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Consciousness eclipsed: Jacques Loeb, Ivan P. Pavlov, and the rise of reductionistic biology after 1900

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Abstract

The life sciences in the 20th century were guided to a large extent by a reductionist program seeking to explain biological phenomena in terms of physics and chemistry. Two scientists who figured prominently in the establishment and dissemination of this program were Jacques Loeb in biology and Ivan P. Pavlov in psychological behaviorism. While neither succeeded in accounting for higher mental functions in physical-chemical terms, both adopted positions that reduced the problem of consciousness to the level of reflexes and associations. The intellectual origins of this view and the impediment to the study of consciousness as an object of inquiry in its own right that it may have imposed on peers, students, and those who followed is explored.

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1. Introduction

The current acceptance of consciousness as a suitable object of study in the life sciences came late in the 20th century (Flanagan, 1984). By that time other biological processes—physiology, biochemistry, genetics, embryology, and even many aspects of brain function—had long since

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been subsumed into the reductionist program seeking to explain biological phenomena in terms of physics and chemistry. The very success of this explanatory reductionism (Audi, 1999) may have dampened interest among many in the life sciences community in a subject as ethereal and elusive as consciousness. Instead, after the initial promise of numerous 19th century studies of psychophysics, hypnosis and dissociative disorders, color perception, sensory physiology, memory, attention, and much more, all of which was viewed in terms of conscious experiences, the subject was relegated, for the most part, to philosophy, mysticism, or (at best) "soft" science, and stayed there, languishing as a scientific subject, until the last decade of the 20th century (Baars, 1986, 2003; James, 1890). (Maybe *fin des siècle* epochs focus everyone, even molecular biologists, on such ultimate questions.)

Now that the subject has been rehabilitated, the question arises as to why something so fundamental to our understanding of ourselves was effectively suppressed as a topic worthy of scientific consideration for so long. Simply to say that the tools were not available for probing it does not suffice, as that deficiency has rarely stood in the way of academic efforts; indeed, one cannot know if current tools are adequate until they are actually tried. Moreover, many of the behavioral tests used to discriminate and subdivide aspects of consciousness (e.g., trace vs. delay conditioning) do not require advanced technologies.

A more compelling explanation may be found in the form that biological reductionist thinking assumed in its account of behavior in general and of mental activity in particular. These accounts can be traced to two dominating figures in early 1900s: Jacques Loeb in biology, and Ivan P. Pavlov in psychological behaviorism. Together, they played a key role early in the century in the establishment and dissemination of the ideology of explanatory reductionism to biology and psychological behaviorism. It is striking that equally famous scientists of the period, such as Sir Charles Sherrington and Karl Lashley, who advocated a more integrated conception of neural functioning, had less overall influence—even though they cited solid and reliable evidence.

2. Jacques Loeb and the theory of "animal tropisms"

Educated in the heyday of German physiology in the 1880s, Jacques Loeb (1859–1924) brought an anti-dualist perspective to questions of behavior and perception (Pauly, 1987; Wozniak, 1993). His early work was in physiological psychology, working with human subjects. He studied the relationship between physical and mental work by measuring the amount of physical force that a subject could exert on a dynamometer while concentrating on the effort, as opposed to when they were concentrating on mental arithmetic. From there, he descended the phylogenetic ladder to dogs, where he studied the effects on spatial perception of unilateral brain lesions, believing that the bilateral anatomical symmetry of individuals dictates their perception of space. His interests were coalescing around the idea that separation of activity into sensation and movement was artificial, and that there was a unifying explanation for all such phenomena. Above all, he wanted to avoid the need to invoke purely psychological factors.

The tenor of the reductionistic movement in science is well described by Miller (1962):

In Germany, the science of physiology was controlled by four men: Hermann Ludwig von Helmholtz, Emil Du Bois-Reymond, Ernst Brücke, and Carl Ludwig. These men formed

a private club in Berlin whose members were pledged to destroy vitalism ... And it was in this intellectual atmosphere that the pioneer psychologists were educated. Freud was Brcke's student; Pavlov studied under Ludwig; Wundt was Du Bois-Reymond's student and Helmholtz' assistant. With physiology reduced to chemistry and physics, the next step was to reduce psychology to physiology. (1962, pp. 193–194)

In Britain T.H. Huxley extended this mechanistic approach to consciousness. He wrote:

