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Psychobiology and Social Psychology: Past, Present, and Future

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Social psychology and psychobiology have a rich historical connection, although over the last half century these two disciplines have seemingly become estranged. To a significant extent, that alienation arose from an archaic and nonviable model of behavioral biology that retarded the development of both disciplines. With the emergence of modern biological perspectives, this impediment no longer limits fruitful collaborations among social psychologists and psychobiologists. Indeed, some of the most exciting contemporary developments are emerging from the areas of social neuroscience, cognitive neuroscience, and behavioral neuroscience. We review the history of links between social psychology and psychobiology, the factors that led to the segregation of these subdisciplines, and the modern biological perspectives that provide the basis for reintegration of these disciplines.

Social psychology and psychobiology share a richly intertwined, if not always harmonious, history. The Darwinian revolution had immense impact on psychology, as it focused attention on the biological origins of behavior and emphasized the continuity between the human and the animal mind. This perspective fostered a view of psychology as a biological science, despite its deep historical roots in philosophy, and promoted a natural conceptual evolution toward biological models of psychological processes (Cofer & Appley, 1964). Darwin himself became a pioneer in that development, with the publication of *Expression of the Emotions in Man and Animals* (Darwin, 1872/1998).

Among the benefactors of the Darwinian era were the instinct theorists, who were now emboldened by a solid evolutionary substrate for their views on the nature and origins of "purposive" behavior. Instincts were central to the thinking of many early psychologists, including notables such as James (1890). Evolutionary perspectives and instinct theories contributed to the emergence of the fields of behavioral genetics and a branch of psychobiology (comparative psychology) that sought to elucidate laws and principles of behavior, largely through animal studies. In the first social psychology textbook, *An Introduction to Social Psychology,* McDougall (1908) outlined a theory of personality, with instincts and their associated "emotions" at the central core.

Instinct theories, however, came under increasing and often blistering attacks. Among other failings was their teleological focus, their devolution into massive instinct "lists," and their failure to mature into predictive, explanatory, and hypothesis-generating theoretical systems. Sharp criticisms came from social psychologists, as in F. H. Allport's (1924) *Social Psychology* and Bernard's (1924) volume *Instincts: A Study in Social Psychology*. The assault on instincts was not limited to social psychologists. Equally strident voices emanated, for example, from clinical psychology in Dunlap's (1919) *Journal of Abnormal Psychology* article "Are there any instincts?" and from comparative psychology in Kuo's (1924) *Psychological Review* piece, "A psychology without heredity."

Clearly, the instinct adventure was a failure for social psychology, but it was also a failure for psychobiology and for psychology in general. Although instinct models flourished in the post-Darwinian era, with its focus on biology and evolution, it would be a misattribution to ascribe the ultimate fall of instinct theories to their biological focus. The demise of instinct theories was not the failure of the biological perspective, but the failure of an inappropriate and ill-conceived biological model. Both social psychology and psychobiology were betrayed by the prevailing instinct theories, and both needed to seek

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alternative paradigms, models, and theoretical schemas.

Among the early critics of the instinct concept were Watson and Morgan (1917), who argued that genetically endowed "instincts" could at best account for a very limited range of behavior. Later, Watson (1924) developed and formalized his concepts in his first volume *Behaviorism.* The early work of Thorndike (1898, 1927) on learning and *The Law of Effect,* and that of Pavlov (1927) on conditioning processes, together with Watson's views on behaviorism, would forever remodel psychological thinking. Although McDougall (1908) recognized the important role of experience in shaping the expression of instincts, there now emerged the specter of a generalized learning mechanism that could liberate the organism from the otherwise immutable dictates of heredity. According to this view, although learning processes may be indirectly dependent on genetically endowed motivational mechanisms, the direction and form of learned behaviors were not so constrained.

Behaviorism and the emphasis on learning assumed preeminence in experimental psychology for several decades. Great empirical and conceptual strides were made during this era. The Hull–Spence model of drive, reinforcement, and learning (e.g., see Spence, 1960) dominated much of the field of psychobiology. Comparative psychologists were busy with attempts to enumerate the laws and principles governing learning, and the emerging field of "physiological psychology" often focused on the neural mechanisms of learning (Beach, Hebb, Morgan, & Nissen, 1960; Hebb, 1949), or the brain mechanisms underlying the putative drives that motivate or reinforce that learning (Hebb, 1955; Stellar, 1954).

Social psychology was also heavily influenced by the prevailing emphasis on learning processes. The emergence of social learning theories during this era (Dollard, Doob, Miller, Mowrer, & Sears, 1939; Dollard & Miller, 1950; Miller & Dollard, 1941) had not only historical significance but also continues to have an impact on research and concepts in social psychology (Bjoerkqvist, 1997; Liao & Cai, 1995; Miller, Shoda, & Hurley, 1996; Smith & DeCoster, 1998). The synergism between social psychology and psychobiology was illustrated by the publication of the first edition of *A Handbook of Social Psychology* (Murchison, 1935), which included 8 (of 22) chapters on animal models of social behavior. Among these was a chapter on nonhuman primates, authored by Yerkes and Yerkes, who would later be instrumental in establishing the federally funded Yerkes Regional Primate Research Center in Atlanta, where social psychological studies of primates have continued.

