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Neuroscience and Biobehavioral Reviews xx (xxxx) 1–18

NEUROSCIENCE AND
BIOBEHAVIORAL
REVIEWS

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Review

Anatomical functional and cognitive determinants of semantic memory disorders

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Received 26 May 2005; received in revised form 15 September 2005; accepted 21 November 2005

Abstract

Contemporary debates on the ‘semantic memory’ construct revolve around three main topics: (1) the functional and anatomical relationships between episodic and semantic memory; (2) the format of semantic representations and their relationships with the underlying sensory-motor processes; (3) the categorical organization of semantic memory. The aim of the present review is to demonstrate that there is a common thread linking these different aspects of semantic memory. This thread is represented by the interdependence of mechanisms involved in the construction of semantic memory and the content of semantic representations. In particular, I suggest there is a continuity between: (a) the mechanisms of acquisition of episodic and semantic memory; (b) semantic representations and sensory-motor processes preliminary to the acquisition of these representations. This continuity has important implications for the format of semantic representations and the brain structures subserving the organisation of various categories of knowledge

Keywords: Semantic memory; Episodic memory; Perceptual activities; Format of semantic representations; Modality-specific semantic disorders; Category-specific semantic disorders; Verbs–nouns; Living things–artefacts; Neuro-anatomical correlates

Contents

1. Introduction

In spite of persisting controversies over the models proposed by Tulving (1972, 1984, 1991) and by Squire (Squire and Zola-Morgan, 1988, 1991; Squire, 1992) for classifying different types of memory, most authors acknowledge that: (a) short-term memory (or working memory) must be considered

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doi:10.1016/j.neubiorev.2005.11.001

apart from permanent forms of encoded information; (b) within long-term declarative memory a distinction must be made between episodic and semantic memory. This distinction was originally proposed by Tulving (1972), who used the term semantic memory to denote comprehension of language (memory of words and concepts) and the term episodic memory to account for acquisition and retention of a particular kind of information in a particular context. In his first model, Tulving assumed that both kinds of memory derive from a common process and only differ in degree of over-learning. According to this interpretation, material stored in episodic memory results from a single exposure to a given stimulus, whereas material stored in semantic memory results from repeated exposures to stimuli belonging to the same category of knowledge. At a later time, however, Tulving (1984) defined episodic and semantic memory as two different 'neurocognitive' systems, allowing acquisition and retention of different kinds of information and subtended by specific neuroanatomical mechanisms. Furthermore, in these new versions of his model Tulving (1984 and 1991) extended the content of the term semantic memory to encompass general knowledge of the world.

The construct of semantic memory as a specific neurocognitive system was at least in part suggested by the Warrington (1975) description of three patients who showed a selective defect of word meaning and of visual representations in the early stages of a slowly progressive focal cortical atrophy, in spite of intact linguistic skills, visual-perceptual functions and general intellectual abilities. In the following years, other comprehensive studies of patients with a selective impairment of semantic memory were reported (e.g. Schwartz et al., 1979) and Snowden et al. (1989) coined the term 'semantic dementia' to describe a form of fronto-temporal dementia, showing a selective deterioration of semantic memory as a consequence of a focal atrophy of the left temporal lobe.

In this review, I will restrict my attention to the components of word meaning and of conceptual representation originally taken into account by Tulving (1972), and will disregard other aspects of the general knowledge of the world. In particular, I will focus on three main topics discussed in contemporary debates on semantic memory, namely: (1) the functional and anatomical relationships between episodic and semantic memory systems; (2) the format of semantic representations and their relationships with the underlying sensory-motor processes; (3) the categorical organization of semantic memory.

2. Functional and anatomical relationships between episodic and semantic memory

Before starting this discussion of the functional and anatomical relationships between episodic and semantic memory, it must be acknowledged that this traditional dichotomy is not universally accepted and that important objections have been raised to it from various points of view.

For example, Moscovitch and Nadel (Nadel and Moscovitch, 1997; Moscovitch and Nadel, 1998; Moscovitch et al., 2005) proposed alternative models from the neuroanatomical and clinical point of view and Funnell (2001) from the cognitive and developmental standpoint.

However, since the episodic–semantic distinction certainly constitutes the standard model of declarative memory organization, in the first part of this section I will discuss the problems raised by this dichotomous classification, in order to see, in the second part of the section, whether similar conclusions can also be extended to the alternative models of declarative memory.

2.1. Anatomical and functional problems raised by the distinction between episodic and semantic memory systems

According to the standard model, episodic and semantic memory are subtended by different neuroanatomical structures. This is based on the fact that disorders of episodic memory (amnesic syndromes) are typically due to bilateral lesions of the hippocampus and/or of other components of the Papez circuit (Papez, 1937), whereas selective disorders of semantic memory mainly result from damage to the left temporal neocortex. It is not clear, however, whether episodic and semantic information is acquired through distinct memory systems or whether both kinds of information are acquired through a common process. Data suggesting the complete independence of semantic knowledge from the mechanisms of acquisition of episodic memory consist mainly of single-case studies (e.g. Knowlton and Squire, 1994, 1996; Verfallie et al., 1995; Haslam et al., 1997), which have shown that some amnesic patients with hippocampal lesions and severe anterograde amnesia can acquire new semantic information. Vargha-Khadem et al. (1997) also supported this viewpoint. These authors reported developmental data, obtained from three children with severe amnesia resulting from hippocampal damage, who were able to attend mainstream school and obtain a low average level of literacy and factual knowledge, in spite of severe spatial and temporal disorientation and of day-to-day memory disorders. However, both clinical data and some neuroanatomically based computational models of long-term memory do not support the hypothesis of a complete independence between the mechanisms of acquisition of episodic and semantic memory. From the clinical point of view, two lines of evidence suggest that episodic memory may contribute to preserving or restoring some areas of meaning in semantic dementia. The first is the Snowden et al's (1994, 1995) observation that repeated autobiographical experience with certain categories of stimuli helps to maintain at least a partial knowledge of the corresponding word meaning in semantic memory. Thus, a patient who showed a massive anomia and a generalised loss of meaning across various semantic tasks, produced appropriate but very unusual words in spontaneous reports of personal activities, suggesting that concepts may be maintained in semantic memory by current personal experience with certain kinds of stimuli. Therefore, even if their general conceptual knowledge is impoverished, these patients retain a partial information about some conceptual islands, which is progressively constrained to the particular context these concepts have been experienced in.

The second line of evidence suggesting a facilitatory effect of current experience upon semantic memory is the Graham and Hodges (1997), Hodges and Graham (1998) demonstration that the temporal gradient for famous persons knowledge is different in amnesic patients with presumed early Alzheimer's disease and in patients with semantic dementia (SD). The former showed the temporally-graded retrograde memory loss originally described by Ribot (1881) in which memories from the recent past are more impaired than those from the distant past, whereas the latter were significantly better at retrieving memories from a recent time period, than from distant time periods. Indeed, Graham et al. (1999) questioned the semantic nature of knowledge updated by autobiographic experience in semantic dementia, stressing the fact that this knowledge mainly consists of fragmented 'semantic like' information, that does not generalise across similar instances. However, Snowden et al. (1995) had already at least in part acknowledged this fact.

These authors recognised that the conceptual islands retained by these patients were progressively constrained to the particular context in which these concepts had been experienced. Therefore the problem raised by these observation is to evaluate whether semantic memory consists of a static store of generalised abstract notions or of a dynamic system that has systematic interactions with experience it continuously learns from. This question was strongly stressed by Funnell (2001) and will be considered in some detail in the second part of this section. For the moment, I would simply underline the fact that these lines of clinical investigation show that intact episodic memory structures can have some influence on material stored in a memory system that is not strictly autobiographical. This suggests that mechanisms of acquisition of episodic and semantic memory may partially overlap.

From the computational point of view, the neuroanatomically-based models proposed by McClelland et al. (1995) and by Murre (1997) assume that the hippocampal complex and the temporal neocortex play an interactive, yet separable role in long-term memory storage. More precisely, the hippocampal complex could play a temporary role in the process of consolidation of new sensory experiences, whereas repeated reinstatement of these experiences over time could allow them to become permanently represented in the temporal neocortex. According to Hodges and Graham (1998) this dual stages process could allow more efficient organisation of the semantic store and potentiation of the synaptic connectivity required to encode new experiences. The gain of storing efficiency is suggested by McClelland et al. (1995) demonstration, using computer based simulation of semantic memory, that the direct integration of newly acquired information into the existing knowledge database can have a negative impact on the integrity of established knowledge and in particular of concepts that have some features in common with the new items. It might, therefore, be advantageous for the brain to utilise an initial temporary store, before adding new semantic knowledge to that previously acquired. The potentiation of synaptic connectivity should be required by the fact that we need a system that can make rapid synaptic adjustments to incoming stimuli to encode new experiences, but that the temporal neocortex does not have dense enough synaptic connectivity to interconnect distant sites in the short time in which an event is experienced. In Murre (1997) model, the hippocampus (which has a high number of reciprocal pathways, potentially mediating the transfer of information over time from the hippocampal system to the neocortex) could solve this conundrum, serving as an intermediate linking site between experienced events and their representation in the temporal neocortex.

