Integrating Neuroscience, Psychology, and Evolutionary Biology Through a Teleological Conception of Function

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Abstract

The idea of integrating evolutionary biology and psychology has great promise, but one that will be compromised if psychological functions are conceived too abstractly and neuroscience is not allowed to play a contructive role. We argue that the proper integration of neuroscience, psyychology, and evolutionary biology requires a telelogical as opposed to a merely componential analysis of function. A teleological analysis is required in neuroscience itself; we point to traditional and curent research methods in neuroscience, which make critical use of distinctly teleological functional considerations in brain cartography. Only by invoking teleological criteria can researchers distinguish the fruitful ways of identifying brain components from the myriad of possible ways. One likely reason for reluctance to turn to neuroscience is fear of reduction, but we argue that, in the context of a teleological perspective on function, this concern is misplaced. Adducing such theoretical considerations as top-down and bottom-up constraints on neuroscientific and psychological models, as well as existing cases of productive, multidisciplinary cooperation, we argue that integration of neuroscience into psychology and evolutionary biology is likely to be mutually beneficial. We also show how it can be accommodated methodologically within the framework of an interfield theory.

Keywords: Neuroscience, evolutionary psychology, interfield theory, evolution, teleology, function, functionalism, brain mapping, language processing.

I. Introduction

Evolutionary psychology is often pitched as an attempt to integrate psychology and biology (Barkow, Cosmides, & Tooby, 1992). The contribution of biology, as the name “evolutionary psychology” implies, is from evolutionary biology. As such, it is not a particularly new endeavor. In the wake of Darwin, theorists such as James and Spencer sought to understand psychological processes from an evolutionary perspective. One objective of proponents of an “evolutionary psychology” such as Tooby and Cosmides (1992) is to counter what they call “the Standard Social Science Model,” which has emphasized environmental determinants of human behavior and denied or minimized nativistic components, especially “the evolved architecture of the human mind.” One can question whether one needs to emphasize nativism in order to give proper weight to the “architecture of the human mind” (see Elman, Bates, Johnson, Karmiloff-Smith, Parisi, & Plunkett, in press, for an anti-nativistic, emergentist perspective that still seeks to identify architectural features of the human mind; see also Wimsatt, 1986). Yet, from our perspective a more serious objection to this endeavor is that the advocates of evolutionary psychology, while including neuroscience in their list of disciplines included in their attempt at integration, do not really draw on neuroscience. While not endorsing the specific theoretical claims put forward by proponents of evolutionary psychology such as Cosmides and Tooby, we nonetheless advocate the integration of neuroscience, psychology, and evolutionary biology, and show how this is best served by a teleological view of function.

One can identify at least two reasons for the apparent lack of serious integration. The first is a bias within some parts of evolutionary biology itself. Mayr (1961) introduced the distinction between ultimate and proximate explanations of a trait: the ultimate explanation is an evolutionary explanation of the trait's origin through a process of natural selection, while the proximate explanation focuses on the physiological and biochemical processes (including genetic ones) instantiating the trait in particular organisms. While Mayr certainly did not dismiss the importance of proximate explanations, the very vocabulary of "ultimate cause" suggests that an evolutionary explanation is more significant. The second factor is that often appeals to neuroscience are viewed as attempts to *reduce* the psychological phenomena, thereby not giving it its proper due. We shall discuss this in section four below. In all likelihood, however, there is a third, less principled, factor that accounts for the tendency to overlook neuroscience--until recently, much of the work in neuroscience has appeared to be at too low a level of organization to provide much help. With the development of powerful techniques in the fields of cell and molecular biology, it became possible for neuroscientists to study in detail processes involving individual neurons, such as the role of ion potentials in synaptic processes, but these are quite far removed from psychological function. However, neuroscience also has a long tradition of research into higher-level processes, such as determining the brain components involved in specific psychological processes which, until recently, were not as familiar to those outside of the field. The introduction in the last decade of new techniques, such as positron emission tomography (PET) and functional magnetic resonance imaging (functional MRI), as well as new computational procedures have greatly expanded the potential for neuroscience to contribute to specifying the architecture of the mind (see, for example, Posner & Raichle, 1994).

Although neuroscience is in a very promising position to contribute to a joint enterprise with psychology and evolutionary biology, there is a further stumbling block to its proper integration into it. This has to do with the concept of function. There are at least two broad ways of construing function in biology, psychology, and the philosophies thereof. The first, a *non-teleological* construal, focuses on the interactions of processes within a system without special attention to their contributions outside the system (for examples, see Fodor, 1968, and Cummins, 1975). In section three, we discuss in detail the componential interpretation of function as a prominent example which lacks an explicit teleological commitment. While it has played a prominent role in the development of functionalism as a stance on the mind-body problem, it is also evident in biology. It is common to refer to the disciplines involved in developing what Mayr called proximate explanations, for example, physiology and biochemistry, as parts of functional biology. "Functional" here serves to mark two contrasts, one with evolution, and another with underlying anatomical structure.

The second major way of construing function is a *teleological* perspective on function, which emphasizes the links with natural selection. Wimsatt (1972) and Wright (1976) were two early advocates of this notion of function, but it has recently been advocated in some areas of philosophy of psychology (e.g., by Millikan, 1984, Dretske, 1988, and Lycan, 1987). The key here is that a function of a component is identified in terms of contributions that component makes to the ability of the system of which it is a part to meet the selection pressures operating on it. We develop and defend this conception of function in section 3; but before that, in section 2, we motivate the teleological perspective through an analysis of how considerations of function figure in neuroscience itself in the foundational activity of identifying the brain's parts.

Evolutionary psychology itself employs a teleological conception of function; yet, as we have noted, it has been slow to develop a significant role for neuroscience. In section 4, we argue that this is the nonetheless the proper extension of the commitment to multi-level integration espoused by most exponents of evolutionary psychology. As we mentioned above, one of the concerns about appealing to neuroscience is a fear of reductionism--a fear that an appeal to neuroscience will displace the potential contributions of psychology and the evolutionary perspective. However, one need not use reductionism as the model for integrating neuroscience into psychology and evolutionary biology. Adopting a stratified view of nature, we can recognize how different levels can play both constraining and heuristic roles with respect to inquiry at other levels. The pattern of integration of neuroscience with psychology and evolution may better be construed from the perspective of what Darden and Maull (1977) characterize as an interfield theory. We will characterize interfield theories in section 5 and offer a detailed example of how an interfield theory might develop that includes evolutionary, psychological, and neuroscientific perspectives.