There was a sense during that period that a comprehensive, meaningful social science would require an integration of social psychology and psychobiology. Considering the scientific status of the social sciences relative to that of the physical sciences, Murchison (1935), in the preface to the first social psychology handbook, beseeched serious students of social psychology to

> reflect concerning the problems of social mechanics that are basic enough to require identification and analysis before progress can even begin in this field. Whatever those mechanisms may be, they are certain to be essential components of *all social behavior in all social bodies in all social situations whatever* [italics added]. The social scientist must discover those mechanisms, or there will never be a social law. (p. IX)

Although both psychobiology and social psychology benefitted from research and theory on learning, and from interactions between the disciplines, both were also hampered by what increasingly had become the straightjacket of behaviorism. Especially pernicious was the radical behaviorism of Skinner (see Evans, 1968), who eschewed scientific explanations of behavior that appeal to something going on in another universe, such as the mind or the nervous system. Although Skinner may have emerged from the psychobiological tradition, his extremist form of behaviorism excluded meaningful accounts of behavior in the terms of biology (except in a trivial sense). It also failed to admit many emerging concepts and theories from social and cognitive psychology.

In his presidential address to the first annual meeting of the American Psychological Association (APA) Division of Personality and Social Psychology, G. W. Allport (1947) railed against what he termed "motorized psychology"—a mechanistic psychology that would deny the influence of factors like attitudes or intentions. Many social psychologists followed suit. Again, however, the rejection of radical behaviorism should not be equated with a rejection of the biological perspective. Indeed, psychobiologists also rejected this extremist behaviorism, because it denies a fundamental tenant of psychobiology—that there is substantial benefit to the study of behavior from approaches that extend across subdisciplinary domains or levels of analysis. These include the social as well as the neuropsychological, neurochemical, and neurophysiological levels.

A phoenix is rising, however, from the ashes of historical behavioral biology. It is based not on a biological paradigm that happens to be transiently in vogue at the moment, but on a progressively emerging contemporary psychobiology that is richly grounded in, and calibrated by, the constraints of cross-disciplinary data, concepts, and perspectives. Of equal importance, given this interdisciplinary grounding, modern psychobiology now has the scientific authority to significantly impact on other disciplines and levels of analysis. There were, of course, growing pains in the emergence of modern behavioral neuroscience from its roots in historical psychobiology. At times, the methods, empirical data, and concepts of psychology seemed incompatible or at least inharmonious with the developing neuroscience perspective. At an early point in the 1970s and 1980s, many psychobiologists rejected their psychological heritage, and sought identification with disciplines such as physiology, pharmacology, or neurochemistry. Other psychobiologists with greater prescience were instrumental in establishing the interdisciplinary Society for Neuroscience (in 1970), which is the premier association for behavioral neuroscience that today has more than 25,000 members. This initiative resulted in gradually increasing communication and integration across levels of analysis, whereby conceptual and methodological barriers that once stood as disciplinary fortresses now seem archaic and regressive.

This multilevel interdisciplinary perspective, which seeks to integrate information derived from levels of analysis ranging from psychology to molecular biology, is now increasingly embraced by the rapidly developing fields of behavioral neuroscience, cognitive neuroscience, behavioral medicine, behavior genetics, psychoneuroimmunology, and social neuroscience. In fact, it is the thesis of this article that the explosive developments in these fields is causally, rather than serendipitously, related to the recognition of the value of multilevel analyses and the biological perspective.

Modern Behavioral Biology

So what is the new biological paradigm or perspective that has fostered the recent explosive developments in both behavioral neuroscience and social neuroscience? There are many factors, but by far the most important is the recognition that evolution not only endowed us with primitive functions like reflexes and a sex drive, but it sculpted the awesome information processing capacities of the highest levels of the brain. Although the conceptual domain of some early evolutionary social psychological theories may have stopped at the limbic system, evolution did not. All behaviors are not invariably adaptive, either in terms of our immediate survival or in the proliferation of our genes. Likely related to the multiplicity of unforeseen adaptive challenges that terrestrial organisms may encounter, natural selection continued to craft complex neural systems that can defy primitive genetic imperatives. For an organism to be generally adaptive it must be eminently flexible, and evolution has seen to it. As cogently articulated by the cognitive neuroscientist Pinker (1997) in his book, *How the Mind Works,* "The ultimate goal of natural selection is to propagate genes, but that does not mean that the ultimate goal of people is to propagate genes" (p. 24). He later elaborated:

> Well into my procreating years I am, so far, voluntarily childless, having squandered my biological resources reading and writing, doing research, helping out friends and students.... By Darwinian standards I am a horrible mistake, a pathetic loser.... But I am happy to be that way, and if my genes don't like it, they can go jump in the lake. (p. 52)

The new behavioral biology is fundamentally different from the old, not just because it is now endowed with a technical armamentarium that permits probing of the lowest levels of neuronal molecular biology (although these developments are far from irrelevant). It is not merely because an interdisciplinary approach can increase the probability of federal funding (in fact, the opposite is sometimes the case), nor is it attributable to an abject denial of our scientific heritage—in fact, appropriately conceptualized instinct models may offer meaningful accounts of some aspects of behavior. Rather, modern behavioral biology is distinct because it recognizes that natural selection and evolution progressed beyond the limbic system, and continue to mold the highest level cortical substrates that underlie cognitive operations. In contrast to the justifiable wrath of G. W. Allport (1947) concerning motorized psychology and the extant biological models of the time, the vision of contemporary behavioral biology is increasingly focused on the manner in which the mind is realized in the brain. Modern behavioral neuroscience is as interested in constructs such as attention and cognition as it is in issues such as why people seek food and water.[1]

The notable 19th-century neurologist Jackson (1884/1958), in an essay on "Evolution and dissolution of the nervous system," emphasized the hierarchical structure of the brain and the rerepresentation of functions at multiple levels within this neural hierarchy. Implicit in his message was the fact that information is processed at multiple levels of organization within the nervous system, but it would be almost 100 years before this concept was comprehensively embraced by behavioral biology. Primitive protective responses to