2.2. *The relationships between autobiographical experience and semantic memory according to alternative models of declarative memory*

As I have already mentioned at the beginning of this section, the traditional dichotomy between episodic and semantic memory was recently challenged from the anatomical and clinical point of view by Moscovitch and coworkers' (Nadel and Moscovitch, 1997; Moscovitch and Nadel, 1998; Moscovitch et al., 2005) 'multiple trace theory' of and from a more theoretical perspective by Funnell's (2001) reinterpretation of semantic memory in terms of script theory (Shank and Abelson, 1977; Shank, 1982). Since a detailed discussion of these models exceeds the scopes of the present review, I will limit myself to presenting some of their main arguments and showing that these alternative models stress the continuous interaction between the hippocampal (autobiographical memory) system and the temporal neocortex, which plays a critical role in the representation of context-free and generalisable semantic memories.

The 'multiple trace theory' (Moscovitch et al., 2005) aims to fractionate episodic, semantic and spatial memory, by showing that there are important differences among different types of these memories and the structures that mediate them. To be sure, this theory claims that all consciously apprehended information is rapidly and automatically encoded by the hippocampal complex, which binds the neocortical neurons that represent that experience into a memory trace. A memory trace of an episode therefore consists of a bound ensemble of hippocampal and neocortical neurons, which represent a memory of the consciously experienced event. However, if each autobiographical memory trace is unique and is permanently mediated by the hippocampal system, the creation of multiple related traces facilitates the extraction of the neocortically mediated common information and its integration with pre-existing knowledge. The outcome of this process of increasing 'semanticization' is the formation of semantic memories, that can exist independently of the hippocampal complex and are permanently represented in specialised neocortical structures. However, since episodic and semantic memory have a common origin and differ simply on the basis of a repetition process that triggers (in the case of semantic memory) a process of 'semanticization', which strips the information from its actual context, they are better conceived as the ends of a continuum, rather than as qualitatively different forms of memory.

Funnell (2001) reached very similar conclusions in her stimulating reinterpretation of semantic memory disorders from a cognitive perspective based on the theory of event scripts (Shank and Abelson, 1977; Shank, 1982). Funnell's (2001) review of theoretical, clinical and developmental evidence led her to subscribe to Kintsch's (1980) claim that episodic and semantic memory form end points of a continuum, extending from completely context dependent episodes to truly general knowledge. Starting from these premises, she proposes a model that represents meaning at three levels: first as specific event knowledge; second as general (typical) event knowledge; and finally, at the most abstracted level of representation, as concepts isolated from context and represented at different levels of specificity.

As evidence to support her model, Funnell (2001) cited Snowden et al's (1994, 1995) previously mentioned observation that repeated autobiographical experience with certain categories of stimuli helps maintain partial knowledge of the corresponding word meaning in semantic memory, and Graham et al's (1999) queries about the semantic nature of this knowledge, which mainly consists of fragmented 'semantic like' information, that does not generalise across similar instances. Returning to the general problem that motivated the first section of this review, I can, therefore, conclude that authors who subscribe the distinction between episodic and semantic memory and (even more) authors who question this traditional dichotomy acknowledge that there is an overlap between the mechanisms of acquisition of autobiographic and of more general semantic knowledge.

3. The format of semantic representations and their relations with the underlying sensory-motor processes

In the previous section of this review I showed that most authors accept the distinction between episodic and semantic memory, but that processes involved in the acquisition of semantic knowledge are still controversial. Some authors suggest that the mechanisms of acquisition of episodic and semantic memory are completely independent, whereas others suggest that the structures involved in the acquisition of the former (namely the hippocampal complex) also play an important role in the first stages of acquisition of the latter.

A partly similar, but much more complex, situation can be found when we consider the relationships between semantic representations and sensory-motor processes preliminary to the acquisition of these representations. Indeed, all authors make a clear distinction between perceptual processes and conceptual-semantic representations, and describe semantic memory as consisting of three stages (input processes, stored representations and output processes). However, regarding the format of these representations and their relationships with the sensory-motor processes involved in their acquisition there is no consensus. In fact, there are two main lines of thought on this subject.

Authors who hold that perceptual and conceptual processes result from the activity of interrelated, but completely independent systems support the first line of thought. According to this view, the hierarchical stages of perceptual analysis proceed up to the level of a three-dimensional structural description, which includes a complete perceptual specification of objects prior to their meaningful recognition. At this stage no trace of the previous sensory-motor mechanisms is supposed to persist, since (according to Anderson and Bower, 1973; Pylyshyn, 1973, 1981; Seymour, 1979; Phillis and Cristie, 1977; Snoodgrass, 1984; Chambers and Reisberg, 1985 and, more recently, Humphreys and Riddoch, 1988; Riddoch et al, 1988; Caramazza et al., 1990; Patterson and Hodges, 2000; Coccia et al., 2004) the format of semantic representations, accessed through these structural descriptions, is conceived as abstract, amodal and propositional.

The second line of thought is defended by authors who refute the hypothesis of a central, amodal, abstract semantic system and assume that the semantic representations are stored in the same format in which they have been perceived, or that they keep the stamp of the perceptual mechanisms through which they formed. Two different positions can be distinguished in this second line of thought. The more radical view, defended by Warrington, Shallice and coworkers (Warrington, 1975; Warrington and McCarthy, 1994; Shallice, 1988; McKenna and Warrington, 2000) postulates the existence of multiple modality-specific semantic systems, in which objects are represented in the same format they are perceived in.

A weaker view is proposed by authors who, for parsimonious reasons, do not accept the hypothesis of multiple modality-specific semantic systems, but also refute the notion of a static, abstract and amodal semantic system. This last line of thought draws on cognitive models proposed by Kolers and Brison (1984); Allport (1985); Jackendoff (1987), who, reacting against the notion of abstract, propositional, amodal conceptual representations, envisaged concepts as activity patterns, distributed across different perceptual and motor attribute domains. For the sake of simplicity, later in this chapter I will use the terms '*amodal*' to refer to the first model, '*modality-specific*' to the second model and '*multimodal*' to the third model.

3.1. The debate between supporters of the unitary 'amodal' and the multiple, 'modality-specific' semantic systems

Although the principle of parsimony leads most authors to assume that a single amodal store is the most logical and intuitive system for storing semantic representations, some important clinical data seem difficult to reconcile with this prevalent theoretical viewpoint.

The first strong source of evidence inconsistent with the single amodal semantic system (and stressed by supporters of the multiple, modality-specific semantic hypothesis) consists of data, obtained in a condition usually labelled optic aphasia (Freund, 1889; Beauvois, 1982). In this condition, resulting from an ischemic vascular lesion in the territory of the Left

Posterior Cerebral Artery, patients cannot name visually presented objects, even though they are able to name them when they are presented in a non-visual modality and to mime their use on visual presentation.

These data suggest it is possible to access part of a semantic representation (e.g. the form of an object, its functional context, its typical use and so on) without necessarily having access to other parts, such as its name or other linguistically coded aspects of the same representation. Warrington and Shallice (Warrington and Shallice, 1979; Shallice, 1988; McCarthy and Warrington, 1991) took this dissociation as evidence of a distinction between two different semantic subsystems labelled, respectively, ‘visual semantics’ and ‘verbal semantics’. Caramazza et al. (1990) accepted empirical evidence showing privileged access from a particular modality of input (in this case visual) to a subset of the information (in this case perceptual and functional) defining the meaning of a concept. They claimed, however, that this fact does not necessarily demonstrate that semantic representation is organised into modality-specific sub systems. They also argued that privileged accessibility is an asymmetrical property of the semantic system, which applies only to perceptual predicates, because these predicates can be informative about the functional properties of an object; words, however, which have an arbitrary relationship to their meaning, bear no information about their referents in the world. Thus, various aspects of the meaning of the object ‘fork’ (such as the fact that forks have tines and a handle, and can be used for eating) are related to perceptually salient properties of this object, but not to phonological features of the corresponding word. Therefore, Caramazza et al. (1990) proposed an alternative model of semantic access—the privileged access unitary content hypothesis (PAUCH)—that allows ‘privileged accessibility’ without requiring that the system be organised into modality-specific subsystems.

