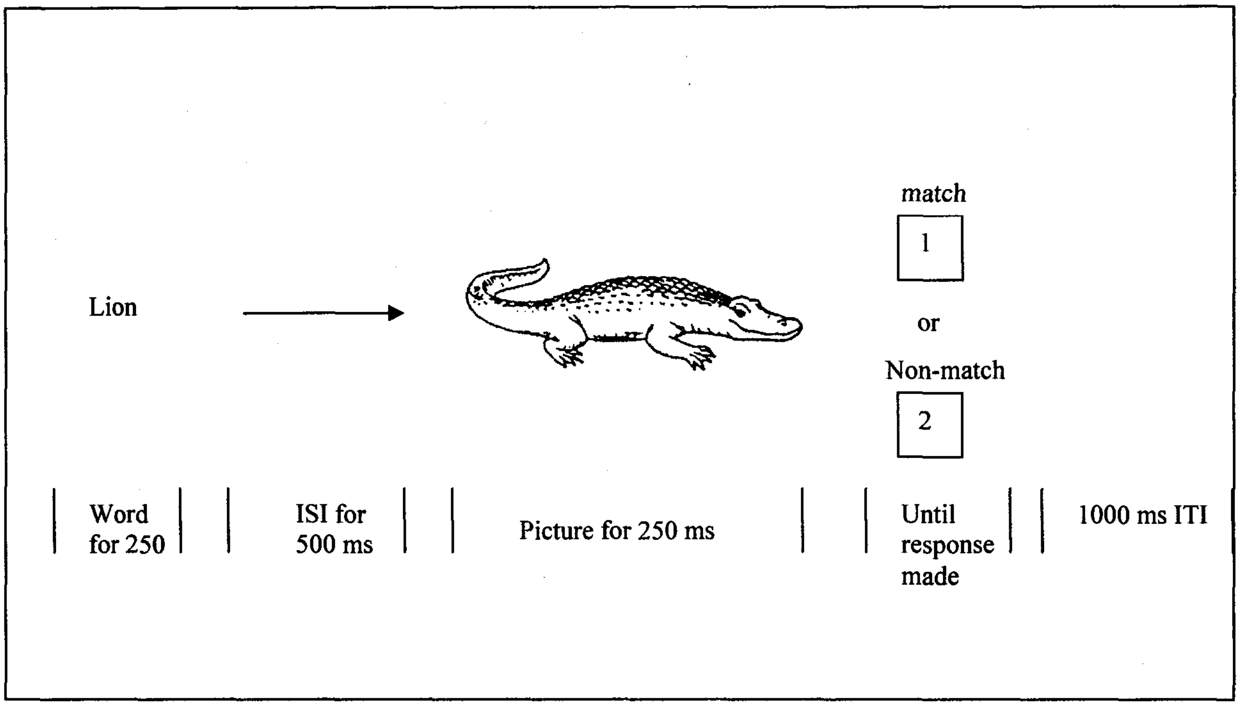
Following the practice trials the participants began the test trials. Each participant responded to 72 picture-word pairs, 36 of which represented animals and 36 of which represented items of clothing. They were given the same instructions as during the practice trials.

There were 18 pictures of animals and 18 pictures of items of clothing. Each picture was presented once in the upright position and once in the inverted position. All of the pictures were presented in random order. Half of the 18 animals and the 18 articles of clothing were paired with a matching word and the other half of the pictures were paired with non-matching words. Half of the participants responded to one half of the 18 items as non-matching and the other half of the participants responded to the other half of the items as non-matching.

All of the non-matching words were taken from the same category as the picture that followed them. For example, for both the practice and experimental trials the words were presented on the screen for 250 ms, were followed by a 500 ms interstimulus interval (ISI), which was followed by the picture for 250ms. The screen remained blank until a response was made. Each response was followed by a 1000 ms intertrial interval (ITI). The general procedure of a single trial is illustrated in Figure 1. The line drawings were taken from Snodgrass and Vanderwart (1983). The drawings were presented on a PC monitor with a black background, approximately 60 cm in front of the participants.

The pictures were presented and the RT's recorded with "Direct RT" software.

Figure 1: Illustrates the task sequence and the duration of each part of the sequence. The word is first presented for 250 ms, followed by an ISI of 500 ms during which time the screen is blank, followed by the picture for 250 ms, immediately followed by the response phase, during which time the screen remained blank until a response was made. Each trial was separated by a 1000 ms ITI during which time the screen remained blank.

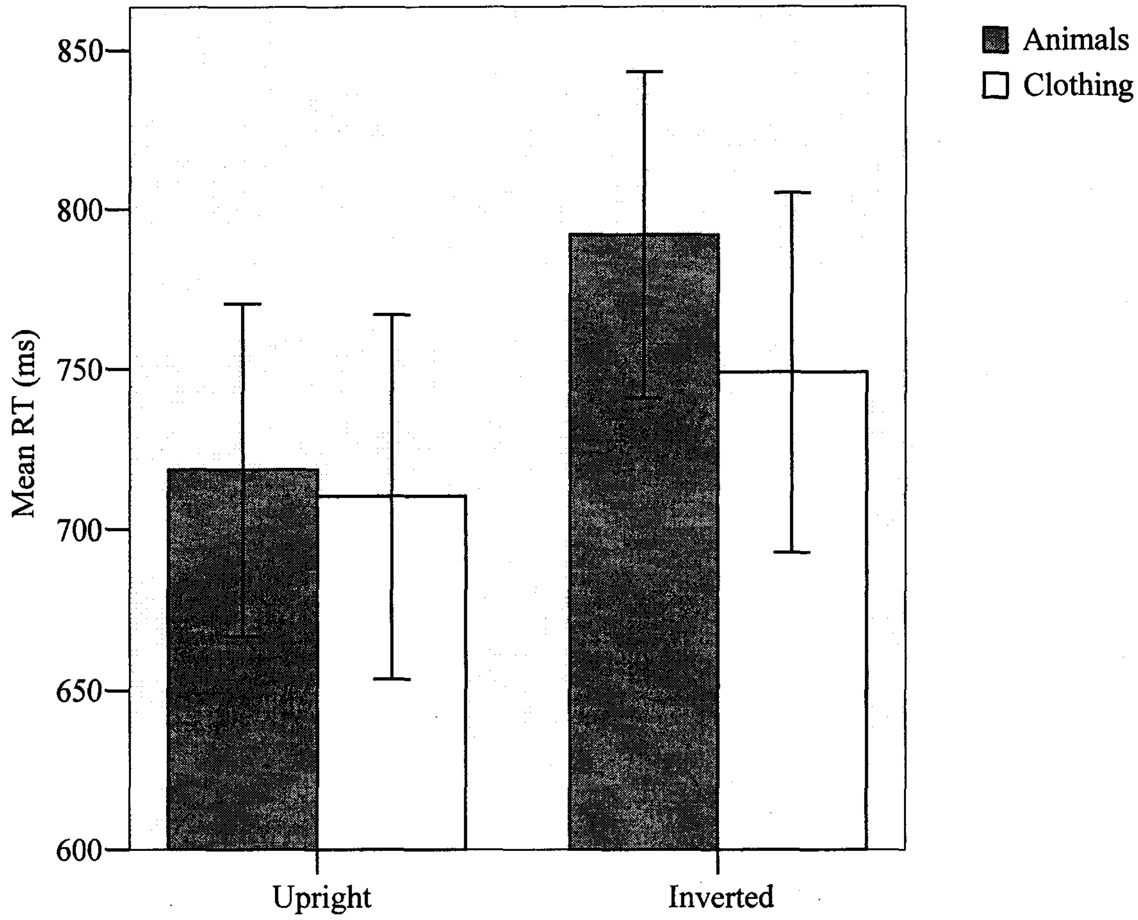


Results

Outliers with RTs greater than 1500 ms were eliminated from the analysis per the recommendations of Ratcliff (1993) to maximize the power of the analysis. After removal of outlier RTs greater than 1500 ms, correct RTs were entered into a two-way repeated measures ANOVA. The factors were Category with two levels (animals and clothing) and Picture Orientation also with two levels (inverted and upright). There was a main effect of Picture Orientation, $F\ (1, 29) = 39.472, p < .001$, and Category, $F\ (1, 29) = 4.311, p = .047$. There was an interaction between Picture Orientation and Category, $F\ (1, 29) = 4.581, p = .041$ with longer RTs for inverted pictures and a greater inversion effect for animals than for clothing (Figure 2).

An error analysis was performed using a chi-square test. There was no effect of category $\chi^2\ (1) = 2.105, p = .156$, or of inversion $\chi^2\ (1) = .896, p = .344$ on the error rates. The overall error rate was 3.4 %.

Figure 2: Presents the mean RTs (ms) with error bars (95% confidence intervals) for participants to indicate whether a picture matched the word that preceded it. Each bar represents a different picture condition: Animal Upright (n = 30) (where "n" refers to the number of subjects); Animal Inverted (n = 30); Clothing Upright (n = 30); and Clothing Inverted (n = 30).



EXPERIMENT 2

In this experiment participants were required to categorize the same set of pictures that were matched to words in Experiment 2. A categorization task was chosen because it was assumed that the relationships among the features would only be necessary to distinguish animals at an individual level. Thus, at a categorical level visual crowding is no longer an issue for animals and they can be distinguished based on simple feature identification. Therefore, unlike Experiment 1, it was predicted that RTs for the animals would be equal to or faster than the RTs for the clothin items that were presented in both the upright and inverted orientation.