Consciousness ... would appear to be related to the mechanism of the body ... simply as a [side] product of its working, and to be completely without any power of modifying that working, as the [sound of] a steam whistle which accompanies the work of a locomotive ... is without influence upon its machinery. (quoted in James, 1890/1983, p. 135)

Along these lines, Jacques Loeb's orientation eventually led him to simpler, invertebrate organisms, in which the responses to discrete stimuli could be more easily controlled and studied in isolation from any behavioral complexity or "mental" phenomena. Initially, this led him to work on the perception of light (heliotropism) in fly larvae and gravity (geotropism) in the cockroach, from which he extrapolated to higher animals and humans the idea that such simple tropic responses could account for many, apparently more complex, perceptual phenomena (Loeb, 1888a, 1888b). In a more extensive study of the caterpillar *Porthesia*, he concluded that three tropisms (helio-, geo-, and contact irritability) accounted for the majority of the animals' behavior (Loeb, 1890). Ten years later, he summarized his theory as follows:

The explanation of [these tropisms] depends first on the specific irritability of certain elements of the body surface, and, second, upon the relations of symmetry of the body....These circumstances force an animal to orient itself toward a source of stimulation in such a way that symmetrical points on the surface of the body are stimulated equally. In this way the animals are led without will of their own toward the source of stimulus or away from it. (Loeb, 1900)

Tropisms and instincts, which accounted for much of an animal's behavior, were simply combinations of reflexes. Any phenomena not categorizable as tropisms could be attributed to associative memory:

[There are] two following peculiarities of our central nervous system: First, that processes which occur there leave an impression or trace by which they can be reproduced even under different circumstances than those under which they originated ... second ... that two processes which occur simultaneously or in quick succession will leave traces which fuse together, so that if later one of the processes is repeated, the other will necessarily be repeated also. (Loeb, 1900)

And associative memory took care of any "higher functions:"

I think it can be shown that what the metaphysician calls consciousness are phenomena determined by the mechanism of associative memory ... I think that we are justified in substituting the term activity of associative memory for the phrase consciousness used by the metaphysicians ... We will then consider the extent of associative memory in

the animal kingdom instead of the extent of consciousness among animals ... For the present, we can say that if any animal can learn, that is, if it can be trained to react in a desired way upon certain stimuli (signs), it must possess associative memory. (Loeb, 1900)

American biologists were well primed to receive Loeb's work and thought favorably. Most of them had, in fact, been trained in Germany as chemists, physiologists, or embryologists, and were trying hard at that time to follow the German university model for the conduct of science. As Loeb's reputation grew, he was sought after by aspiring American academic institutions. After a short sojourn at Bryn Mawr College, an institution in the vanguard of recruiting the new breed of scientist in America, in 1892 he went to the University of Chicago, one of the most innovative of the new-style American universities.

While on the faculty in Chicago, Loeb had a profound influence on a young graduate student, John B. Watson (Buckley, 1989; Pauly, 1987). The origins of many of Watson's behaviorist views (Watson, 1913) can be traced to Loeb's influence and writings. But Loeb influenced a much wider audience than just his university students. He became a scientific celebrity after his successful achievement of parthenogenesis in the laboratory, a foreshadowing of today's preoccupation with genetic engineering and cloning, and this afforded him a platform to a popular audience. This accomplishment reinforced Loeb's belief that all of life's processes would eventually be explicable in terms of chemistry and physics. Parethenogenesis made Loeb into one of the first scientist/celebrities in American culture, and in articles for popular magazines such as *McClure's*, he disseminated his ideas and asserted that human capabilities differed from animal tropisms in degree only (Snyder, 1902). After moving to The Rockefeller Institute in 1910, where he became a central figure in that institution's rise to preeminence in American science, he wrote a popular book, *The Mechanistic Conception of Life* (1912), placing his research findings firmly in the context of the worldview expressed in its title and spreading that message to a wide audience.

Loeb's influence on 20th century science was deep and lasting. He was the prophet of what became its dominant scientific ideology and directly influenced such pioneering figures in the triumph of that ideology as the geneticists Thomas Hunt Morgan and Hermann J. Muller, the cell biologist E.B. Wilson, and the biochemist John H. Northrop. Most striking of all, his impact on J.B. Watson and William J. Crozier set the tone and the agenda for the behaviorist perspective in psychology (Pauly, 1987). Crozier was B.F. Skinner's mentor at Harvard, and Skinner acknowledged the importance of Loeb's books in his own development (Skinner, 1976). Even Pavlov acknowledged Loeb's influence in the first of his "Lectures on the Work of the Cerebral Hemisphere," citing his concepts of associative memory and animal tropisms (Pavlov, 1924).