II. Functional considerations in the brain-mapping research of neuroscience

In order to set forth the advantages of the teleological view of function that we defend, it is first necessary to show how it is motivated by some particular features of neuroscientific research, especially those which concern the mapping of the brain. One factor about neuroscience research which has largely escaped notice by philosophers is the critical role functional considerations play in fixing the taxonomy of brain. Unless one follows in the tradition of investigators such as Marie-Jean-Pierre Flourens (1794-1867), Constantin von Monakow 1853-1930, Kurt Goldstein (1878-1965), or Karl Lashley (1890-1958), who, to varying degrees, held to holistic, or equipotentiationist[1] interpretations of brain action, one needs to identify component parts within the brain. For those who are not neurological cognoscenti, it is easy to assume that this can be done in either purely anatomical terms or, if physiological considerations are important, only low-level neurophysiological considerations need to be taken into account. They picture opening up the skull and finding this grey bumpy mass, riddled throughout with neurons and who knows what else, divided into two more or less equal hemispheres, with a prominent bump hanging off the back; various protrusions and fissures will be apparent, and they may easily assume that these will be sufficient for defining the parts of the brain. Yet to be informative, a far more fine-grained taxonomy is required; accordingly functional considerations, frequently requiring considerations of overt behavior and psychological theories of the processes involved in producing this behavior, often play a crucial role in developing an adequate map the brain. In order to understand the importance of function in mapping the brain, it is first necessary to consider some additional features of this research (for details, see Mundale, 1996, chapter 1).

In practice, of course, neuroanatomists use more than easily observable physical characteristics such as fissures and protrusions to identify brain regions. For example, they examine the types of neurons prevalent in different areas of the brain and their projection patterns. Beginning in the late 19th century, a variety of chemical stains were developed which selectively stain some of the microscopic constituents of brain matter. Minute slices of the brain, appropriately stained and prepared, reveal differential patterns, layers, and regions when viewed under a microscope. There are, of course, many different stains and methods for applying them, and they do not all yield the same results. Depending on the stain, the pattern may indicate differences in the density, type, distribution, etc., of nerve cells, nerve fibers, or neurochemicals. Methods which reveal patterns of *cell* type, density, and distribution, are known as cytoarchitectonic methods. However, not all of the differences that can be marked in neuroanatomical terms make for useful decomposition of the brain into components; accordingly other criteria, functional criteria, must be invoked to determine which cytoarchitectural distinctions are important. The cytoarchitectural distinctions, though, do provide useful clues about where divisions of functional importance may lie within the brain.

One of the most renowned researchers in this area is Korbinian Brodmann (1868-1918), a figure of enduring influence whose map of the brain's cortex continues to be used (albeit with slight modifications) in today's current neuroscientific literature. While Brodmann employed a variety of methods, his map of the cortex was primarily based on cytoarchitectonic patterns and was divided into 52 separate areas. Brodmann was not the only researcher of his time to advance a map of the cortex. Unlike many of the alternative maps, however, his has endured, since many of the regions he identified have proved to be functionally significant. Brodmann's area 17, for example, has been identified as important in visual processing, and accordingly is often referred to as “the visual cortex.” Likewise, Brodmann's area 4 constitutes the motor cortex, and areas 1, 2 and 3 the sensory cortex. Kandel, Schwartz, and Jessell (1991, p. 293), in one of the most authoritative texts of general neuroscience, report that "Brodmann's areas have consistently been found to correspond to distinctive functional fields, each of which has a characteristic pattern of connections."

Brodmann was a staunch localizationist, as would be predicted, and he was unwavering in his support of the principle that physical differentiae of the brain demarcate functional boundaries. On several occasions, he expresses support for this principle. He argues, for example, that:

> . . .where we find within the organism or within an organ new types of cells we assume a qualitatively characteristic function. Why should the cortex with its cells make an exception? The cells of the two glands such as the kidney and liver are histologically not nearly as different from each other as for instance, in the same central nervous organ, a 'motor' giant pyramidal cell and the small granular cell .... (Brodmann, 1909, p. 289; transl., von Bonin, 1960, p. 204).

In the approximately one hundred year history of this sort of research, Brodmann's faith has often been confirmed; it has repeatedly proved to be the case that different brain areas revealed by neurohistological criteria have turned out to have specific psychological functions associated with them. If this were not the case, of course, it is difficult to see any point in such research. We would be left with just an interesting mosaic of patterns, regions, and types, but without any sense of what they might signify - an uninterpreted map, in other words.

In addition to considering psychological activities associated with cortical regions, Brodmann emphasized that the brain is an evolved product; it has been refined, modified, and specialized like any other organ, by the forces of natural selection. An evolutionary perspective suggests identifying homologous traits in different species and attending to how the structure involved is preserved or changes in light of functional demands made on the two species. Thus, not only did Brodmann study human brains, but he also prepared comparative maps of the brains of dozens of other species as well. As we shall note in developing an example in section 5, comparative studies establishing homologies have turned out to be fruitful in developing a functional understanding of the brain. Such a focus on function is teleological in the sense we shall develop in the next section, and it is apparent throughout his writings that Brodmann's philosophical approach to the brain and its functions is profoundly teleological. This is especially evident when he discusses the basic assumptions governing his research, of which the following passage is representative:

> It is a basic biological fact that the function of an organ is correlated with its histological structure. Since every organic form is a product of its development, since, furthermore, its development is the sum of many biological processes, the evolution of organic form, its appearance by

> histological differentiation is in the last instance a *physiological problem*. Function creates its organs. This seems to justify even him who is generally not used to deduce the function of an organ from its structure, to draw certain conclusions from the structural similarity or dissimilarity of its parts, in brief from the special differentiation of internal structure to the function of the whole as well as of the parts.
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> Although my localizing studies began from a purely anatomical viewpoint and I only wanted to solve anatomical questions, the final goal was from the beginning to push ahead the knowledge of function . . . . (Brodmann, 1909, p. 285; von Bonin, transl., 1960, p. 201).

The outlook expressed by Brodmann still resonates in modern brain mapping research. Thus, many contemporary researchers employ an approach which integrates structural and functional considerations in mapping the brain, integrating information from many different levels (see, for example, Carmichael and Price, 1994, or Felleman and Van Essen, 1991). "FACTS" is an acronym in the neuroscientific community which stands for the criteria most commonly employed to define brain areas: functional, architectonic, connective, topographic, and structural. The functional criterion is straightforward, in the sense that it refers to what the putative area does. Architectonics usually refers either to cytoarchitectonics, or to myeloarchitectonics, which refers to differential patterns of nerve fibers rather than nerve cells. Connectivity simply refers to how a region is connected to other regions, its major neuronal inputs and outputs. Topography refers to the way some parts of the brain contain maps or representations of corresponding sensory regions. The somatic sensory cortex, for example, has a topographic map of the entire sensory (tactile) surface of the body, and the visual cortex has a map of the entire visual field. Structural criteria are also fairly straightforward, and may refer to the form and appearance of the layers present in a given region of cortex, for example.

Turning specifically to the importance of function, we note first that there are several different functions subserved by the brain: physiological, regulative, hormonal, sensory, motor, psychological, and others.[2] Our particular concern is with the use of psychological functions in mapping the brain, and how this ultimately ties in with an evolutionary perspective. The role of psychological function is particularly apparent at the macro level of research, especially at the level of such innovative radiographic techniques as the PET scan, functional MRI, and others used to map the brain. An example drawn from current PET research helps illustrate the role psychological functions -- in this case, language functions -- play in mapping the brain.