Methods

Participants

Participants were 30 right-handed undergraduate students from the University of Windsor, ranging in age from 18 to 40 who volunteered for the study for course credit.

Materials and Procedure

Participants were asked to indicate whether a line drawing represented a living or a man-made item. The participants were then instructed that they were going to perform several practice trials before beginning the test trials. Thirty practice trials were conducted in which the participants were instructed to indicate whether the line drawing represented a living or a man-made item by pressing "1" for living and "2" for man-made. They were told that the pictures may be inverted or upright and to respond as quickly and as accurately as possible.

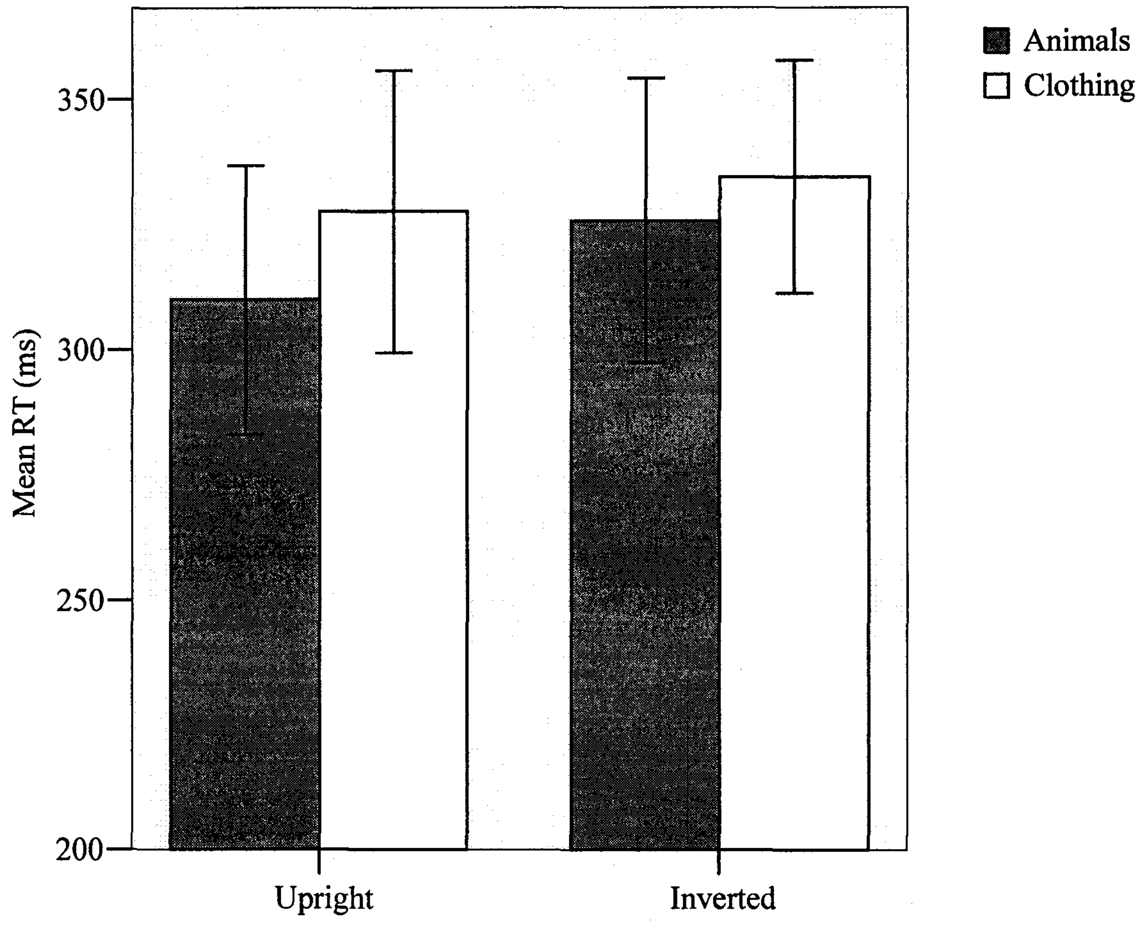
Participants responded to the same pictures used in Experiment 1 presented under identical conditions, for the same duration.

Results

The correct RTs were subjected to a two-way repeated measures ANOVA. Outliers greater than two standard deviations from the mean of all RT's were removed from the data set. The factors were Category with two levels (animals and clothing) and Picture Orientation also with two levels (inverted and upright). There was a main effect of Picture Orientation, $F\ (1, 29) = 7.793, p = .009$ and Category, $F\ (1, 29) = 8.427, p = .007$. The interaction between Picture Orientation and Category was not significant, $F\ (1, 29) = .879, p = .356$ (Figure 3). The RTs were longer when the pictures were inverted and when they were pictures of clothing. Unlike the picture-word matching task, RTs were not significantly longer for inverted animals than for inverted clothes.

An error analysis was performed using a chi-square test. There was no effect of category $\chi^2\ (1) = .258, p = .612$, or of inversion $\chi^2\ (1) = .064, p = .800$ on the error rates. The overall error rate was 2.9 %.

Figure 3: Presents the mean RTs (ms) with error bars (95% confidence intervals) for the participants to indicate whether a picture represented a living or a non-living item. Each bar represents a different picture condition: Animal Upright (n = 30); Animal Inverted (n = 30); Clothing Upright (n = 30); and Clothing Inverted (n = 30).



EXPERIMENT 3

In this experiment participants were again asked to state whether a set of animals and a set of man-made objects matched words that preceded them, thereby requiring that they be identified at an individual level. The animals used in this experiment were the same as those used in Experiment 1, but instead of using clothing, the non-living items were selected from categories that were believed to be more visually crowded. The non-living items used were vehicles, furniture, and buildings. These categories were chosen because of their assumed visual crowding that would require differentiation based on the spatial relationships of their features. The proposed model results in the prediction that these non-living items would be processed in a similar way to the living items, thereby nullifying the interaction observed in Experiment 1.

Methods

Participants

Participants were 30 right-handed undergraduate students from the University of Windsor, ranging in age from 18 to 40 who volunteered for the study for course credit.

Materials and Procedure

The materials and procedures were identical to those used in Experiment 1 except that the man-made items used were selected from the sub-categories of vehicles, furniture, and buildings. All of the non-matching words were taken from the same sub-categories.

Results

The correct RTs were subjected to a two-way repeated measures ANOVA. All RTs greater than 1500 ms were removed from the data set. The factors were Category with two levels (animals and non-living items) and Picture Orientation also with two levels (inverted and upright). There was a main effect of Picture Orientation, $F(1, 29) = 41.753, p < .001$, but not of Category, $F(1, 29) = .797, p = .379$. There was no interaction between Picture Orientation and Category, $F(1, 29) = .356, p = .555$ (Figure 4). The RTs were longer when the pictures were inverted. Unlike the results of Experiment 1, RTs were not increased more for the living items when they were inverted compared to the inverted non-living items (Figure 5).

An error analysis was performed using a chi-square test. There was an effect of category $\chi^2(1) = 12.857$, $p = .000$, but not of inversion $\chi^2(1) = .400$, $p = .527$ on the error rates. The overall error rate was 4.4 %.

A repeated measures ANOVA was completed with the RT data from Experiments 1 and 3, with the Experiment (1 and 3) as a between subjects variable. Outliers were removed at 1500ms. There was an effect of Experiment, $F(1, 58) = 5.483, p = .023$, reflecting faster overall reaction times in Experiment 3 compared to Experiment 1. There was an interaction between Experiment and Category, $F(1, 58) = 4.782, p = .033$. Neither the Experiment and Orientation, $F(1, 58) = .129, p = .721$, nor the Experiment, Category, and Orientation, $F(1, 58) = 1.042, p = .312$ interactions approached statistical significance.

Figure 4: Presents the mean RTs with error bars (95% confidence intervals) for the participants to indicate whether a picture matched the word that preceded it. Each bar represents a different picture condition: Animal Upright (n = 30); Animal Inverted (n = 30); Non-living Upright (n = 30); and Non-living Inverted (n = 30). The animal items were the same as those used in Experiment 1, but instead of clothing, items were selected from vehicles, furniture, and buildings.