Loeb's legacy for the study of consciousness is his outright denial of its relevance and his contention that no explanation is required, beyond that of reflexes, tropisms, and and associative memory. He proselytized that there was a simple, mechanistic explanation for every aspect of living things. When this view was combined with Pavlov's mechanism for associative memory, to which Loeb attributed all of our higher order mental functions, there was no further need to consider consciousness as anything other than an illusion or epiphenomenon.

3. I.P. Pavlov and the theory of "conditional reflexes"

The Russian born physiologist and psychologist Ivan P. Pavlov (1849–1936) was, like Loeb, another disciple of the 19th century German physiological reductionists. Pavlov was awarded one of the first Nobel prizes (1904) in recognition of his pioneering work on the physiology of digestion and its associated pancreatic and gastric secretions (Pavlov, 1897). It was during subsequent studies of salivation, and their differences from pancreatic and gastic secretions in his now immortalized canine subjects—Bierka, Milkah, Ikar, Umnitza, Visgun, Zlodey, Pingiel, Rijiy, Gryzun, Arleekin, Ruslan, Chingis Kahn, Murashka, and 37 others (see Tully, 2003)—that he stumbled upon the phenomenon of the "conditional reflex" (Pavlov, 1927).

Beginning in 1894, Pavlov described the digestive system as a "chemical factory." For him, the digestive glands responded purposefully, precisely, and regularly to different foods, producing secretions of the necessary quantity and proteolytic power for optimal digestion of an ingested foodstuff (Pavlov, 1897; Todes, 1997).

This digestive machine, however, was inhabited by a "ghost"—by the psyche and its capricious, highly individualized manifestations in the secretory responses of laboratory dogs. Pavlov emphasized that in salivation "the participation of the psyche emerges clearly, so psychology almost entirely overshadows physiology." This "dominance of psychology" was clear from "the fact that appropriate types of saliva are secreted both when a tested substance is put into the mouth and when it is only used to tease the dog" (Pavlov, 1897). The qualities of this "mind," however, presented an obstacle to Pavlov's standardized investigatory path. Previously, he had recognized the importance of the psyche but had treated it as a blackbox (Todes, 1997).

The way out of this conundrum, one that brought the phenomena back into the realm of reductionist physiology, came from one of Pavlov's students, A.T. Snarskii. Drawing on physiologists and psychologists who had addressed the problem of "purposeful behavior" in animals, including Jacques Loeb, Wilhelm Wundt, William James and I.M. Sechenov, Snarskii (1901) asserted that "psychic secretion" reflected not high-level processes such as will, choice, and judgment, but rather the relatively low-level "habitual" process of "visual associations ... that united new impressions with preceding ones: elementary memory" (Todes, 1997). Morever, "...this act is accomplished entirely stereotypically, automatically, through a well-trod path. The consciousness of the dog plays no 'important' role; it 'chooses' nothing and in itself does not 'determine' the activity of the salivary glands" (Snarskii, 1901; Todes, 1997).

Another of Pavlov's students, I.F. Tolchinov, then "...proposed that the phenomena of salivation during irritation of the dogs at a distance by foodstuffs be considered a reflex at a distance, which was accepted by Professor I.P. Pavlov, who termed it a conditional reflex, as distinct from the unconditional reflex received when the mucous membrane of the roof of the mouth is irritated directly by edible and inedible substances." (Todes, 1997; Tolochinov, 1912). By 1903, Pavlov was reporting these findings at international conferences and by 1907 had converted his entire laboratory to the study of conditional reflexes (Todes, 1997).

Within a decade, Pavlov had developed this perspective into an entire world view. Tasting, smelling, and eating was the 'food reflex,' fear a 'defensive reflex,' and submissiveness the 'slavery reflex.' He went on to propose a "freedom reflex," a 'reflex of religion,' an 'investigatory reflex' as shown by exploration and curiosity, a 'self-defence' reflex, and a 'reflex of purpose.'