[1]This is documented by a Medline search. The APA *Journal of Comparative and Physiological Psychology* (*JCCP*) became *Behavioral Neuroscience* (*BN*) in 1983. In the *JCCP* years (from 1965–1982), the number of articles retrieved by the keyword *attention* was only about 25% of the number retrieved by *hunger* or *thirst*, and the number retrieved by *social* was about 80% of the latter. During the 1980s period of *BN*, those proportions had shifted considerably, as either *attention* or *social* now retrieved about 160% of the number retrieved by *hunger* or *thirst*. That trajectory continues into the 1990s period of *BN*, over which the keywords *attention* or *social* each retrieved about 700% more articles than did *hunger* or *thirst*.

aversive stimuli are organized at the level of the spinal cord, as is apparent in flexor (pain) withdrawal reflexes to noxious stimuli that can be seen even after spinal transections. These primitive protective reactions are expanded and embellished at higher levels of the nervous system (see Berntson, Boysen, & Cacioppo, 1993). The evolutionary development of higher neural systems, such as the limbic system, endowed organisms with an expanded behavioral repertoire, including escape reactions, aggressive responses, and even the ability to anticipate and avoid aversive encounters. However, it was not until the emergence and elaboration of the cerebral cortical mantle that the ultimate protective strategies were fully developed in humans. These include not only the ability to anticipate potential danger but also to weigh alternative tactics for dealing with it, including the establishment of social organizations such as governments and militaries.

Social and cognitive mechanisms are not localized to a single neural level, but are represented at multiple levels of the nervous system. At progressively higher levels of organization, there is a general expansion in the range and relational complexity of contextual controls and in the breadth and flexibility of discriminative and adaptive responses (Berntson et al., 1993). Higher level systems confer greater behavioral variability and adaptive flexibility, but do not eliminate lower behavioral mechanisms. Thus, evolutionary forces have more rigidly canalized some aspects of behavior, such as those organized at subcortical levels, but have also forged higher level interacting neural systems. A behavioral biology or evolutionary social psychology that restricts its focus to these more primitive levels is necessarily incomplete.

Adaptive flexibility has costs, however, given the finite information processing capacity of neural tissue. Greater flexibility implies a less rigid relation between inputs and outputs, a greater range of information that must be processed, a slower serial-like mode of processing, and an increased susceptibility to miscalculation. Consequently, the evolutionary layering of higher processing levels onto lower substrates has considerable adaptive advantage, in that lower and more efficient processing levels may continue to be utilized, and may be sufficient in some circumstances. Pain withdrawal reflexes are fast, and rarely lie. A pain stimulus is an obligatory condition for the rapid invocation of the flexor withdrawal reflex. Given the hierarchical organization of the nervous system, however, an invoked reflex does not necessarily manifest in a reflexive response. Information is processed at multiple levels of the neuraxis, and reactions to that information may be quite divergent across levels. Priority in the control of behavior may shift among these levels. Practiced drivers on a familiar thoroughfare may be largely unaware of the control behavior they exercise in driving, which can be mediated by relatively low-level automated processing mechanisms. However, in unfamiliar or treacherous terrain, such as a narrow and winding mountain road, every control action may become thoughtful and deliberate. Similarly, although people have powerful pain withdrawal reflexes, they can be overridden by higher level processes under some circumstances (e.g., if a child was caught in a fire).

An Illustration of Multiple Levels of Processing

Higher level neural systems do not always dominate, however, and the multiple levels of neural processing may even come into conflict. In a project (Boysen & Berntson, 1995) designed to study the possible use of deception in chimpanzees, an initial stage entailed training the animals in a simple choice selection task between two quantities of candies. Animals were presented with two discrete candy arrays, and their task was to select one of the choice options. A reversed reward contingency was imposed, such that the animals were reinforced with the nonselected array, whereas the selected array was given to a passive observer animal. Consequently, the animal could optimize payoff by selecting the smaller candy array, and thus receive the larger reward. This was a simple task, or so it seemed, that would be mastered in a few trials. In fact, even after hundreds of trials of differential reinforcement, the animals could not be trained to reliably select the smaller of the two candy arrays (Boysen & Berntson, 1995).

This was a startling result, as the chimpanzees in this study (Boysen & Berntson, 1995) were among the most highly trained and cognitively sophisticated nonhuman animals in the world. They were accomplished in the use of numeric symbols (Arabic numerals) both receptively and expressively, and could demonstrate logical reasoning in a transitive inference task. Seemingly, this was one of the most elementary tasks in which they had engaged. Nevertheless, trial after trial, they continued to select the larger candy array, thereby receiving the smaller reward, and no improvement in performance was apparent even with extended training.

We asked why such intelligent animals could not learn to optimize performance in such a simple task. That was the wrong question, and that became apparent with further analysis of performance. Overall, the animals tended to select the larger candy array, and this tendency increased as the numerical disparity between the array choices increased. That is, their performance became even less optimal under the very conditions in which they stood to benefit the most by selecting the smaller array. Was this a violation of the basic principles of reinforcement? A learning failure?

The answer to those questions is no. Arabic numerals were then substituted (mounted on a placard) for the candy arrays. The same reversed reward contingency was in effect, with the animals receiving the number of candies corresponding to the nonselected numeral as a reward. Under these conditions, performance became more optimal on the very first trial (Boysen, Berntson, Hannan, & Cacioppo, 1996). Animals now reliably selected the smaller Arabic numeral and thus received the larger reward. Moreover, opposite the pattern with candy arrays, performance became more optimal with larger numeric disparities between the choice stimuli, consistent with the greater payoff differential. It appears that the animals had indeed learned the rules of the game, but were unable to implement that implicit knowledge with candy arrays as choice stimuli. When candy arrays were again introduced, performance plummeted, and when Arabic numerals were reintroduced as stimuli, performance was again immediately optimized.