From the viewpoint of the amodal semantic model, the main advantage of the PAUCH hypothesis is that it elegantly explains optic aphasia patients’ spared ability to mime the use of objects they are unable to name (Beauvois, 1982; Gil et al., 1985; Manning and Campbell, 1992; Campbell and Manning, 1996; Teixeira-Ferreira et al., 1997). Drawing on a Riddoch et al.’s (1988) thesis Hillis and Caramazza (1995) claimed that the miming activities of patients with optic aphasia are non-semantic acts, that may be mediated by perceptual attributes and can be explained by the perceptual affordances of objects whose use is mimed. By interpreting the spared mimic activities of patients with optic aphasia as non-semantic acts, Hillis and Caramazza (1995) rejected the hypothesis assuming that different modalities may preferentially access different components of the semantic system and defended the unitary, amodal, propositional model of semantic memory. Upon closer scrutiny, however, this interpretation seems rather implausible, because the perceptual affordances allowing inferences about some general functions of objects cannot provide the specific information needed to mime its use. Thus the view of a tool with a handle and a blade obviously suggests the object is used to cut, but will not tell us whether the object is a razor, a knife or a sword, namely objects that require very different miming activities.

Furthermore, Caramazza et al.’s (1990) claim that privileged accessibility is an asymmetric property of the semantic system, resulting from the affordances pictures (but not words) can have about certain properties of objects, cannot explain two further dissociations I will discuss in the next parts of this review, namely: (a) the fact that in ‘optic aphasia’ items belonging to some lexical categories (namely those denoting action knowledge and body parts knowledge) can be named much better than those denoting common objects, such as living things and artefacts (Gainotti, 2004); (b) the observation that in the absence of any visual-perceptual disorder some patients can draw much more information from words than from pictures.

Campbell and Manning (1996) have already discussed the problem of the selective sparing of action naming in patients with ‘optic aphasia’, with respect to the PAUCH hypothesis. These authors acknowledged that the hypothesis hardly explains why action naming may be selectively spared in ‘optic aphasia’. However, since the discussion of this question requires a preliminary analysis of the principles underlying the brain organization of different categories of knowledge I will delay a detailed consideration of this question to a later section of this review and I prefer to take into account now the problem of the different information that some patients can draw from words or from pictures, in the absence of any visual-perceptual disorder. This problem stems from studies conducted in patients with selective semantic memory disorders, resulting from either focal atrophy of the left temporal lobe (semantic dementia) or from a circumscribed vascular lesion of the right hemisphere, in which opposite forms of semantic memory disorders have been described by various authors. For example, McCarthy and Warrington (1988); Lauro-Grotto et al. (1997a) reported a prevalent difficulty in understanding the names, rather than the pictures, of objects, whereas McCarthy and Warrington (1986); Warrington and McCarthy (1994) described greater difficulty understanding pictures than words. Although these findings have been interpreted as consistent with the multiple, modality-specific semantic system hypothesis, Lambon Ralph et al. (1999); Patterson and Hodges (2000) reported different results and a different interpretation in a different group of patients with semantic dementia. These authors found that knowledge elicited from words and from pictures was highly correlated in these patients, even if the rate of success was higher for pictures than for words. The correlation between knowledge elicited from words and pictures was at variance with predictions based on the multiple semantic systems hypothesis and the higher rate of success with pictures was attributed to the fact that pictures afford certain properties of objects, whereas words have no affordance. In an attempt to clarify these conflicting results, Snowden et al. (2004) followed the same line of research in patients with degenerative lesions of the right and left temporal lobes. They reasoned that, since people’s faces and names are arbitrary, they could represent a potentially valuable means of addressing the unitary vs multiple semantic systems debate.

Semantic dementia patients with predominantly left temporal lobe atrophy identified faces better than names and performed better on the picture than on the word version of the semantic memory ‘Pyramids and Palm Trees’ test (Howard and Patterson, 1992) (Fig. 1), whereas patients with right temporal lobe atrophy showed the reverse pattern of performance.

These data were considered incompatible with a unitary amodal model of semantic memory and with a strict multiple modality-specific semantic systems account; they were considered consistent with a model, like the one proposed by Lauro-Grotto et al. (1997b), that views semantic memory as an integrated multimodal network in which different areas are accessed by different channels and store modality-specific information. Under normal circumstances, the various components of the net are interconnected, allowing retrieval of the entire representation from any input channel, but in pathological conditions one or more components of the net can be preferentially damaged, giving rise to dissociations in performance. More specifically, Snowden et al (2004) regarded the left temporal lobe as particularly important for verbal information and the right temporal lobe for visual information. Furthermore, in parallel with the notions of ‘convergence zones’, put forward by Damasio (Damasio, 1989; Damasio et al.,1990) and of ‘transmodal areas’ advanced by Mesulam (1998); Snowden et al. (2004) proposed that the anterior temporal lobes do not store concepts, but bind together components of information distributed through different sensory modalities.

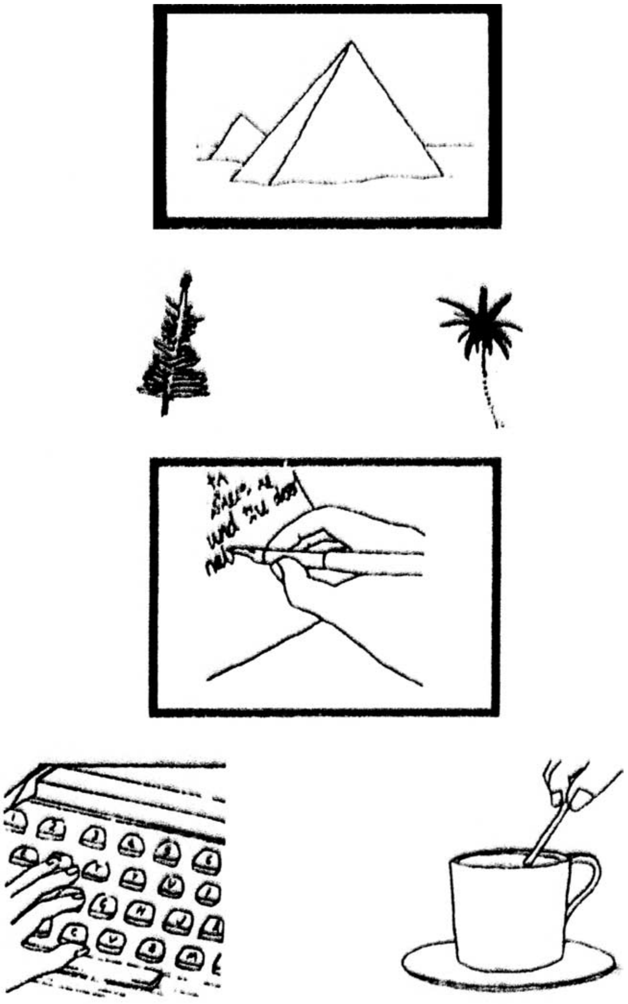

Fig. 1. In the upper part of the figure is reported an item of the ‘Pyramis and Palm Trees’ test, whereas in the lower part is reported an item of the ‘Kissing and Dancing’ test. In both tests patients must choose which of two drawings reported at the bottom of the page fits better with a target picture placed at the top. However, in the ‘Pyramis and Palm Trees’ test selection is based on conceptual relationships among objects, whereas in the ‘Kissing and Dancing’ test it is based on conceptual relationships among actions. (Partly modified from Bak and Hodges, 2003).

My own position is very similar to that proposed by Snowden et al. (2004). However, for the sake of clarity, I will now state the main points.

The first point is that for theoretical reasons I do not agree with a strict version of the multiple modality-specific semantic systems hypothesis. The reasons for this disagreement are, on one hand that a semantic representation cannot by definition be modality-specific, because it results from the convergence/integration of information coming from different modalities and, on the other hand, the conviction that a literal version of this hypothesis is implausible, because it postulates a duplication of information across different subsystems.

The second point is that the unitary amodal semantic model can be criticised not only from the empirical point of view (because of its inability to account for the above mentioned aspects of optic aphasia and of semantic dementia), but also because it is not necessarily more parsimonious (in terms of neural activity) than the multiple modality-specific semantic model. As a matter of fact, unitary abstract models do not offer an explicit model, that explains how perceptual information coming from different sensory modalities can be transformed into a set of abstract propositions. This problem of the mechanisms required to translate modality-specific information into abstract information becomes even more relevant if we accept Damasio’s (1989) model, which suggests that semantic representations are not localised in a static store, but must rather be conceived as a dynamic process of recollection of fragmented perceptual-motor features. In this case, it would be necessary to evaluate the costs for the brain of this bidirectional transcoding mechanism, or, in any case, to acknowledge that an abstract, amodal system is not necessarily very parsimonious.