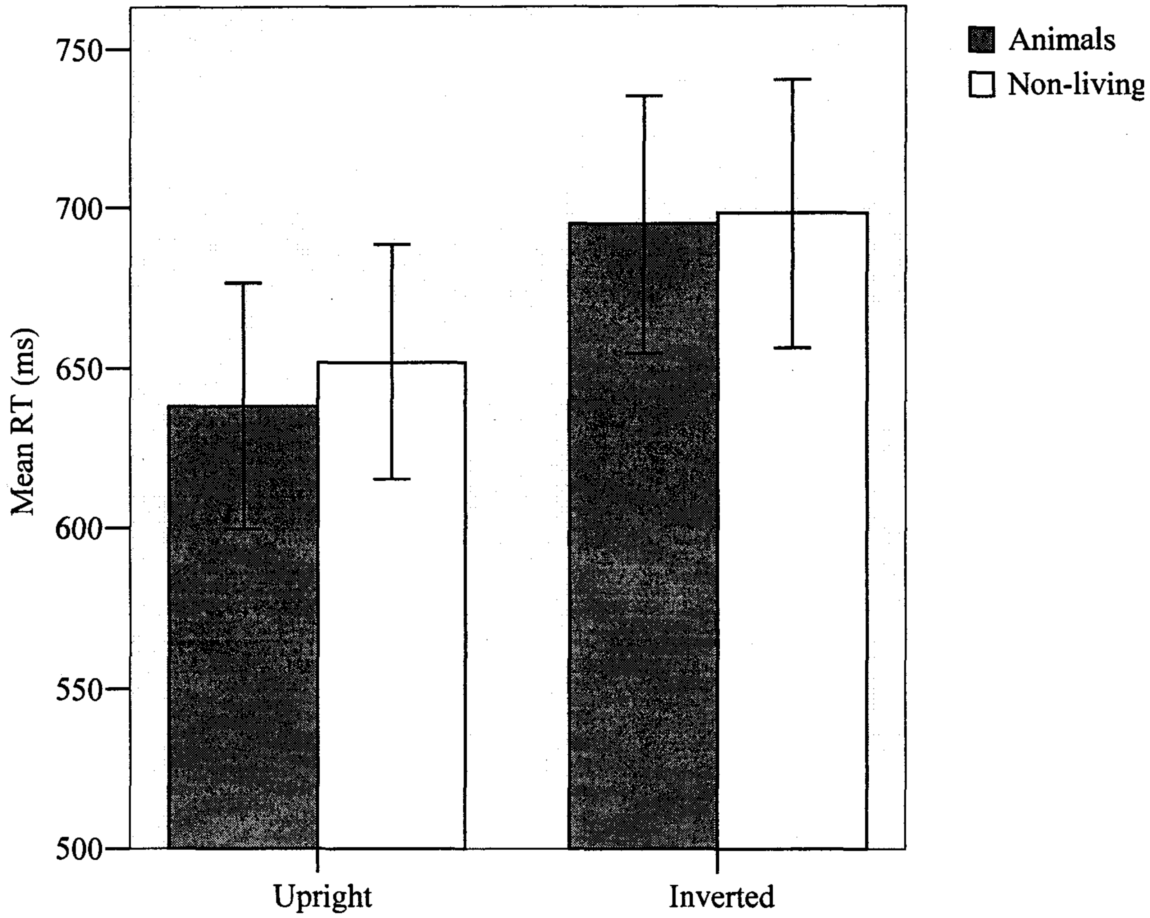
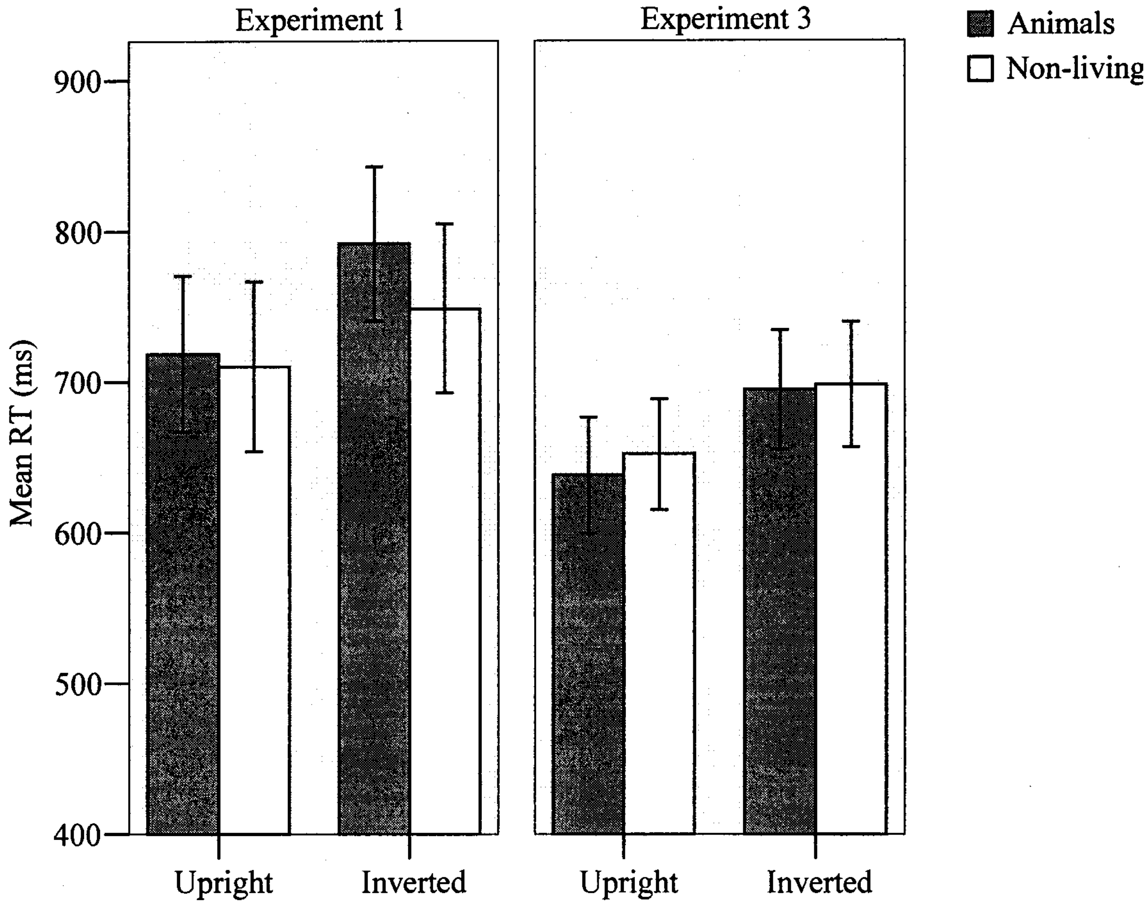


Figure 5: Presents the mean RTs with error bars (95% confidence intervals) shown in Figure 1 and Figure 3 included in a single figure. The different picture conditions include Animal Upright, Animal Inverted, Non-living Upright and Non-living Inverted.



DISCUSSION

The results of Experiment 1 were consistent with the predictions of the hypothesis that identifying individual living things is more dependent on the relationships between features than is the identification of non-living things. The RT's were increased by picture inversion for both categories, but to a greater extent for the animals. According to the proposed model, the increase in RT's for the animals occurred because of a disruption to the known relationships between the features of such items, in addition to the disruption caused by feature inversion. The increase in RT's for the clothing, on the other hand, was more limited to the effects of the disruption to feature detection because quantitative knowledge of the relationships between features is not necessary for differentiation of items within this category.

An alternative explanation is that the animals are more difficult to recognize because of some confounding factor such as visual complexity or a greater number of features in living things. If the recognition of animals requires processing of a greater number of features and we predict that inversion also effects feature recognition, then inversion would be expected to affect animals more, simply because more inverted features need to be processed. However, this is not supported by the RT's for the pictures in the upright orientation which were equal for animals and clothing (actually faster for animals, but the difference was not statistically significant).

It still seems possible that a difference between the stimulus properties of the categories could account for the differences rather than the processing differences required to distinguish between members of the two categories. To control for this, in Experiment 2 a group of participants performed a categorization task with the same set of stimuli used in Experiment 1 in both the upright and inverted orientations. Again, inversion increased the response times across both categories of items. In contrast to Experiment 1, however, inversion of the pictures did not increase RT's more for animals than for clothing. This is not consistent with the suggestion that the interaction found in Experiment 1 was the result of general stimulus differences between the two categories, but indicates that the processing of animals in Experiment 1 was different from the processing of clothing.

The proposed model results in the prediction that the interaction observed in Experiment 1 would not occur during a categorization task because configural processing of the items is only required to differentiate between the highly similar members of animals at an individual level. At the categorical level animals need only to be differentiated from clothing and this can be done by simple feature detection.

Animals were categorized faster than clothing in both the upright and inverted conditions. This provides support for the visual crowding hypothesis that states that categorization proceeds quickly for living things because there is greater overlap of the features of living things (Humphreys and Riddoch, 1987).

An important element of the current hypothesis that differentiates it from hypotheses of semantic category deficits that emphasize a categorical organization of semantic memory is that other objects that belong to categories that are visually crowded will tend to be processed in a manner that is similar to that for animals. In Experiment 3 the inversion effect for animals observed in Experiment 1 was contrasted to a group of non-living things that were believed to come from more visually crowded categories. Because of this, it was hypothesized that the interaction that was observed in Experiment

1 would not occur in Experiment 3. The results of testing showed an effect of inversion for both animals and for the non-living things, in the absence of an interaction between category and inversion, confirming the original hypothesis.

In contrast to Experiments 1 and 2 in which there was no effect of category or inversion on error rates the results of Experiment 3 revealed higher error rates for the non-living things. Based on these findings it could be argued that the non-living things used in Experiment 3 were more visually difficult to process than the animals and this is why inversion caused increased reaction times, rather than the configural processing of such items. However, this is not consistent with the observation that the number of errors actually decreased when the non-living things were inverted.

An analysis of the RTs across Experiments 1 and 3 revealed significantly faster RTs during Experiment 3. This was true for both the new set of non-living items and for the identical set of animals used in Experiment 1. Because RTs were also faster for the "animals" category this is likely the result of the characteristics of the sample rather than an effect of experimental variables.

