Associative Agnosias and the Functions of the Left Hemisphere*

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ABSTRACT

Associative agnosias are traditionally regarded as perceptual, and ideational apraxia as motor, deficits, but they can be understood as amnesias for generic knowledge, caused by bilateral or unilateral left-hemispheric cortical lesions. Current theories of hemispheric specialization explain these syndromes' mandatory link with left-hemisphere damage, and are validated by this link. This link reflects the multiple nature of generic, categorical representational systems, not all reducible to natural language, and the left hemisphere's principal role as their substrate, regardless of their dependence on language. The distinction between processing novel information, and processing based on well-established, routinized representations, captures a fundamental difference between the functions of the right and left hemispheres. The complementary link of apperceptive agnosias with right- and associative agnosias with left-hemisphere lesions is an expression of this general principle in the posterior cortex. Future studies of the neuroanatomy of agnosias in animals may offer insights into the evolutionary continuities of hemispheric specialization.

Two significant developments have recently taken place in neuropsychology. First, several novel theories of hemispheric specialization have been put forth. Secondly, there has been a surge of studies of agnosias informed by cognitive theory. Although these two efforts are highly relevant to each other, relatively few attempts have been made to connect them. This paper attempts to integrate the two domains, and conceptualize associative agnosias and ideational apraxia in light of the current models of hemispheric specialization and integration.

ASSOCIATIVE AGNOSIAS AS CORTICAL AMNESIAS

A class of neuropsychological syndromes exists which can be conceptualized as "cortical amnesias", or more accurately, "amnesias for generic knowledge." These syndromes are rare but well-known, and they are referred to as associative agnosias, or asymbolias. It has been argued that, in spite of their traditional designation as forms of agnosia, these syndromes can be naturally understood as deficits of semantic memory (Warrington, 1975; Zaidel, 1986).

The visual form of associative agnosia, known as the "visual object agnosia" (or "associative blindness", or "psychic blindness,") was first described by Freud (1891) and Lissauer (1890). Although the existence of this syndrome in its pure form has been questioned, work by Albert, Reches, and Silverberg (1975), De Renzi and Spinnler (1966), Hécaen and Albert (1978), Hécaen and Angelergues (1963), Hécaen, Goldblum, Masure, and Ramier (1974), Luria (1980), McCarthy and Warrington (1986), Rubens and Benson (1971), and Warrington (1975) have demonstrated its reality.

A patient with a visual object agnosia "can see an object shown to him but cannot appreciate its character or meaning" (Hécaen & Albert, 1978, p. 194). Upon visual examination of an object, the patient can accurately describe its sensory and perceptual components, and even copy it (Rubens & Benson, 1971), but is unable to identify the object by name or describe its function through language or imitation. Hécaen and Albert (1978) give an example of a patient describing a bicycle as "a pole with two wheels, one in front, one in back," and a pen and a cigar as "cylindrical sticks of variable lengths" (p. 195). Sometimes the patient ventures a deduction regarding the meaning of the object which is perceptually justified but wrong, e.g., identifying glasses as "a circle, then another circle, and some sort of crossbar...it may be a bicycle" (Luria, 1980, p. 161).

Visual object agnosia can hardly be construed as a linguistic deficit, since there is no mandatory association with aphasia or anomia, and it is limited to the visual modality. As soon as the patient examines the object tactilely or listens to its characteristic sound, he can immediately name the object and give its correct description.

The deficit implicit in visual object agnosia appears to be that of defective categorical identification. An item can be perceptually analyzed but not identified as an exemplar of a category. To account for such a selective deficit, one has to postulate, following Warrington (1975), a deterioration of, or impaired access to, generic engrams which provide the description for large, potentially infinite classes of equivalent objects.

The gross-neuroanatomical picture of visual object agnosia involves either an isolated left occipital, left occipito-temporal area (Hécaen & de Ajuriaguerra, 1956; Hécaen, Goldblum, Masure & Ramier, 1974; McCarthy & Warrington, 1986; Nielsen, 1937; 1946) or a bilateral posterior lesion most prominent in the left occipital or occipito-temporal areas (Hécaen & Albert, 1978; Hoff & Pötzl,

1935; von Stauffenberg, 1918). Presence of left mesial occipital damage or its disconnection from sensory input, appears therefore to be mandatory in this syndrome (Bauer & Rubens, 1985; Nielsen, 1937). This assertion is further supported by an asymmetric pattern of the sensory input disconnection from the knowledge base; cases of the visual object agnosia limited to the left visual field following severance of the splenium of the corpus callosum have been reported (Nielsen, 1937), in the absence of known cases characterized by the opposite pattern, i.e., right visual field agnosia.