The methodology involved in PET imagery is fairly well known, so we will just highlight the major components here. Since areas of the brain metabolize glucose and oxygen in proportion to their activity level, and since both of these are borne by the blood, increased metabolism corresponds to increased local blood flow. Prior to the PET scan, radioactive tracers (usually radioactive oxygen) are injected into the blood stream and it is the ensuing decay that PET images indirectly record. During the PET scan, the subject performs specific mental tasks, allowing researchers to detect which areas of the brain are most metabolically active during the performance of those tasks. These tasks are ones for which psychological studies have already provided analyses into sub-tasks. Areas of the brain are thereby distinguished in terms of their functional significance. Since many of the tasks are complex, several different areas of the brain are usually activated. However, subtraction techniques have been developed which allow researchers to pinpoint areas associated with just a particular element or sub-function of the overall task. If one has two tasks, for which the task analysis of the second differs in one or more additional subtasks not involved in the area, then by subtracting the activation pattern produced in performance of the first task from that produced in performance of the second task researchers can isolate areas involved specifically in the additional subtasks (see Stufflebeam & Bechtel, 1997, for an analysis of the epistemic assumptions involved in PET research).

In a series of studies (Petersen, Fox, Posner, Mintun, and Raichle 1989; Petersen, Fox, Snyder, and Raichle 1990; Petersen and Fiez, 1993), PET researchers at Washington University investigated how the brain processes various kinds of visually presented linguistic stimuli. The stimuli presented were grouped into the following four categories: (A) false fonts (a string of letter-like forms), (B) consonant strings (i.e., “gdnk”, orthographically irregular), (C) pseudowords (i.e. “tweal”, orthographically regular), and (D) real word common nouns. From all of the images resulting from presentation with the above stimuli, a "control" image, produced by the subject's staring at a simple fixation point, was subtracted. The subtraction of the fixation point image was designed to remove areas associated with general, passive, visual processing -- leaving images more particularly and distinctively associated with each task.

These experiments revealed a distinction between how the brain processes stimuli types A-B and how it processes types C-D. In other words, the distinction in the images seemed to correspond to the orthographic regularity of the stimuli. Anatomically, stimuli C and D produced activation in a specific area of the left extrastriate cortex which A and B did not. This research serves to both identify an area of the brain and associate a function with it. Thus, they report their findings in terms of psychological functions:

> Rules of spelling and orthography are specific to each language. The presence of a left-lateralized area in posterior, extrastriate cortex that distinguishes between letter strings that do and do not conform to English spelling rules argues that access to information specific to English orthography is present very early in the visual processing stream. These areas may represent the neural mechanism underlying the perceptual advantage that words and pseudowords show over irregular letter strings. Furthermore, such an area may be the cortical site for priming of word perception occurring at a presemantic level. (Petersen, Fox, Snyder, and Raichle, 1990, p. 1043)[3]

While this particular research focuses on components of language processing, PET has also been used to investigate other mental processes such as are involved in emotion, visual processing, attention, clinical/psychiatric disorders, etc. In all of these cases, the significance of the intricate brain activation patterns that result would be fairly meaningless except for the linkage with psychological processes. Moreover, in picking psychological processes to study with brain imaging, researchers are concerned to use tasks involving psychological processes that are likely to be significant in human life. The set of tasks one might ask subjects to perform during a PET scan is virtually infinite, but the images produced in most of these tasks would be of limited interest. Each would show the brain "lighting up" in a particular way; and the possible patterns of lighting up again is likely to be virtually infinite. Each would suggest a new way to map the brain. Without some basis for selection, there would be no way to select between ways of mapping the brain. What psychologists rely on, as we have tried to show in this section and will continue to discuss in subsequent sections, are psychological functions that are thought to be important in human activity.

To this point, we have been concerned mainly with the role of psychology in neuroscientific research concerned with brain mapping, but this is only one side of the interdisciplinary project we address below. We will also discuss cases which illustrate the importance of neuroscientific research for psychology as well. But before doing so, we will discuss more directly the particular view of function most appropriate to the brain mapping project described above, and also most appropriate to what we take to be the interdisciplinary goals and projects of evolutionary psychology.

III. A Teleological View of Function

Darwin's goal in applying the theory of natural selection to organisms was to explain the presence of traits which made those organisms highly adapted to the demands of their specific environments. These traits seemed to serve the ends or goals of the organisms, and it was natural to identify these goals or ends as the functions of the trait. Prior to Darwin, philosophical consideration of function dates back at least to Aristotle. In his four-part division of causal kinds, efficient, material, formal, and final, it was the final cause which specified the goals or ends served by something -- a kind of account we now term "teleological". As science turned to seeking mechanistic explanations, teleological explanations fell into ill repute and were criticized because they seemed to give causal powers to the future. In other words, teleological explanation focuses on goals or ends, but goals or ends lie in the future, and may or may not be realized; any legitimate causal explanation, it was argued, must appeal to events that happened in the past, not outcomes that may or may not be realized. Darwin's explanation in terms of natural selection provided just such a causal explanation of adaptive traits. But, ironically, it also provided the basis for resuscitating teleological function statements: one could identify the function of a trait by focusing on an organism's ancestors and how possession of the trait by these ancestors favored them in satisfying selection forces operating on it (Wimsatt, 1972; Wright, 1976). The current organism with the trait thus exists because of the selective advantage that trait offered to its ancestors.

This view of function can be generalized beyond biological contexts as long as the essential components of a selectionist process are present: variation and selective retention (Lewontin, 1970). Thus, in engineering contexts, we can identify the function of a component in terms of how selection by designers led to the inclusion of similar parts in subsequently produced systems. In cultural contexts we can identify the function of a behavior by identifying how the behavior has been acquired because of selection forces operating on previous instances of that behavior.[4]

One question that arises in developing this notion of function is whether we really need to focus on ancestral organisms and the selection forces operating on them, even when those are no longer operating, or whether it is sufficient to consider currently operating selection forces. Wright (1976) and Millikan (1984, 1989) argue that we must appeal to selection forces operating on ancestral organisms in identifying functions; Bechtel (1986) argues for considering currently operating selection forces, though recognizing that this requires a distinction between functional analyses and functional explanations. For our purposes here we need not settle this conflict. What is critical is that a teleological notion of function makes central reference to selection forces. Moreover, following on a distinction developed by Machamer (1977), we should note that teleological function statements form a bridge between two levels of theory--one that describes the behavior of an entity, often in terms of the interaction of its parts, and one at which that entity is evaluated in terms of its ability to satisfy certain selection criteria.