In sum, the results are consistent with the hypothesis that the animals used were processed in a more holistic fashion compared with clothes. Furthermore, the categories of furniture, vehicles, and buildings appeared to be processed in a similar manner to animals. However, the conclusion that animals are processed more holistically is dependent on the hypothesis that inversion affects holistic processing. Evidence for this comes from research into prosopagnosia which is discussed in the following section.

Prosopagnosia, Expert Object Identification, and Living Things

The explanation of deficits for living things provided in the present paper is similar to theories offered to explain the deficits of patients with prosopagnosia. Such patients are believed to have difficulties with "holistic" processing or "configural" processing (Farah, Wilson, Drain, & Tanaka, 1998). Patients with prosopagnosia will often describe their experience of face perception as seeing the parts individually and losing the whole or the gestalt (Farah, 2004). Although there are a number of different theories elaborating on the process of configural processing the majority of researchers agree that faces are processed more holistically than other objects (Farah et al., 1998). In all elaborations of configural processing the relationships among features are considered paramount for accurate perception, as is proposed in this paper.

Farah, Tanaka, and Drain (1995) tested whether the holistic representation of faces could explain the face inversion effect. The "face inversion effect" is the term used to describe the difficulty that normal individuals have recognizing inverted faces. Farah et al., (1995) taught participants to identify random dot patterns and then tested their ability to recognize the patterns either upright or inverted. Half of the patterns were presented in a manner that encouraged part-based representations. This was done by having each part made up of a distinctive colour. The other half of the patterns were presented with all dots being black, thereby encouraging a holistic representation. All of the test patterns were presented in black. Testing revealed no effect of orientation for the patterns that had been encoded in a part-based manner, but a significant inversion effect for those that were represented holistically.

In a second experiment, participants learned to recognize a set of faces. Again, half of the faces were learned in a part-wise manner and half were learned holistically. To encourage part-wise encoding half of the faces were presented in an “exploded” form, such that the parts of the faces were presented separately. The other half of the faces were presented normally. All of the faces were then tested in a normal format. There was only an inversion effect for the faces that were learned normally. The inversion effect was absent when the faces were learned part-wise. These results are consistent with the hypothesis that the inversion effect is the result of a disruption to holistic processing and supports the current conclusions that living things are processed more holistically.

The inversion effect is not unique to face recognition, but has been observed under conditions requiring expert object recognition as well, suggesting that holistic processing is important for both tasks. Expert recognition refers to the differentiation of visually similar items within a category by an individual that has a great deal of experience with that category. For instance, Diamond and Carey (1986) showed that dog recognition by dog experts was sensitive to inversion effects that were comparable in magnitude to the face inversion effect. In contrast, non-dog experts showed only a face inversion effect in the absence of a dog inversion effect. The authors argued that the holistic processing of faces is actually a specific instance of expert object recognition and any other items that are processed “expertly” will be processed holistically.

Further support for the hypothesis that expert object identification relies on holistic processing comes from two studies performed by de Gelder and colleagues. De Gelder, Bachoud-Levi, and Degos (1998) found that normal subjects produced an inversion effect for both faces and a set of subtly different shoes. Shoes were chosen because they tend to be highly visually similar, but have a number of different exemplars. Also, much like faces, shoes have a canonical orientation. de Gelder and Rouw (2000) extended these findings with a prosopagnosic patient who showed an "inverted inversion effect" for the set of faces and the set of shoes. The inverted inversion effect refers to the improved learning and recognition of items that are presented inverted in patients with prosopagnosia. This is believed to occur because the holistic processing module is engaged when the item is presented upright even though that module is damaged (Farah, 2004).

Guathier and Tarr (1997) specifically tested the effects of expert object processing by training a group of participants to discriminate "greebles". They examined whether such participants who were trained to discriminate one set of pictures of greebles would then show configural processing of a new set of unfamiliar greebles. "Greebles" are digitally created three-dimensional objects each with four protruding parts organized in approximately the same configuration. Each greeble was a member of one of two genders and one of five families. The five families were defined by a different central part shape. The genders were differentiated by the orientation of the other parts relative to the central part. Although some of the parts were very similar to each other, each was unique to the individual greeble. The authors reported that their group of greeble experts were slower to identify the parts of novel greebles when those parts were in a different configuration than during training. This was only the case for greebles presented in the upright orientation. Novice identification of parts was not sensitive to the configuration used during the study phase. These results suggest that the "experts" had learned a configural representation of the parts of the greebles similar to that observed in facial recognition.

Gautheir, Tarr, Anderson, Skudlarski, and Gore (1999) provided further support for the hypothesis that holistic face processing is simply an example of expert object recognition by examining activity in the fusiform face area (FFA) during processing of greebles and faces. To do this the authors examined the difference in FFA activity on fMRI between upright and inverted faces and between upright and inverted greebles. Prior to training there was a greater difference in FFA activity between upright and inverted faces than between upright and inverted greebles. Following training with greebles (and with faces as a control condition) the difference in activity in the FFA between matching of upright greebles versus matching of inverted greebles increased dramatically. This area was also more activated in passive viewing of greebles by experts than by novices. It was concluded that expertise is one factor that encourages activation in the FFA.

The results of the current experiments suggest that the individual identification of animals requires more holistic processing than the individual identification of clothes. Furthermore, other objects that come from visually crowded categories may also be processed holistically as indicated by the significant effect of inversion for buildings, vehicles, and furniture. This form of processing may be similar to that observed for shoes (de Gelder et al., 1998), expert dog identification (Diamond and Carey, 1986), and expert greeble identification (Gauthier and Tarr, 1997). The processing of visually crowded categories may be an example of expert object processing.

Research mentioned in the introduction of this paper also supports the hypothesis that living things are processed by regions of the brain that have been implicated in the expert object recognition research discussed above. Gerlach et al. (1999) found that larger parts of the right inferior temporal and anterior fusiform gyri were recruited for living objects compared to artefacts. Whatmough et al. (2002) reported that naming of animals compared with the naming of tools was associated with increased regional Cerebral Blood Flow (rCBF) in the fusiform and inferior temporal gyri bilaterally. Moore and Price (1999) found that naming of living objects compared to naming of non-living artefacts resulted in increased rCBF in the posterior portion of the right middle temporal gyrus and the anterior temporal lobes. In a meta-analysis Gainotti (2000) found that deficits for living things were associated with inferior temporal lobe damage, in contrast to deficits for non-living things which were associated with fronto-temporo-parietal lesions. All of the above findings are consistent with the hypothesis that living objects are more visually similar and are processed more holistically than are non-living things.

Semantic Deficit or Visual Agnosia?

The results of the current experiments in conjunction with the literature on the anatomical processing of living things provides strong evidence in favour of the hypothesis that living things are processed more holistically than are non-living things. Furthermore, it seems likely that this is the result of the visual crowding of the category of living things (Humphreys & Riddoch, 1987). It is difficult for the current results to be accommodated by many of the prevailing theories of category specific deficits because they focus on damage to "semantic memory" as the locus of the deficits and were not intended to address the perceptual processing of objects. However, for this same reason the results do not refute any of the hypotheses regarding the organization of semantic memory.

The results are best interpreted within the visual crowding hypothesis and provide a possible mechanism by which visual crowding affects the process of differentiating between objects. It is possible to incorporate this mechanism within the HIT account (Humphreys & Forde, 2001), much like the visual crowding hypothesis has been. Within this model the re-entrant activation of visual processing would be represented by entry into a “holistic processing module” which would only be required to differentiate between living things and other items from visually crowded categories. Damage to this area would then lead to a category specific deficit for living things.

It is clear that any model explaining category specific deficits will have to account for differences in holistic processing between categories. Research indicates that areas of the fusiform gyrus may be necessary for such processing to take place and, therefore, any damage to this area is likely to result in deficits processing those objects that require holistic processing to be differentiated.

The question remains as to whether a holistic processing deficit can account for the deficits observed in patients with a dissociation between their knowledge for living and non-living things. It is possible that for certain living items an inability to differentiate individual items visually would result in a loss of all “semantic” information for those items as well. For instance, animals may be differentiated almost entirely based on their subtly different visual features for most individuals. Therefore, if they cannot be differentiated at the visual level they cannot be differentiated semantically. In contrast, an individual may differentiate people based on their face, their voice, and their relationship to that individual. If this individual is no longer able to differentiate faces because of a holistic processing deficit this will result in prosopagnosia, but all knowledge of people they have relationships with will not be lost because of the intact connections to voice information and relationship information that can also be used to differentiate individuals. This provides a reasonable explanation for why prosopagnosia and "semantic" category deficits for living things are so highly correlated (Farah, 2004).

Thomas and Forde (2006) recently came to a similar conclusion in their examination of a patient with a category specific deficit for living things. This patient was faster at identifying local compared to global letters (letters made up of smaller letters) and showed no local-to-global or global-to-local interference effects in a selective attention task. From this the authors hypothesized that it was this difficulty processing visual information globally that resulted in the patient's category specific deficit for living things.

This hypothesis allows for variability in the presentation of deficits resulting from an inability to process the spatial relationships among details depending on the individuals learning history. For instance, some individuals may present with only a visual agnosia for living things if they have adequate connections in other modalities to distinguish between individual items (i.e. verbal, auditory, gustatory, tactile, or motor). Such patients have been identified in the literature (Arguin, Bub, & Dudek, 1996; Humphreys & Riddoch, 1987).