For these reasons, I agree with models (such as the one proposed by Lauro-Grotto et al., 1997b) that consider the semantic system as an integrated multimodal network, keeping the influence and the flavour of the prevailing input and output modalities in its various parts. Within this context, I would subscribe to a broad and modified version of the distinction, proposed by Warrington and Shallice (1979); Shallice (1988); McCarthy and Warrington (1991), between a ‘visual semantic’ and a ‘verbal semantic’ system. According to this broad version, the term ‘visual semantic system’ refers to an integrated convergence of perceptual information, where the visual modality plays the greatest role, and the term ‘verbal semantic system’ stands for a semantic system that is mainly organised in linguistic terms. In this case, the distinction between 'verbal semantic' and 'visual semantic' system could be very useful, because it reflects the characteristics of the multimodal networks typical, respectively, of the right and left hemisphere. This interpretation is consistent with Coslett and Saffran's (1989, 1992) distinction between a right hemisphere semantic structure mainly based on the integration of perceptual data and a left hemisphere semantic system, intimately connected with naming abilities.

Some data recently obtained in semantic dementia patients seem to support this equivalence between the broad acceptance of the term 'visual semantics' and the convergence of perceptual information (mainly consisting of visual data) typical of the right hemisphere semantic system. On one hand, Barbarotto et al. (1995); Evans et al. (1995), Gentileschi et al. (1999, 2001) and Gainotti et al. (2003) have shown that the selective progressive defect in recognising familiar people shown by patients with right anterior temporal atrophy must be considered as a multimodal semantic (rather than as a modality-specific face recognition) defect. On the other hand, Gainotti et al.'s (2003) detailed analysis of patient C.O. showed that this patient's ability to recognise familiar people was much more impaired through the visual (face) and auditory (voice) perceptual modalities than trough the verbal (person's name) semantic access. It is, therefore, possible to suppose that the person-specific semantic knowledge represented in patient's C.O. right hemisphere was based more on a convergence of perceptual (visual and auditory) data than on an integration of these perceptual data with verbally-coded information.

Coming back to the much more general problem of the relationships between semantic representations and perceptual processes preliminary to their acquisition, Rogers et al. (2004) recently obtained data that raise doubts about the assumption of complete independence between the last stages of the perceptual processing (structural description) and the corresponding semantic representations. These authors tried to investigate the impact of semantic degradation on (lexical and) object decision tasks, i.e. on tasks that are currently used to assess the integrity of the corresponding structural description. The variables considered in this study were the typicality of objects (and words), their frequency and familiarity and the degree of semantic degradation. Results showed that (lexical and) object decision tasks are impaired in semantic dementia patients and that this impairment mainly concerned atypical and less familiar objects and did so increasingly in patients with greater semantic deterioration. These data are not surprising, since Patterson et al. (1994) and Gainotti et al. (1995) have already shown that within the language domain a severe semantic impairment can have a deleterious influence upon (pre-semantic) purely lexical tasks.

In any case, they support the view of ongoing interactions between perceptual and semantic representations, rather than the independence between modality-specific perceptual channels and the unitary, abstract, amodal semantic system.

4. The categorical organization of semantic memory

In the introductory part of this chapter I acknowledged Warrington's (1975) seminal role in identifying selective defects of semantic memory in patients with focal cortical atrophies. In a very influential series of papers, the same author also proposed that semantic memory may be categorically organized in the brain, because different brain lesions can provoke different sorts of category-specific disorders, selectively affecting abstract words (Warrington, 1975, 1981), action names/verbs (Baxter and Warrington, 1985; McCarthy and Warrington, 1985), biological entities (Warrington and Shallice, 1984; McCarthy and Warrington, 1991) and man-made artefacts (Warrington and McCarthy, 1983; 1987).

However, Warrington's contributions in this field go beyond the identification of different kinds of category-specific semantic disorders and the proposal that semantic knowledge may be categorically organised in the brain. Discussing the contrast between category-specific disorders for living things and artefacts, Warrington and McCarthy (1983) and Warrington and Shallice (1984) also advanced a general hypothesis about the brain representation of semantic knowledge, which challenged the traditional views about the cortical representation of concepts and offered a general key to understanding the basic mechanisms subserving category-specific semantic disorders. This general hypothesis, labelled the 'differential weighting hypothesis' contrasted both traditional associationistic views, which assumed that concepts generically result from the convergence of multiple sensory modalities in cortical association areas, and with the abstract, amodal and propositional models of semantic knowledge proposed by Anderson and Bower (1973), Pylyshyn (1973, 1981), Phillis and Cristie (1977) and Seymour (1979). Although the 'differential weighting' hypothesis acknowledged that concepts are based on the linkage of the output of various perceptual systems, it also stressed the different weight these sensory modalities have in the acquisition of different categories of knowledge. Within this context, the dissociation between living beings and artefacts was viewed as the consequence of the different weighting of visual-perceptual and functional attributes in identifying members of living and artefacts categories.

This interpretation was consistent with the theoretical models concerning the functional bases of conceptual activity proposed in the same years by several cognitive psychologists, such as Kolers and Brison (1984), Allport (1985) and Jackendoff (1987), who reacted against the notion of abstract, propositional, amodal conceptual representations. These authors suggested that the organisation of semantic representations reflects how the information most relevant for their development has been acquired. This theoretical construct also fits with connectionist models (e.g. Ballard, 1986; Churchland and Sejnowski, 1988; Farah and McClelland, 1991), which hold that information processing and storage are closely interconnected in a network, since information is stored as a pattern of activity in the connections between the units of the net which process a given type of information.

From the anatomical point of view, the differential weighting hypothesis and the above mentioned cognitive models predict a close relationship between cortical areas crucially involved in processes of storage/retrieval of a given category and the localisation of the brain mechanisms that have contributed most to the development of that category.

In the present discussion of the categorical organization of semantic memory, I will focus on the two main dissociations that have emerged as most important in the study of category-specific semantic disorders, namely, the contrast between the semantic-lexical representations of actions/verbs and, respectively, of objects/nouns and (within the latter) the contrast between the semantic representations of biological entities and, respectively, of artefacts. In both domains, I will first report some clinical and experimental data that support the dissociation and will then discuss the principal interpretations that have been advanced to explain these data. I will then take into account the anatomical locus of lesions found in these category-specific semantic disorders and discuss their consistency with the set of predictions based on the 'differential weighting hypothesis'. This set of predictions will be labelled 'the sensory-motor model of semantic knowledge' (Gainotti, 1990, 2004, 2006; Saffran and Schwartz, 1994; Gainotti et al., 1995; Martin, 1998; Martin and Chao, 2001). In the last part of this section I will briefly discuss the results of neuroimaging experiments that have studied the brain areas activated by different semantic categories in normal subjects; then, I will report the results of a recent review I made to further check the 'sensory-motor model of semantic knowledge', by investigating category-specific naming disorders in patients with visuo-verbal disconnection/'optic aphasia' (Gainotti, 2004).

4.1. Disorders in production and comprehension of object and actions names in brain-damaged patients

Goodglass et al. (1966) carried out the first study that suggested a differential impairment of nouns and verbs in patients with different aphasic syndromes. These authors noticed that patients with fluent aphasia are particularly impaired in naming objects (producing nouns), whereas non-fluent aphasics are more impaired in naming actions (producing verbs). This double dissociation was afterwards further investigated both in single-case studies (e.g. Marin et al., 1976; Miceli et al., 1983; McCarthy and Warrington, 1985; Zingeser and Berndt, 1988; Caramazza and Hillis, 1991; Breedin et al., 1994; Miozzo et al., 1994; Shapiro et al., 2000) and in group studies (Miceli et al., 1984, 1988; Zingeser and Berndt, 1990; Tranel et al., 2001), with particular attention to agrammatic patients, among non-fluent aphasics and to anomic patients among fluent aphasics. All these studies showed that: (a) agrammatic patients are particularly impaired in naming actions, whereas anomic patients are selectively unable to name objects (Miceli et al., 1984; Zingeser and Berndt, 1988, 1990; Breedin et al., 1994; Miozzo et al., 1994); (b) the same kind of dissociation can be observed in comprehension of nouns and verbs (McCarthy and Warrington, 1985; Miceli et al., 1988; Breedin et al., 1994); (c) some (anomic or agrammatic) patients show a selective disorder (for nouns or verbs) only in production, whereas other patients show a category-specific disorder (for nouns or verbs) in both production and comprehension (McCarthy and Warrington, 1985; Miceli et al., 1988; Zingeser and Berndt, 1988; 1990; Caramazza and Hillis, 1991; Breedin et al., 1994; Miozzo et al., 1994; Breedin and Martin, 1996; Silveri and Di Betta, 1997; Hillis et al., 2002).