To appreciate what is at stake in a teleological conception of function we need to contrast it with a competing, non-teleological view, which we refer to as the componential view. In this view, the function of a component is simply the way in which it interacts with other components in carrying out some activity in the system (Fodor, 1968; Cummins, 1975). A function is anything something does in the course of a system's operation, without consideration as to how it promotes satisfaction of selection criteria. The metaphor most often invoked is to a computer, in which the system's software specifies the operations or functions to be executed, while electrical activities in the hardware realize this function. When this view is applied to human beings and other sufficiently cognitive organisms, the brain is the hardware, the mind is the software, and each mental state is a computational state of the system. While the componential view of function has lost considerable ground in some areas of philosophy (particularly the philosophy of biology) this view still predominates in much of cognitive science, especially in information processing modeling.

The componential view of function not only has the effect of cutting off the attribution of function to an entity from the selection factors operating on the system; it also has the unfortunate effect of making the lower levels of organization which are responsible for producing the behavior of the entity irrelevant to understanding the function itself. This is because, it is argued, just as the same software can be run on many different kinds of computers, with very different hardwares, the same activities could be performed by many different kinds of physical systems. What matters to understanding mental functions when construed this way is not their underlying brain states, but the role they play in relation to other inputs and outputs of the system. Thus, if two people in similar circumstances both happen to believe that a thunderstorm is imminent, what matters to identifying the state each is in is *not* their underlying physical states, which supposedly have nothing interesting in common, but the functional relation of their state to such inputs as, say, the sound of thunder and darkening skies, other internal states, such as fears about lightening and desires to stay dry, and such possible outputs as closing the windows and searching for an umbrella.

Many criticisms have been levelled against the componential view of function; however, we will concentrate our attention on those most pertinent to the contrast with the teleological concept. First, the categories invoked are often construed so abstractly as to apply to all possible cognizers, whether human or not, whether organic or not. While we do not deny that it may be useful for some purposes to abstract from differences and focus on commonalities that can only be identified at a high level of abstration, there are many contexts in which such abstraction is not useful. One such context is where one is trying to understand the operation of particular systems (e.g., the psychological processes working in humans). In this case, moving to too high a level of abstraction may be disasterous since we lose the particulars of species-specific (or otherwise more narrowly shared) cognitive and behavioral characteristics.[5]

To use Putnam's example, *hunger* may be construed so broadly as to be considered functionally equivalent across a wide variety of those able to be in such a state - humans, octopi, spiders, frogs, etc.- with obviously various physical systems[6]. Hunger, in this case, can be seen, for example, as the functional intermediary of such an input as *detection of energy depletion*, and an output of *energy seeking behavior*. However, if one is interested in the more specifically, and perhaps more uniquely *human* features of hunger, such as how it affects performance on language tasks, then we are not interested in generalizing over the extreme range of physical variability Putnam considers, but only over cases in one species. When we restrict our focus, inquiry that considers specific features of the human nervous system becomes theoretically useful. This, rather than Putnam's level, is the one at which most scientific research is carried out.

There is another reason why the componential view of function is inadequate for science: it focuses evaluation of the system merely on serial or step-wise analysis of inputs and outputs, and that at the level of the functional system as a whole. There is a failure to recognize both the interactive processes taking place at the lower level of the separate components of the system, as well as those at the higher level of the context or environment in which the system itself is operating. As Bechtel (1986, p.40) explains, “Organized systems, on the one hand, are only adaptive given particular environment contexts”, and “On the other hand, environments can only select among systems that occur in it; hence, the occurrence of lower level systems constrains what is selected." Failure to recognize relationships at these different levels has obvious liabilities for theory construction, as cognitive or psychological theories may be advanced which are either biologically implausible at the lower level, or which, given the higher level environmental scenario, would be maladaptive and unlikely to have evolved. We discuss such constraints further with regard to evolutionary psychology in the next section. Also, recognition of the limitations on the "raw" biological material available for implementational adaptation can lead not just to constraints but also to heuristically useful perspectives. Given the principle of evolutionary conservatism, we can sometimes use one species to understand processes in another species where, due to other complexities, they may not be as easily identified. We return to this point in connection with Terrence Deacon's work, below.

The next problem with componential functionalism has often been discussed by several different commentators, including Lycan (1994), Block (1978), and Bechtel (1986). There are subtle variations of this problem and of the remedies proposed by each of the many commentators, so we will provide here just a general summary. The problem, basically put, is that a componential view of function, in itself, provides no means of distinguishing between behaviors and traits which are functional, and those which are merely operational consequences or by-products. All causal effects must be counted as functions even if some are not theoretically significant. The seriousness of this problem is obvious when one is dealing with an extremely complex system such as the brain, in which there are many more causal processes occurring than we can study. We need some means of focusing on those causal processes which are important. Those will be the ones that enable the overall system to perform the tasks that are important for it to perform.

A teleological framework helps address this problem because it provides an evaluative backdrop against which to make such a determination: one evaluates whether or not a given feature helps the system better cope with the demands of its environment. Those which serve to enhance the organism's survivability count as functions; those which play no role in furthering the survival or adaptability of the organism do not. The human appendix, for example, while functional for our evolutionary antecedents, has no present purpose. (Unless it turns out to be dysfunctional, it is simply not worth investigating its causal activities.) The heart pumps blood, and we consider that to be its function and it is theoretically important to understand how it does so. However, it also makes heart sounds which, at least until the advent of modern medicine, were not functional. (In the new environment with modern medical techniques for diagnosis and possible intervention to fix damaged systems, the generation of these sounds may turn out to have a function. This once again emphasizes the need to evaluate function in the context of a specific environment.)

Finally, we wish to make one last point about a non-teleological construal of function, and show more explicitly why a teleological perspective not only accords better with certain features of neuroscientific research, but also provides a better framework for interdisciplinary cooperation. In a version of componential functionalism known as *homuncular* *functionalism*, the component psychological processes that figure in an explanation of a psychological task are known as *homunculi*, component agents which perform parts of the overall task. In the version of homuncular functionalism developed by Dennett (1978) and Lycan (1981), the analysis of psychological performance into homunculi can be carried out recursively, identifying homunculi within each homunculus, until "components are *seen* to be neuroanatomical structures" (Lycan, 1994, p. 320, emphasis added)[7]. The problem with this claim is the suggestion that the neuroanatomical structures that realize psychological homunculi are simply there to be seen. That is, that they are identified independently of functional considerations. Given our earlier discussion of how psychological states play an integral role in defining neurological kinds, such a non-teleological construal of homuncular functionalism represents a very poor conception of neuroscience. In other words, the very determination of the identity of neuroanatomical structures, the process we referred to as "mapping the brain", is grounded in functional considerations at the very outset, and the notion of function that is employed in mapping the brain is teleological. Thus, without a teleological perspective, we could not complete the homuncular program.