The tactile form of associative agnosia has also been described and is usually referred to as "pure astereognosia" (Hécaen & Albert, 1978) or "tactile asymbolia" (Wernicke, 1894). This syndrome can be construed as the tactile equivalent of visual object agnosia. The patient is unable to identify the object by touch although he can easily do so with reliance on other sensory systems. Although Dejerine (1914) argued that the deficit is rooted in the impairment of elementary somesthesis, "pure astereognosia" can be observed. It consists of an inability to make tactile identification of objects as members of meaningful generic classes, even though the patient's ability to describe separate tactile properties of the stimulus is intact (Hécaen & Albert, 1978; Luria, 1980). The deficit is bilateral, affecting both hands, but is caused by a unilateral, left temporo-parietal lesion (Foix, 1922; Goldstein, 1916; Lhermitte & de Ajuriaguerra, 1938). Bilateral pure astereognosia without elementary sensory deficits or aphasia, caused by a unilateral lesion can be best interpreted as deterioration of and/or impaired access to somatosensory generic engrams which provide categorical representations of large, potentially infinite classes of equivalent objects.

The auditory form of associative agnosia has also been described following posterior left hemispheric lesions (Faglioni, Spinnler, & Vignolo, 1969; Kleist, 1928; Spinnler & Vignolo, 1966; Vignolo, 1982). The deficit involves an inability to understand the "meaning" of nonverbal sounds and noises, i.e., associate them with the correct source. Purely auditory perceptual aspects of analysis are, however, intact. Vignolo (1982) termed this syndrome "semantic associative" auditory agnosia as opposed to "discriminative" auditory agnosia in which auditory perception *per se* suffers.

In order to complete the discussion of syndromes associated with the loss of generic knowledge, one has to consider certain forms of apraxia. It has been argued that procedural knowledge is spared in "classical", diencephalic and medial temporal lobe amnesias (Cohen & Squire, 1980; Squire & Cohen, 1984). A cortical syndrome is known, however, which can be interpreted as a form of "procedural amnesia". This is "ideational apraxia", originally described by Liepmann (1900; 1908) as the disintegration of skilled, overlearned, object-oriented movements, presumably due to the disintegration of, or impaired access to, "motor engrams". Although individual motor components are intact, their integration into coherent motor programs fails (Hécaen & Albert, 1978). The affected "motor engrams" are generic in the sense that they describe motor programs invariant across a variety of specific circumstances, applicable to any

object of a given class and executable by any limb. The deficit is bilateral and general rather than segmental with respect to body parts (Hécaen & Albert, 1978), but it can be produced by a unilateral, circumscribed lesion limited to the posterior parietal and temporo-parietal regions of the left hemisphere (De Ajuriaguerra, Hécaen, & Angelergues, 1960; De Renzi & Lucchelli; 1988; De Renzi, Pieczulo, & Vignolo, 1968; Hécaen & Albert, 1978).

The symbolic, generic nature of ideational apraxia and its kinship with associative agnosias has been emphasized by Denny-Brown (1958), De Renzi and Lucchelli (1988), and Morelaas (1928). As in the case of associative agnosias, the deficit in "ideational apraxia" appears to be higher-order and selective. It does not have to be associated with an underlying elementary somatosensory, motor or movement imitation deficit, or with a general intellectual or attentional deterioration (De Ajuriaguerra et al., 1960; De Renzi & Lucchelli, 1988; De Renzi et al., 1968). Although ideational apraxia can be associated with severe aphasic disorder and share the locus of the critical lesion with aphasia (De Renzi et al., 1968), most authors consider it autonomous from a language disorder (De Renzi & Lucchelli, 1988; Goodglass & Kaplan, 1963; Liepmann, 1900).

Visual object agnosia, tactile asymbolia, associative auditory agnosia and ideational apraxia are often caused by bilateral lesions of the posterior cortex. It is therefore thought that either hemisphere can mediate the functions whose breakdowns lead to these syndromes, although probably in different ways. On the other hand, these syndromes can be caused by unilateral lesions of the left but not of the right hemisphere. It is therefore likely that the left hemisphere is more efficient in controlling these functions and plays the leading role in their mediation under normal conditions.