These findings (Boysen et al., 1996) imply a powerful interfering response bias in this task, perhaps related to the perceptual features of the candy arrays. The task interference appears to be related to a primitive disposition to select a larger quantity of food, which would likely have adaptive value in the evolutionary history of the species. In the contrived environment of the experimental psychologist, however, such a disposition can lead to suboptimal choices. Although this primitive disposition may have introduced an interfering bias in response selection, it did not preclude higher level processing and learning of the reward contingencies, as that learning was expressed immediately on introduction of the Arabic numerals.

These results (Boysen et al., 1996) can be understood within the framework of the multiple levels of processing within the nervous system. The findings illustrate that multiple processing levels, although generally coordinated, may under some conditions lead to very different behavioral conclusions. These results suggest that an important function of symbols is that they can come to represent selective abstract features of their referents (e.g., numerosity), without the perceptual imperatives that may have been endowed on those referents by evolution. That is, higher level cognitive processing of information may serve as a powerful liberating force from the dictates of a more primitive evolutionary biology. Indeed, this was likely an important factor in the emergence of human intellect, culture, and civilization.

Relevance to Social Psychology

Multiple levels of processing, implied by the hierarchical structure of the nervous system, likely underlie important aspects of social psychology. The Elaboration Likelihood Model (Petty & Cacioppo, 1986) asserts that there are distinct routes to persuasion, some being more peripheral (based on factors such as context, authority, etc.) and others more central or rationally based. The conditions under which the peripheral route predominates are those in which inadequate knowledge is available, or higher level cognitive processing is otherwise diminished. In humans, mere exposure to novel stimuli has been shown to alter evaluative judgments of those stimuli in subsequent tests (Zajonc, 1968). Similarly, simple somatomotor posturing can bias evaluative judgments of stimuli in the absence of preexisting knowledge, a condition that favors the peripheral processing route (Cacioppo, Priester, & Berntson, 1993; Priester, Cacioppo, & Petty, 1996). However, the effectiveness of peripheral routes is greatly reduced for stimuli that have an existing associative meaning (Cacioppo, Marshall-Goodell, Tassinary, & Petty, 1992). The powerful interference observed in chimpanzees, despite knowledge of the payoff rules, suggests that one consequence of continued phylogenetic development of cognitive mechanisms is an enhanced ability of higher level mechanisms to overcome more primitive dispositional biases. The availability of animal models that parallel human cognitive and behavioral processes can provide an important link between social psychological phenomena and their underlying neurobehaviorial mechanisms.

Although we carry a primitive evolutionary undercarriage that is generally but not always adaptive, the real psychological significance of evolution is that it has progressively endowed organisms with the cognitive machinery that allows more elaborate and flexible processing of information. This can be a tremendously liberating force from the fixed dictates of primitive dispositions arising from our genetic heritage, allowing for the regulation, shaping, and integration of more primitive levels of organization. Although conflicts may develop across levels of organization under certain circumstances, generally there is a synergism rather than an antagonism among levels, and between biological and cultural determinants of social behavior.

A feature of the antiquated behavioral biology of the past is that it failed to progress conceptually beyond the level of the limbic system. In contrast, contemporary behavioral neuroscience fully recognizes the multiplicity of processing levels, and embraces those aspects of cognition and behavior that derive from the highest levels of neural organization. These are the levels that underlie the most complex psychological processes, and are most closely related to what may be termed the *mind.* The behavioral biology of the past, which was appropriately rejected by social psychologists, was a mindless biology. In contrast, contemporary behavioral neuroscience is highly mindful. It is clear that what we have learned about the physiology of thirst and body water balance offers few insights into the drinking behavior of an alcoholic in a bar. For this understanding, we will need a knowledge base ranging from the genetic and neurochemical predispositions to the rewarding effects of alcohol, to the cognitive and sociocultural factors that dispose toward alcohol usage. In short, a multilevel approach will be necessary to unravel this vexing social problem. Given the hierarchical structure of the brain, and the multiple levels of processing, biological determinants are no longer equated with fixed, innate mechanisms.

Principles of Multilevel Analyses

The central tenet of the emerging discipline of social neuroscience is simple: Social psychology and psychobiology will mutually benefit by greater integration among our subdisciplines. Both lower and higher levels of neural organization can contribute to psychological processes, and a crucial focus for the future is how moderator variables come to determine the relative contributions of these levels of processing in a given context. This knowledge can transform generalizability failures into comprehensive theoretical integrations. Does this raise the specter that social psychology will be overwhelmed, supplanted, or otherwise rendered subservient to psychobiology? The dirty little secret of reductionism is that, in the recorded history of science, there has never been a discipline that has been obliterated by reduction to a lower level of analysis. The emergence of subatomic physics did not render biochemistry obsolete. To the contrary, it offered the basic conceptual framework within which biochemistry and neurochemistry have flourished.

Cross-disciplinary constraints from one level of analysis to another come not only from lower strata in the reductionist hierarchy. As previously discussed, early instinct theories were felled in large part by social psychologists, and radical behaviorism buckled under the assault of the cognitive revolution. The intellectual sword of multilevel analysis cuts both ways. It is not the subjugation of one discipline or level of analysis to another, as higher level analyses often provide the fundamental subject matter and guiding concepts for lower level disciplines. Rather, multilevel analysis affords a mutual calibration among disciplines that enriches both. This entails a reciprocal anchoring of disciplines in the knowledge base of the other, and offers insights that can dramatically enhance progress of each of the subfields. Disciplinary or subdisciplinary isolation poses a real threat to the survival of a field. At best, such isolationism is inefficient, often requiring the rediscovery of basic principles that have been well-established in other disciplines. This applies to lower as well as higher levels of analysis. Although genes may rigidly encode their specific gene product, the behavioral effect of gene expression may be far less fixed. Indeed, behavioral geneticists increasingly recognize that