IV. Bringing Neuroscience into the Integration of Psychology and Evolutionary Biology

One of the positive features of the program of evolutionary psychology is its promise to invoke evolutionary considerations in developing psychological analyses. Such an appeal to evolution opens up the potential for a teleological view of function. But evolutionary psychologists tend not to carry this approach through to its natural conclusion. While they may advance evolutionary analyses of psychological traits, they tend not to extend the evolutionary analysis down to lower levels. Rather, the information processing psychological analyses to which they appeal have more the character of non-teleological functional analyses. They thereby fail to take advantage of an appeal to the resources of neuroscience that a fully teleological view would afford. This would generate a multi-level framework integrating neuroscience, psychology, and evolution.

It is important to note that by a scientifically integrated, multi-level framework of explanation, we do not mean a reductionistic one. Attempts at integration in the past have often taken the form of a reduction, some forms of which planned not only a reduction to the lower-level theory, but eventually, an outright dismissal of the higher-level theories. One characterization of this type of integration is in terms of the form of theory reduction advocated by proponents of "the unity of science" (see Nagel, 1961). While recent champions of the reduction model, such as the Churchlands (P.S. Churchland, 1986; P. M. Churchland, 1984), make it clear that theory reduction justifies rather than eliminates the higher-level theory, a successful reduction suggests nonetheless that it is possible to dispense in practice with the higher-level theory. Most scientists do not construe reduction as *theory* reduction, but they too construe reduction as redirecting one's energies toward the lower level; thereby in practice they dispense with the higher level. To the extent that scientific integration is understood in terms of reduction, therefore, it has helped to fuel an anti-biological spirit in traditional social science.

However, reduction is not the only means of integration. One can accept that nature is hierarchically organized, as the reductionist does, without construing higher-level processes *simpl*y as consequences of lower-level processes. Rather, one can allow that each level has its own processes, with important constraints occurring between processes at each level. One branch of support for a stratified view of nature stems from Herbert Simon, who suggests that a scaling of energy forces involved in building structures makes for a hierarchy of levels:

> Thus, protons and neutrons of the atomic nucleus interact strongly through the pion fields, which dispose of energies of some 140 million electron volts each. The covalent bonds that hold molecules together, on the other hand, involve energies only on the order of 5 electron volts. And the bonds that account for the tertiary structure of large macromolecules, hence for their biological activity, involve energies another order of magnitude smaller--around one-half of an electron volt. It is precisely this sharp gradation in bond strengths at successive levels that causes the system to appear hierarchic and to behave so (Simon, 1973, p. 9).

One need not take literally Simon's scale of energy forces to nonetheless accept the view that the structures put together at one level can be organized by different principles working on these whole structures. Recognizing this stops the quest for dismissing higher-level principles.

Once we recognize a stratified view of nature, we must offer another argument to support drawing the linkages between these levels, lest we endorse the radical autonomy of levels advocated by Fodor (1975). But that is readily forthcoming if we consider the constraints each level places on the others. The constraints the lower level places on the upper are fairly straight-forward: generally there are only a limited number of ways to put pieces together into wholes.[8] Atoms can only bond with each other in limited ways, and this, for example, places limits on the sort of biochemical pathways evolution could select. The constraints in the other direction are perhaps not as apparent, but they are nonetheless real. When an atom becomes bound into a molecule, its fate is significantly determined by the molecule. The molecule, or any other system with an integrated structure, places top-down constraints on its components. For another example, the possibilities and limitations on human actions are significantly affected by the character of the society one lives in. This top-down effect becomes even more significant when we take the role of evolution into effect. Selection operates on overall behaviors of a system existing at a given level; it thereby also selects for and against the components of those systems.

In such a stratified universe, one will frequently have to take into account multiple levels of organization, and develop explanations that link multiple levels. Accordingly, in dealing with psychological characteristics of individuals, one will have to consider both the social context of the individual and the neural processes within the individual. The teleological view we have advocated recognizes this, and seeks to take advantage of it.

One of the benefits of the integrated view we advocate, to which we have already alluded, is that it is more likely to foster development of realistic explanations. In other words, it can circumvent the possibility of positing psychological models which could not be physically realized within the human brain and nervous system. In pushing this claim, we are merely extending the argument made by Cosmides, Tooby, and Barkow (1992), against disciplinary isolation, which they say leads to the following problems:

> As a result, one finds evolutionary biologists positing cognitive processes that could not possibly solve the adaptive problem under consideration, psychologists proposing psychological mechanisms that could never have evolved, and anthropologists making implicit assumptions about the human mind that are known to be false. (p. 4)

To take a simple case, no one would find it reasonable, for example, to posit theories about human predatory behavior which depended on our having the echolocating ability of bats, because we do not have that sensory processing ability.

More generally, then, one should not posit psychological mechanisms which, in order to function properly, place processing demands upon the brain which we know to be biologically unrealistic. In playing chess, for example, the human brain does not compute a list of all logically possible outcomes at each stage of the game and then choose the optimal move at each turn (unless the game is nearly over and there are only a few possibilities left). As Bechtel and Richardson (1993) explain,

> A general brute force solution for chess is obviously out of the question. Some means must be found to limit the search to a computationally tractable number of alternatives. In the face of complex problems, humans typically engage in heuristic search, examining only a small subset of the abstractly possible alternatives . . . . We are organisms limited in memory, attention, and patience. . . . A psychologically realistic model of human problem-solving must incorporate the heuristic assumptions imposed by human problem-solvers (p. 12)

Cherniak (1986) makes a similar point in urging us against theories which assume the maximally rational agent, because maximal rationality often entails computational paralysis.

To summarize, biological realism can be a powerful evaluative tool for theories currently proposed, in that theories which are inconsistent with current neuroscientific knowledge cannot reflect the way human beings actually carry out the psychological task under consideration. Further, it can be heuristically powerful as well, in that neuroscience can provide clues for theory building at the psychological levels.

Having just discussed the theoretical advantages of an integrated account with neuroscience, it would now be useful to discuss cases of a more practical nature which illustrate more concretely the benefits to be gained from the scientific integration of psychology and neuroscience. In section two, we discussed the crucial role psychological functions play in mapping the brain, thus providing an example of an area of neuroscientific research that is usefully informed and guided by psychology. This example is typical with regard to such complex systems as language, memory, emotion, and perception, where functional considerations at the psychological level guide neurological research in such a way that physically distinct and disparate areas within the brain are put together into complex systems which themselves are not obvious at the merely neurophysiological level.

But the converse case also holds: neuroscience has had, and likely will continue to have, a powerful influence within psychology. There are several different areas which we could point to as indicators of this kind of productive integration, but we will focus here on just one example that promises to have great impact in reconnecting the study of cognition with the study of emotion, two topics that have recently been pursued largely in isolation from each other.

The cortex of the frontal lobe is a functionally diverse area, and among those functions that have been thought to be associated with it are memory, emotion, personality, learning, species-specific socially appropriate behavior, and others. The orbitofrontal subregion of the frontal cortex (the surface which lies just above the eyes, extending forward from the rest of the brain) is somewhat functionally distinct from the rest of the frontal cortex, and has been the object of extensive human and animal studies. Data from human studies allows a less precise degree of regional localization, since the data has to be gathered indirectly, or after the fact, say, from those who suffered from some sort of accidental injury to this area, or from the result of surgical excision or lesioning made necessary by such diseases as cancer or epilepsy.

