

**COMPUTATIONAL ANALYSES AND HEMISPHERIC ASYMMETRIES**  
**IN VISUAL-FORM RECOGNITION**

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Much of contemporary theory in cognitive neuroscience adheres to a theoretical framework in which behavioral abilities are understood as arising from the operations of and interactions between relatively independent processing subsystems of the brain. Although these subsystems may be only weakly modular (e.g., Farah, 1994), a primary goal for the field is to discover the broad architecture of interconnected subsystems and to pinpoint the particular functions performed by the various subsystems. In other words, the goal is to understand how the brain is “carved at its joints” (e.g., Kosslyn & Koenig, 1992) or, perhaps more appropriately given weak modularity, “stretched at its interconnections” into relatively independent functional entities. This quest for component subsystems is especially important in understanding functional hemispheric asymmetries. Theories that are cast in terms of how component subsystems operate more or less effectively in different hemispheres are providing more powerful and compelling explanations than those that rely on general principles or fundamental dichotomies (see Hellige, 1993a).

In order to theorize about the function of any system, one must characterize how inputs are mapped to outputs by the system. Inputs, outputs, and the couplings between the two are needed to describe any function; if one of these three elements is missing or vague, no matter which one, a function per se cannot be described. Hence, if one’s goal is to delineate and understand the function of a neural processing subsystem, one must theorize not only about what it produces as output, but also about what it accepts as input and which inputs will be used to signal the production of which outputs. This somewhat obvious point helps to illuminate some of the important questions to consider when doing the difficult job of stretching the brain at its interconnections, functionally speaking.

An effective strategy to follow when hypothesizing about neural processing subsystems is to consider clues about inputs, outputs, and their mappings from the perspectives of different levels of explanation (Marr, 1982). Useful computational clues come from considerations of the goals that should be satisfied by the relevant subsystems, what information is available to the relevant subsystems to help achieve these goals, and what sort of strategy would be useful for achieving the appropriate goals given the available information. Useful implementational clues include aspects of the underlying physical substrate that suggest how inputs may be represented, where the inputs come from, how outputs may be represented, where the outputs are sent to, and how the mechanism may operate to map inputs to outputs.

In this chapter, we consider such clues to hypothesize about the subsystems involved in visual-form recognition. First, we theorize that two relatively independent subsystems underlie different aspects of visual-form recognition and that each subsystem operates more effectively in one cerebral hemisphere than in the other. Then, we summarize the results from behavioral studies that support the separate subsystems theory. Next, we offer computational analyses and describe results from a computational modeling study that illuminate the contradictory natures of the internal processing strategies that these subsystems may use. Finally, we summarize the results from additional behavioral studies that support the computational theory.

*VISUAL-FORM SUBSYSTEMS*

Visual-form recognition is an essential human ability. By most accounts, it entails the activation of a previously stored visual-form representation that corresponds best to the currently processed input form. Generally, the neural mechanisms involved in this ability appear to operate in occipital-temporal and inferior-temporal cortex of the brain (e.g., Buckner et al., 1995; Petersen & Fiez, 1993; Schacter et al.,

1995; Sergent, Ohta, & MacDonald, 1992; Squire et al., 1992), in a region that may be a homologue to the occipital-temporal “what” pathway in nonhuman primate vision (as opposed to the occipital-parietal “where” or “action” pathway; Felleman & Van Essen, 1991; Goodale & Milner, 1992; Haxby et al., 1991; Ungerleider & Mishkin, 1982). These areas accept retinotopically coded inputs from primary visual cortex (Fox, Miezin, Allman, Van Essen, & Raichle, 1987; Kosslyn et al., 1993; Tootell, Silverman, Switkes, & De Valois, 1982), and they appear to send output representations that signal a recognized form to non-visual subsystems (e.g., phonological, conceptual/associative, motoric, etc.) as well as to other visual subsystems (e.g., the occipital-parietal “where” or “action” pathway).

### ***Computational Constraints***

Careful considerations of our visual abilities, in terms of goals and strategies, suggest that these visual-form areas do not perform a single or simple process. Given retinotopically coded images of forms that appear in the world, visual-form subsystems accomplish at least two essential goals. First, they underlie the ability to recognize *abstract categories* of forms. For example, when reading a book, a reader usually categorizes word forms at only the coarse level of classification needed to access the appropriate meanings associated with the words. More concretely, one categorizes forms at the coarse level in which all of the forms in Figure 1 belong to the same category and hence produce the same output. However, visual subsystems also underlie another important ability, that of recognizing *specific instances* within the same abstract category of form. For example, to recognize a signature, one usually categorizes a letter string at the fine-grained level needed to distinguish a restricted set of the many possible ways in which the same letter string can appear. More concretely, one categorizes forms at the fine-grained level in which the forms in Figure 1 produce different outputs.

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 Insert Figure 1 about here  
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According to many theories, these two abilities should be accomplished in a single, undifferentiated processing subsystem (for general computational theories, see Knapp & Anderson, 1984; McClelland & Rumelhart, 1985; for object recognition theories, see Hummel & Biederman, 1992; Tarr, 1995; see also most theories of word recognition). However, the two abilities seem to place contradictory demands on the relevant processing mechanisms. To recognize abstract categories, it should be useful for a subsystem to ignore the visually distinctive information that differentiates specific instances in a category and to focus on the information that is relatively invariant across instances. For example, only the shared information between the two input forms in Figure 1 is very useful for accomplishing the goal of recognizing the common abstract category. Note that the relatively invariant information across the forms in Figure 1 is only found in *parts* of the larger wholes (see top of Figure 2). In contrast, to recognize specific instances, it is necessary for a subsystem to focus on just the sort of information that may be effectively ignored when recognizing abstract categories. For example, the information that distinguishes the inputs in Figure 1 must be processed to accomplish the goal of discriminating the forms. It is important to note that the visually distinctive information that differentiates the forms in Figure 1 in addition to the specific instances of other words is found in the *wholes* of those forms (see bottom of Figure 2).

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 Insert Figure 2 about here  
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### ***Implementational Constraints***

In addition, considerations of findings in the neuropsychological literature suggest that there are important differences in how visual-form subsystems operate across the different physical substrates of the left hemisphere (LH) and right hemisphere (RH). First, subsystems in the LH and RH play important roles in word recognition and face recognition, respectively (e.g., Damasio & Damasio, 1983; Geffen, Bradshaw, & Wallace, 1971; Petersen & Fiez, 1993; Rhodes, 1985; Sergent et al., 1992; Sergent & Bindra, 1981). Second, recognition of word, face, and object forms appears to be performed through two, not one or three, independent capacities. In a review of the visual associative agnosia literature, Farah (1990, 1991) noted that only a subset of the logically possible combinations of impaired abilities exhibited by individual brain-damaged patients are found frequently. The combinations indicate that two kinds of visual recognition capacities are susceptible to damage, one involving word and sometimes object recognition (and affected by LH damage), and the other involving face and sometimes object recognition (and affected by RH damage). These results have direct implications for abstract-category and specific-instance recognition, to the extent that word recognition usually relies on abstract-category processing, face recognition usually relies on specific-instance processing, and object recognition likely relies on different processes (abstract versus specific) in different circumstances.