> for behaviors with smaller genetic effects (such as those likely to characterize most of the effects of a gene knockout), there can be important influences of environmental conditions specific to individual laboratories, and specific behavioral effects should not be uncritically attributed to genetic manipulations such as targeted gene deletions. (Crabbe, Wahlsten, & Dudek, 1999, p. 1672)

Principle of Multiple Determinism

It is increasingly apparent that problems and issues in genetics as well as psychology will not be fully understood by studies restricted to a single level of analysis, regardless of the specific level selected (Anderson, 1998; Cacioppo & Berntson, 1992). A process or event at one level of organization may have antecedents and determinants both within and across organizational levels, as encapsulated in what has been termed the *principle of multiple determinism* (Cacioppo & Berntson, 1992). In prairie voles, oxytocin, vasopressin, adrenal glucocorticoids, and other hormones, along with experiential factors, exert important influences on mate selection, the establishment of monogamous relationships, and on parenting behavior (Carter & Altemus, 1997; Carter, DeVris, & Getz, 1995). Similar hormonal–behavioral relations have been documented in other mammalian species (Insel, 1997; Nelson & Panksepp, 1998). In view of the elaborations of higher level processing mechanisms in humans, it is not surprising that sociocultural and interpersonal factors assume greater significance in mate selection and maternal–infant attachments. Nevertheless, it is increasingly recognized that, in addition to the obvious role of gonadal hormones in sexual function and potency, a broader range of hormonal influences may modulate attraction and affiliation, as well as maternal–infant and paternal–infant attachments in humans (Flemming, Ruble, Krieger, & Wong, 1997; McCarthy & Altemus, 1997; Nelson & Panksepp, 1998; Rosenblatt, 1994). These relations do not represent the obligatory dictates of a one-way biological mandate on behavior. In fact, hormonal status is known to be modulated by psychological states and processes. We will return to this reciprocal pattern of modulation between psychological and biological determinants.

Neither social psychologists nor psychobiologists can, or should, directly concern themselves with all possible levels of analysis. A corollary to the principle of multiple determinism is that mapping relations across levels of organization becomes more complex as the number of intervening levels increases. Although it is certainly worthwhile to adopt a broad scientific perspective, specific research programs would probably achieve maximal benefit by attention to more proximate levels of analysis (both higher and lower). If this perspective was embraced generally by those pursuing distinct levels of analysis, it may be sufficient to ensure the ultimate integration among disciplines.

As previously considered, disciplines are not obliterated by reduction to a lower level of analysis, as there are efficiencies in higher level organizations of information. The essential features of Beethoven's Ninth Symphony may be captured by the sequential digital data on a compact disc (CD), and examination of that data set may be sufficient to identify the piece. It may be faster, easier, and likely more enjoyable to simply play it out. Similarly, although a horse race may be characterized by specifying all relevant, temporally unfolding synaptic interactions and neuromuscular events of each of the participant horses, it would not be a particularly parsimonious account, and probably not nearly as much fun as watching the race, or even listening to the energetic narrative of a race announcer. This is not to say that a mapping across levels would be worthless. Indeed, it would be invaluable. Of the bewildering number of cellular events underlying the performance of the horses, a subset will relate to psychological concepts such as motivation, and the myriad social interactions among the horses as well as between the horses and their jockeys. Understanding this subset would undoubtedly yield insights into the psychological states and processes, and the neurological mechanisms and dynamics that make for a good horse race.

Principle of Nonadditive Determinism

As important as is the issue of efficiency, there is another reason why higher levels of analysis will always be with us. That is that the properties of more basic elements at lower levels of organization may only become apparent when these elements interact with others at a higher level of organization. Although the whole may not be greater than the sum of its parts, the properties of its parts may only, or more readily, be knowable by the properties of the whole. This has been articulated as the *principle of nonadditive determinism* (Cacioppo & Berntson, 1992). Although the essential features of Beethoven's Ninth Symphony may be fully captured by the sequential digital data on a CD, the esthetic impact of that data is more efficiently processed by auditory perceptual mechanisms. There is no magic involved, as the perceptual qualities relate to specific temporal patterns of the data, but identification of the relevant patterns that correspond to specific perceptual qualities could not be derived readily from the digital data stream alone.

An illustration of this principle comes from recent studies on the impact of social stress on immune function. In a study (Padgett & Sheridan, 1999) of the effects of social reorganization on immune processes in mice, the social structure of a mouse colony was disrupted by introduction of an unfamiliar mouse. Two social reorganization cycles were given before and two after the animals were inoculated intranasally with an influenza virus. In a socially stable control group, about 8% of the animals died of the resulting infection. In the social stress group, however, about 70% of the animals died—from the flu. Despite comparable hypothalamic–pituitary–adrenal (HPA) activation, as evidenced by similar corticosteroid levels, the social stressor had a substantially greater impact on immune function than did a standard physical stressor (restraint stress), which was associated with only a 15% mortality rate. Similarly, herpes simplex was found to be reactivated by social stress in mice, whereas physical stressors such as restraint and shock were largely ineffective (Padgett et al., 1998). In these cases, psychosocial stresses were translated into physiological signals that modulated the expression and pathological impact of virally transmitted host–pathogen genes.