Various authors gave a different interpretation of the cognitive defects underlying these category-specific disorders for nouns and verbs. Thus, the association between agrammatism and verb retrieval led Miceli et al. (1984, 1988) to suggest that the underlying defect was located at the syntactic level. On the other hand, based on the observation of two patients with a modality-specific defect in verb production (in the oral and respectively in the written modality), Caramazza and Hillis (1991) suggested that the cognitive defect concerned the lexical level, selectively affecting verbs as a specific grammatical category. This interpretation has been strengthen by report of other patients showing selective difficulty in producing verbs in the oral or in the written modality (Rapp and Caramazza, 1998; Hillis et al., 2002). Finally, Damasio and Tranel (1993), Gainotti et al. (1995), Gainotti (1998) and Bird et al. (2000) argued that, at least in patients who show a selective impairment for nouns or verbs in both production and comprehension, the defect has to be located at the semantic level.

It seems clear from the above interpretations and from data gathered in more recent years, that the greatest uncertainties concern the clinical features and the cognitive defects underlying category-specific disorders for verbs. This can be explained both theoretically and factually. The former derive from controversies over the relationships between semantic and syntactic aspects of verb representations (Pinker, 1989; Jackendoff, 1990), whereas the latter refer to the observation that a very heterogeneous set of disturbances is usually grouped under the 'category-specific impairments for verbs' heading (see Marshall et al., 1996; Gainotti, 1998; Marshall, 2003; Shapiro and Caramazza, 2003, for different viewpoints on this subject). In any case, since some category-specific verb disorders are certainly due to a disruption of the semantic representation of actions, I will focus my attention on this more circumscribed problem later in this paper. In particular I will try to clarify whether the anatomical locus of lesion is different in patients with a category-specific impairment for action names and object names and whether the neuroanatomical correlates of these category-specific disorders are consistent with the predictions based on the 'sensory-motor model of semantic knowledge'.

As for the neuroanatomical correlates of disorders selectively affecting nouns and verbs, both direct and indirect evidence suggests an association between action name deficit and left frontal areas and between object name deficit and left temporal pathology. The indirect evidence is based on the standard anatomical locus of lesion in agrammatism (where selective verb disorders are usually observed) and in aphasic anomia, where disorders are limited to the production and comprehension of names of objects. Direct evidence consists of results of experimental studies, conducted in normal subjects by Shapiro et al. (2001) and Cappa et al. (2002) using repetitive transcranial magnetic stimulation (rTMS), to modify the excitability of the left prefrontal cortex during object and action naming tasks and of neuroimaging data, originating from patients with vascular, neoplastic and degenerative syndromes (Damasio and Tranel, 1993; Daniele et al., 1994; Bak and Hodges, 1997; Cappa et al., 1998a; Rapp and Caramazza, 1998; Tranel et al., 2001; Hillis et al., 2002; Tranel et al., 2003; Saygin et al., 2004). Results of rTMS experiments show that the left prefrontal cortex is selectively involved in action naming, whereas neuroimaging data confirm that a selective impairment of action names is associated with left frontal lesions, and a defect of object names is found in patients with left temporal pathology.

Although in some of these studies (e.g. Rapp and Caramazza, 1998; Tranel et al., 2001; Shapiro et al., 2001; Hillis et al., 2002) data concerning verbs have been interpreted within the framework of the grammatical category hypothesis, data obtained in other investigations (e.g. Damasio and Tranel, 1993; Daniele et al., 1994; Bak and Hodges, 1997; Tranel et al., 2003; Saygin et al., 2004) clearly point to a disorder affecting the semantic representation of actions in patients with left frontal lesions. Patients with this kind of lesion location were, for instance, particularly impaired on tasks designed by Tranel et al. (2003) to tap into the conceptual knowledge of actions and on non-linguistic tasks of action comprehension (pantomime interpretation) designed by Saygin et al. (2004).

Furthermore, Bak and Hodges (2003) obtained other data suggesting that selective verb disorders observed in patients with left frontal lesions are due to a disruption of the semantic representation of actions. These authors found a double dissociation between frontal and temporal variants of Fronto-Temporal Dementia on two conceptual tests (Fig. 1), one based on objects (the ‘Pyramids and Palm Trees’ test, devised by Howard and Patterson (1992)) and the other on actions (the ‘Kissing and Dancing’ test, devised by Bak and Hodges (2003)). Patients with the left frontal variant were more impaired on the Kissing and Dancing’ test, whereas patients with left temporal atrophy (Semantic Dementia) were more impaired on the ‘Pyramids and Palm Trees’ test.

Taken together these data are consistent with the ‘sensory-motor model of semantic knowledge’, which assumes that the brain areas damaged in a given form of category-specific semantic disorder were previously involved in the acquisition of sensory-motor information crucial for the development of that category. From this point of view, it is logical to expect that a selective inability to name or understand action names will usually be due to a lesion of the parts of the left frontal lobe, where action schemata are planned and represented and which become active not only when a motor schema is actually executed, but also when it is recognized in other subjects (Gallese et al., 1996; Rizzolatti et al., 1996; Rizzolatti and Arbib, 1998) or simply imagined (Decety et al., 1997).

Further support for this model comes from recent detailed investigations of the neural substrate of verb meaning, conducted with neuroimaging techniques by Grossman et al. (2002) and with neurophysiological procedures by Pulvermuller et al. (2001). In an fMRI study Grossman et al. (2002) observed, that a different pattern of activation is associated with verbs of motion and verbs of cognition, since only the former (which represent events involving action planning) activate the prefrontal cortex, whereas the latter (which contain few associated sensory-motor features) activate the left postero-lateral temporal cortex. On the other hand, Pulvermuller et al. (2001) showed that different parts of the frontal lobe are recruited by verbs denoting different kinds of actions. Using high resolution EEG recordings, these authors investigated the brain activity elicited by verbs referring to actions performed with the face (e.g. ‘talking’) and with the lower limb muscles (e.g. ‘walking’). Face-related action verbs produced the strongest activity over the left Sylvian fissure, close to the part of the motor cortex that represents face movements, whereas leg-related action verbs produced the strongest in-going currents at the vertex, close to the cortical representation of the leg movements.

4.2. *Disorders in identifying living things and man-made artefacts in brain-damaged patients*

The most frequently reported instance of a category-specific semantic disorder consists of a striking dissociation between a severe inability to recognise living beings and a preserved capacity to identify man-made artefacts. Warrington and Shallice (1984) first reported the main characteristics of this syndrome in four patients who had partially recovered from herpes simplex encephalitis. These characteristics have been confirmed with surprising regularity by other authors, who have investigated the pattern of cognitive impairment and/or the distribution of the anatomical lesions associated with this form of category-specific semantic disorder (e.g. Basso et al., 1988; Pietrini et al., 1988; Sartori and Job, 1988; Silveri and Gainotti, 1988; Sirigu et al., 1991; Hart and Gordon, 1992; Laiacona et al., 1993; Sartori et al., 1993; Sheridan and Humphreys, 1993; De Renzi and Lucchelli, 1994; Gainotti and Silveri, 1996; Forde et al., 1997; Kolinsky et al., 2002).

From the cognitive point of view, these patients show a severe inability to identify animals, fruits, flowers and vegetables, which is independent from the verbal or pictorial modality through which information is presented and the patient’s response is expressed and is in contrast with a relatively spared capacity to identify artefacts and body parts. The opposite dissociation, namely a prevalent impairment of artefacts and body parts, has been much less frequently reported (e.g. Warrington and McCarthy, 1983, 1987; Hillis and Caramazza, 1991; Sacchett and Humphreys, 1992; Cappa et al., 1998b) and is, in any case, much less impressive than the previously described selective inability to identify living beings.

In spite of the dramatic and selective nature of category-specific semantic disorders for biological entities, some authors have advanced the hypothesis that they may be an artefact of stimulus selection. Thus, Funnel and Sheridan (1992), Stewart et al. (1992) and Gaffan and Heywood (1993) raised the question of whether category specific deficits for living things might not simply reflect the fact that these items tend to be of lower frequency, lower familiarity and greater visual complexity than non-living things. These authors reported patients in whom the category-specific semantic deficit disappeared when living and non living categories were carefully matched for frequency, familiarity and visual complexity.

Although methodological caution is certainly important, and I have even shown (Gainotti, 2005) that in single case studies gender-related familiarity effects can explain the prevalent impairment of some semantic categories, they cannot explain the most prototypical instances of category specific semantic disorders. As a matter of fact, (1) many patients continue to show disproportionate difficulty in naming or recognising living things even when frequency, familarity and visual complexity are taken into account (Warrington and Shallice, 1984; Hart and Gordon, 1992; Laiacona et al., 1993; Sartori et al., 1993; Sheridan and Humphreys, 1993; Farah et al., 1996; Gainotti and Silveri, 1996, etc.); (2) some patients show a disproportionate deficit for the (supposedly easier to process) category of non-living things; (3) some authors have reported instances of patients who showed opposite category-specific deficits, when tested with the same stimuli (Hillis and Caramazza, 1991; Gainotti and Silveri, 1996; Silveri et al., 1997). Thus, in spite of these specific objections and of more general methodological critiques, such as the ones Laws (in press) recently addressed to the existing literature on category-specific naming disorders, it remains unquestionable that some kinds of brain lesions (which will be considered later in some details) give rise to a specific disruption of knowledge of biological entities.