One of the most famous human cases of this sort of frontal lobe damage is known as "EVR", and Damasio, Tranel, and Damasio (1990) provide a recent evaluation of his case in relation to frontal damage and sociopathic behavior. In 1975, due to a malignant tumor, EVR underwent bilateral excision of a large section of his frontal lobe. While he showed no demonstrable postoperative deficits in either memory or intelligence (in the usual sense), the transformation which *was* observed has been described as (acquired) sociopathic behavior. Pre-operatively, EVR was a responsible businessman with wife and family; postoperatively, he exercises very poor judgment and planning, fell into bankruptcy through a series of bad business ventures, is twice divorced, and is incapable of holding a job and supporting himself. Damasio's group interprets EVR's deficiency as the inability to associate the *consequences* of a given course of action with the *action* itself. The authors describe his deficit as a loss of the ability to associate the past punishment/reward value of a given action with a present similar action. They tie the punishment/reward aspect of the situation directly to visceral, bodily states, which they say provide the basis for the higher emotive, or affective value of the action. Generally stated, this case presents some evidence that the frontal lobe in humans is somehow necessary for the eventual pairing of circumstances with outcome.

But the "circumstances" turn out to be quite complex stimuli (i.e. a business venture), and the "outcome" can have sensory, visceral, affective, and cognitive components.

The first point we wish to make about this example, is that even the grossest psychological categories, such as cognitive, affective, and perceptive (sensory) do not pick out distinct neuroanatomical areas. In monkeys, the neurological specificity can be tied to a functionally complex, single kind of cell[9]. Even a single cell, then, or a single region in humans, cuts across psychological boundaries, involving cognitive, emotive, and even sensory aspects. As the neurological story develops, these findings may force us to reconsider the interrelation between psychological categories such as emotion, intelligence, rationality, and personality. The case of EVR, as well as other case of frontal lobe damage, such as Phineas Gage, already point to a crucial link between reason and emotion. Antonio Damasio, in *Descartes' Error*, explicitly draws this moral: “Flawed reason and impaired feelings stood out together as the consequences of a specific brain lesion, and this correlation suggested to me that feeling was an integral component of the machinery of reason.” (1994, p. xii)

Alternatively, one might view the neuroscientific evidence as calling for another option. EVR's case, in particular, finds us scrambling for the appropriate psychological descriptions. His problems are not *quite* a matter of loss of intelligence or rationality, not *quite* a memory disturbance, not *quite* within the usual range of emotional difficulties, and so on. His problems have elements of all these things, but none capture his deficits very adequately, even when we combine them. In this case, we might decide to create a *new* psychological category, which, by definition, would capture the strange sorts of deficits exhibited by frontal lobe patients such as EVR (there have been other similar cases, so the resulting psychological category would not just have a single instance).

Of course, depending on other neuroscientific and psychological data, we might decide to leave things just the way they are. Decisions of taxonomic addition and/or revision would have to be undertaken in light of a more comprehensive empirical, as well as pragmatic considerations, and infrequently would a single case be strong enough reason for adjustment. In this section we have argued for the integration of neuroscience into the broader program linking psychology and evolutionary biology. Next, we will show how the integration we propose can be accommodated methodologically as an example of an interfield theory proposed by Darden and Maull.

V. Integration Through An Interfield Model

We begin this section with a general characterization of interfield theories as first described by Darden and Maull (1977). Rather than focusing on reductive relations between scientific *theories*, Darden and Maull concentrated on the more practical aspects of how actual scientists, working in separate *fields*, may bring the resources of their different perspectives to bear on problems not resolvable within the confines of any single field. Thus, their concern was not to show how higher-level theories may reduce to lower-level theories, but to show how an integrated theory can be developed that connects phenomena studied in the different fields. Darden and Maull propose a preliminary classification of the kinds of interfield relationships which such theories may involve: these include relations between parts and wholes, causes and effects, and structures and functions.

While they discuss several historical cases of interfield cooperation, one of their central examples concerns the relationship between cytology and genetics in developing the theory that genes, identified after the rediscovery of Mendel by geneticists as the units of heredity, were located on structures which cytologists called "chromosomes" due to their stainability. This discovery allowed cytologists to make sense of the processes of meiosis and mitosis, and allowed geneticists to understand why Mendelian factors came in pairs. Eventually geneticists such as T. H. Morgan were able to use the linkage between genes and chromosomes to explain why some traits assorted randomly, while others seemed to be linked, and to map genes onto chromosomes (see Darden, 1991). Originally set forth as a means of relating *two* different fields, it is obvious that their framework can be extended among any number of fields (including both those that do, and those that do not cross levels of organization). Darden herself explores a three-tiered, “multi-field” relationship among the levels of Mendelian genetics, mathematical population genetics, and experimental and field studies of populations (Darden, 1986).

In addition to avoiding any sense of dispensing with the higher level, as reductive analyses suggest, another virtue of the interfield theory approach to integration is that it works with incomplete theories as a vehicle of discovery. For example, by postulating a relation between genes and chromosomes, researchers were able to use whatever was discovered about one to address questions about the other. Establishing interfield relations between neuroscience, psychology, and evolutionary biology offers the same type of promise. To show what this might be, we offer one example of how, in the study of human language processing, a very fruitful attempt to integrate behavioral or psychological perspectives with neuroscientific perspectives has been pursued for well over a century.

Against the Cartesian tradition exemplified by Flourens, which rejected the localization of cognitive functions, especially higher cognitive functions such as language, Paul Broca (1861) argued that a specific region in the left frontal cortex was responsible for language production. He drew this conclusion from studies of patients who exhibited deficits in language production without apparent loss of language comprehension or other cognitive ability and who, on autopsy, were shown to have suffered neural damage in this area (although generally the damage was far more widespread by the time of autopsy, rendering the specific localization controversial). Subsequently, Karl Wernicke (1874) identified another group of patients who appeared to suffer deficits in language comprehension and had lesions in the temporal cortex. The two neural regions involved (as well as the deficits associated with them) are frequently identified by the names of these scientists who attached functional significance to them.

Wernicke's analysis was developed in the context of an associationist psychology according to which cognitive performances were due to associations between simple ideas. Within such a framework, what were localized in the brain were specific associations or connections between ideas--associations between ideas involved in comprehension in Wernicke's area and between ideas involved in production in Broca's area. In addition, the associationist framework analyzed overall performance in terms of associations between sensory processing (performed in Wernicke's area in the case of language) and motor processing (performed in Broca's area in the case of language). This raised the prospects of further deficits in the connections between these areas; Wernicke provided evidence of such deficits and termed them “conduction aphasias". This general framework for thinking about the psychological processes involved in language, in which a sharp distinction is drawn between comprehension and production, was further developed in this century, especially by Geschwind (1974).