The critical, mandatory lesions leading to ideational apraxia and to associative agnosias share the same general territory – the posterior portion of the left hemisphere. Both ideational apraxia and associative agnosias entail the degradation of, or impaired access to, generic knowledge base. They involve the deterioration of, or impaired access to, long-term, generalized, categorical representations which enable us to perceive the world in terms of pre-specified, invariant classes. In characterizing these syndromes, Teuber referred to them as "percepts stripped of their meaning" (1968). A consistent and parsimonious picture emerges of these syndromes as cortical amnesias for generic knowledge, both declarative and procedural.

ASSOCIATIVE AGNOSIAS AND MULTIPLE CODES

Associative agnosias and ideational apraxia may co-occur with language disturbances. The question has been asked whether these syndromes constitute separate deficits (i.e., represent the impairment of separate cognitive functions) whose neuroanatomical territories overlap with, or are proximal to, those of aphasias, or whether they are secondary to aphasias in terms of the underlying cognitive mechanisms (Hécaen & Albert, 1978).

Three kinds of argument can be offered that, while related to language disorders, asymbolias are not, strictly speaking, secondary to them. The first two arguments are empirical. Although asymbolias may co-occur with language disorders (De Renzi et al., 1968; Vignolo, 1982; Warrington, 1975), it is by far not always the case, and asymbolias without aphasia or anomia have been described (Albert, Reches & Silverberg, 1975; De Renzi et al., 1968; Humphreys & Riddoch, 1987; McCarthy & Warrington, 1986; Rubens & Benson, 1971). Since the converse is also possible (aphasias without associated symbolic agnosias), one can argue that double dissociation exists between aphasias and the above-described symbolic disorders. Lack of clear-cut association between the severity of aphasia and that of ideational apraxia has also been noted (Goodglass & Kaplan, 1963).

Secondly, even if one assumes that associative agnosias are secondary to a language disorder, this explanation is not sufficient, since it does not account for the modality-specificity of agnosias. A simple language-based explanation would predict a massive associative agnosia affecting generic identification simultaneously in all modalities. In order to account for the modality-specificity of associative agnosias, one would have to adopt a "language plus" explanation, the "plus" accounting for their specificity.

The third argument is conceptual. The ability to categorize the world and identify objects as members of generic classes antedates language in evolution and therefore has to be viewed as more basic. That the neuroanatomical locus of such processes in monkeys closely corresponds to the one in humans (Cowey, 1982; Dean, 1976), argues strongly that the human functions of categoric object recognition are closely linked to their phylogenetic prototypes at least in some aspects.

It has been proposed that a multitude of representational systems, interrelated yet separate, are operative in human cognition, and that these systems cannot be all reduced to natural language on either evolutional or functional grounds (Goldberg & Costa, 1981; Goldberg, Vaughan, & Gerstman, 1978). Clinical studies have led to similar conclusions (Beauvois, 1982; Warrington, 1982; Zaidel, 1986).

The existence and exact nature of such multiple, distinct representational systems, the type of information they contain, and their relationship to sensory modalities have been the subject of debate. In the cognitive literature, the debate revolves around these alternatives: Are verbal and pictorial processes mediated by separate semantic systems (Paivio, 1971), or by one, amodal, propositionally expressed semantic system (Pylyshin, 1973)? More recent cognitive models attempt to incorporate the elements of both positions. They rest on the assumption that both form-specific and form-invariant components are present in representations, probably hierarchically arranged (Snodgrass, 1984; Vanderwart, 1984).

In the neuropsychological literature the debate reflects competing interpretations of associative agnosias and modality-specific aphasias (Riddoch, Humphreys, Coltheart, & Funnell, 1988; Shallice, 1988). Central to this debate is the distinction between "perceptual" and "functional and associative" informa-

tion about things. "Being sweet" and "growing in bunches" are elements of the perceptual account of the category "grapes", and "being the precursor of wine" and "growing in the South" are the elements of its "functional and associative" account. Perceptual information can be discerned in the image of the object itself, whereas the more abstract "associative" and "functional" information must be inferred by using some of its perceptual properties as surrogates or markers. Both types of information are represented in our knowledge about things (Miller & Johnson-Laird, 1976).

Beauvois (1982), Shallice (1987), Warrington (1975), and others postulate the existence of separate verbal and nonverbal semantic systems, each containing generic descriptions which include both "perceptual" and "functional and associative" accounts of things. This position mandates the existence of multiple, modality-specific parallel systems in which information is duplicated to a high degree, but in modality-specific ways.