This is not to say that all reports of category specific deficits for living things can be accounted for by this mechanism. Although such patients are rare, De Renzi and Lucchelli (1994) have reported on a patient with deficient knowledge for living things with intact face recognition abilities.

Humphreys and Forde (2001) distinguished between two types of patients with deficits for living things that have been described in the literature. One type, such as the patient reported on by Caramazza and Shelton (1998), has an inability to perform accurately on an object decision task for living things in addition to deficits for living things on tasks presented in various modalities. This is the type of patient that, according to the present model, would also present with difficulties with face recognition. Humphreys and Forde argue that this type of patient has difficulties distinguishing between visually similar items because of a disruption to the process of re-entrant activation. Such a patient could also be conceptualized as having an impaired ability to process the configural relationships in visual object identification.

Another type, such as the patient described by Laiacona et al. (1997), has deficits for living things with an intact ability to perform object decision tasks. Humphreys and Forde (2001) argue that this type of patient has category specific damage at the semantic level, as opposed to the visual recognition level. The difficulty with classifying patients as having a "semantic" deficit because of intact object recognition is that intact object recognition may not, in fact, equate to intact configural processing abilities. Individual object identification is likely to require a more fine grained analysis of the visual properties of an object than is required for object decision tasks. Furthermore, object decision tasks will very greatly from study to study based on the different parts that have been connected to create non-objects. Perhaps a more accurate test of configural processing abilities would be a test of facial recognition.

CONCLUSIONS

The results of the current study indicate that living things are processed more by their holistic configuration than are non-living artefacts. Such processing is hypothesized to be similar to that observed for facial recognition and expert object recognition and requires the application of an image-based processing model (Tarr & Vuong, 2002). Given these findings it is possible that prior instances of category-specific deficits for living things have resulted from an inability to process the spatial relationships between the features of living things. Previous research suggests that this may be because of the increased visual crowding of living things (Humphreys & Riddoch, 1987b). The results of this study support this hypothesis, showing that other types of non-living artefacts that are more visually crowded can also be affected by disruption to the configural relationships that differentiate the items. The fact that prosopagnosia is so highly correlated with category-specific deficits for living things supports this hypothesis.

The reverse pattern of deficits, category specific deficits for non-living artefacts, is not addressed by these results. However, research suggests that action knowledge is particularly important for processing this category of items (Gerlach et al., 2002).

Future investigations of patients with category specific deficits for living things must be careful to examine the visual processing abilities of such individuals, particularly with respect to configural processing. The object decision task may not be entirely sensitive to deficits of configural processing depending on the nature of the "non-objects" that are created. Perhaps a more accurate indication of configural processing abilities would be a test of facial recognition.

REFERENCES

Arguin, M., Bub, D., & Dudek, G. (1996). Shape integration for visual object recognition and its implication in category-specific visual agnosia. *Visual Cognition, 3,* 221-275.

Basso, A., Capitani, E., & Laiacona, M. (1988). Progressive language impairment without dementia: A case study with isolated category-specific semantic defects. *Journal of Neurology, Neurosurgery, and Psychiatry, 51,* 1201-1207.

Biederman, I. (1987). Recognition-by-components: A theory of human image understanding. *Psychological Review, 94,* 115-147.

Binkofski, F., Buccino, G., Dole, C., Seitz, R. J., & Freund, H. J. (1999). Mirror agnosia and mirror ataxia constitute different parietal lobe disorders. *Annuls of Neurology, 96,* 51-61.

Brousseau, G. & Buchanan, L. (2004). Semantic category effect and emotional valence in female university students. *Brain and Language, 90,* 241-248.

Bullier, J. (2002). Neural basis of vision. In Pashler, Hal & Yantis, Steven, (Eds.) *Steven's Handbook of Experimental Psychology (3rd Ed.): Sensation and Perception.* (pp. 1-40). John Wiley and Sons: New Jersey, US.

Buxbaum, L. J., Shwartz, M. F., & Carew, T. G. (1997). The role of semantic memory in object use. *Cognitive Neuropsychology, 14,* 219-254.

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

Caramazza, A., Hillis, A. E., Rapp, B. C., & Romani, C. (1990). The multiple semantics hypothesis: Multiple confusions? *Cognitive Neuropsychology, 7,* 161-189.

Chao, L. L., Haxby, J. V., & Martin, A. (1999). Attribute-based neural substrate in posterior temporal cortex for perceiving and knowing about objects. *Nature Neuroscience, 2,* 913-919.

Chao, L. L & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *Neuroimage,(12),* 478-484.

Damasio, A. R. (1990). Category-related recognition defects as a clue to the neural substrates of knowledge. *Trends in Neuroscience, 13,* 95-98.

De Gelder, B., Bachoud-Levi, A. C., & Degos, J. (1998). Inversion superiority in visual agnosia may be common to a variety of orientation polarised objects besides faces. *Vision Research, 38(18),* 2855-2861.

De Gelder, B. & Rouw, R. (2000). Paradoxical configuration effects for faces and objects in prosopagnosia. *Neuropsychologia, 38(9),* 1271-1279.

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

Devlin, J. T., Gonnerman, L. M., Andersen, E. S., & Seidenberg, M. S. (1998). Category-specific semantic deficits in focal and widespread brain damage: A computational account. *Journal of Cognitive Neuroscience, 10,* 77-94.

Diamond, R. & Carey, S. (1986). Why faces are and are not special: an effect of expertise. *Journal of Experimental Psychology, 115,* 107-117.

Farah, M. J. (2004). *Visual Agnosias (2nd Ed.).* MIT Press: Cambridge, Massachusetts.

Farah, M. J., & McClelland, J. L. (1991). A computational model of semantic memory impairment: modality specificity and emergent category specificity. *Journal of Experimental Psychology: General, 120,* 339-357.

Farah, M. J., Tanaka, J. R., & Drain, H. M. (1995). What causes the face inversion effect? *Journal of Experimental Psychology: Human Perception and Performance, 21,* 628-634.

Farah, M. J., & Wallace, M. A. (1992). Semantically-bounded anomia: Implications for the neural implementation of naming. *Neuropsychologia, 30,* 609-621.

Farah, M. J., Wilson, K. D., Drain, H. M., & Tanaka, J. R. (1998). What is "special" about face perception? *Psychological Review, 105,* 482-498.

Forde, E. M. E., Francis, D., Riddoch, M. J., Rumiati, R., & Humphreys, G. W. (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.

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.

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

Gainotti, G. (2000). What the locus of brain lesions tells us about the nature of cognitive deficits underlying category-specific disorders: a review. *Cortex, 36,* 539-559.

Gainotti, G., & Silveri, M. C. (1996). Cognitive and anatomical locus of lesion in a patient with a category-specific semantic impairment for living beings. *Cognitive Neuropsychology, 13,* 357-390.

Gainotti, G., & Silveri, M. C., Daniele, A., & Guistolisi, L. (1995). Neuroanatomical correlates of category-specific semantic disorders: A critical survey. *Memory, 3,* 247-262.

Gale, T. M., Done, D. J., & Frank, R. J. (2001). Visual crowding and category specific deficits for pictorial stimuli: A neural network model. *Cognitive Neuropsychology,* 18, 509-550.

Garrard, P., Patterson, K., Watson, P. C., & Hodges, J. R. (1998). Category-specific semantic loss in dementia of Alzheimer's type. *Brain, 121,* 633-646.

Gauthier, I., Behremann, M., & Tarr, J. J. (1999). Can face recognition really be dissociated from object recognition? *Journal of Cognitive Neuroscience, 11,* 349-370.

Gautheir, I. & Tarr, J. J. (1997). Becoming a "greeble" expert: Exploring mechanisms for face recognition. *Vision Research, 37,* 1673-1682.

Gelman, R. (1990). First principles organize attention to and learning about relevant data: Number and the animate-inanimate distinction as examples. *Cognitive Science, 14,* 79-106.

Gelman, S. (1988). The development of induction within living kind and artefact categories. *Cognitive Psychology, 20,* 65-95.

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

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

Gonnerman, L. M., Andersen, S. E., Devlin, J. T., Kempler, D., & Seidenberg, M. S. (1997). Double dissociation of semantic categories in Alzheimer's disease. *Brain and Language, 57,* 254-279.

Goodale, M. A., Milner, A. D., Jakobson, L. S., & Carey, D. P. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature, 349,* 154-156.

Guistolisi, L., Bartolomeno, P., Daniele, A., Marra, C., & Gainotti, G. (1993). Category-specific semantic impairment for living things in the early stages of Alzheimer's disease: Further evidence from a study on single cases. *Journal of Clinical and Experimental Neuropsychology, 15,* 403.

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

Hummel, J. E. (1998). Where view-based theories break down: The role of structure in shape perception and object recognition. In: Dietrich, E. Markman, A. (Eds.), *Cognitive Dynamics: Conceptual Change in Humans and Machines.* MIT Press, Cambridge MA.

Humphreys, G. W., & Forde, E. M. E. (2001). Hierarchies, similarity, and interactivity in object recognition: "Category-specific" neuropsychological deficits. *Behavioural and Brain Sciences, 24,* 453-509.

Humphreys, G. W., & Riddoch, M. J. (1987b). On telling your fruit from your vegetables: A consideration of category-specific deficits after brain damage. *Trends in Neuroscience, 10,* 145-148.