### ***Relatively Independent Visual-Form Subsystems***

Although these considerations do not rule out the possibility that a single subsystem underlies both abilities, they do lead to the theory that relatively independent subsystems underlie visual-form recognition. We have hypothesized that an *abstract visual-form (AVF) subsystem* underlies recognition of abstract categories of forms, processes relatively-invariant input information through the use of a parts-based internal processing strategy, and operates more effectively in the LH than in the RH. In contrast, a *specific visual-form (SVF) subsystem* underlies recognition of specific instances of forms, processes visually-distinctive input information through the use of a holistic internal processing strategy, and operates more effectively in the RH than in the LH. These subsystems may operate relatively independently in large part because they rely on contradictory internal processing strategies. In the next section, we summarize initial behavioral evidence in support of this theory. Afterward, we use computational analyses and modeling to suggest a concrete specification of these internal processing strategies and to illuminate their contradictory natures.

#### ***BEHAVIORAL EVIDENCE FOR RELATIVELY INDEPENDENT SUBSYSTEMS***

We have tested the AVF/SVF subsystems theory in the following studies. The initial behavioral tests utilized divided-visual-field presentations of visual forms during the test phases of various memory experiments.

### ***Rationale for Divided-Visual-Field Studies***

We use the divided-visual-field technique as a tool to help test whether a single visual-form subsystem operates in a fairly unitary manner in the brain or two subsystems operate in a relatively independent manner. Our rationale is similar to the rationale that interactions between task and field of visual presentation are needed to adequately study laterality effects in this paradigm (Hellige, 1983). Of course, in a divided-visual-field presentation, the information presented directly to one hemisphere must cross brain commissures to be processed by the other. The important implication is that mechanisms in the first hemisphere obtain higher quality information (e.g., Dimond, Gibson, & Gazzaniga, 1972; Gross, Rocha-Miranda, & Bender, 1972) and obtain it more quickly than mechanisms in the other hemisphere. Thus, if the characteristic processing of one hypothesized subsystem (e.g., AVF processing) is performed

more effectively when high quality visual input is processed initially in one hemisphere (e.g., left) than in the other, whereas the characteristic processing of a different hypothesized subsystem (e.g., SVF processing) is performed more effectively when high quality visual input is processed initially in the *other* hemisphere (e.g., right) compared with the one yielding the first advantage, then two sorts of processing must rely on two sets of neural circuitry that operate at least relatively independently.

Note that, taken alone, such behavioral results do not suffice to indicate the extent to which the subsystems are lateralized or the degree to which they are modular. They only indicate that at least relatively independent subsystems are involved and that they are at least weakly lateralized. Further investigations utilizing additional methodologies are needed to clarify the unresolved issues. For example, further methods are needed to determine whether one subsystem operates in only one hemisphere, whether both subsystems operate with asymmetric efficiency in each hemisphere, etc.

### ***Visual Repetition Priming***

In one study, we examined repetition priming for visual word forms (Marsolek, Kosslyn, & Squire, 1992). Subjects were asked to read lists of common words presented in the central visual field during an initial encoding phase. Half of the words were presented in all lowercase letters (e.g., “convince”), and half were presented in all uppercase letters (e.g., “PRIMARY”). Afterward, in a presumably unrelated second phase of the experiment, subjects completed word stems (three-letter beginnings of words that can be completed to form many common words; e.g., “con”) to form the first words that came to mind. Each stem was presented in the left or right visual field. Repetition priming was exhibited when they produced word completions that corresponded to words that were viewed earlier in the experiment with a greater-than-chance tendency. The results were that such priming was greater when stems were presented in the same letter case as previously presented words, compared with the different letter case. More important, this letter-case-specific priming effect was found when the stems were presented directly to the RH (briefly in the left visual field) but not when they were presented directly to the LH (briefly in the right visual field). In a related study, Marsolek, Squire, Kosslyn, & Lulenski (1994) discovered that, in certain experimental conditions, the same pattern of results is obtained when subjects use the stems as cues to help them explicitly recall previously seen words.

These results suggest that the structural changes that underlie visual memory effects may be qualitatively different across subsystems that operate asymmetrically in the two hemispheres. Structural changes that underlie storage of the visually distinctive information that differentiates specific instances in an abstract category of form (e.g., lower- vs. uppercase versions of the same word) are instantiated more effectively in the RH than in the LH. Given that this sort of information storage should be characteristic of an SVF subsystem, the results indicate that an SVF subsystem, but not an AVF subsystem, operates more effectively in the RH than in the LH.

### ***Task Demands in Visual Repetition Priming***

In a similar study, we examined how task demands may influence priming in visual-form subsystems (Burgund & Marsolek, 1996). All subjects read lists of common words and pronounceable nonwords (half of each in all lowercase letters, and half of each in all uppercase letters) that were intermixed and presented in the central visual field during initial encoding. Then, in the test phase of one experiment, subjects performed a standard perceptual identification task by identifying briefly presented letter strings and writing them down, without following any particular instructions on how to write the strings. In the test phase of a different experiment, subjects performed a form-specific perceptual identification task by identifying briefly presented letter strings and writing them down in the *same letter case* as they had appeared on the computer monitor. Repetition priming was measured as the

tendency to identify and report letter strings that had been viewed earlier in the experiment more accurately than letter strings that had not been processed previously. The results were that letter-case-specific priming was greater when test items were presented directly to the RH than when they were presented directly to the LH (as observed in word-stem completion studies; Marsolek et al., 1992, 1994), but this was true only when the form-specific perceptual identification task was performed and not when the standard perceptual identification task was performed (cf. Koivisto, 1995).

These results suggest that task demands directly affect which subsystems are recruited in different priming tests. Performance in the standard perceptual identification task may be influenced by processing in an AVF subsystem to a greater degree than by processing in other subsystems, because letter-case-specific information does not need to be processed for accurate performance (unlike in the form-specific perceptual identification task). In addition, there is only one correct response per trial in this task, which may have the effect that the most efficient subsystem for the job (i.e., an AVF subsystem) dominates the production of a response (unlike in the word-stem completion task, in which the large number of “correct” responses per stem may have the effect that various subsystems contribute to the production of a response). Of course, performance in the form-specific perceptual identification task should be influenced highly by an SVF subsystem, because letter-case-specific information must be processed for accurate performance. In light of these task demands, the results further support the AVF/SVF subsystems theory.

### ***Visual Classification***

In another experiment, we investigated classification of novel visual forms (Marsolek, 1995). Subjects first learned to associate labels to categories of unfamiliar letterlike forms, and each form was presented in the central visual field during learning. Afterward, subjects were asked to classify test forms using the newly-learned categories. The results were that they classified the previously unseen prototypes of the newly learned categories (each prototype was the central tendency of the instances in one category) more effectively when they were presented directly to the LH than to the RH. In contrast, subjects classified the previously seen specific instances more effectively when they were presented directly to the RH than to the LH (and they did not classify previously unseen non-prototype instances differently depending on hemisphere of presentation).