Such effects are not limited to animals. Parallel findings of stress effects on susceptibility to viral infections and other markers of immune function have also been reported for humans, with social stressors being particularly potent (Cohen et al., 1998; Cohen, Tyrrell, & Smith, 1991; Glaser, Kiecolt-Glaser, Malarkey, & Sheridan, 1998; Kiecolt-Glaser, Malarkey, Cacioppo, & Glaser, 1994). A meta-analytic review (Uchino, Cacioppo, & Kiecolt-Glaser, 1996) of the extant human literature revealed that perceived social isolation is associated with a variety of altered physiological functions, such as blood pressure regulation, catecholamine levels, and immune reactions. A causal link in these relations was suggested by findings of improved physiological functioning after interventions that served to reduce social isolation (Uchino et al., 1996). The role of psychological variables in these relations is indicated by the fact that subjective indexes of social isolation are often better predictors of stress and health than objective indexes (Seeman, 1996; Uchino et al., 1996). These examples demonstrate the potent influence of social relations on physiological and immunological function, and illustrate how the order in physiological, pharmacological, or immunological data may not be fully understandable from the vantage of a single level of analysis. Rather, comprehensive accounts of psychophysiological relations will likely require multiple analyses across distinct levels of functional organization.

Principle of Reciprocal Determinism

A final principle that characterizes the relations among levels of organization is the *principle of reciprocal determinism,* which asserts that there can be mutual influences among higher and lower levels of organization in the determination of behavior. As considered earlier, social stressors can lead to activation of the HPA axis and other signaling pathways that impact on physiological and immune functions. In rats, a low-reactive HPA system produces an adult who is low in stress reactivity and is attentive to offspring, showing increased levels of licking and grooming of the pups (Liu et al., 1997). The latter are important for the offspring to develop into low-reactive adults, who in turn attend to and frequently lick and groom their own pups (Liu et al.). Similarly, genotypic high-reactive infant monkeys develop into high-reactive adults (e.g., high HPA reactivity to stress, aggressive, and maladaptive social behaviors) when raised by their biological mothers or surrogate mothers who are also highly reactive (Suomi, 1999). When raised by low-reactive mothers, however, these same infants develop into low-reactive adults (Suomi, 1999). Patterns of parental care can modulate genetic actions and shape glucocorticoid binding in the hippocampus and cortex, leading to altered stress reactivity and social behavior in adulthood (Meaney et al., 1996; Meaney, Sapolsky, & McEwen, 1985). Genetic constitution clearly impacts on physiology, but what appears to be a genetic influence on physiological function may well be mediated by a behavioral variable. Such influences are not limited to animals, as the early loss of a parent, poor quality family relationships in humans, or both, have been reported to be associated with higher blood pressure and enhanced HPA reactivity in infancy (Hertsgaard, Gunnar, Erickson, & Nachmias, 1995) and adulthood (Luecken, 1998).

Summary

The principles articulated previously emphasize the important contributions to the scientific enterprise of multiple levels of analysis. They further illustrate the reasons why a one-way reductionism is an empty enterprise, rather than a threat to social psychology. However, we should seek a reductionism that allows a closer mapping of constructs from differing levels of analysis, and permits a representation of higher level constructs in the vocabulary and models of lower levels of analysis. This is what science ultimately demands. By the same token, the terms and constructs of lower levels of analysis will be equally vitalized and enriched by knowledge gleaned from higher levels of analysis, and this is increasingly recognized in contemporary behavioral neuroscience. The emphasis on interdisciplinary approaches and multilevel analyses is not a fad. It is the future. A discipline that fails to embrace this perspective threatens its very survival, and is in jeopardy of an isolationism that can only diminish itself as well as the broader scientific community. Multilevel analyses cannot be coerced, and if they were, they would not likely be productive. There is a continuing need for analyses restricted to a single level. Rather, what is important is a multilevel perspective that will ultimately foster multilevel analyses as the scientific problem dictates, and as interdisciplinary collaborative opportunities present themselves.

Contemporary Social Neuroscience Perspective

A fundamental organizational feature of the nervous system lies in the basic hierarchical structure of multiple processing levels. Not a strict hierarchy in the formal sense, but a more complex set of interacting levels, with parallel and serial processing components, and both ascending and descending communication between proximate and remote levels—what has been referred to as a heterarchy (see Berntson, Boysen, & Cacioppo, 1993). This heterarchical organization is not limited to sensorimotor processes or primitive reflex organizations, but also extends to the highest levels of neurobehavioral and cognitive functions. Although there are distinguishable levels and components of this system, they are highly interactive. Consequently, an understanding of a target level of functional organization, as gleaned from a single level of analysis, may be accurate but is likely to be incomplete. Sources of variance in behavior and cognition, arising from divergent levels of organization, would be relegated to the error term in disciplinary approaches that limit their vision exclusively to a single level of analysis.

For social psychologists, biological parameters should be viewed as theoretical elements, not merely dependent (or independent) variables. Available methods now permit not only the monitoring of biological systems in humans but also allow explicit manipulations of biological states. The latter range from simple noninvasive experimental procedures (e.g., postural change that can alter the balance of sympathetic and parasympathetic activity; Cacioppo et al., 1994), to pharmacological manipulations (e.g., autonomic blockades or HPA modulation; Berntson et al., 1994; Malarkey, Lipkus, & Cacioppo, 1995), to neuropsychological studies of naturally occurring brain insults (e.g., Kline & Kihlstrom, 1998). Although behavior is the ultimate product of neurobiological systems, the fact remains that psychological processes can have an impact on this biology. Indeed, the third principle articulated—the principle of reciprocal determinism—is particularly relevant, as it captures the mutually interacting influences among the varied levels of neurobehavioral organization. Of the multitude of reciprocal influences across levels of organization, an especially intriguing subset may be of particular interest to social neuroscience. This relates to bottom-up influences from lower level systems that can exert subtle biases on higher level processes, paralleling the top-down modulations of lower level systems by higher neural mechanisms.