Humphreys, G. W., & Riddoch, M. J. (1987a). *To see but not to see: A case study of visual agnosia.* Hillsdale, NJ: Lawrence Erlbaum Associates.

Humphreys, G. W., & Riddoch, M. J. (1999). Impaired development of semantic memory: Separating semantic from structural knowledge and diagnosing a role for action in establishing stored memories for objects. *Neurocase, 5,* 519-532.

Humphreys, G. W., Riddoch, M. J., & Quinlan, P. T. (1988). Cascade processes in picture identification. *Cognitive Neuropsychology, 85,* 67-103.

Jarvis, B. G. (2002). *Direct RT Research Software* (2002 version). New York: Empirisoft.

Jones, E. G., & Powell, T. P. S. (1970). An experimental study of converging sensory pathways within the cerebral cortex of the monkey. *Brain, 93,* 793-820.

Kolinsky, R., Fery, P., Messina, D., Peretz, I., Evinck, S., Ventura, P., Morais, J. (2002). The fur of the crocodile and the mooing sheep: A study of a patient with a category-specific impairment for biological things. *Cognitive Neuropsychology, 19,* 301-342.

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

Logothetis, N. K., Paulis, J., Poggio, T. (1995). Shape representation in the inferior temporal cortex of monkeys. *Current Biology, 5(5)*, 552 – 563.

Mandler, J. M., Bauer, P. J., & McDonough, L. (1991). Separating the sheep from the goats: Differentiating global categories. *Cognitive Psychology, 23,* 263-298.

McRae, K., de Sa, V. R., & Seidenberg, M. S., (1997). On the nature and scope of featural representations of word meaning. *Journal of Experimental Psychology: General, 126,* 99-130.

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

Moss, E. H., & Tyler, L. (1997). A category-specific semantic deficit for non-living things in a case of progressive aphasia. *Brain and Language, 60,* 55-58.

Moss, E. H., & Tyler, L. (2000). A progressive category-specific deficit for non-living things. *Neuropsychologia, 38,* 60-82.

Moss, E. H., Tyler, L., Durrant-Peatfield, M., Bunn, E. M. (1998). Two eyes of a see-through: impaired and intact semantic knowledge in a case of selective deficit for living things. *Neurocase, 4,* 291-310.

Ratcliff, R. (1993). Methods for dealing with reaction time outliers. *Psychological Bulletin, 114,* 510-532.

Riddoch, M. J. & Humphreys, G. W. (2004). Object identification in simultanagnosia: when wholes are not the sum of their parts. *Cognitive Neuropsychology, 21,* 423-441.

Saumier, D., Arguin, M., & Lassonde, M. (2001). Prospagnosia: a case study involving problems in processing configural information. *Brain and Cognition, 46,* 255-259.

Shallice, T. (1988). Specialisation within the semantic system. *Cognitive Neuropsychology, 5,* 133-142.

Silveri, M. C., Daniele, A., Guistolisi, L, & Gainotti, G. (1991). Dissociation between knowledge of living and non-living things in dementia of the Alzheimer's type. *Neurology, 41,* 545-546.

Silveri, M. C., & Gainotti, G. (1988). Interaction between vision and language in category-specific semantic impairment. *Cognitive Neuropsychology, 5,* 677-709.

Silveri, M. C., Gainotti, G., Perani, D., Cappelletti, J. YU., Carbone, G., & Fazio, F. (1997). Naming deficit for nonliving items: Neuropsychological and PET study. *Neuropsychologia, 35,* 359-387.

Snodgrass, J. G., & Vanderwart, M. (1980). A standardized set of 260 pictures: Norms for name agreement, image agreement, familiarity, and visual complexity. *Journal of Experimental Psychology: Human Learning and Memory, 6,* 174-215.

Stewart, F., Parkin, A. J., & Hunkin, N. M. (1992). Naming impairments following recovery from herpes simplex encephalitis. *Quarterly Journal of Experimental Psychology, 44,* 261-284.

Tarr, M. J. & Bulthoff, H. H. (1998). Image-based object recognition in man, monkey and machine. *Cognition, 67,* 1 – 20.

Tarr, M. J. & Vuong, Q. C. (2002). Visual object recognition. In H. Pashler & S. Yantis (Eds.) *Steven's Handbook of Experimental Psychology. Volume 1: Sensation and Perception* (pp. 287 – 314). New York, NY: John Wiley & Sons.

Tarr, M. J., Williams, P., Hayward, W. G., & Gauthier, I. (1998). Three-dimensional object recognition is viewpoint-dependent. *Nature Neuroscience, 1(4),* 275-277.

Thomas, R. & Forde, E. (2006). The role of local and global processing in the recognition of living and nonliving things. *Neuropsychologia, 44,* 982-986.

Thompson-Schill, S. L., Aquirre, G. K., D'Esposito, M., & Farah, M. J. (1999). A neural basis for category and modality specificity of semantic knowledge. *Neuropsychologia, 37,* 671-676.

Tyler, L. K., Moss, H. E., Durrant-Peatfield, M. R., & Levy, J. P. (2000). Conceptual structure and the structure of concepts: A distributed account of category specific deficits. *Brain and Language, 75,* 195-213.

Warrington, E. K. (1975). The selective impairment of semantic memory. *Quarterly Journal of Experimental Psychology, 27,* 635-657.

Warrington, E. K., & McCarthy, R. (1983). Category-specific access dysphasia. *Brain, 106,* 859-878.

Warrington, E. K., & McCarthy, R. (1987). Categories of knowledge: further fractionations and an attempted integration. *Brain, 110,* 1273-1296.

Warrington, E. K., & McCarthy, R. (1994). Multiple meaning systems in the brain: A case for visual semantics. *Neuropsychologia, 32,* 1465-1473.

Warrington, E. K., & Shallice, T. (1984) Category-specific semantic impairments. *Brain, 107,* 829-859.

Whatmough, C., Chertkow, H., Murtha, S., & Hanratty, K. (2002). Dissociable brain regions process object meaning and object structure during picture naming. *Neuropsychologia, 40,* 174-186.

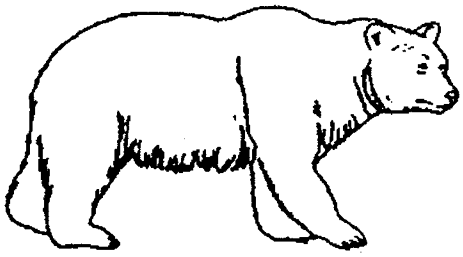
Whatmough, C., Chertkow, H., Murtha, S., Templeman, D., Babins, L., & Kelner, N. (2003). The semantic category effect increases with worsening anomia in Alzheimer's type dementia. *Brain and Language, 84,* 134-147.

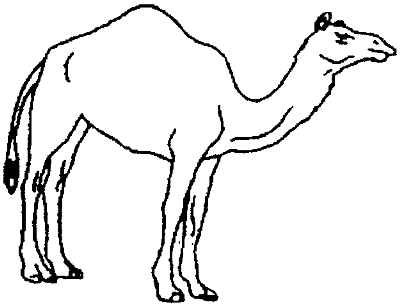
Van Orden, G. C., Pennington, B. F., & Stone, G. O. (2001). What do double dissociations prove? *Cognitive Science, 25, 111-172.*

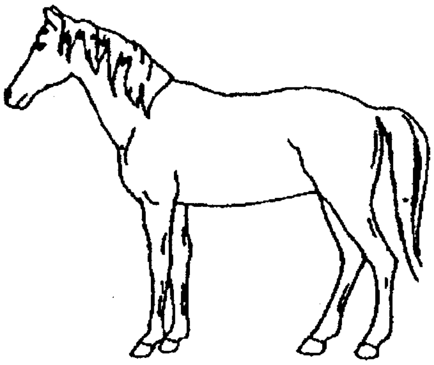
Zannino, G. D., Perri, R., Giovanni, A., Carlesimo, P. P., & Caltagirone, C. (2002). Category-specific impairments in patients with Alzheimer's disease as a function of disease severity: a cross-sectional investigation. *Neuropsychologia, 40,* 2268-2279.