'All life, all its improvements and progress, all its culture are effected through the reflex of purpose, are realized only by those who strive to put into life a purpose. '... the comforts of life (the aim of practical people), right laws (aspired to by statesmen), knowledge (the goal of educated people), discoveries (the treasures of scientists), virtues (the ideal of righteous people), etc.' (Pavlov, 1927)

Even '...the tragedy of the suicide lies in the fact that he has an inhibition, as we physiologists would call it, of the reflex of purpose...' (Pavlov, 1927)

Enormous international acclaim greeted Pavlov's reports on conditional reflexes. Prominent philosophers like Bertrand Russell took his claims seriously. Paul de Kruif called him 'The Liberator of Mankind... the Pasteur of the human brain and heart... Russian Saint of Science... this grey-bearded old Light of the North has discovered the way not to change human nature but to alter the human heart through the human brain.' L.A. Andreyev celebrated him as 'The Great Teacher and Master of Science' (Andreyev, 1937), and Gantt, Pavlov's translator, wrote that 'Pavlov's [method] will permanently elevate him among the Great Scientists.' Pavlov seemed to provide the scientific key for a new, socialist utopia and despite his unceasing criticism of the Soviet government, he received more lavish support from Lenin than he had ever received from the Tsarist government (Todes, 2000).

Nor was the utopian vision simply a characteristic of Pavlov's followers. As he himself explained, "Our work will result in the success of eugenics—the science of the development of an improved human type...with the most perfected nervous system..." (Todes, 2000). In line with this viewpoint, Pavlov's attributions of any and all psychological states to conditional reflexes has much in common with the eugenicist Charles Davenport's wholesale explanation of human behavior in terms of a gene for pauperism, a gene for shiftlessness, a gene for alcoholism, a gene for feeble-mindedness, and so on (Cravens, 1978; Davenport, 1911). Both perspectives offer a unitary, explanation for the complexities of human behavior.

Pavlov's findings began to be disseminated in England in 1906 when he delivered the Huxley Lecture (Pavlov, 1906). His message was taken up avidly by Jacques Loeb in America, who saw the findings as confirmation of his view that behavior in higher animals and humans was not fundamentally different from that in lower organisms:

The manifestations of associative memory are generally discussed by the introspective psychologists, who as a rule are not familiar with or do not appreciate the methods of the physicist. There have been made repeated attempts to develop methods for the analysis of associative memory, among which thus far only one satisfies the demands of quantitative science, namely Pawlow's method....[The] influence of an associative memory image is as exactly measurable as, e.g., the direct illumination of the eye; and moreover that what we call a memory image is not a 'spiritual' but a physical agency....[An] enlargement of the tropism theory might include human conduct also if we realize that certain memory images may exercise as definite an orienting influence as, e.g., moving retina images or sex hormones. (Loeb, 1918)

Early on in the formulation of behaviorism, J.B. Watson (Loeb's former student, see above) took up "conditioned-reflex" experiments in his own laboratory at Johns Hopkins University (Buckley, 1989), and thereafter actively promoted Pavlov's universal reflex explanation in the

West (Russell, 1921; Skinner, 1976; Watson, 1916, 1925). For the young B.F. Skinner, Pavlov was not just an influence, but his hero, as well as the most cited author in Skinner's (1938) *The Behavior of Organisms* (Catania & Laties, 1999).

Pavlov did not reject consciousness as completely as Watson and Skinner. But he set the tone. And like Loeb, Watson, and Skinner, his ideas were disseminated at least as much through the popular media as through scientific publications. In the decades after 1900 the goal of reducing all behavior to reflexes became popular in the United States and Britain among social reformers, journalists, philosophers, and radical behaviorists. Many physiologists and psychologists remained skeptical; but their voices were not heard by the public (Baars, 1986, 2003).

The reflex hypothesis encountered a crisis when an article appeared in 1930 by Karl Lashley, who began as a student of J.B. Watson's. Lashley argued that while reflex pathways could explain some spinal mechanisms, they failed to account for basic facts about the brain. "...[In] the study of cerebral functions we seem to have reached a point where the reflex theory is no longer profitable. And if it is not serviceable here, it can scarcely be of greater value for an understanding of the phenomena of behavior..." (Lashley, 1930). There was no evidence for stereotyped reflexive responses in animals with intact brains.

