Evolution of neuroarchitecture, multi-level analyses and calibrative reductionism

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Evolution has sculpted the incredibly complex human nervous system, among the most complex functions of which extend beyond the individual to an intricate social structure. Although these functions are deterministic, those determinants are legion, heavily interacting and dependent on a specific evolutionary trajectory. That trajectory was directed by the adaptive significance of quasi-random genetic variations, but was also influenced by chance and caprice. With a different evolutionary pathway, the same neural elements could subserve functions distinctly different from what they do in extant human brains. Consequently, the properties of higher level neural networks cannot be derived readily from the properties of the lower level constituent elements, without studying these elements in the aggregate. Thus, a multi-level approach to integrative neuroscience may offer an optimal strategy. Moreover, the process of calibrative reductionism, by which concepts and understandings from one level of organization or analysis can mutually inform and ‘calibrate’ those from other levels (both higher and lower), may represent a viable approach to the application of reductionism in science. This is especially relevant in social neuroscience, where the basic subject matter of interest is defined by interacting organisms across diverse environments.

Keywords: calibrative reductionism; emergence; complexity; nervous system; evolution; social neuroscience

1. INTRODUCTION

There has been an historical bias among many scientists and intellectuals, partly because of disciplinary boundaries, that humans can be understood as isolated, individual information-processing systems. Humans are a fundamentally social species, however, and by definition, social species create emergent organizations beyond the individual—structures ranging from dyads and families to groups and cultures. These emergent social structures evolved hand in hand with neural, hormonal, cellular and genetic mechanisms to support them because the consequent social behaviours helped organisms survive, reproduce and care for offspring sufficiently long that they too reproduced, thereby ensuring their genetic legacy. The profound influence of the social environment on neurobiological structure and function has led some to consider the central nervous system of social mammals, especially of humans, as a social brain [1–3]. Although social psychologists have a long history of the study of social processes apart from its biological origins and mechanisms, with the recent explosion of developments in the neurosciences, it is now clear that the biological perspective can not only inform social systems, but also may be necessary for a comprehensive understanding of social processes. This raises the critical issue as to how we are to understand the relations between social and biological processes. A neurological account may provide a sufficient explanation for simple reflexes. The complexities associated with navigating social systems in primates, however, have led to the evolutionary development of some of the most complex networks of the brain [1,2], entailing multiple interacting circuits. Although social processes arise from the operations of brain circuits, the complexity of these networks has thus far precluded a clear mapping between social and neurological processes. Moreover, with this complexity may come emergent properties of systems that are not

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One contribution of 15 to a Theme Issue ‘Top-down causation’.
readily derivable from the underlying biological components. The issues of complexity, emergence and reductionism are relevant to all systems and sciences [4], of course, but become especially acute with increasing complexity and interaction, as is the case for the highest-level social functions of the brain and the emerging discipline of social neuroscience [5]. In the present paper, we outline an approach to multi-level analysis and calibrative reductionism, whereby observations, knowledge and concepts of higher (e.g. social behavioural) and lower (e.g. physiological) levels of analysis can mutually inform and calibrate those of other levels.

Evolution has firmly planted sociality, emotionality and meaning making in our genome. An early view was that our genotype (or the pattern of gene encoding in DNA) is the ultimate, bottom-up determinant of our phenotype—the characteristic expression of genetic information into physical, psychological and behavioural manifestations [6]. But it is now apparent that this bottom-up model may be overly simplistic. Noble [7, p. 3001] asserts:

Relating genotypes to phenotypes is problematic not only owing to the extreme complexity of the interactions between genes, proteins and high-level physiological functions but also because the paradigms for genetic causality in biological systems are seriously confused.

It is now clear that the phenotype derives from an interaction between the genotype and the environment and that the environment and the phenotype, in a top-down fashion, can regulate the genotype [7,8]. Epigenetic reprogramming of the genome and its expression in neurons (via methylation of DNA among other means) occurs during development in an environmentally dependent fashion [8,9]. In addition to DNA methylation, the epigenome (the chromatin-based chemical environment of the DNA) can regulate gene expression by altering accessibility of the essential transcriptional machinery [8]. This top-down regulation of the genome belies simple bottom-up models of causality and illustrates the complexity of biological systems—of particular note, the human brain. The implication of these and related studies is that aspects of genetic expression, which were thought to be encapsulated within each living cell far from the reach of personal ties or social influences, are in fact subject to modulation by the social environment [10]. This complexity poses challenges for how we are to understand neuro-psychological processes and even what a fundamental understanding of these processes would look like and how it should be pursued.