Generally, the prototypes of these visual-form categories possessed a large amount of the visual information that remained relatively invariant across the different instances in one category. In fact, each prototype contained a larger amount of this relatively invariant information than did any of the other specific instances in its category. Hence, the results indicate that the information that is useful for an AVF subsystem (relatively invariant information) is stored more effectively in the LH than in the RH. In contrast, the previously seen specific instances of course contained visually distinctive information. Hence, the results indicate that the information that is useful for an SVF subsystem is stored more effectively in the RH than in the LH. Note that a RH advantage for processing the previously seen specific instances was obtained even though the demands of the categorization test task may have favored processing in an AVF subsystem more than processing in an SVF subsystem. We suggest that an SVF subsystem contributed to performance in this task nonetheless, because all of the forms were unfamiliar preexperimentally, and an SVF subsystem should store novel visual forms especially well. This reasoning for this hypothesis (see below) stems from our analyses of the internal processing strategies for AVF and SVF subsystems.

### ***CONTRADICTORY INTERNAL PROCESSING STRATEGIES***

Many previous theories of functional asymmetries have emphasized distinctions that can be understood in terms of analytic/parts-based processing versus holistic processing in the left and right

hemispheres, respectively (e.g., Bever, 1980; Bradshaw & Nettleton, 1981; Corballis, 1989; Diamond & Carey, 1986; Farah, 1990, 1991; Levine & Calvanio, 1989). Unfortunately, little attention has been given to explicating precisely the differences between these two kinds of processes (see Marshall, 1981, for important problems with analytic vs. holistic distinctions). In addition, little attention has been given to clarifying the conditions under which each kind of processing should be recruited or on explaining why the two kinds of processing appear to operate in different parts of the brain.

In this section, we offer computational analyses suggesting that one visual-form subsystem (an AVF subsystem) performs parts-based processing, because that sort of processing is required for effective recognition of *abstract categories per se*. Another visual-form subsystem (an SVF subsystem) performs holistic processing, because that sort of processing is required for effective recognition of *specific instances per se*. This analysis illuminates a concrete specification of the distinction between--and the contradictory natures of--parts-based versus holistic internal processing. In addition, we discuss how results from a neural network modeling study supplement and directly test this computational reasoning.

### ***Neural Network Models of Visual-Form Recognition***

We have examined relatively simple feedforward neural network models that receive “retinotopically-coded” bit-mapped inputs, in an effort to investigate how parallel distributed processing systems might accomplish the task of recognizing such input forms (Marsolek, 1994). Each network was composed of three layers of processing units: an input layer, a hidden layer, and an output layer. Input units were connected to hidden units via weighted interconnections, and in turn hidden units were connected to output units via weighted interconnections. In each processing trial, an input form was presented to the network as a pattern of activation across the two-dimensional array of input units. These input forms were just smaller than the array of input units, and in one trial an input form was presented in either the upper-right, lower-right, lower-left, or upper-left region of the array. After an input form was presented, activation flowed across the first set of weighted connections to activate the hidden units, and in turn activation flowed across the second set of weighted connections to activate the output units. Weights on the internal connections modulated the flow of activation between layers.

Each network was trained to perform input-to-output mappings through the use of an error-correction procedure (backpropagation-of-error; Rumelhart, Hinton, & Williams, 1986). This sort of training was used to guide each network to discover a set of weights across its internal connections that allowed the intended input-output mappings to take place. When such networks are trained to accomplish input-output mappings that apparently take place in certain areas of visual cortex, they tend to discover mapping solutions that the relevant neural subsystems appear to use (e.g., Churchland & Sejnowski, 1992; Lehky & Sejnowski, 1988; O'Reilly, Kosslyn, Marsolek, & Chabris, 1990; Zipser & Andersen, 1988). Note that any neural implausibility of the specific backpropagation training process used in this study was not important, in part because networks that use training algorithms that are very similar to backpropagation, yet are biologically plausible, tend to produce results that are highly similar to those found with backpropagation (see, e.g., Mazzoni, Andersen, & Jordan, 1991).

The input patterns and the target output patterns in our networks were random-dot patterns that adhered to statistical similarity constraints. However, in the following discussion we describe the models as though word forms like “BEAR,” “bear,” “**bear**,” “*bear*,” etc., served as input patterns, simply for clarity.

### ***AVF, SVF, and Intermediate Input-Output Mappings***

Each network was trained to solve *two* of the following three input-to-output mapping problems, with the three mapping problems examined in different pairs across different networks. In AVF

mappings (see Figure 3), the uncorrelated input patterns “BEAR” and “bear” (note the visual dissimilarities between these forms), in addition to the correlated input patterns “*bear*” and “**bear**” (note the visual similarities between these forms), were all mapped to the same output representation. However, in SVF mappings (see Figure 4), each specific instance (e.g., “BEAR,” “bear,” “*bear*,” and “**bear**,” etc.) was mapped to a different output representation. Furthermore, in an intermediate-level mapping problem (see Figure 5), the correlated input patterns “BEAR” and “*BEAR*” were mapped to the same output representation, yet the input patterns “bear” and “*bear*,” which were correlated with each other but not with “BEAR” and “*BEAR*,” were mapped to a different output representation. Note that the input patterns were the same for all three mapping problems; only the mappings to output representations differed across the three mappings.

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 Insert Figures 3, 4 and 5 about here  
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We examined whether the internal architectures of the networks affected their abilities to perform different pairs of mapping problems. One set of networks was trained to perform both AVF and SVF mappings of input patterns through different subsets of output units, half of the output units allocated to the AVF task and the other half to the SVF task. Some of these networks were unified or “unsplit” models, in which all hidden units were connected to all output units. However, other networks were “split” (e.g., Rueckl, Cave, & Kosslyn, 1989), in that one subset of the hidden units was connected only to the AVF output units and the other subset was connected only to the SVF output units. In this way, split networks had separate subcomponents devoted to the different mapping tasks, but unsplit networks accomplished the two tasks through a unified model.

Results were that, after an arbitrary number of training trials, models with separate subcomponents performed the AVF and SVF mappings more efficiently than unified models. (These split networks also outperformed networks with the same number of hidden-to-output unit connections as the split networks but with no systematic splitting of the hidden units into separate pools allocated to the different mappings.) It is important to note that this separate-subnetwork advantage did not extend to models that performed both AVF and intermediate-level mappings. Furthermore, the separate-subnetwork advantage did not extend to models that performed both SVF and intermediate-level mappings (see also Knapp & Anderson, 1984; McClelland & Rumelhart, 1985). Hence, split networks did not always outperform unsplit networks; they did so in this study only when AVF and SVF mappings, in particular, were performed in the same networks.

The split networks described above were strongly split networks in that they contained a strong modularity in their internal architectures. Strong modularity was not necessary, however, for the separate-subnetwork advantage. AVF and SVF networks that were weakly split (such that one subset of hidden units was dedicated to the AVF task, another to the SVF task, and a third to both tasks) also outperformed unsplit networks, even though weakly-split AVF and intermediate networks and weakly split SVF and intermediate networks did not outperform their unsplit counterparts.