However, the interpretation of this pattern of categorical impairment remains very controversial, because three main theoretical accounts have been proposed for category-specific semantic disorders for living and non-living things. The first and more influential model is the one Warrington and Shallice put forward in their 1984 seminal paper. It assumes that the living/non-living distinction may be the by-product of a more basic dichotomy, concerning the differential weighting of visual-perceptual and functional attributes in identifying members of biological and, respectively, of artefacts categories. According to this interpretation, which has been called the 'sensory-functional theory', identification of a particular exemplar of a living category relies crucially on visual features, whereas identification of a of man-made artefact depends critically on functional attributes, i.e. the subtly different functions artefacts were designed for.

More recently, Caramazza and Shelton (1998) proposed a second theoretical model. It starts with a factual objection to the 'sensory-functional theory', namely with the observation that a greater impairment of the visual-perceptual rather than of the functional associative properties of the disrupted category is not necessarily present in patients with a category-specific defect for living things. This objection, which is supported by much empirical data (see Caramazza, 1998; Capitani et al., 2003, for review) is not necessarily inconsistent with the 'sensory-functional theory'. This is because Farah and McClelland (1991) using computer simulation showed: (a) that it is possible to produce a category-specific defect for living things by preferentially damaging sensory inputs and (b) that both perceptual and functional attributes of biological entities are equally disrupted in this computational model of a category-specific defect. In any case, starting from the weakness of the 'sensory-functional theory' and from the observation that animals and plant life can be independently affected in individual patients [for example, animals were. selective impaired in patients KR (Hart and Gordon, 1992) and EW (Caramazza and Shelton, 1998), whereas fruits and vegetable were selectively affected in patients MD (Hart et al., 1985), TU (Farah and Wallace, 1992), and FAV (Crutch and Warrington, 2003), Caramazza and Shelton (1998) proposed that category-specific defects may be due to the disruption of different evolutionary-adapted dedicated neural mechanisms for the domains of 'animals' (potential predators), 'plant life' (possible source of food and medicine) and 'artefacts'. This model is usually labelled the 'domain specific knowledge systems' hypothesis.

The third and last theoretical model, proposed by Gonnerman et al. (1997), assumes that different levels of interconnections may exist within the semantic structure between shared (perceptual and functional) attributes of living and non-living things. Thus, in living beings, the fact of having eyes and ears is correlated with the properties of seeing and hearing, whereas in artefacts similar interconnections are much less important. According to Gonnermann et al. (1997), this difference may be more important than the differential weighting of perceptual and functional attributes to explain category-specific semantic disorders. This last model is often labelled the 'intercorrelations among semantic features' hypothesis.

The main criteria that have been used by various authors to support or disprove these theoretical models are the following: (a) the relative impairment of visual and functional knowledge in patients with selective damage to the living or non-living categories; (b) the detailed pattern of impaired and spared categories that can be found in these patients; (c) the results of computational studies, using computer simulation to produce category-specific defects for living or non-living things.

Less frequently considered, although potentially relevant from the theoretical point of view, are the neuroanatomical correlates of category-specific semantic disorders, because each of the above mentioned theoretical models makes a different set of predictions about extent and localization of the underlying brain pathology. Thus, the sensory/functional hypothesis, which stresses the importance of visual-perceptual attributes in the semantic representation of living categories, and the relevance of functional attributes in the semantic representation of artefacts, leads to the prediction that lesions provoking a category-specific semantic impairment for living things should encroach upon brain structures playing a critical role in processing and integrating high level visual knowledge, whereas those provoking a selective deficit for artefacts should encroach upon brain areas involved in manipulation and physical use of objects.

Less clear are the predictions made by the ‘domain-specific knowledge systems’ hypothesis; however, Caramazza (1998) and Caramazza and Shelton (1998) explicitly claimed: (a) that dedicated neural circuits for domain-specific knowledge systems, representing all types of perceptual and conceptual information relevant to that category of knowledge exist within the central nervous system; (b) that, because of the affective/emotional components associated with flight and feeding responses to animals and plants, it is not implausible that the assumed neural circuits for these biological categories involve the limbic structures.

Still different are the predictions made by the ‘inter-correlations among semantic features’ hypothesis, because this model assumes that the severity of brain damage, rather than its precise anatomical location, plays a major role in provoking a category-specific defect for living or non-living entities. Indeed, Gonnerman et al. (1997) argued that biological entities, which have many more interconnected features in their semantic structure than artefacts, should be more resistant to mild diffuse damage of the semantic system. This hypothesis was validated by a computer simulation study, that showed that with a small degree of damage to the system there is a greater impairment of artefacts, whereas with increasing damage, there is a dramatic decline of the living categories. However, on the basis of a different connectionist model, Moss et al. (1998); Tyler et al. (2000) predicted the opposite type of interaction between prevalent impairment of biological or artefact categories and stage of disease progression. In any case, according to these models, the severity of lesions should be more important than their anatomical location in determining category-specific semantic disorders.

Since our knowledge of the neuroanatomical correlates of category-specific semantic disorders for living beings and artefacts is almost completely based on single-cases studies, I tried to more thoroughly investigate the problem by making a detailed and systematic review (Gainotti, 2000) of all the available anatomo-clinical reports of patients showing a category-specific semantic disorders for living things and artefacts. In this review I took into account some cognitive and anatomical variables that could differentially influence the results obtained. These variables were: (a) the locus of cognitive impairment (distinguishing semantic, lexical and visuo-perceptual disorders); (b) the aetiology of the disease; (c) the neuroanatomical locus of lesion.

Out of the 47 patients who showed a selective impairment for living beings, and who met the inclusion criteria, the deficit concerned the semantic level in 38. From the aetiological point of view, most of these patients suffered from three diseases, caused by lesions that usually encroach upon the anterior parts of the temporal lobes, namely herpes simple encephalitis in 20/38 patients, head trauma in seven and semantic dementia in five. The very high prevalence of herpes simple encephalitis among these patients is worth-stressing, because this disease, although rather uncommon was responsible for all the cases Warrington and Shallice reported in their 1984 seminal paper and for about one half of all cases reported in the literature. A detailed analysis of lesion location in the patients I investigated for my review (Fig. 2) showed that: (a) within the temporal lobes, lesions were usually bilateral, but asymmetrically distributed, with a clear prevalence for the left side and (b) almost invariably the anterior, medial and inferior parts of the temporal lobes were impaired, whereas the lateral and posterior parts were spared. On the other hand, in the 10 patients who showed a category-specific impairment for artefacts, the deficit concerned the semantic level in six. All these patients also showed a defect in recognising body parts and were affected by vascular lesions in the territory of the left middle cerebral artery, which usually involved the fronto-parietal areas (Fig. 3), provoking a severe, non-fluent aphasia.

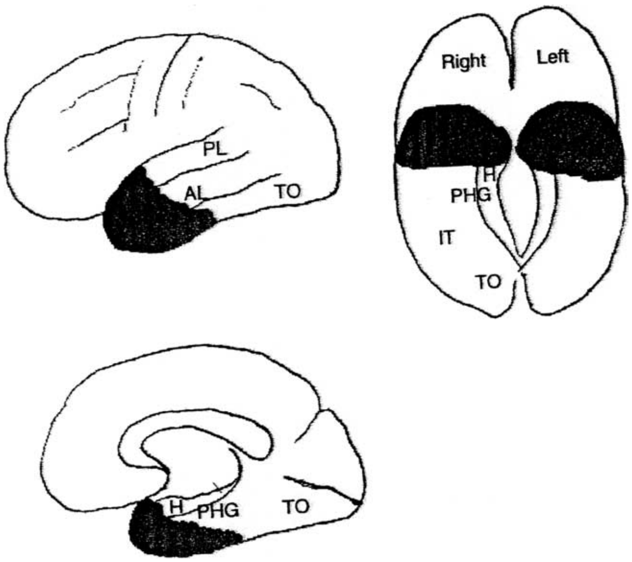

Fig. 2. Schematic representation of the anatomical locus of lesion found in patients with a category-specific semantic impairment for biological entities. H: hippocampus; PHG: parahippocampal gyrus; TP: temporal pole; IT: inferior temporal gyrus; AL: antero-lateral temporal cortex; PL: postero-lateral temporal cortex; TO: temporo-occipital cortex. (Partly modified from Gainotti, 2002).