The alternative position has been stated by Riddoch et al., (1988), who propose the existence of multiple, modality-specific representational systems for "perceptual" information, but of only one, amodal system for "functional and associative" information. They refer to the latter as the "semantic" system and the former as "presemantic systems". This appears to be in agreement with the position of Goodglass (1980) who proposed that lexical knowledge is based on supramodal semantic representations. According to Goodglass, word concepts can be accessed or "aroused" via different sensory routes, but with varying degrees of ease.

For the purposes of this analysis, it is important to clarify, on what these competing cognitive and neuropsychological positions agree, and on what they disagree. Both positions agree on the hierarchic nature of stored, generic knowledge base, with "perceptual" and "associative/functional" levels of representation. Both positions accept the multiplicity of modality- or form-specific "perceptual" representational systems, but they disagree on whether there is one or more "associative/functional" representational system(s). Only the latter system(s) is(are) called by the above authors "semantic", whereas the former ones are called "presemantic". This terminology is somewhat misleading and contains a misnomer. It should not blur the fact that both kinds of representations are categorical in the sense that both represent stored, pre-existing, generic knowledge base of large, potentially infinite classes of eguivalencies, which serve as the basis for the recognition and classification of specific exemplars. In that sense, both kinds of representations are "semantic", but they mediate different aspects, and possibly different levels of semantic knowledge.

One concludes that the existence of multiple representational systems for *certain* aspects of the knowledge base is not in dispute either in the cognitive or neuropsychological literature. What is being debated, is the existence of a single, superordinate, amodal representational system superimposed upon them.

At least up to a certain level of integration, then, the "total" generic engram of an object is distributed, dimensionalized along sensory modalities into multiple

components. Isolated, modality-specific associative agnosias and ideational apraxia are likely to reflect selective breakdowns along these dimensions, of the ability to use the corresponding nonverbal representations. This can be either due to their degradation, or due to an impaired access to them. It is beyond the scope of this paper, nor is it critical for this analysis, to chose between the two alternatives. Humphreys and Riddoch (1988) specify several possible types of such breakdowns, e.g. impaired access to perceptual, "presemantic" representations, impaired "semantic" representations, or the impairment of the route from a specific "presemantic" system to the (invariant) "semantic" one.

MULTIPLE CODES AND THE LEFT HEMISPHERE

The selective association between asymbolias and posterior left hemispheric damage then becomes extremely important from a theoretical standpoint, since it elucidates the nature of hemispheric specialization. It indicates that not only verbal, but also nonverbal representational systems and their use are mediated with particular reliance on the posterior portions of the left hemisphere.

Until recently, there were no well-articulated theories capable of acommodating as special cases the selective relationship between associative agnosias and the left hemisphere. Therefore, the assumption shared by some authors that an underlying language deficit invariably accounts for asymbolias of the left hemisphere (most recently criticized by De Renzi and Lucchelli, 1988) may have been made by *default*, despite rather than due to the existing evidence, for the lack of a better explanatory framework. Likewise, the reluctance by some authors to accept the possibility that a unilateral, left hemispheric lesion could be sufficient in causing an associative agnosia, may reflect the lack of a compelling model which would make such an association plausible on theoretical grounds, once the notion of a hidden language disorder has been discarded.

Recently, several novel theories of hemispheric specialization capable of accommodating the selective relationship between associative agnosias and the left hemisphere have been proposed. These theories were formulated independently of the agnosia findings. In other words, the agnosias literature was not used as the empirical basis in formulating these theories. This means that the predominant association of associative agnosias with the left hemisphere can be understood in the context of broader theoretical models. Conversely, the neuroanatomy of associative agnosias provides an independent (not used in the theory-building) empirical domain validating the predictions implicit in these theories. Once the nonverbal nature of asymbolias is accepted, the selective association between them and the left hemisphere damage provides a powerful support for the theories of hemispheric specialization to be discussed below.

Without disputing the critical role of the left hemisphere in natural language, several authors have postulated its broader role. Goldberg and Costa (1981), Goldberg et al. (1978), Kosslyn (1987), and Tucker and Williamson (1984) have

proposed that the left hemisphere is critical for processing in terms of any categorical representational system, regardless of its association with natural language.