The idea that SVF and intermediate mappings are compatible with one another in this study (Marsolek, 1994), as well as in other computational studies (see Knapp & Anderson, 1984; McClelland & Rumelhart, 1985), is one aspect of the present theory and models that is different from Kosslyn's (1987; Kosslyn, Chabris, Marsolek, & Koenig, 1992) theoretical distinction between coordinate and categorical spatial relations encoding and from Jacobs and Kosslyn's (1994) neural network models of “coordinate shape” and “categorical shape” processing. Their coordinate-categorical mapping distinction is very similar to our SVF-intermediate mapping distinction, in that one of the tasks (SVF or coordinate) involves mapping visually similar inputs to different output representations and the other task (intermediate or

categorical) involves mapping visually similar inputs, *and only inputs that are similar to them*, to the same output representation. Yet, we find that SVF and intermediate mappings are compatible, whereas Jacobs and Kosslyn (1994) conclude that different mapping solutions are useful for coordinate-shape and categorical-shape processing in their neural network models.

The apparently inconsistent results across these modeling studies may be resolved with the help of additional analyses (Marsolek, 1994). In our study, the projective fields of the hidden units in all split networks were held to a constant size across the pools of AVF, SVF, and intermediate-level hidden units. The projective field of a hidden unit is determined by its connections to the output units (Lehky & Sejnowski, 1988), thus split networks with a larger number of output units devoted to the SVF mapping than to the intermediate mapping would have SVF hidden units with larger projective fields than those of the intermediate-mapping hidden units. This is important because methodological difficulties arise when the two subsets of hidden units in a split network do not have the same-sized projective fields, which was the procedure used by Jacobs and Kosslyn (1994). When SVF hidden units have larger projective fields than intermediate-level hidden units, we have found that split networks outperform their unsplit counterparts, in restricted conditions, but the result is equivocal (Marsolek, 1994). The split advantage in this situation could be due to facilitation from splitting networks into large and small projective-field subnetworks (which may have to do with optimal learning rates being proportional to fan-in and fan-out of processing units in networks like these; cf. Plaut & Hinton, 1987), regardless of whether contradictory mapping tasks are performed in the separate subnetworks.

Therefore, we conclude that AVF and SVF mappings, but not the other pairs of mappings, are performed more efficiently through separate subnetworks than through unified networks. These results indicate that the internal processing strategies that are useful for parallel distributed processing systems to perform AVF mappings and the internal processing strategies that are useful for such systems to perform SVF mappings may interfere with one another or are contradictory in some way. In what ways are the strategies contradictory? Our computational argument is that different internal processing strategies are useful for subsystems that perform AVF and SVF recognition. Parts-based processing should be useful for an AVF subsystem because the relatively invariant information of the forms in one category tend to be found in their parts (see Figure 2). In contrast, holistic processing should be useful for an SVF subsystem because the visually distinctive information that differentiates specific instances of forms is found in the holistic structures of the forms (see Figure 2). A single, undifferentiated mechanism cannot perform both parts-based and holistic processing effectively. For proper assessment, this hypothesis requires the following explication.

### ***Assumptions***

Two important assumptions are needed for the computational analysis offered here. First, visual-form subsystems (and artificial networks that simulate them) receive the retinotopically-mapped representations of input forms that are currently being captured by selective attention mechanisms. That is, visual selective attention serves to filter out extraneous inputs and acts to “surround” the form that currently is being processed, regardless of the location or size of the form as it appears on the retina (e.g., LaBerge, 1995). Such a selective-attention filter may operate at least in part before processing in visual-form subsystems of the inferior temporal cortex, because cells in the inferior temporal region do not change their response selectivities appreciably when visual forms change locations and sizes yet remain within the receptive fields of the cells (Schwartz, Desimone, Albright, & Gross, 1983). This assumption is needed to account for effects of size and location invariance in visual-form priming; changes in size and location of forms between initial encoding and subsequent test do not greatly influence priming effects (Biederman & Cooper, 1992; Cooper, Schacter, Ballesteros, & Moore, 1992).

The analogy in the network models is that input forms are conceptualized to be scaled so that they are just smaller than the input grid in any one trial, regardless of their sizes or locations on the “retina” in some earlier stage of processing.

The second important assumption is that visual-form priming is produced by structural changes in visual-form subsystems (and in artificial networks that simulate them). This assumption is needed to account for relatively long-term priming effects, which can last for several days in the case of object priming, even for amnesic patients (Cave & Squire, 1992). Long-term priming must be supported through some kind of physical change that serves to store information for a period of time (possibly through local synaptic changes such as in long-term potentiation in visual cortex; Artola & Singer, 1987; Komatsu, Fujii, Maeda, Sakaguchi, & Toyama, 1988). The analogy in the network models is that priming is supported by small changes in the previously established weights on the internal connections of the networks due to recent processing of a prime stimulus (and the accompanying backpropagation-of-error). Different kinds of weight changes can be considered in these network models, depending on the kind of information they represent.

### ***Parts-Based Internal Processing***

Imagine the receptive fields that would develop in these network models during training (the receptive field of a hidden unit is determined by its connections to the input units). If each hidden unit in a network were to have a relatively large absolute weight value on only a few of the connections feeding into it and very small weight values (perhaps 0) on the other connections, then each hidden unit would be connected functionally to only a few input units. If different hidden units were sensitive to different subsections of the input array, such that any one hidden unit were to be sensitive to only a part of any one input form, this would be an example of a network with a parts-based internal representation strategy. Such a network may utilize what is called a “sparse” or “local” coding strategy (see Churchland & Sejnowski, 1992). In this case, different hidden units necessarily represent different parts of any one input form.

Note that this kind of internal processing strategy should be useful for an AVF subsystem. For example, an efficient internal representation for the abstract category in Figure 1 may be activation of the hidden units that are sensitive to that category's relatively invariant information (see Figure 2), coupled with little or no activation of the hidden units that are sensitive to the parts that are found in the visually distinctive information that differentiates specific instances in that abstract category or to the parts that are found in other abstract categories. Indeed, examinations of the trained networks described above (Marsolek, 1994) indicate that this sort of internal processing strategy is used in the AVF portions of split networks. The hidden units in these AVF subnetworks develop receptive fields that utilize a relatively parts-based strategy.

The priming in such a network necessarily would be parts-based. Because the activation of any one hidden unit represents only one part of an input form, small weight changes on the connections feeding into different hidden units would yield priming for relatively independent information about different parts of an input form. Hence, different parts of the same input form should be primed relatively independently in such a subsystem. Indeed, behavioral results summarized below support this hypothesis.