However, starting in the late 1950s a different framework for thinking about language was introduced in linguistics by Noam Chomsky, according to which comprehension and production no longer mark the major divide; instead Chomsky distinguished the different types of knowledge that were involved--syntactic, semantic, and pragmatic. Inspired by Chomsky, a new generation of neuropsychologists reanalyzed deficit patients and saw a different pattern. Whereas on the traditional analysis Broca's aphasics were not supposed to show deficits in comprehension, they did exhibit comprehension deficits in atypical sentences in which syntactically encoded information (e.g., in closed class vocabulary such as prepositions) is essential for comprehension. In most sentences, semantic cues are sufficient for determining the meaning, and even in sentences in which proper processing of closed class vocabulary is essential, Broca's aphasics can supply proper interpretations if time constraints are removed (Bradley, Garrett, and Zurif, 1980). Subsequent work has shown that similar comprehension problems are experienced by children, a result that coheres well with evidence that full myelination of nerves in Broca's area does not occur until near puberty (Friederici, 1996).

What we have seen so far are situations in which psychological conceptions of cognitive processing led to the identification of specific brain regions in terms of their putative functions, and in which subsequently new models of cognitive activity led to new characterizations of the functions of these regions. Interpreting functions of structures on the basis of deficits when those structures are lesioned is in general problematic. While a lesion at a site might induce a deficit in a function, that site might not be the locus of the function, but only of some ancillary activity. But the general claim that Broca's area is involved in language processing is robustly confirmed not just through deficit studies, but also through stimulation research and imaging studies.

What is more interesting than this “direct localization” (Bechtel & Richardson, 1993), however, is determining how Broca's area is involved in language processes. Developing such an explanation requires working at a finer level of organization in which a finer taxonomy of brain regions is identified and the role of these sub-regions in language processing is identified. One avenue to developing such an account employs much the same tools as we have already noted, except uses them at a more micro scale. But another approach applies the evolutionary perspective on function as a critical guide. We will briefly sketch how both lines of research have developed. (This is a rapidly developing area of research, and the conclusions that the researchers we discuss have reported to date may well be modified in the future. We are not committed to the correctness of the claims researchers have advanced, but to the methodology employed.)

Drawing upon the electrical stimulation research of Penfield & Roberts (1959) and Ojemann (1983) , Deacon (1992) distinguishes four successive lateral tiers of what he refers to as the "ventral frontal language region (VFLR)" (a portion of the frontal cortex that extends beyond what has traditionally been referred to as "Broca's area") which differ in their patterns of connectivity. Electrical stimulation of each area yields a different response. Stimulation in the most caudal area results in discrete movements of muscles and interferes with voluntary movements, while stimulation in the next rostral tier interferes with the ability to produce sequences of oro-facial movements. Stimulation in the third tier, moving rostrally, interferes with grammar and naming, while stimulation in the most rostral tier results in speech hesitations. In addition to sending reciprocal processes to each other, each of these areas also sends processes to different specific sensory areas. Moreover, all of these areas send efferents down to the brain stem, but the more caudal tiers project directly to brainstem motor nuclei while the more rostral tiers do so by a more indirect route. This suggests to Deacon a complex control system governing the vocal system:

> Because efferent pathways from all these frontal areas indirectly reach motor nuclei by numerous parallel multisynaptic pathways, the control of final motor output is almost certainly the result of the coordinated action of these many converging parallel pathways, each simultaneously contributing different forms of output information. The highly indirect pathways of the ventral prefrontal areas, though very likely not programming the details of muscle movements, may provide programming for large-scale units of behavior which regulate the execution of movement sequences and provide the anticipatory frame or "motor envelop" within which more specific behaviors can be organized. The discrete motor performances that constitute stock phrases, words, or morphemes are likely programmed by motor cortex in conjunction with striatal and cerebellar circuits, whereas the temporal organization and flexible gating of these modular behaviors are likely regulated by numerous parallel projections originating from ventral prefrontal areas (Deacon, 1992, p. 59).

While this decomposition and localization within the ventral frontal language area is not yet sufficiently developed to provide a complete account of the ways in which this area contributes to language production, it does suggest how detailed knowledge of the underlying neuroanatomy and neurophysiology may guide the development of a processing theory. To our knowledge, this decomposition and localization has not yet been employed by psychologists or computational modelers, but it seems an ideal candidate for inspiring further cognitive modeling and research.

Ethical restrictions limit researchers ability to investigate further the computational contributions of the various components of the ventral frontal language area, but this is where comparative anatomy and an evolutionary analysis may be fruitful. While many people have seen the call systems of various animals as closely linked to the human speech system, Deacon (1989) provides evidence to show that this is not the case. Animal call systems are principally under the control of subcortical circuits (the exception is the cingulate cortex) involving limbic and diencephalic structures as well as periaqueductal gray and adjacent tegmentum or parabrachial nuclei. In particular, structures in the ventral frontal language area are not involved. Nonetheless, using tracer studies one can map connections between the homologous sections of the monkey's brain, and the pattern of connectivity seems much the same as electrical stimulation and PET studies indicate for humans. This at first seems surprising since monkeys do not speak. But Deacon proposes a resolution to this puzzle. Allometry is a means of measuring the growth of one part of a organism in relation to the whole organism or other parts. In the progression from monkeys to humans, areas such as the prefrontal cortex have expanded much more than other brain regions. Since connectivity patterns are determined by each area of the brain first sending out processes to appropriate targets followed by the selective culling of these processes, if in humans the prefrontal cortex has expanded abnormally, then it would send out many more processes to the same targets than the monkey's prefrontal cortex, and after culling would be much more connected to those targets. Deacon thus proposes that these prefrontal areas in the ventral frontal language area have, in humans, overwhelmed the connections to the vocalization system stemming from the subcortical areas. Accordingly, while the human call system is much diminished (laughter and crying being examples of retained calls), the ventral frontal language area has taken over.

This now opens a route for determining the kind of processing being carried out in the ventral frontal language area: we can study the sorts of processing it is involved with in monkeys. Studies in monkeys suggest that this area figures centrally in performance in a conditional association paradigm in which the animal must determine a subsequent response in light of the outcome of a previous behavior (Petrides, 1982). This suggests that what the homologous area contributes in humans is ability in conditional associations. Deacon (1992) offers some suggestive comments as to how this sort of computational ability can, together with a functionalist approach to grammar (Bates & McWhinney, 1982), contribute to an account of the evolution of human linguistic abilities in terms of the coevolution of brain and language.