Goldberg and Costa (1981) have proposed that the functional differences between the two hemispheres are at least in part characterized by the following distinction: The right hemisphere is critical for initial orientation in the task and for processing novel information to which none of the representational systems pre-existing in the subject's cognitive repertoire can be successfully applied. The left hemisphere, on the other hand, is critical in any processing which relies upon well-routinized representational systems ensconced in the subject's cognitive repertoire, verbal and nonverbal alike. The left hemisphere's dominance for language is viewed as a special case of this more general principle. The advantage of the left hemisphere in applying fixed, pre-existing representations is related by Goldberg and Costa to the greater facility of the left hemisphere for storage of, and access to, previously accumulated information, in particular to compact codes capable of representing large, potentially infinite classes of specific stimuli in invariant ways. Whereas the right hemisphere ensures processing in terms of multiple purpose basic primitives, the left hemisphere ensures processing in term of derivative, second-order, specialized codes (Goldberg et al., 1978). Right-to-left shifts of hemispheric control over processing certain types of material takes place as a function of the development and routinization of representational systems applicable to these materials.

Three types of evidence are marshalled by Goldberg and Costa to support their hypothesis: cross-sectional studies comparing patterns of hemispheric advantage in healthy, task-naive and task-sophisticated subjects; laboratory simulations of longitudinal studies eliciting within-experimental changes in hemispheric advantage as a function of growing task-proficiency in healthy subjects; and studies of the cognitive competencies of isolated, single hemispheres in hemispherectomized and callosotomized/commissurotomized patients.

Long-term, generic engrams which describe open classes of equivalent stimuli form fixed, well-routinized representational systems enabling one to categorize the world in invariant terms. They support the processes impaired in associative agnosias and ideational apraxia. The formation and routinization of such multiple representational systems constitute the end-points of right-to-left shifts of hemispheric control over particular cognitive domains proposed by Goldberg and Costa. The left hemisphere is intimately linked to "symbolic" functions, because it is the repository of acquired representational systems – verbal and nonverbal, "semantic" and "presemantic" alike – once they have become highly developed and routinized. When the left hemisphere's capacity to serve as the repository or user of such fixed, invariant codes is compromised, "generic amnesias", or asymbolias develop.

Tucker and Williamson (1984) formulated similar ideas, linking the function of the right hemisphere to an "expansive", exploratory cognitive mode, and the function of the left hemisphere to a "restrictive" cognitive mode which is charac-

terized by reliance on fixed, highly routinized and stable operations, and therefore, presumably, on well-developed representations. Tucker and Williamson muster extensive biochemical evidence to support their position.

Kosslyn (1987) also proposed a broader role for the left hemisphere by investing it with the function of categorical processing. He attributes the emergence of this broad function to a "snowball" effect set off by the primary left hemisphere's dominance for speech. By contrast, the right hemisphere is invested by Kosslyn with the function of a "rapid search controller", a notion similar to Goldberg and Costa's "initial orientation to novelty", or to Tucker and Williamson's "expansive" exploratory mode.

Kosslyn's account of the genesis of the left hemisphere's dominance for categorical processing is causatively opposite to that offered by Goldberg and Costa (1981). Kosslyn views it as secondary, derivative from the left hemisphere's fundamental dominance for certain aspects of language, whereas Goldberg and Costa regard the categorical nature of left hemisphere's function as the broad, fundamental principle of which language dominance is but a special case. In spite of this difference, it is important that several independently formulated theories invest the left hemisphere with a very broadly conceived categorical processing which embraces both linguistic and non-linguistic, "associative/functional" and "perceptual" representational systems. Associative agnosias interpreted here as "generic amnesias" can be viewed as selective breakdowns of the ability to use such nonverbal, perceptual representational systems of the left hemisphere.

Recognizing an exemplar as a member of a generic class and imagining a prototypical exemplar of that class is likely to rely on the same or similar representations in the long-term store (Farah, 1985; Goldberg & Tucker, 1979; Kosslyn, 1987). An interesting line of evidence on the leading role of the left hemisphere in processes dependent on nonverbal generic representations arises from the studies of mental imagery. In an extensive literature review, Farah (1984) found a strong association between the damage to the posterior portion of the left hemisphere and loss of imagery. By using priming techniques, Farah (1986) has also shown that in normal subjects the left hemisphere is better at multipart image generation.

TYPES OF AGNOSIAS AND HEMISPHERIC INTERACTION

The close relationship to memory for generic knowledge, is what distinguishes *associative* agnosias from another broad category of phenomena, the so-called *apperceptive* agnosias. Apperceptive agnosias affect the capacity for physical (rather than categorical) identification of unique exemplars, e.g., capacity for perceptual constancy under varying angles of observation, or varying conditions of illumination, in the absence of elementary perceptual deficits such as brightness discrimination (Humphreys & Riddoch, 1987; Kertesz, 1987). Appercep-

tive agnosias are regarded as more purely perceptual in nature in that they rely less on long-term, pre-existing, generic and context-free representations, and have been linked by some authors to "contextual" memory (Damasio, 1985; Humphreys & Riddoch, 1987).