Lashley's article was widely read, and his evidence undisputed, yet the hypothesis was not abandoned by behaviorists; it merely assumed a new guise. Under the influence of B.F. Skinner, all behavior was taken to involve 'stimulus—response contingencies' without evidence for a physiological reflex (Skinner, 1931, 1953, 1976). Skinner thereby saved the behaviorist movement.

Like Pavlov and Watson, Skinner claimed that his ideas applied to all animals and humans without testing them in natural situations. Much later, when Breland and Breland (1961) conducted operant (Skinnerian) training in 38 different species, they found numerous limits on the method, and intrusions of untrained actions. In nature, such 'unconditioned' behavior is likely to be much greater.

Pavlov's influence on the 20th century was even greater than that of Loeb. Loeb may have inspired the ideological bent and style of modern biology, but Pavlov provided the rationale and a pseudo-mechanistic explanation to account for mental activity.

4. Sherrington's inconsistencies with the Loebian/Pavlovian view

Sir Charles Sherrington, one of the most distinguished physiologists of the time, took a very different tack from Pavlov. Sherrington was a pioneering student of reflex actions. His classic work *The Integrative Action of the Nervous System* (1906) came out only two years after Pavlov's work was first published in the West. It presents numerous experiments on reflexes.

Sherrington was critical of Descartes' mechanistic idea that

Cat, dog, horse, etc. were trigger-puppets which events in the circumambient universe touched off into doing what they do. It lets us feel that Descartes can never have kept an animal pet.

Sherrington and others demonstrated that simple reflexes can be seen mainly when the spinal cord is isolated from the cortex. Under those conditions animals actually become "trigger puppets."

Experiment to-day does, however, put within reach of the observer a puppet-animal which conforms largely with Descartes' assumptions. (The cerebral cortex) can be removed under anaesthesia, and on the narcosis passing off the animal is found to be a Cartesian puppet: It can execute certain acts but is devoid of mind. Thoughts, feeling, memory, perceptions, conations (voluntary actions), etc.; of these no evidence is forthcoming."

"Thus, the (spinal) cat set upright on a 'floor' moving backward under its feet walks, runs or gallops according to the speed given to the floorway. In the dog a feeble electric current on the shoulder brings the hind paw of that side to the place, and performs a rhythmic grooming of the hairy coat there. If a foot tread on a thorn that foot is held up from the ground while the other legs limp away. Milk placed in the mouth is swallowed; acid solution is rejected. The dog shakes its coat dry after immersion in water.

Yet spinal reflexes are impoverished:

But when all is said, if we compare such a list (of spinal reflexes) with the range of situations to which the normal dog or cat reacts appropriately, it is extremely poverty stricken. It contains no social reactions, it fails to recognize food as food: It shows no memory, it cannot be trained or learn: it cannot be taught its name. The mindless body reacts with the fatality of a penny-in-the-slot machine. (p. xii)

To Sherrington, reflexes showed one level of integration. But they also raised the question of a higher level: What is it that the brain does to guide and organize spinal activities?

In healthy animals reflexes are subordinate to the conscious and voluntary control of the cerebral cortex. That is where goal-directed action is organized, where food and danger are recognized, social action is directed, and competing sensations are unified. A striking example Sherrington explored was the unitary perception of the world when two different images are presented to the two eyes. In recent years this has proved to be one of the most productive methods for studying visual consciousness (e.g., Logothetis & Schall, 1989).

In physiology Sherrington was as prominent as Pavlov. He received a Nobel Prize and coined basic terms like "neuron" and "synapse." But he did not make utopian claims, he was not famous to the general public, and Pavlovians ignored him.

5. Lashley's evidence against brain reflexes

Karl Lashley began as a student of John B. Watson, the first famous radical behaviorist in psychology. In a 1923 paper Lashley noted with approval how behaviorism was "spreading like wildfire." Seven years later, in a classic article, he has changed his mind. While reflex pathways could account for some spinal mechanisms, they failed to explain basic facts about the brain. He wrote,

The notion of the reflex arc was developed in studies of spinal preparations (animals whose brains were disconnected from their spinal cords). Under these simple conditions something like a point for point correspondence between receptor cells and muscle groups could be demonstrated, as in the case of the scratch reflex."