### ***Holistic Internal Processing***

Now imagine another possibility in these network models. If each hidden unit in a network were to have relatively large (but varying across units) absolute weight values on perhaps all of the connections feeding into it, then each hidden unit would be connected functionally to the whole (or at least a very

large portion) of the input array. If different units were differentially sensitive to different parts of the whole input array, such that different hidden units were sensitive to slightly different aspects of the whole of any one input form, this would be an example of a network with a holistic internal representation strategy. (For advantages in using “coarsely” coded representations like these, see Ballard, 1986; Hinton, McClelland, & Rumelhart, 1986.) In this case, the hidden units would not represent different parts of an input form explicitly as such, only implicitly as portions of the whole form to which perhaps every unit is sensitive.

This kind of internal processing strategy should be useful for an SVF subsystem. For example, an efficient internal representation for the specific instance “BEAR” may be a distinct pattern of activation across perhaps all of the hidden units, each of which may be slightly differentially sensitive to all of the information in that particular input form. Indeed, examinations of the trained networks described above (Marsolek, 1994) indicate that this sort of internal processing strategy is used in the SVF portions of split networks. The hidden units in these SVF subnetworks develop receptive fields that utilize a relatively holistic strategy.

The priming supported by such a network would be holistic. Because the activation of any one hidden unit represents holistic structure, small weight changes on the connections feeding into any one hidden unit would yield priming for the wholes of forms. Hence, different parts of the same input form could not be primed independently in such a subsystem. Indeed, behavioral results summarized below support this hypothesis.

In addition, it is worthwhile to note that the holistic priming supported by such a network should be useful for priming of unfamiliar forms. At some level, every unfamiliar form has parts (in the limit, various sorts of edges) that are familiar; it is the holistic structure of any unfamiliar form that contains the information that makes it unfamiliar. Hence, the novel aspects of unfamiliar forms should be primed more effectively in a holistic processing network than in a parts-based processing network. This hypothesis is also supported by behavioral results summarized below.

### ***Contradictory Strategies***

It should be clear that a single, undifferentiated network could not implement both a parts-based and a holistic processing strategy. The same mechanism could not represent parts explicitly as such and *not* represent parts explicitly as such. Although the parts-based and holistic processing strategies described above are relatively extreme versions of both, less extreme versions of the two strategies also may be contradictory. The relatively invariant information associated with an abstract category like in Figure 1 is present in some subset of the information in any one input form, a subset that necessarily is smaller than the amount of visually distinctive information that differentiates any one specific instance in that category (i.e., the holistic structure of that instance). Likewise, the visually distinctive information that differentiates specific instances in Figure 1 is present in the holistic information in these inputs, a set of information that necessarily is larger than the relatively invariant information for that abstract category (i.e., parts of the forms). Hence, efficient internal representations for AVF categorizations should involve parts-based coding of a relatively small amount of information per form, whereas efficient internal representations for SVF categorizations should involve holistic coding of a relatively large amount of information per form. It would be difficult for a single mechanism to store both kinds of information effectively (*only* the relatively invariant information for the abstract category *as well as* the visually distinctive information that differentiates specific instances in that category). In other words, it would be difficult for a single mechanism to accomplish both AVF and SVF recognition effectively.

Given that contradictory strategies (parts-based vs. holistic) are useful for accomplishing different goals (AVF vs. SVF categorizations), and both goals are vitally important for survival, selective pressures

may have led to the evolution of relatively independent processing subsystems with the different subsystems utilizing different computational strategies. Note that the claim here is not that it would be impossible for a single subsystem to accomplish both AVF/parts-based and SVF/holistic processes or that these processes are incompatible per se. Instead, the reasoning involves considerations of relative efficiency and of course should be tested. Next, we summarize behavioral evidence in support of our computational theory.

#### ***BEHAVIORAL EVIDENCE FOR PARTS-BASED VERSUS HOLISTIC PROCESSING***

In further behavioral studies, we have tested directly whether an AVF subsystem utilizes a parts-based internal processing strategy whereas an SVF subsystem utilizes a holistic processing strategy. Recent behavioral studies using divided-visual-field presentations of memory test items and studies using an interhemispheric communication paradigm support these hypotheses.

#### ***Visual Repetition Priming***

The computational theory is supported by a recent study of visual priming using the word-stem completion task (Marsolek et al., 1995). In this study, some of the word stems (and hence the beginnings of their corresponding words) were composed of letters with visually *dissimilar* lower- and uppercase structures (e.g., “bea” / “BEA”), whereas the other items were composed of letters with visually *similar* lower- and uppercase structures (e.g., “sco” / “SCO”). Like the priming studies described above (Marsolek et al., 1992; 1994), subjects read lists of words presented in the central visual field during an initial encoding phase. Half of the words were presented in all lowercase letters, and half were presented in all uppercase letters. Then, subjects completed word stems to form the first words that came to mind during a presumably unrelated second phase of the experiment.

Results indicate that the parts-based information that is common to “BEAR” and “bear” is stored in an AVF subsystem that operates more effectively in the LH than in the RH. Same and different letter-case priming did not differ when the dissimilar stems were presented directly to the LH (even though same-case priming was greater than different-case priming when these stems were presented directly to the RH). For example, “BEAR” primed “bea” as well as “bear” primed “bea” in LH stem presentations. (Note that this effect apparently is supported by visual subsystems per se, because “BEAR” primes “bear” to a greater degree than hearing the word bear primes the visual form “bear” [Bowers, in press].) In contrast, the holistic information that differentiates even structurally similar forms, like “SCOOP” and “scoop,” is stored in an SVF subsystem that operates more effectively in the RH than in the LH, albeit through interactions with the hippocampal formation (see several chapters in Schacter & Tulving, 1994; Cohen & Eichenbaum, 1993; McClelland, McNaughton, & O’Reilly, 1995; Squire, 1992). This qualification is needed because only explicit memory as measured in word-stem cued recall, but not repetition priming as measured in word-stem completion priming, produces greater same-case than different-case memory for the similar-case items in RH presentations. For example, when “scoop” had been presented earlier in the experiment and “sco” was the test cue, that word was recalled more readily than when “SCOOP” had been presented earlier and “sco” was the test cue, in RH but not in LH presentations of the cues.

#### ***Visual Priming for New Associations***

In further experiments, we examined visual priming for new associations between previously unrelated words (Marsolek, Schacter, & Nicholas, 1996). During the encoding phase, subjects read lists of word pairs, one word presented above the other in the central visual field for each pair. Half of the pairs were presented in all lowercase letters, and half were presented in all uppercase letters. Afterward, subjects completed word stems that were presented beneath complete context words in a presumably

unrelated test phase. Letter-case-specific priming in stem completion was found only when the context words were the same words that had appeared previously above the primed completion words during initial encoding and when the two items in a test pair (context word and word stem) were presented directly to the RH. When the context words were different words from those which had appeared above the primed completion words during initial encoding, no letter-case-specific priming was obtained in stem completion. These results indicate that priming for novel holistic information (i.e., one word form as it appears above another word form) is supported by a subsystem that distinguishes lower- versus uppercase versions of the same word and operates more effectively in the RH than in the LH, as predicted from the computational theory described above.