Warrington (1982) proposed a two-stage hierarchic model of visual object-recognition (superimposed on elementary sensory processes). According to this model, the first stage consists of the physical object identification. It is presumed that while either hemisphere can contribute to these processes, the right hemisphere is more efficient and dominant for it under normal circumstances (Damasio, 1985; Warrington, 1982). Breakdown of these processes leads to some form of apperceptive agnosias. Their underlying neuroanatomy is opposite to that of associative agnosias. Although apperceptive agnosias are often seen following bilateral posterior cortical damage (Damasio, 1985; Damasio, Damasio, & Van Hoesen, 1982), they can be caused by unilateral right but not left hemispheric lesions (De Renzi, Scotti, & Spinnler, 1969; Warrington, 1982; Warrington & James, 1988; Warrington & Taylor, 1973). The second stage consists of semantic object identification. Although either hemisphere can contribute to it, the left hemisphere is more efficient and dominant for these processes under normal conditions. Breakdown of these processes leads to some form of associative agnosia.

Physical object identification is concerned with recognizing the object as "its own self," across various conditions of observation (e.g., distance, angle, illumination, etc.). Semantic object identification is concerned with recognizing the object as a member of a generic category. Physical object identification emphasizes that which is specific to the object. Semantic object identification emphasizes that which is in common across many objects. Face recognition is by definition a task of physical identity because the purpose is to identify the specific John Smith as opposed to Bob Taylor. Object recognition is fundamentally different because the emphasis is on that which is common across the whole class of objects: a tall black chair is equivalent to a squat white one according to the functional criteria of the "chair" class. Generic identification probably relies on more compact, invariant and generalized codes than does physical identification.

It is likely that generic identification, due to its reliance on compact and generalized representations, is more directly based on stable, stored memory representations, whereas physical identification always has a strong element of *de novo* computations. Physical identification entails coping with a much greater degree of stimulus variability than generic identification, often along continuous dimensions, and therefore cannot be as readily accomplished with reliance on pre-existing templates or fixed perceptual criteria. Every case of physical identification requires substantial transformation and recomputation of the stimulus pattern before it can be connected with the memory traces of the "original".

The foregoing discussion of the differences between generic and physical identification follows Kosslyn's (1987) distinction between categorical representations (left-hemisphere dominance) and coordinate representations (right-

hemisphere dominance), and Bernstein's (1967) distinction between topological and metric representations. The former are more generalized and can be captured to a greater degree (although not completely) in terms of qualitative features, or in terms of an observable number of prototypical templates. The latter encode quantitative variations within broad ranges, which cannot be easily approximated by a small number of pre-existing templates. The former can be stated in relatively compact propositional or prototypical descriptions, whereas the latter are too informationally rich to afford an explicit account of every possible variation, or even to come close to it. Associative agnosias reflecting selective breakdowns of predominantly left-hemispheric processes can be therefore more meaningfully interpreted as memory deficits, or "generic" cortical amnesias, than the apperceptive agnosias which reflect the breakdowns of predominantly right hemispheric processes and are characterized by a stronger perceptual component.

Humphreys and Riddoch (1987) criticized the associative-apperceptive distinction as too crude and failing to operationalize specific types of deficits and ways of testing for them. They propose that the lack of neuroanatomical consistency of findings may be a consequence of the lack of such clearly operationalized cognitive criteria. Humphreys and Riddoch propose a more elaborate taxonomy of agnosias, which includes the following types: impaired shape processing, impaired transformation processes (e.g. from an unusual to a canonical view), impaired integration processes (e.g., integrating local shape descriptions), loss of stereoscopic vision, impaired access to form knowledge (i.e., to generic, modality-specific perceptual stored representations), impaired semantic knowledge (i.e., associative/functional, presumably amodal knowledge of things), and impaired access to semantics via a particular modality route.

This classification refines the associative-apperceptive distinction but does not refute it, since the types of agnosias proposed by Humphreys and Riddoch fall neatly into one or the other category. The last three types imply an impaired ability to access or otherwise use generic, pre-existing knowledge base, and are therefore associative. The first four types are not linked to the breakdown of such processes nearly to the same extent and mostly involve breakdowns of episodic, context-dependent representations and *ad hoc* computations; they are therefore apperceptive.