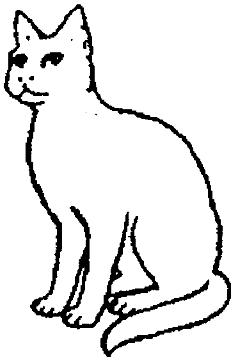
APPENDIX A: Stimulus set

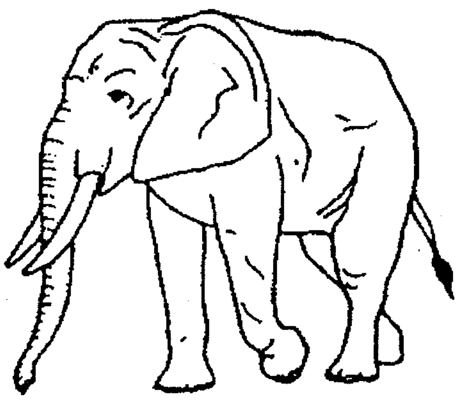
Animals

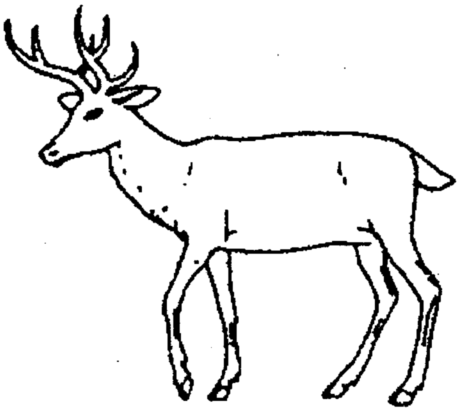


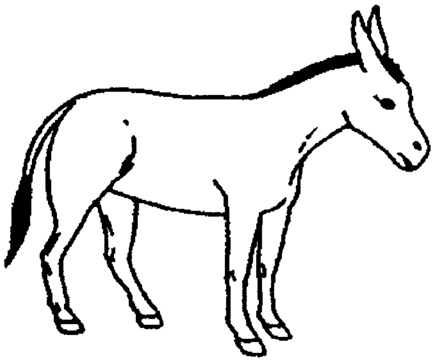


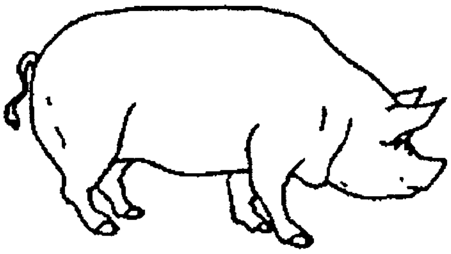


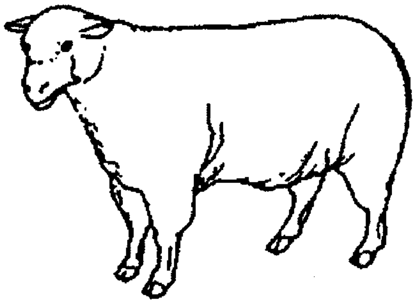


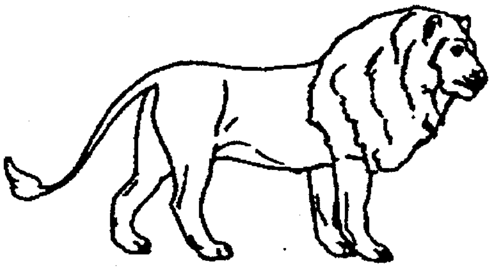


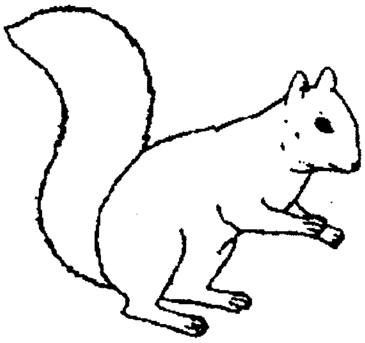


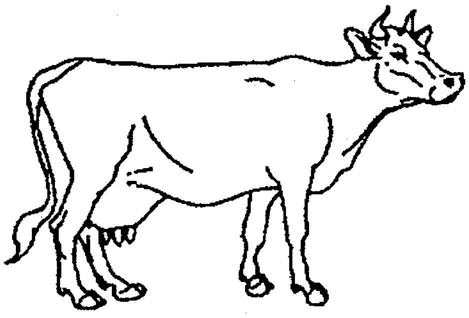


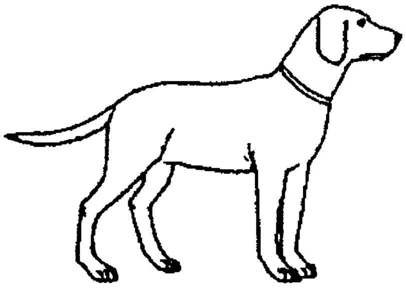


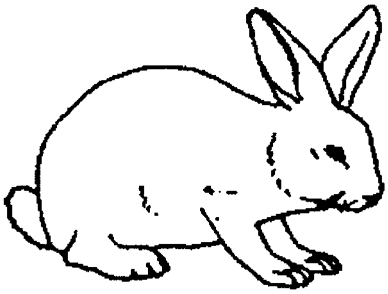


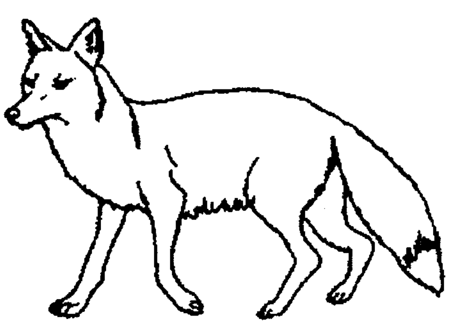


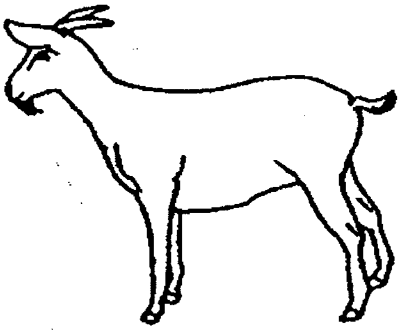


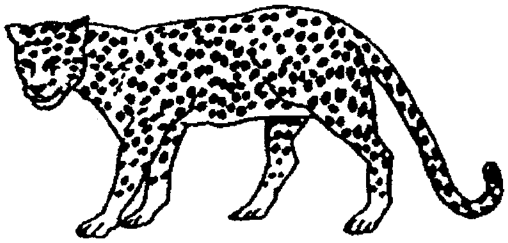












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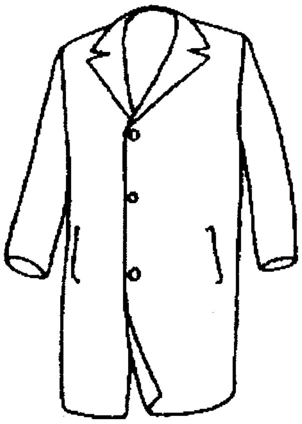

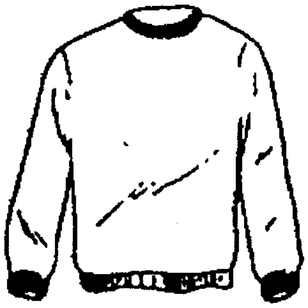

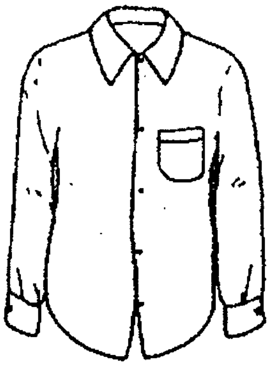

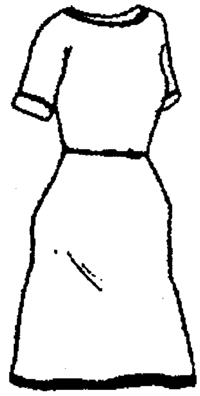

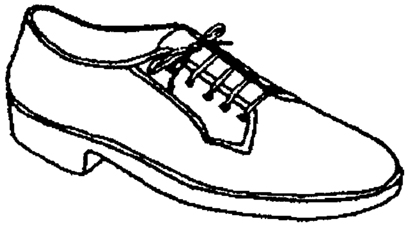

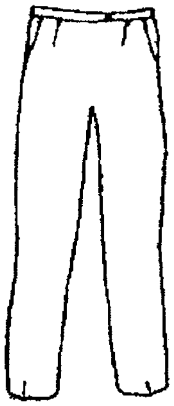

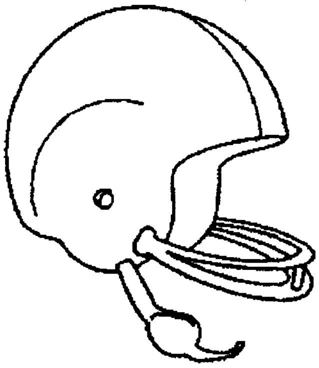

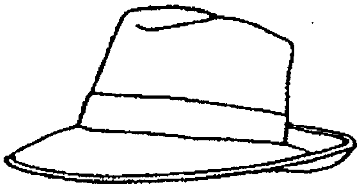

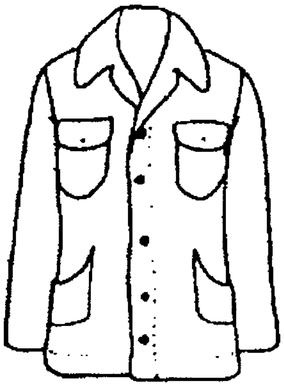

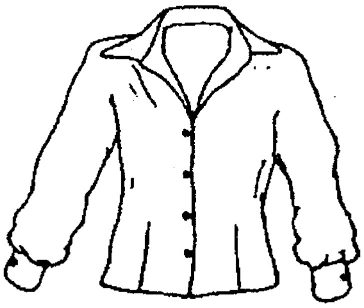

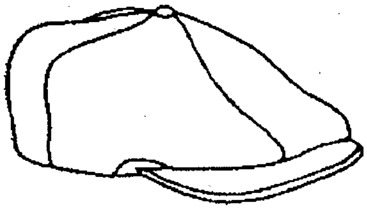

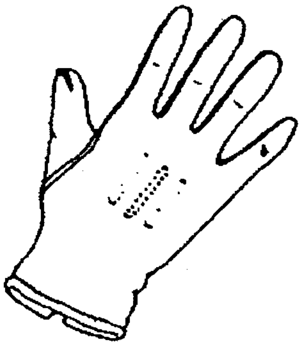

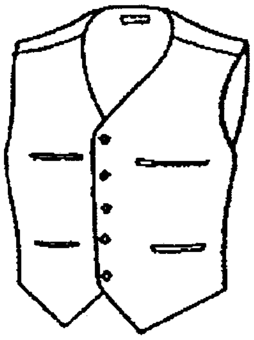

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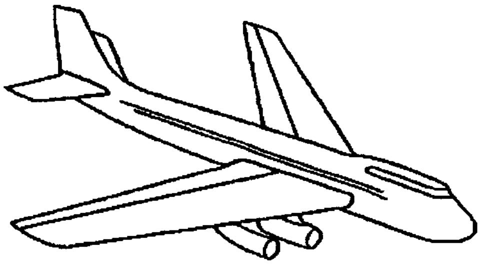