Central to this effort will be mereological understandings of the relations of the parts to the whole and the interactions among systems and levels of organization. Contemporary developments in neuroscience and psychology are beginning to shed light on the general organizational and functional features of neural architecture that inform neuropsychological relationships. We will explore the evolutionary development of the nervous system and its implications for epistemological approaches to neuroscience. We will also articulate the construct of calibrative reductionism, which offers a conceptual framework for organizing knowledge and pursuing programmatic transdisciplinary, multi-level neuroscientific research. This approach is consistent with the multi-level integrative mechanistic view of Craver and colleagues [11,12], and focuses on the evolutionary origin of multi-level processes and pragmatic implications for scientists.

2. MEREOLOGICAL CONSIDERATIONS AND REDUCTIONISM

The observation that novel properties of aggregates may emerge from the combinatorial structure of the constituent elements has long been posed as an argument against some forms of reductionism. Illustrations of these complexities abound. The neuropeptide oxytocin, for example, has recently received much attention for its role in pair-bonding, trust and social relations. Oxytocin was first isolated and synthesized by Vincent du Vigneaud (Cornell Medical College, 1953), for which he received the Nobel Prize for Chemistry in 1955. Oxytocin is relatively simple, as biomolecules go, consisting of a sequence of nine amino acids (cysteine–tyrosine–isoleucine–glutamine–asparagine–cysteine–proline–leucine–glycine). Each of these amino acids is composed of various combinations of precisely the same atomic elements (carbon, hydrogen, oxygen and nitrogen), with the exception of cysteine, which also has a sulphur atom. What differentiates the rest of these amino acids, then, is not the constituent elements, but the combinatorial organization of those elements (see also [13,14]). Indeed, two of them (leucine and isoleucine) have the exact same chemical composition (C9H19NO2), differing only in how the elements are bound together (the location of the methyl group; figure 1). This story replays itself at a more macro level.

As illustrated in figure 2, oxytocin contains both isoleucine and leucine. Although these two amino acids are composed of the exact same elements, switching the locations of these amino acids within the oxytocin molecule reduces the biological activity by over 90 per cent. Other distinct combinations of carbon, hydrogen, oxygen and nitrogen comprise two additional amino acids, phenylalanine and arginine. If these two amino acids are substituted, respectively, for isoleucine and
leucine in the oxytocin molecule (figure 2), there results a different hormone, vasopressin, with totally distinct properties and actions (antidiuretic and vasopressor). Again, the functional impact of these hormones is defined not simply by the constituent atomic elements, but by how those elements are combined into amino acids, and in turn by how those amino acids are sequenced into protein. One might argue that this is just another example of classical chemistry, but it is not. Even with the understanding of peptide biochemistry and the knowledge that oxytocin can have powerful effects on social processes, it remains the case that there is nothing intrinsically social about oxytocin. There is no inherent coding of social information or disposition in the molecule—no proper social characteristic. There is nothing in the basic chemistry of oxytocin or its constituent elements that could, in an obligatory fashion, predict its role in social processes. In the absence of a critical receptor molecule, it is just another sequence of amino acids. Although peptide chemistry has been with us since amino acids first formed, the social role of oxytocin did not exist prior to the evolutionary sculpting of the vertebrate brain. With a slightly different evolutionary trajectory, however, the situation might be quite different. We will return to this point later.

Again, there is nothing inherently socio-functional about the oxytocin molecule. Its socio-biological properties could not be derived from or related to the properties of its constituent elements studied in isolation. Rather, those properties are revealed only by studying this molecule in its biological and environmental context. It becomes endowed with its social power only by virtue of its ability to interact with another protein, the oxytocin receptor, and the cascade of neural sequelae triggered thereby. Indeed, recent evidence suggests that single nucleotide polymorphisms in the gene specifying the oxytocin receptor may alter these functions and dispose towards outcomes as diverse as diminished empathy and autism [15,16]. Even with the obligatory receptor interaction, however, one might still argue that this is simply peptide chemistry. Complex chemistry perhaps—but chemistry nonetheless. But there is another evolutionary contribution that goes well beyond peptide chemistry—that is, the location of the oxytocin receptor within the brain and the specific neurons that bear this receptor. Research on voles, sometimes referred to as field mice, illustrate the importance of this localization. The prairie vole is monogamous, displaying prolonged pair-bonding. This pair-bonding is attributable to the evolutionary development of an oxytocinergic neural system within the brain, including a critical brain structure (the nucleus accumbens) that underlies pleasure and reward [17]. Evolution took a slightly different turn for the closely related montane vole, a polygamous animal that does not pair bond. Although the montane vole also has oxytocin receptors in the brain, they are less expressed in the nucleus accumbens [18]. The role of oxytocin in social processes is not dictated by peptide chemistry, and no amount of knowledge about basic peptide chemistry could predict this role, in the absence of knowledge about higher level neural circuits and their evolutionary exigencies. The role of oxytocin in social processes is an emergent property of interactions in complex systems, at least from an epistemological perspective. While it might be argued that the social effects of oxytocin are indeed properties of the constituent elements of the relevant molecules (oxytocin and its receptor), the fact remains that those properties could only be known by studies at a higher level of organization and analysis as well as a social neuroscientific perspective.