In reality, however, certain perceptual processes are dependent both on pre-existing generic and *ad hoc*, specific information. It is known, for instance, that various forms of constancies benefit from the subject's knowing the meaning of the object. This may indicate that the match of two non-canonical representations of an object is mediated by referring them to the canonical, prototypical one when such is available. The classic apperceptive-associative classification and the more elaborate one, proposed by Humphreys and Riddoch, may represent degrees of approximation by finite taxonomies of a right-left continuum of perceptual processes in terms of the underlying hemispheric substrates.

The position occupied on this continuum by a particular perceptual task in a

given individual at a given level of proficiency will depend on the extent to which it relies upon pre-existing generic representations (linguistic or non-linguistic, propositional and amodal or prototypical and modality-specific alike), as opposed to *ad hoc* computations, and on how exclusive is the dependence on one or the other. The relatively greater reliance on stored generic representations will correspond to a relatively greater dependence on the left hemisphere, and the relatively greater reliance on *ad hoc* computations will correspond to a relatively greater dependence on the right hemisphere. Task-specific learning and the emergence of appropriate stored representations is accompanied by the shift from a predominantly right-hemispheric to a predominantly left-hemispheric locus of cognitive control.

The position of a cognitive-perceptual task on such a continuum in a given individual will determine its vulnerability following a lateralized brain lesion in that individual. This implies a substantial degree of individual differences in the neuroanatomy of agnosias which is determined by a wide range of experiential, educational and vocational factors.

IN SEARCH OF PARSIMONY AND EVOLUTIONARY CONTINUITY

One of the foremost challenges of science is the search for fundamental, parsimonious principles capable of bringing together specific observations. Studies of hemispheric specialization have resulted in numerous specific findings, and any attempt to tabulate them will produce a rather long list. Is the true nature of hemispheric specialization best captured by long lists of specific findings, or is it possible to understand these numerous findings as expressions of certain general, parsimonious principles? The impetus behind this paper was to espouse the latter approach.

Neocortical functional organization can be viewed as being fundamentally bilaterally symmetrical (Goldberg, 1989). Superimposed upon this fundamentally symmetrical organization is hemispheric specialization which can be captured, according to this approach, by a small number of parsimonious principles – or possibly even by a single principle, – which reflect(s) the functional properties of each hemisphere as a whole. These few, parsimonious principles of hemispheric specialization are *expressed* in a multitude of specific ways as they interact with the anterior-posterior dimension. This paper is devoted to the interaction between the left-right and anterior-posterior cortical dimensions as it pertains to the posterior cortex.

It has been proposed earlier (Goldberg & Costa, 1981) that the distinction between processing novel information and processing in terms of pre-existing, well-routinized representational systems constitutes a parsimonious, fundamental principle capturing the functions of the two hemispheres. In this paper I further propose that the selective link of the two broad categories of agnosias, associative and apperceptive, with the lesions of one or the other hemisphere,

reflects *an expression of this general principle of hemispheric specialization in the posterior cortex*. This expression takes the form of the left posterior cortex supporting those aspects of perception which rely upon well-routinized, generic representations serving as the knowledge base for large classes of equivalent objects, and the right posterior cortex supporting those aspects of perception which substantially rely upon *de novo* computations.

The exploration of the interaction of the novelty-routinization principle of hemispheric specialization with the anterior-posterior dimension as it pertains to the anterior cortex, and the expression of this principle in the frontal cortex, is among the future challenges for the neuropsychology of hemispheric specialization.

Contemporary theories of hemispheric specialization in humans fall into two groups, characterized by two opposing premises. The first, and by far the more accepted one, is that the lateralization of language is fundamental and the lateralization of other cognitive functions is secondary to, and derivative from it (Corballis, 1983; Kosslyn, 1987; Levy, 1974). This position emphasizes the uniqueness of human hemispheric specialization and implicitly suggests an evolutionary discontinuity of cerebral functional organization.

The second position is that language lateralization is a consequence and/or a special case of a more fundamental principle of asymmetric hemispheric specialization. Although still a minority position, it has been taken recently by a number of authors (Bogen & Bogen, 1969; Goldberg & Costa, 1981; Goldberg et al., 1978; Hamilton & Vermeire, 1988a,b; in press). By divesting natural language of its cardinal role in hemispheric specialization, this position opens — implicitly or explicitly — the avenue for tracing the evolutionary *continuity* of the development of functional cerebral lateralization and for the search of homologies across species.