### ***Interhemispheric Communication of Visual-Form Information***

In another behavioral study, we examined interhemispheric transfer of visual-form information (Nicholas & Marsolek, 1996). Subjects were asked to compare two visually presented letters in each trial. The two letters appeared in the same visual field in half of the trials, but in different visual fields in the other half of the trials, similar to a task used by Banich & Belger (1990) who presented three letters per trial and asked subjects to compare the bottom-most letter to the other two in each trial. With such a procedure, interhemispheric transfer of information *must* have taken place when the comparison letters were presented across hemispheres (briefly displayed in different visual fields) but not necessarily when they were presented within a hemisphere (briefly displayed in the same visual field). We took advantage of this circumstance in experiments investigating two visual comparison tasks. Results indicate that AVF and SVF subsystems are differentially affected by interhemispheric transfer of visual-form information in ways that are predictable from the computational theory described above.

In an AVF comparison task, subjects decided whether the pairs corresponded to the same letter of the alphabet (e.g., “a” and “A,” “s” and “S”) or not (e.g., “a” and “Q,” “s” and “P”). In this task, they performed more accurately in across-hemisphere trials than in within-hemisphere trials. However, this across-hemisphere advantage was found for similar-case letters (e.g., s/S), but not for dissimilar-case letters (e.g., a/A) which yielded no within- or across-hemisphere advantage. Current theories of interhemispheric communication (Banich & Belger, 1990; Belger & Banich, 1992; Hellige, 1993b) would not predict this finding, yet the AVF/SVF subsystems theory may account for it. The effects of noise produced by interhemispheric transfer of similar-case letters may not be as detrimental as the effects of noise produced by interhemispheric transfer of dissimilar-case letters, in the AVF task. That is, noisy versions of the relatively invariant information in similar-case letters may be processed by an AVF subsystem more effectively than noisy versions of the relatively invariant information in dissimilar-case letters, because there is more relatively invariant information per letter for similar-case items than for dissimilar-case items to help overcome the noise. Hence, the relatively invariant information needed to make AVF categorizations of similar-case letters, but not dissimilar-case letters, may cross brain commissures effectively enough to take advantage of the benefits of distributing the processing of the two letters across the two hemispheres (cf. Banich, 1995; Dimond & Beumont, 1971).

In an SVF comparison task, subjects decided whether the letters in a pair were physically the same (e.g., “a” and “a,” “S” and “S”) or not (e.g., “a” and “A,” “s” and “S”). In this task, they performed more accurately in within-hemisphere trials than in across-hemisphere trials. Hence, SVF processing apparently cannot take advantage of the benefits of distributing the processing of the two letters across the two hemispheres. Interestingly, this within-hemisphere advantage was found for similar-case letters (e.g., s/S), but not for dissimilar-case letters (e.g., a/A) which yielded no within- or across-hemisphere advantage. Current theories of interhemispheric communication (Banich & Belger, 1990; Belger & Banich, 1992; Hellige, 1993b) would not predict this result, but the AVF/SVF subsystems theory would.

The visually distinctive information needed to make SVF categorizations of dissimilar-case letters may not cross brain commissures (to take advantage of neural distribution) effectively enough to produce an across-hemisphere advantage. Moreover, the visually distinctive information needed to make SVF categorizations of similar-case letters may be so fine-grained that it crosses brain commissures so ineffectively that a within-hemisphere advantage is produced. Indeed, by hypothesis, an SVF subsystem should be fairly sensitive to the noise produced by interhemispheric transfer of information, because it may treat noise as the kind of “visually distinctive” information that it is tuned to process when it is called upon to perform SVF categorizations.

#### *CONCLUSIONS AND IMPLICATIONS*

A fundamental aspect of the architecture of our neural processing subsystems appears to be that relatively independent subsystems underlie AVF versus SVF recognition. In this chapter, we have summarized research that supports this conclusion through an integration of behavioral studies and computational analyses and models. We have highlighted considerations of the inputs available to visual processing subsystems, the goals that these subsystems must satisfy to underlie important visual abilities, and plausible internal processing strategies that these subsystems could use to achieve the appropriate goals given the available input. All of these considerations are combined to characterize explicitly the functions--and contradictory natures of--relatively independent AVF and SVF subsystems. We conclude that an AVF subsystem operates more effectively in the LH than in the RH, and it uses a parts-based internal processing strategy to focus on the relatively invariant information in visual-form inputs, which allows it to recognize abstract categories of visual forms effectively. In contrast, an SVF subsystem operates more effectively in the RH than in the LH, and it uses a holistic internal processing strategy to capture the visually distinctive information in visual-form inputs, which allows it to recognize specific instances of forms effectively.

One set of results from previous research that we have not mentioned heretofore is consistent with our conclusions and may help to illuminate an important feature of our theoretical approach. In divided-visual-field studies, subjects identify and discriminate high spatial-frequency information more effectively when it is presented directly to the LH than to the RH, whereas they identify and discriminate low spatial-frequency information more effectively when it is presented directly to the RH than to the LH (e.g., Christman, Kitterle, & Hellige, 1991; Kitterle, Christman, & Hellige, 1990; Kitterle & Selig, 1991). Of course, these asymmetries may help to explain why LH advantages are found when subjects process the local parts of hierarchically arranged stimuli whereas RH advantages are found when they process the global forms of these stimuli (Robertson & Lamb, 1991; Van Kleeck, 1989), given that relatively high spatial-frequency information should be useful for processing the local forms and relatively low spatial-frequency information should be useful for processing the global forms (Sergent, 1982).

These findings are consistent with our theory for the following reasons. A subsystem that has evolved to perform AVF recognition should perform parts-based processing effectively. An individual cell in such a subsystem should receive information from a relatively small portion of the input array, and hence the cell optimally should be tuned to a high spatial-frequency band. It is important to note that the cell also may be sensitive to even higher frequencies in some conditions, but it may not be very sensitive to substantially lower frequencies (e.g., Sergent, 1989). It is also important to note that a collection of such cells, each receiving information from different but overlapping portions of the input, should be very sensitive to even higher frequencies than an individual cell's optimal frequency, through the use of a distributed representation (cf. Hinton et al., 1986). Furthermore, this collection of cells may be able to respond to relatively low frequencies as well, given that different cells in the distributed representation should respond differently due to the different levels of overall activation that are present in their different portions of a low spatial-frequency input.

In contrast, a subsystem that has evolved to perform SVF recognition should perform holistic processing effectively. An individual cell in such a subsystem should receive information from a relatively large portion of the input array, and hence it optimally should be tuned to a low spatial-frequency band. Of course, by the same analysis as above, the cell also may be sensitive to higher frequencies in some conditions, but not to substantially lower frequencies (e.g., Sergent, 1989). Furthermore, a collection of such cells, each receiving slightly different information from large portions of the input, should be sensitive to higher frequency information than that to which an individual cell in the subsystem is sensitive (cf. Hinton et al., 1986), and the collection of cells should be sensitive to lower frequencies as well.

Thus, both subsystems may process high and low spatial-frequency information, but not with the same efficacy. Assuming that the optimal frequency band for most individual cells in a subsystem determines the optimal range of frequencies for distributed representations in that collection of cells, and assuming roughly the same number of cells per subsystem, we conclude the following. Compared against one another, an AVF subsystem should process relatively high spatial-frequency information more effectively than an SVF subsystem, and an SVF subsystem should process relatively low spatial-frequency information more effectively than an AVF subsystem.