Bottom-Up Influences

Multiple levels of processing, implied by the hierarchical structure of the nervous system, may help clarify aspects of social cognition and behavior. Although the evaluative disposition and associated interference displayed by chimpanzees in the candy selection task may have been inherent in chimps, acquired evaluative dispositions in humans can operate similarly. Evaluative predispositions (attitudes) can be formed in humans through classical conditioning (Cacioppo, Marshall-Goodell, et al., 1992). The experimental stimuli were neutral words and pronounceable nonwords that were matched in terms of structural features and participants' prior attitudes and affect. A differential conditioning procedure was used such that the word was paired with electric shock, the nonword was paired with shock, or the word and nonword were paired randomly with shock. A simulation experiment in which participants read descriptions of the conditioning procedures revealed that they expected (and believed the experimenter anticipated) simply that whatever stimulus was paired with electric shock would become disliked. In accord with latent inhibition, however, we posited that conditioning would be more apparent for nonwords than for words because of the preexposures to the former class of stimuli. Results confirmed that more negative attitudes were formed when nonwords were paired with shock than when words were paired with shock.

Research by LeDoux and colleagues (LeDoux, 1995) on conditioned fear reactions to acoustic stimuli, indicates that projections from the auditory thalamus to the amygdala bypass the cortex and constitute a sufficient subcortical mechanism for affective learning. Although an adequate subcortical mechanism exists for simple conditioning, more complex contextual conditioning appears to be dependent on a cortical link (LeDoux, 1995). Similarly, visually masked fear stimuli can trigger autonomic reactivity in humans, despite the fact that the stimuli are not seen or recognized (Ohman, 1996). A more recent imaging study revealed that masked fear stimuli preferentially increase activity in thalamic–amygdala circuits, and decrease amygdala–cortical activity, relative to nonmasked stimuli that were consciously perceived (Morris, Ohman, & Dolan, 1999). These findings are consistent with the thesis that the acquisition and representation of affective (evaluative) dispositions can operate at multiple, interrelated levels of the neuraxis. Moreover, the lower level processing systems may exert important biases on higher attentional, cognitive, and affective reactions (Berntson, Sarter, & Cacioppo, 1998; Ohman, 1996).

These data are reminiscent of Nisbett and Wilson's (1977) and Gazzaniga and LeDoux's (1978) proposition that individuals can come to feel certain ways about stimuli and can even construct rationalizations for their feelings, although not really knowing why they come to feel as they do about people, objects, or events around them. The results of our simulation study indicated that people's declarative knowledge about classical conditioning led them to believe that whatever stimulus was associated with electric shock would also become disliked. Our results, however, conformed to animal studies showing that individuals felt more negatively about a novel stimulus than a familiar stimulus that was paired with electric shock. These data suggest a process by which individuals can come to feel differently toward stimuli in their world even though they do not comprehend the true basis for these differential feelings. Work on split-brain patients further suggests that people spontaneously confabulate to explain their feelings, with sometimes humorous results to the experimenter with all the facts. To the patient who is trying to construct a meaningful world from disparate parts, however, the confabulations are sensible and sober (Gazzaniga & LeDoux, 1978).

The evidence reviewed previously is consistent with the view that racial prejudice may rest in part on the conditioned evaluative predispositions that coexist with egalitarian beliefs, leaving people unwittingly of two minds about members of racial minorities. Thus, it may be verbal beliefs and evaluative attitude representations that are more likely to influence and predict behavioral intentions, but lower level (e.g., conditioned) evaluative predispositions that are more likely to influence a variety of affective and unintentional behaviors—the kinds of behaviors that have been shown to be most likely to reveal prejudice in contemporary research on stereotypy (cf. Clark & Squire, 1998). Contrary to the notion in modern racism that people are of one mind but two faces, work in social psychology and in the neurosciences raises the possibility that individuals who report being egalitarian but find themselves acting in a discriminatory fashion are speaking truthfully, in a sense, when they say that their actions were not premeditated or intentional. Their actions may not reflect what they see to be the behavioral implications of their beliefs. Symbolic representations provided a different glimpse into the minds of the chimps; similarly, words and rating scales may provide an accurate yet incomplete glimpse into human prejudices.

Bottom-Up Influences Arise Not Only From Lower Neural Systems

Since James's (1890) suggestion that strong emotions may represent the perceptual consequences of visceral afferent feedback, there has been a continuing history of research and theory on the role of visceral afference in affective reactions (for a review, see Cacioppo, Berntson, & Klein, 1992). Although studies on patients with spinal injuries have suggested that visceral feedback is not essential for emotional reactivity, this conclusion must be tempered by the fact that major visceral afferent systems remain intact in people with spinal injuries. Moreover, rather than constituting the sole basis for emotional reactions, a more likely role for visceral afference is in the priming of central systems underlying affective response (see Cacioppo et al., 1992). Recent research offers considerable support for the view that visceral afferent input can exert important modulatory influence over higher neural systems.

Invasion of the body by foreign microbes (or mitogens such as lipopolysaccaride) can trigger a neuroendocrine cascade that manifests in many common features of stress reactions (e.g., central catecholamine release, elevated corticosterone levels, anorexia, decreased activity, and hyperthermia). Recent findings suggest that this central stress-like response is mediated by a peripheral immune cytokine (lymphocyte secretion) that is transduced into a neuronal signal and conveyed to the brain via afferent fibers in the vagus nerve (Maier & Watkins, 1998; Watkins, Maier, & Goehler, 1995).

Additional data further indicate that vagal afferent activity can impact on the plasticity of central networks and can modulate memory in humans (Clark, Naritoku, Smith, Browning, & Jensen, 1999). Systemic administration of epinephrine has been shown to potentiate "emotional" memories in rats—an effect that is blocked by beta blockers (McGaugh, Cahill, & Roozendall, 1996; Williams & McGaugh, 1993). Similar to the illness response, these memory affects appear to be mediated by a peripheral feedback signal carried by afferent vagal activity (Clark et al., 1999; Williams & McGough, 1993). Together, these findings suggest an important modulatory role for visceral afferent information on central information processing.