These contrasting patterns of cognitive and anatomical data can, in my opinion, be explained if we contrast the main functions of the antero-medial and inferior parts of the temporal lobes with those of the fronto-parietal areas of the dominant hemisphere.

I would argue that the antero-medial temporo-limbic structures and the infero-temporal lobe (ITL) constitute a cortical network, devised to process high level visual-perceptual knowledge and to integrate it with other kinds of information. The ITL is, in fact, the main component of the ‘ventral stream’ of extra-striate visual processing system, which plays a critical role in object recognition (Ungerleider and Mishkin, 1982; Mishkin et al., 1984; Goodale et al., 1991).

On the other hand, within the medial temporal lobe (MTL) structures, several areas are considered either as rostral regions of the ‘ventral stream’ or as multimodal areas where highly processed visual data are integrated with non-visual properties of objects. Thus, at least in animals, the perirhinal cortex has been considered to be involved in complex visual discriminations (Bussey et al., 2002, 2003) and in visual object representation (Bussey and Saksida,

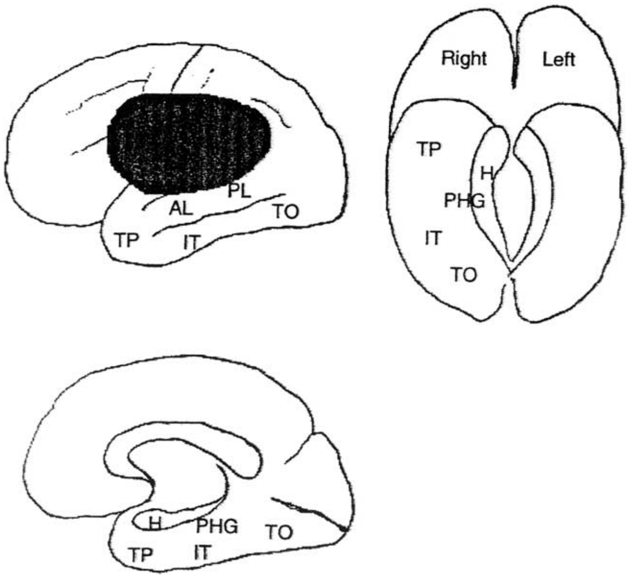

Fig. 3. Schematic representation of the anatomical locus of lesion found in patients with a category-specific semantic impairment for artefacts. H: hippocampus; PHG: parahippocampal gyrus; TP: temporal pole; IT: inferior temporal gyrus; AL: antero-lateral temporal cortex; PL: postero-lateral temporal cortex; TO: temporo-occipital cortex. (Partly modified from Gainotti, 2002).

2002), whereas the entorhinal cortex receives convergent, integrated input from all the sensory modalities (Jones and Powell, 1970; Mesulam et al., 1977; Van Hoesen, 1982), through the parahippocampal and perirhinal cortices (Suzuki and Amaral, 1994). Furthermore, Lee et al. (2005) have recently challenged the view suggesting that in humans the MTL plays an exclusive role in memory functions, and have shown that patients with MTL damage, including the perirhinal cortex, are significantly impaired in discriminating scenes, faces and, to a lesser extent, objects.

Finally, Damasio (1989) and Mesulam (1998) considered the temporal pole as a higher order convergence zone, i.e. as the top of a cascade of densely interconnected cortical processors that binds together the different components of a concept's distributed representation. Inferior temporal lobe, temporo-limbic structures and temporal pole could, therefore, be critically involved in processing, storing and retrieving the representations of those semantic categories whose knowledge is mainly based on sensory (and above all visual) attributes.

A very different set of functions is usually attributed to the dorso-lateral (and in particular to the fronto-parietal) areas of the dominant hemisphere. These areas are, in fact, part of the 'dorsal stream' of visual processing, involved in spatial and action functions (Goodale et al., 1991) and play a very important role both in action planning and in high level somatosensory processing. Therefore, the fronto-parietal areas of the dominant hemisphere subtend those somatosensory and motor schemata that may have contributed critically (through processes of concrete utilization and physical contact) to building the semantic representation of man-made objects.

In this view, the joint impairment of the man-made objects and body parts categories may be due to the fact that the sensory-motor mechanisms that contribute critically to the construction of the semantic representation of man-made objects are also crucially involved in building the representation of the body parts category.

4.3. Brain areas activated by different semantic categories in functional neuroimaging experiments

By and large consistent with the 'sensory-motor model of semantic knowledge', but less clear-cut than neuroanatomical data are the findings provided by functional neuroimaging experiments (see Martin, 1998; Martin et al., 2000; Martin and Chao, 2001; Price and Friston, 2002, Martin and Caramazza, 2003, and Thompson-Schill, 2003 for reviews).

More precisely, the view that the infero-lateral part of the left frontal lobe may be strongly activated by tasks concerned with actions found support in studies dealing with the generation of action words (Martin et al., 1995; Petersen et al., 1988), listening to action-related sentences (Tettamanti et al., 2005) or the observation of meaningful actions (Decety et al., 1997; Grezes et al., 1999; Grezes and Decety, 2001, 2002). However, Warburton et al. (1996) and Tyler et al. (2001) reported no difference between cortical areas activated by nouns and verbs. Analogously, some authors (Perani et al., 1995; Martin et al., 1996; Grabowski et al., 1998; Chao and Martin, 2000) confirmed the activation of the fronto-parietal areas of the left hemisphere in tasks requiring the identification and naming of tools, whereas others (Damasio et al., 1996; Mummery et al., 1996; 1998; Moore and Price, 1999; Perani et al., 1999) did not. Indeed, the latter found a more marked activation in the posterior middle temporal region, which is involved in visual control of actions associated with objects (Martin et al., 1995).

Equally controversial is the relationship between living stimuli and activation of the antero-infero-medial parts of the temporal lobes. According to most authors, living stimuli mainly activate the infero-temporal cortex (Perani et al., 1995) or the antero-medial parts of the temporal cortex (Mummery et al., 1996; Moore and Price, 1999; Devlin et al., 2002a; Phillips et al., 2002). However, Spitzer et al. (1995, 1998) and Perani et al. (1999) reported results at variance with this model. Furthermore, Cappa et al. (1998c), Mummery et al. (1998) and Devlin et al. (2002b) failed to find an association between the anatomical areas activated by visual-perceptual vs functional/associative knowledge and those activated by biological vs artefacts categories as predicted by the sensory/functional hypothesis (see critical reviews in Price and Friston, 2002 and in Devlin et al., 2002a).

Therefore, even if most studies do show evidence of an association between action words and left frontal cortex, between tool knowledge and left fronto-parietal cortex, and between living things and antero-medial-inferior parts of the temporal lobes, there is not an universal agreement on this. There may be two reasons for the different results obtained in lesion studies and in functional imaging experiments: (1) the difficulty of neuroimaging experiments to control variables, such as the methods used for data acquisition, the nature of the stimuli or the experimental design; (2) the greater difficulty of distinguishing between category-specific conceptual and lexical operations in neuroimaging experiments than in lesion studies. This distinction can be easily made in lesion studies, as shown by the separate analysis of semantic, lexical and visual-perceptual defects for living or non-living things I made in my review of the neuroanatomical correlates of these disorders (Gainotti, 2000). On the contrary, in functional neuroimaging experiments, the patient's responses are a conflation of recognition and naming processes, since normal subjects, when requested to perform tasks that involve recognition or naming of various stimuli, are unable to voluntarily suppress one part of the process and execute both semantic and lexical operations.

4.4. Category-specific naming disorders in 'optic aphasia'

One line of research that could also be used to investigate the neuroanatomical organisation of categorical knowledge is the study of impaired and spared categories on visual naming in patients with 'optic aphasia' (or, in any case, with a visuo-verbal disconnection syndrome). This topic was considered worthy of interest for two main reasons—the first is the observation that action naming (Manning and Campbell, 1992; Campbell and Manning, 1996; Teixeira-Ferreira et al., 1997) and body parts naming (Shelton et al., 1998), can be selectively spared in these patients—the second is the observation, made in my previous review of the neuroanatomical correlates of category-specific disorders for living beings and artefacts (Gainotti, 2000), that some patients with a vascular lesion in the territory of the left posterior cerebral artery seemed to show a selective naming impairment for fruit and vegetables (e.g. Farah and Wallace, 1992; Goldenberg, 1992). These observations might suggest that in patients with optic aphasia access to the lexical output mechanisms differs according to categories of knowledge. The more specific set of predictions advanced in this review was prompted by the classical neurological models of 'optic aphasia' and of 'visuo-verbal disconnection' proposed by Freund (1889) and by Geschwind (1965). According to the Freund's (1889) model, a concomitant lesion of the left visual areas and of the posterior parts of the corpus callosum is expected to prevent visual information (processed by the right hemisphere visual cortices) from reaching the left hemisphere lexical output mechanisms, since the inter-hemispheric pathways connecting the right and the left visual cortices pass through the splenium (i.e. the posterior part) of the corpus callosum. Geschwind (1965) noticed that, in spite of this disconnection between right and left hemisphere visual cortices, some visual stimuli are usually correctly named and attributed these residual visual naming abilities to the use of alternative inter-hemispheric callosal pathways. According to this author, the vision of an object arouses associations in other sensory modalities and 'the arousal of such associations permits the finding of an alternative pathway across uninvolved more anterior portions of the corpus callosum'.