Many of these theoretical proposals must be regarded as still tentative. From our perspective, though, what is most important in this work is its role as a model integrated study of structure and function and the promise it offers for an interfield theory of language mechanisms. In this endeavor the discovery of neural mechanisms plays a critical role in suggesting psychological models. But functional psychological models also play a role in guiding the interpretation of the neural evidence. While, as we have noted, the details of Deacon's analysis must be regarded as provisional, what we want to emphasize is how interfield theories can be developed in this area that link neuroscience, psychology, and evolution. Cosmides and Tooby (1992) cite Pinker's and Bloom's (1992) analysis of the evolution of language as their example of how evolutionary psychology might examine language processes. The difference neuroscience plays in the study of language in Deacon's account in contrast to that of Pinker and Bloom is remarkable. For Pinker and Bloom, the fundamental claim to establish is that Chomsky's language organ is the product of natural selection. They do not consider a study at the neuroscience level that could shed light not just on the evolution of language, but also on the mechanism involved in language processing. Deacon comments on attempts like that of Pinker and Bloom:

> The danger of arguments that attribute so much of the explanation of language structure to unanalyzed brain structures created entirely by evolutionary accident is that they simply pass the buck to neurologists and biologists and thereby stifle serious attempts to explain these phenomena in functional and semiotic terms." (Deacon, 1992, p. 51)

That is, by not linking the neuroscience investigation to the functional psychological investigation, neither prospers. We contend that, whether or not the details of his account turn out to be right, Deacon's approach exemplifies the sort of interfield theorizing that can develop if neuroscience is given its due. It appears that this course is more likely to be productive for evolutionary psychology than less integrative alternatives.

Conclusion

To briefly summarize: We have advocated the integration of neuroscience into the attempts to link psychology and evolutionary biology, and have argued that this project is best served by a teleological, as opposed to a componential conception of function. We began discussing the basis of our teleological view of function in section two, where we explored several often-overlooked features of the way neuroscientific research has been and continues to be carried out. A key feature of this research, particularly at the grosser levels, is the critical role psychological functions play in mapping the brain. The concept of function in this case is a thoroughly teleological one. In section three, we advanced a more detailed picture of our teleological interpretation of function, and showed how it is preferable to another prominent view; namely, the componential construal of function, which does not insist on the relevance of the biological or implementational level. We then demonstrated in section four how a teleological version of function provides a means of integrating neuroscience with psychology and evolutionary biology, and addressed the theoretical and heuristic benefits to be gained from this endeavor. Finally, we proposed that an interfield theory, similar to that of Darden and Maull (1977), is the best way to accommodate the interdisciplinary integration we advocate. We also discussed current research areas which, through the productive integration of neuroscience, psychology, and evolutionary theory, exemplify the promise of the interfield model.

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NOTES

1. These two positions are technically distinct, in that holists hold that even if there is some regional specificity, no single component or subset of components can alone explain any product of brain activity, because each product is a complex integration of the activity of the whole brain. Equipotentiationists take a somewhat stronger position in that they often deny even the existence of functionally distinct regions of the brain. For our purposes, however, the main point is that they are both anti-localizationist.

2. It is becoming increasingly apparent that these functional divisions are not as segregated as was once thought. Particularly from the standpoint of the brain's division of labor, such psychological functions as cognition and emotion are not entirely distinct from either sensory or motor functions. Thus, while not a clean division, our intention is primarily to address the more psychologically-oriented functions.

3. Interestingly, this particular study also has some bearing on the question of the innateness of psychological capacities, which as we shall see, has been a major concern of evolutionary psychologists. While the report does not explicitly discuss the issue, it seems likely that what is orthographically regular for a speaker of one language may not be orthographically regular for the speaker of another language. For example, the word "wszystek" is a Polish word, and the word "tvrdy" is a Czech word. Neither is orthographically regular for native English speakers. One would expect the PET images of English speakers when given either of these "words" to resemble the images corresponding to test conditions A and B, above, while one would expect the scans of Polish speakers presented with "wszystek", and Czech speakers presented with "tvrdy", to resemble test conditions C and D above. While experimental confirmation of these predictions has yet to be provided, it is likely that what will turn out to be common across speakers of different languages, and

hence potentially an innate feature of language processing, is just the capacity to differentiate according to orthographic regularity, with what is orthographically regular being relative to the language(s) a person has learned.

4. Note that this does not require that the mechanism of inheritance be genetic. It could be cultural. See Boyd and Richerson (1985).

5. Of course, in looking at psychological or behavioral processes in humans, we are abstracting from individual differences between humans. We do so because, due to common genealogy, we assume that substantially the same processes are operative in all humans. This assumption of course fails in some contexts where it is individual differences that matter. And for some purposes we want to compare one species with another so as to use information about their similarities or differences to gain an understanding of what is happening in one species. For example, research such as Savage-Rumbaugh's (1986) on basic language capacities in bonobo and common chimpanzees is motivated in large part to gain a useful perspective on what constitute basic language processes in us (Bechtel, 1993).

6. Some functionalists hold open the possibility that functional states may be instantiated in non-physical systems.

7. Lycan (1987) in other contexts explicitly endorses a teleological view of function and recognizes that functional criteria enter at all levels of nature's hierarchy. In this passage he may just be characterizing a common view rather than advancing his own. It is a view found in Dennett (1978).

8. This system may seem to be violated in some cases, such as language systems and computers. One of the important features of language is the ability to put words together in virtually unlimited numbers of ways to be able to say almost anything. Similarly, we have designed computers so that we can put together symbolic states in any way so as to achieve universal computation. However, even in these fairly extremely cases, there are constraints. Even if one adopts a universal grammar type perspective, grammars are not equally conducive to saying anything. Moreover, if one adopts a more cognitive perspective on language, and emphasizes, for example, the role of metaphors in structuring language (Lakoff, 1987), one may recognize a great number of constraints on what can be said in any specific natural language. Similarly, while computers are nearly universal machines, the machine language, operating system, and compiled program running on the machine limit at least what can be done easily and what requires complex computation. Especially if we worry about computation in real time, these limitations can become important.

9. See, for example, Thorpe, Rolls, and Maddison (1983), who demonstrate that in the orbitofrontal cortex of monkeys, there are cells which are not just selective for a given sense, (i.e. vision, olfaction, etc.), but also for the affective value (rewarding/aversive) of specific stimuli. They provide the following summary of their findings:

> a number of the apparently sensory responses of orbitofrontal neurons were highly dependent on the meaning of the stimulus. For example,

> the response of a neuron to the presentation of a 1 ml syringe was critically dependent on whether the syringe had recently been used to feed the animal rewarding fruit juice or aversive saline.... Thus, the orbitofrontal cortex seems to possess information on the reinforcement associations of particular stimuli, and seems able to rapidly modify this information in the light of the animal's recent experience. (p. 113)

Thus, in the population of neurons they describe above, the neurons were first sensorially selective, and then affectively selective (either as reward-excitable or averse-excitable). In these cells, changing the affective value of the stimulus, as in the case of the syringe, above, changed the response of the neuron. If it was active when the syringe was aversive, for example, it stopped being active when the affective value of the syringe was changed back to rewarding, by feeding the monkey fruit juice with it instead of saline.

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