Of course, the more general spatial-frequency hypothesis can account for these hemispheric asymmetries as well. The LH may be specialized for processing high spatial-frequency information whereas the RH may be specialized for processing low spatial-frequency information (Sergent, 1982). This hypothesis certainly has been useful for attracting attention to input factors and their roles in hemispheric asymmetries. However, concentration on input factors without their relations to other factors leaves an incomplete picture of hemispheric asymmetries.

Just as one must consider how asymmetries in lower-level processes modulate asymmetries in higher-level processes when hypothesizing about the higher-level processes, one must also consider the goals that the lower-level processes accomplish, as well as the mappings between inputs and outputs that they achieve, in order to explicate the functions of the neural subsystems that underlie the lower-level processes. The functions of relatively independent AVF and SVF subsystems may provide an explanation for the observed spatial-frequency asymmetries, one that is capable of explaining why these asymmetries evolved in the first place, but only after inputs, outputs, and their couplings are examined together. Indeed, consideration of all of the available constraints may be essential when doing the very difficult job of stretching the brain at its interconnections.

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*AUTHOR NOTES*

Preparation of this chapter was supported by the National Institute of Mental Health, Grant MH53959-01; by the McDonnell-Pew Cognitive Neuroscience Center and the Arizona Cognitive Science Program of the University of Arizona; and by the Center for Research in Learning, Perception, & Cognition in conjunction with the National Science Foundation (GER 9454163), the Office of the Vice President for Research, and Dean of the Graduate School of the University of Minnesota.

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**FIGURE CAPTIONS**

*Figure 1.* Different specific instances that belong to the same abstract category of visual form.

*Figure 2.* In the upper display, the relatively invariant information (right) that is common to different specific instances in the same abstract category of visual form (left). In the lower display, the visually distinctive information (right) that distinguishes specific instances in the same abstract category of visual form (left).

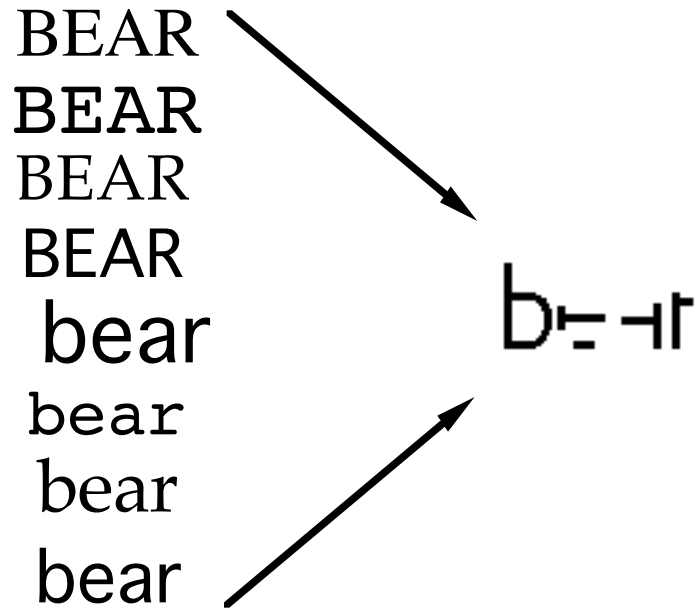
*Figure 3.* AVF mappings of input forms (left) to output representations (right) simulated in neural network models.

*Figure 4.* SVF mappings of input forms (left) to output representations (right) simulated in neural network models.

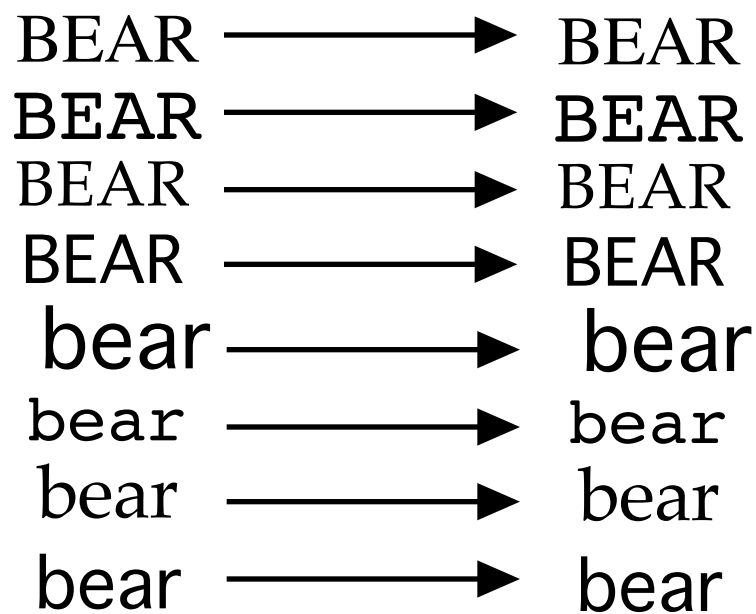
*Figure 5.* Intermediate-level mappings of input forms (left) to output representations (right) simulated in neural network models.