The rationale of my review was to integrate Geschwind's (1965) model with the 'differential weighting hypothesis', because I assumed that residual naming abilities were contingent upon the different weight non-visual attributes have in the representation of different semantic categories. According to this model, in patients with optic aphasia, visual naming should be spared for conceptual categories, such as action names, body parts (and in part artefacts) whose representations are mainly based on non-visual (motor and somato-sensory) information, while it should be impaired for living things (and in particular for fruits, vegetables and flowers), whose representations are mainly based on visual attributes (Fig. 4).

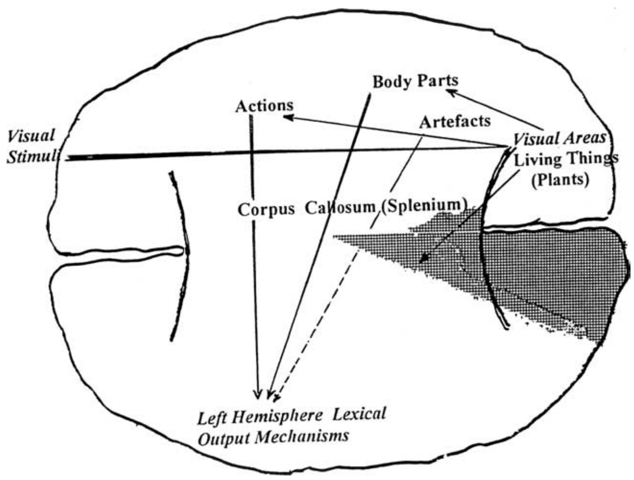

Fig. 4. Schematic representations of the pathways that could be followed to name visually presented members of different semantic categories in patients with 'optic aphasia'. According to the schema, actions and body parts should be named without major difficulties, since the visual stimuli could activate, via ipsilateral connections, the corresponding semantic representations in the frontal and parietal cortices of the right hemisphere. These representations could, in turn, activate the left hemisphere lexical output mechanisms passing through the intact anterior parts of the corpus callosum. Other categories of objects should met a naming difficulty proportional to the weight that visual attributes have in their semantic representations. Accordingly, artefacts should be less impaired than living beings and, within the latter, the most impaired categories should be those of flowers, fruits and vegetables, whose semantic representations are deemed to be heavily based upon purely visual colour information. (Partly modified from Gainotti, 2004).

The predictions relative to body parts and action names were strongly confirmed, because in all optic aphasics in whom these categories were separately taken into account, pictures representing actions or body parts were perfectly or preferentially (in comparison with other categories) named. Less clear results were obtained in the comparison between living things and artefacts, since a trend toward a greater impairment of biological stimuli was found; however, neither the difference between artefacts and living stimuli, nor the difference (within the latter) between animals and plant-life reached statistical significance.

5. Concluding remarks

A common thread links three apparently different facets of semantic memory, such as its relationships to the mechanisms of acquisition of episodic memory, the format of the semantic representations and the mechanisms underlying the categorical organization of semantic memory. This general thread is represented by the stress put on continuity and interdependence (rather than on discontinuity and complete independence) that our survey seems to suggest between: (a) the mechanisms of acquisition of episodic and semantic memory, (b) the format of the semantic representations and the sensory-motor processes preliminary to their acquisition and (c) the organization of semantic categories and the role various sensory modalities have played in their acquisition.

As to the first point, both authors who subscribe to standard distinction between episodic and semantic memory and those who propose alternative models of declarative memory, acknowledge that the hippocampal complex plays a critical role in the acquisition of autobiographical and general knowledge. However, authors who question the traditional episodic/semantic dichotomy go further, assuming that a continuum may exist from the cognitive point of view between autobiographical experience and abstract general knowledge and that the same anatomical structures mediate the end points of this continuum. From the cognitive point of view, Funnell (2001), stresses the influence of the main properties of the script theory on the construction of semantic memory and helds that meaning is represented in semantic memory according to a continuum of levels, i.e. from the most specific and context-bound to the most generalisable and context free. From the functional and anatomical viewpoint this continuum is explained by proponents of the multiple trace theory (Moscovitch et al., 2005) by assuming that semantic memories not only depend on the hippocampal complex for their initial acquisition, but also include episodic components, that continue to depend on the hippocampus. According to this model, attended information is in any case encoded by the hippocampal complex and bound to the neocortical neurons that represent that experience in a memory trace. However, each autobiographic memory is unique and permanently mediated by the hippocampal system, whereas semantic memories are created through a process that extracts information common to multiple related traces and integrates it with pre-existing knowledge, permanently represented in specialized neocortical structures independent from the hippocampal complex. In any case, both autobiographic and semantic traces are mediated by a bound ensemble of neocortical and hippocampal neurons, which act as a pointer or an index for the neurons representing the attended information (Teyler and DiScenna, 1986). This model of information processing, consolidation and retrieval is clearly reminiscent of the dynamic ‘convergence zones’ that, according to Damasio (1989), recollect and bind together the distributed attributes of concepts.

As for the second point, the hypothesis that perceptual activities may proceed within the various sensory modalities up to the level of a ‘structural description’ allowing access to a unitary, abstract, amodal semantic system is inconsistent with clinical and experimental data, which cast serious doubts on the unitary, amodal and abtract format of the semantic representations. From the clinical data, I would list: (a) the difficulty of explaining the spared ability shown by patients with optic aphasia to mime the use of objects that they are unable to name (Beauvois, 1982; Gil et al., 1985; Manning and Campbell, 1992; Teixeira-Ferreira et al., 1997); (b) the fact that in the same syndrome items denoting actions and body parts can be named much better than those denoting common objects (Gainotti, 2004); and (c) the contrasting performance of patients who (in the absence of any visual-perceptual disorder) can draw much more information from words than from pictures (McCarthy and Warrington, 1986; Warrington and Mc Carthy, 1994; Snowden et al., 2004). From the experimental data, Rogers et al.’s (2004) results raise serious doubts about the assumption of complete independence between the last stages of the perceptual processing (structural description) and the corresponding semantic representations, because they show that a severe impairment of semantic memory has a deleterious influence on the object decision tasks, currently used to assess the integrity of the corresponding structural description. Taken together, all these data argue against the hypothesis of complete independence between modality specific processing of different sensory-motor information and amodal, abstract and propositional representation of a conceptual knowledge, acquired on the grounds of the same basic sensory-motor functions. A growing number of authors (see, for e.g. Gallese and Lakoff, 2005) tend, therefore, to acknowledge that conceptual knowledge not only draws its content from the sensory-motor system, but also bears the stamp of the perceptual mechanisms through which it was acquired.

As for the last point, neuroanatomical data obtained in patients with category-specific semantic disorders, and category-specific naming disorders observed in patients with ‘optic aphasia’ consistently show that a close relationship exists between cortical areas crucially involved in processes of organisation/storage/retrieval of a given category and the localization of the sensory-motor functions that have mostly contributed to the development of that category. On one hand, the brain areas damaged in patients with a category-specific semantic disorder (Gainotti, 2000) play a special role in processing just those sensory-motor mechanisms that have critically contribute to the organisation of the disrupted semantic category. On the other hand, the study of residual naming abilities in ‘optic aphasia’(Gainotti, 2004) confirms that a rostro-caudal gradient exists between semantic categories (such as action names and body parts) whose representation are contingent upon motor and somatosensory mechanisms and those (such as living things categories) that rely more crucially upon visual attributes.

All these data are not compatible with a modular approach that views episodic memory, perceptual processing and semantic knowledge as interrelated, but quite independent computational systems. Rather, they are consistent with a distributed model, that considers the semantic system as an integrated multimodal network, strongly interconnected with the episodic memory system and formed by specialized cortical regions, which are accessed by different perceptual channels and store modality-specific information. Under normal circumstances, the various components of the net are interconnected, allowing retrieval of the entire representation from any input channel, but in pathological conditions one or more of its components can be preferentially damaged, giving rise to dissociations in performance, concerning either different perceptual or verbal modalities or different categories of knowledge.

Acknowledgements

I am very grateful to Prof. E. De Renzi for his precious comments to a first draft of this review.

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