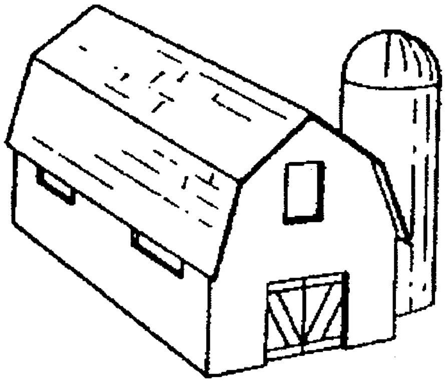

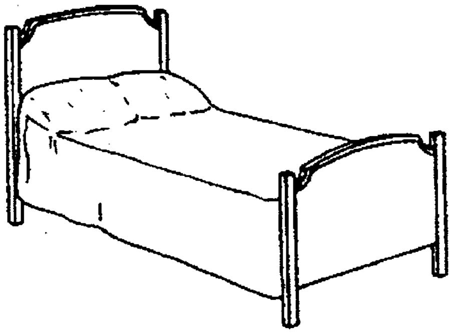

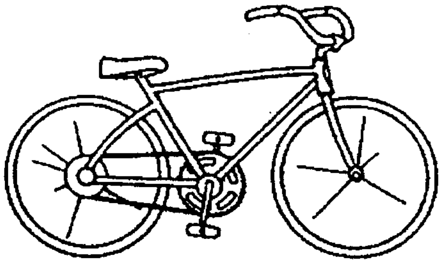

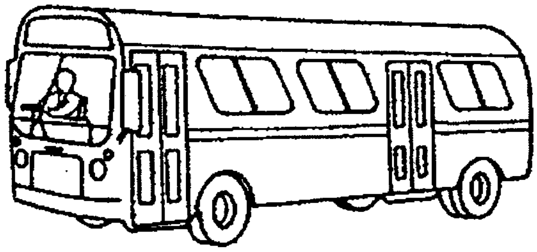

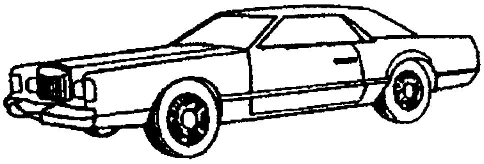

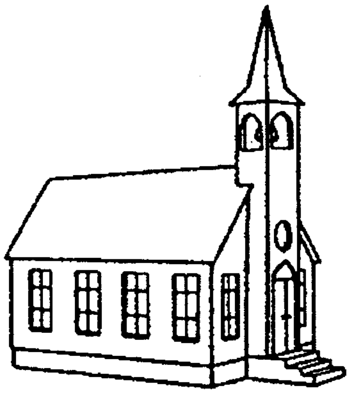

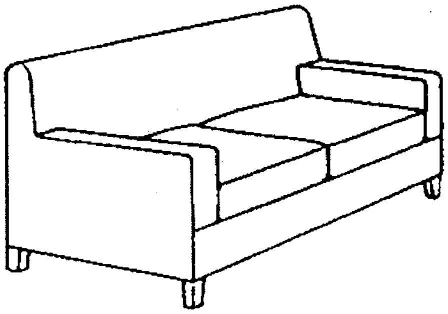

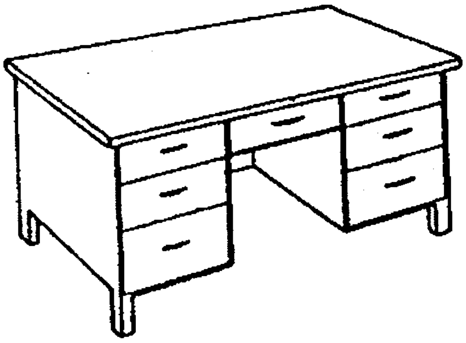

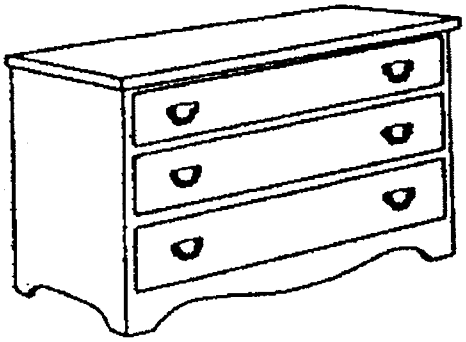

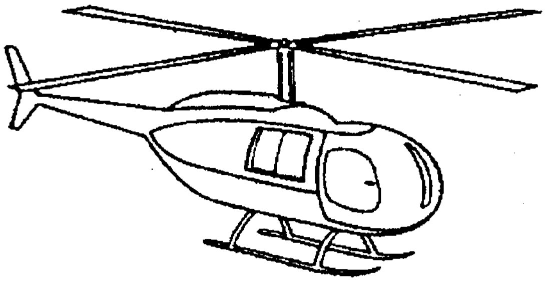

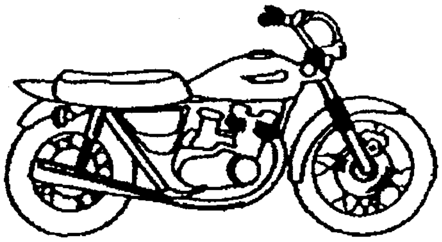

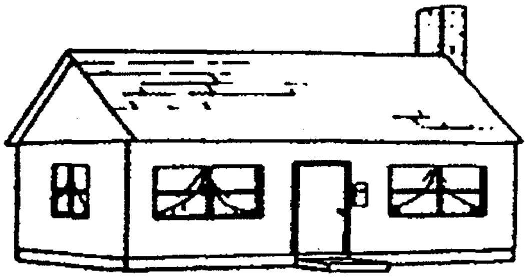

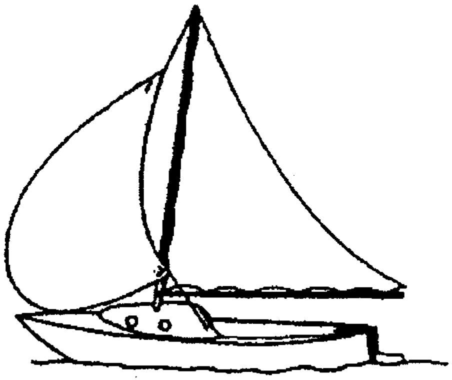

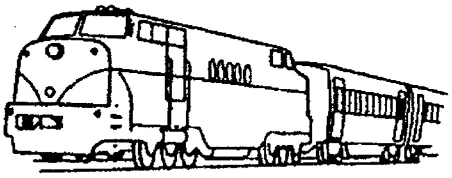

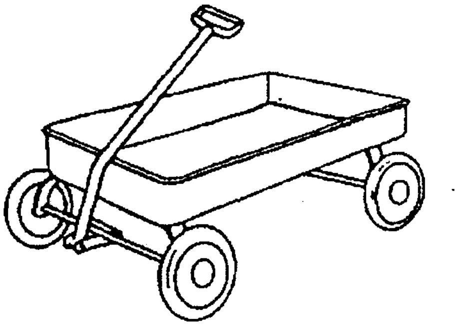

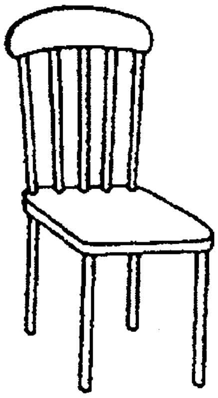

APPENDIX B: ANOVA tables for each experiment

Experiment 1

Effect	**F-value**	**Significance**	**Eta Squared**
Category	(1, 29) = 4.31	.047	.129
Orientation	(1, 29) = 39.47	.000	.576
Category * Orientation	(1, 29) = 4.58	.041	.136

Experiment 2

Effect	**F-value**	**Significance**	**Eta Squared**
Category	(1, 29) = 8.43	.007	.225
Orientation	(1, 29) = 7.79	.009	.212
Category * Orientation	(1, 29) = .88	.356	.029

Experiment 3

Effect	**F-value**	**Significance**	**Eta Squared**
Category	(1, 29) = .80	.379	.027
Orientation	(1, 29) = 41.75	.000	.590
Category * Orientation	(1, 29) = .36	.555	.012

Experiments 1 and 3 Interactions

Effect	**F-value**	**Significance**	**Eta Squared**
Category * Experiment	(1, 58) = 4.78	.033	.076
Orientation * Experiment	(1, 58) = .129	.721	.002
Category * Orientation * Experiment	(1, 58) = 1.04	.312	.018

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