However, "in the study of cerebral functions we seem to have reached a point where the reflex theory is no longer profitable. *And if it is not serviceable here, it can scarcely be of greater value for an understanding of the phenomena of behavior.* (Lashley, 1930, p. 12) (italics added)

The reason for the last point is, of course, that normal behavior always involves the brain. Lashley's critique was therefore not just physiological, but psychological as well.

Lashley presented three arguments against a reflex explanation. First, there simply was no evidence for reflex pathways in the cortex.

An essential element to the reflex theory is the doctrine that all the effects of stimulation are immediately observable in the motor systems. But there is certainly no direct evidence for the existence of any sharply defined reflex paths whose interruption results in the loss of isolated elementary functions. (p. 10)

Thus cerebral cortex is fundamentally different from the spinal cord.

Second, there was no evidence for stereotyped sensory input. In contrast to isolated reflexes, a large class of sensory stimuli were effectively equivalent.

We have a situation where a habit is formed by the activation of one set of receptors and executed immediately upon stimulation of an entirely different and unpracticed group. The equivalence of stimuli is not due to the excitation of common nervous elements.

Finally, there was no evidence for stereotyped reflex-like responses. Instead, habits showed motor equivalence: A maze could be run in many different ways.

Turning to motor activity, we are confronted by an identical problem. If we train an animal in a maze we find little identity of movement in successive trials. He gallops through in one trial, in another shuffles along, sniffing at the cover of the box. *If we injure his cerebellum, he may roll through the maze.* (italics added)

It is as if the maze-trained animal has access to a vast range of actions that will get it to the goal, even when the brain's motor control has been severely damaged.

He follows the correct path with every variety of twist and posture, so that we cannot identify a single movement as characteristic of the habit. I have earlier reported cases of motor habits of limbs which were paralyzed throughout training and whose motor paths consequently could not have been exercised during training...

The same points applied all the way from birds to humans.

Activities ranging from the building of characteristic nests by birds to the activities of man show the absence of stereotyped movements in the attainment of a predetermined goal. (pp. 6–7)

Thus any single goal can be achieved in many different ways, across a vast range of species. This viewpoint finds its present day counterpart in the concept of "degeneracy" (Edelman & Gally, 2001).

In sum, Lashley found no rigid reflex-like sensory or motor functions in the cortex, and no simple reflex pathways. He thought that Pavlov's universal reflex hypothesis did not hold up.

Yet this apparent falsification did little to impede the Pavlovian program in brain physiology.

6. Reductionism and the modern world

One hundred years have passed since Loeb's and Pavlov's seminal writings on behavior. During much of that time, behaviorism reigned supreme in psychology and explanatory reductionism inspired the life sciences to produce the staggering advances in biochemistry, genetics, cell biology, developmental biology, and neurobiology that dominate today's scientific landscape. These movements were a driving force in the application of serious scientific methods to the study of biological and psychological problems that had seemed unapproachable before. In that respect, it represented an important, progressive force. In other respects, it went too far—as in the banishment of consciousness from science. But all things must end, whether good or bad, and behaviorism began to give way in the final decades of the 20th century (Baars, 1986, 2003).

Explanatory reductionism, on the other hand, still reigns supreme in biology, neurobiology, and in much of cognitive science. Its strength has come from the strategy of isolating component parts of a process and characterizing the function of those parts in detail. In neuroscience, this has often taken the form of decomposition and localization of processes (Bechtel & Richardson, 1993; Finger, 1994). Now, however, this strategy is starting to show signs of strain around the edges. It is weak when it comes to supplying explanations for the behavior of large numbers of elements at higher levels of organization. This difficulty applies to many biological problems that involve numerous components interacting as a system, as in metabolic networks, gene networks, cellular organization, and systems level activities in the brain. The problem reaches its pinnacle with attempts to provide a mechanistic explanation for consciousness (Baars, 1996; Crick, 1995; Edelman, 1989; Edelman & Tononi, 2000; Koch, 2004).

We are now approaching the limits of the classical strategy of decomposition and localization. In all of the areas where it has been so effective—genetics, cell biology, and neurobiology—it is becoming clear that mere identification and functional characterization of component parts does not account adequately for higher level phenomena—the parts do not add up in a simple way to give the whole. Systems level explanations for these higher level phenomena are, however, both possible and achievable. But they require something more than the simple reductionism that dominated the last century. New ways of thinking are needed to grapple with the issues of complexity, parallel processes, and emergent properties in biological networks.

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