BEAR  
BEAR  
BEAR  
BEAR  
bear  
bear  
bear  
bear

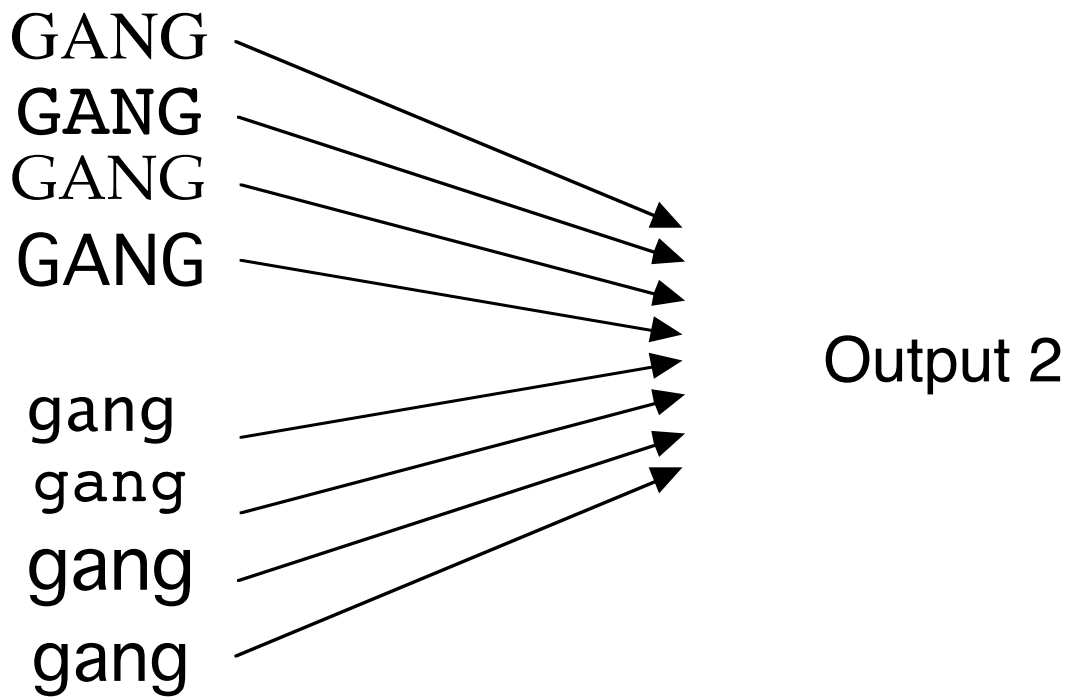
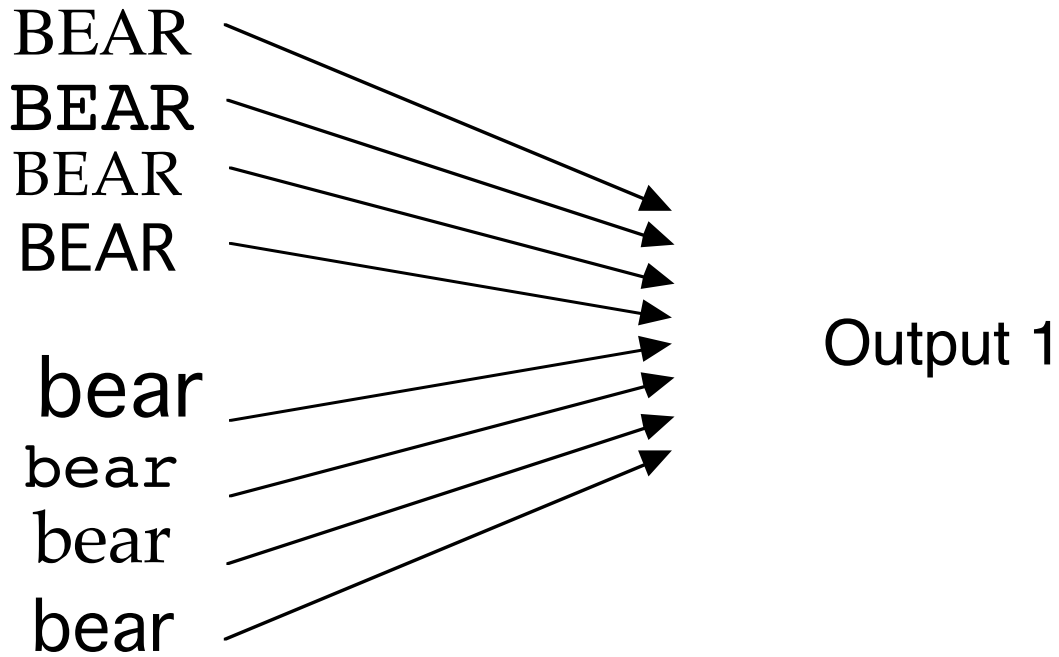
***Relatively Invariant Information***

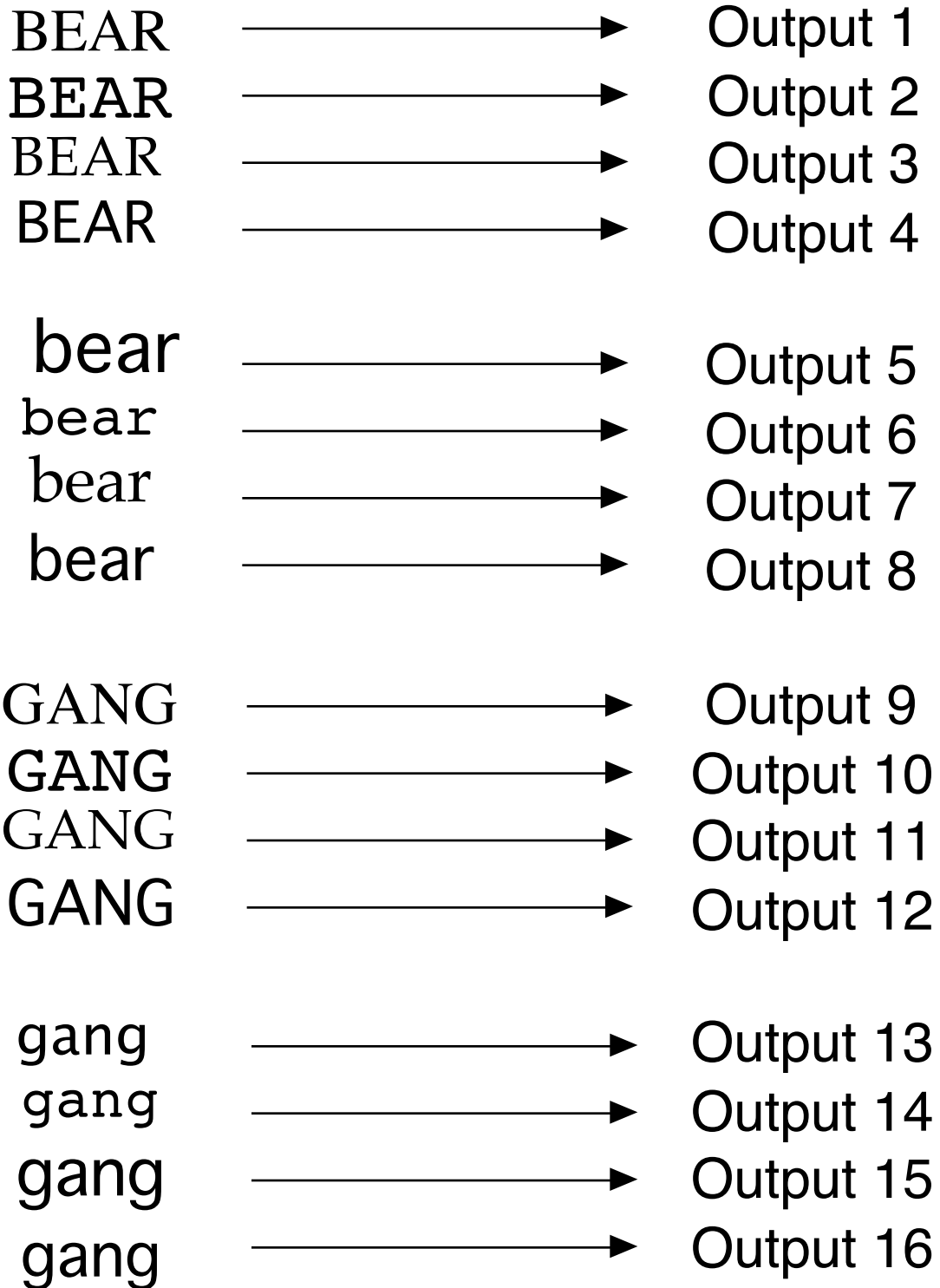


***Visually Distinctive Information***



*AVF Mappings*



***SVF Mappings***

*Intermediate-Level Mappings*