Further findings suggest that visceral afference may come to modulate and bias, more generally, the cognitive and attentional processing of behaviorally relevant stimuli (Berntson et al., 1998). The significance of this perspective is that it focuses on important biological influences on psychological processes that arise not from the inherent organizational features of higher level cognitive substrates, but from more subtle functional biases on these higher level processing substrates that arise from lower level influences. That is, feedback from peripheral biological states can bias the processing of higher level cognitive systems (see Berntson, Sarter, & Cacioppo, 1998). Indeed, there is now an emerging recognition of a symmetry in the reciprocal interplay among levels of organization, entailing both direct and indirect mutual interactions (top down and bottom up) that impact both biological and psychological processes. This interplay can neither be appreciated from the perspective of a primitive model of biology, nor from a social psychology that limits its focus exclusively to higher level processes.

Top-Down Influences Are Generally More Flexible

Important in the further integration of the biological and the social psychological perspectives will be the ability to relate constructs at one level of analysis to those of another. That does not entail a one-way process, as the scientific value of multilevel efforts accrues to both higher and lower levels of analysis. Illustrative of this issue is the traditional view of the sympathetic and parasympathetic branches of the autonomic nervous system being subject to reciprocal central control, with activation of one branch associated with inhibition of the other. This is a conception that arose from the early physiological literature, and continues to the present, although qualifications are increasingly recognized (see Berntson, Cacioppo, & Quigley, 1991). Malliani, Montano, and Pagani (1997) asserted that "in most physiological conditions, the activation of either (sympathetic or parasympathetic) outflow is accompanied by the inhibition of the other" (p. 343).

This opponent pattern of central autonomic control does characterize many lower level cardiovascular reflexes (e.g., baroreceptor reflexes), but is incomplete and noncomprehensive. As previously outlined, higher level systems are generally endowed with much greater flexibility than lower level mechanisms. Consequently, in behavioral contexts, activities of the two autonomic branches may show reciprocal, concordant (coactive), or independent changes. This represents an important expansion and calibration of biological conceptions of autonomic control, which arose to a large extent from the psychophysiological literature and is crucial in understanding psychophysiological relations. For example, heart rate acceleration to standard psychological stressors has been reported to predict immune reactions to stress (Manuck, Cohen, Rabin, & Muldoon, 1991). This predictive relation has not always been found, however, and the amount of variance accounted for may be modest. However, an increase in heart rate in behavioral contexts can arise from sympathetic activation, parasympathetic withdrawal, reciprocal sympathetic activation together with parasympathetic withdrawal, or even sympathetically dominant coactivation of both autonomic branches. These varied patterns may be related to distinct psychological states, and may have differential implications for immune function.

Whereas lower levels of neural organization are generally characterized by relatively fixed response patterns, higher levels foster a broader and more flexible range of responses. Lower level cardiovascular reflexes, such as the baroreceptor heart rate reflex, manifest in a relatively rigid reciprocal pattern of autonomic control, with little variation among individuals (Berntson et al., 1994; Cacioppo et al., 1994). In contrast, social stressors yield a more variable pattern of response, characterized by notable, but stable, individual differences (Berntson et al., 1994; see also Malarkey et al., 1995). This is important, because it is the sympathetic component of heart rate reactivity, rather than heart rate reactivity per se, that is most predictive of immune responses (Cacioppo, 1994). This feature of psychophysiological relations would not have been apparent without the inclusion of higher level analyses.

A parallel can be seen in social psychological studies on the Elaboration Likelihood Model, in which lower level influences (the peripheral route) can lead to relatively simple and mindless changes in attitudes when higher level processes are precluded. In contrast, more mindful influences on attitudes are apparent when conditions favor higher level processing (Cacioppo, Marshall-Goodell, et al., 1992; Petty & Cacioppo, 1986). These findings highlight an important focus for future research in multilevel analyses—the conditions that foster higher versus lower levels of processing in a given context.

Synergism Across Levels of Analysis

The conceptual synergism among levels of analysis is apparent in social psychological research. The documented dissociation between central substrates for positive and negative affect, for example, lends important support to the recent conception of the bivariate nature of affect in humans (Cacioppo & Berntson, 1994). Further information concerning the form of the activation functions of these bivariate affective substrates, derived from basic psychobiological studies in animals, suggested a quantitative refinement of the bivariate model that more effectively accounts for the variance in human affective response (Cacioppo, Gardner, & Berntson, 1999). Additional social neuroscience approaches, including measurements of cerebral electrical activity, provide added support for this view and offer important methods for further exploring the quantitative parameters of affective systems (e.g., Crites, Cacioppo, Gardner, & Bernston, 1995). These multilevel analyses have substantially broadened the conception of affective systems. Although there are many manifestations of affective response that can be subsumed by a bipolar affective dimension, the bivariate model is more comprehensive and corresponds more closely to the known organizational features of neurobehavioral systems, as well as the psychology of affective response.

Summary

In summary, there is much to be gained by multilevel analyses. This approach enriches not only the higher level disciplines but also the lower level disciplines. The modern biological perspective, with its recognition of higher cognitive processing mechanisms, offers a powerful set of analytical tools to social psychologists, including neuroimaging and neuropsychological approaches in human participants. This does not mean that all social psychologists should seek additional training in behavioral neuroscience. An equally viable approach, and one that is increasingly visible, is the development of interdisciplinary teams that can address social psychological as well as psychobiological issues from a multilevel perspective. Most important, however, is the recognition on the part of both social psychologists and psychobiologists, of the value of multilevel analyses.

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