Associative and apperceptive agnosias reflect the breakdown of perceptual processes which are undoubtedly present already in animals and whose existence is not predicated on the availability of natural language. Their differential dependence on the two hemispheres in humans raises the intriguing possibility that the two corresponding forms of perception, one based on pre-existing generic representations, the other on *de novo* computations, are lateralized also in other species.

The existence of hemispheric asymmetries in animals is well established (for review, see Glick, 1985). In many instances a continuity between such asymmetries and human functional lateralization is hard to discern, as in the case of lateralized aspects of bird song (Nottenbohm, 1970; 1980). However, Hamilton and Vermeire (in press) review a number of recent findings, which allow more direct parallels with human cognition.

Discrimination of species-specific calls shows a right- over left-ear advantage in Japanese macaques (Beecher, Petersen, Zoloth, Moody, & Stebbins, 1979; Petersen, Beecher, Zoloth, Moody, & Stebbins, 1978), and is more disrupted following left than right temporal lesions (Heffner & Heffner, 1984; 1986). In split-

brain monkeys, the right hemisphere is better than the left at discriminating monkey faces (Hamilton & Vermeire, 1988a;b). Conversely, the left hemisphere is better than the right at discriminating the direction of movement of a field of dots (Hamilton & Lund, 1970), orientation of gratings (Hamilton, Tieman, & Farell, 1974), and line orientation (Hamilton, 1983; Hamilton & Vermeire, 1988a;b).

The findings of the left-hemisphere advantage for species-specific vocalizations, and the right-hemisphere advantage for facial discrimination in monkeys, agree with the direction of hemispheric advantages for corresponding stimulus types in humans. On the other hand, the findings of the left-hemisphere advantage in monkeys for various forms of spatial judgement appear to be at variance with the corresponding human findings.

However, this apparent discrepancy is insurmountable only if we were to look for hemispheric homologies for *specific cognitive tasks and stimulus classes,* an attempt grossly antithetical to the spirit of this paper and its precursors (Goldberg & Costa, 1981; Goldberg et al., 1978). The basic premise of the approach advocated here is that functional hemispheric asymmetries in humans and cross-species homologies (if such exist) can be only captured by *general principles, which may have different expressions in different individuals and species.*

If one considers the possibility of a fundamental, prelinguistic and phylogenetically early cognitive hemispheric dichotomy shared by several species, then it may be that the novelty-routinization distinction between *de novo* perceptual computations and processing with reliance on stored, pre-existing generic representations, captures an important aspect of this dichotomy. It is not clear what the structural and/or biochemical bases of this functional dichotomy could be and how early in evolution they emerge, but parallels have been found between humans and other species with respect to both structural and biochemical hemispheric asymmetries (for reviews see Glick, 1985; Tucker & Williamson, 1984).

Goldberg and Costa (1981) argued that in humans, the same task may reveal different patterns of hemispheric advantage in different individuals and even in the same individual over time. These differences reflect the *variability of expressions of an invariant underlying principle of hemispheric specialization.* The invariant principle is the predominant reliance of relatively novel cognitive tasks on the right hemisphere, and of relatively well-routinized tasks on the left hemisphere. The variable expressions of this principle may reflect the right-to-left hemispheric shift of the locus of cognitive control as the function of task-relevant cognitive learning in a given individual over time, or varying degrees of left- as opposed to right-hemispheric contribution as a function of varying levels of task-relevant cognitive competencies across individuals.

If this general reasoning is correct, then the fundamental evolutionary homologies of hemispheric specialization are expected to have even more variable expressions across species, due to basic ecological and ethological differences. It may be, for instance, that the left-hemisphere advantage for various visuo-spatial judgements in monkeys reflects their ecology, where precision jumping from

tree to tree is as well-routinized, and processed with reliance on stored representations, as lexical decision-making is in humans. Admittedly, the power of this explanation is limited by its *post-hoc* nature.

The theoretical importance of the hemispheric complementarity of associative and apperceptive agnosias goes beyond supporting a particular view of hemispheric specialization in humans, precisely because it enables us to go beyond *post-hoc* reasoning in thinking about cross-species continuities. By implying a complementary lateralization of two broad categories of perceptual processes, one based on *de novo* computations, the other on pre-existing generic representations, it offers a hypothetical conceptual framework in which specific findings of perceptual hemispheric asymmetries in animals can be understood and reconciled across species. Even more importantly, it offers a general homological principle, based on which specific, falsifiable hypotheses regarding perceptual hemispheric asymmetries in various species can be formulated and tested, by attempting to produce species-specific analogues of associative and apperceptive agnosias with lateralized lesions in animals.

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