In sum, constituent elements may be crucial to the properties of aggregates, but the properties of aggregates cannot always be readily determined from the proper features of the elements studied in isolation. Ontological reductionism holds that there are properties, features and combinatorial rules of the elements that give rise to the properties of the aggregates. But certain aspects of these elements may be knowable only by studying the aggregates and elements in a multi-level integrative fashion [5]. This would pose an epistemological problem for ontological reductionism. We will return below to an alternative and perhaps more useful reductionist model.
3. NEUROEVOLUTION AND NEURAL HETERARCHIES

3.1. Evolution and re-representation of function

Man with all his noble qualities still bears in his bodily frame the indelible stamp of his lowly origin.

Darwin [19]

In his essay ‘Evolution and dissolution of the nervous system’, the noted nineteenth century neurologist John Hughlings Jackson emphasized a multi-level perspective on brain organization and function [20]. Jackson noted that evolution results in a progressive anatomical layering of functional levels within the neuraxis, yielding what he termed a re-representation of function throughout the neuraxis, from the spinal cord to the highest cortical levels. Although higher levels are characterized by elaborated networks with progressively greater flexibility and functional sophistication, these higher levels do not come to replace the lower representations. Indeed, higher systems critically depend on lower substrates for information inputs, pre-processing computations and for achieving motor outputs in a hierarchical-like fashion (figure 3a). There is now ample documentation of a hierarchical dimension of organization across the neuraxis, with relatively simple, reflex-like organizations characteristic of the lowest levels and more complex, integrative substrates featured at higher levels. The vertical gradients in figure 3 illustrate important characteristics of different levels of organization in neural hierarchies. Lower level substrates may be composed of relatively simple circuits, such as the monosynaptic stretch reflex and the flexor (pain) withdrawal reflex. In the work for which he won the Nobel Prize for Physiology or Medicine (1932), Charles Sherrington detailed the circuitry and documented functions of spinal reflexes, which provided an adequate explanation of these lower level processes. Although reflexes can and do interact, the basic circuits are organized in parallel, with limited inputs and outputs, allowing for rapid, efficient processing. The cost of this efficiency, however, is that lower level systems have limited integrative capacity. In contrast, higher level elements receive a much broader array of inputs, requiring more substantive computational processing and integration with associative networks and executive systems for strategic responding. Because of inherent processing capacity limits, even in complex circuits, higher level systems may be subject to a processing bottleneck that necessitates a less efficient, serial mode of information processing. Additional complexities relate to the long ascending and descending pathways that have been documented across neural levels (figure 3b), an organizational pattern that has been termed heterarchical.

The heterarchical neuroarchitecture depicted in figure 3b illustrates the multiple levels of processing and the organizational continuity across levels of the brain and also captures an important distinction between levels of organization and levels of processing. Jackson’s construct of re-representation was expressed in the context of evolutionary layering of the neuraxis, and the resulting hierarchical structural organization. These levels of organization support diverse levels of computational processing. The higher levels of organization in this hierarchy are generally the most highly elaborated and support ‘higher’ or more sophisticated levels of processing. But this relationship is not one-to-one, as different levels of processing may occur within a level of organization, and different levels of (heterarchical) organization may engage in a given level of processing. Although the increasing complexities of progressively more rostral systems preclude a simple Sherringtonian-type circuit analysis of higher functions, many general principles of organization that he articulated apply broadly across levels. As with the oxytocin example, however, the progressive organizational complexity results in emerging functions extending beyond, and not readily derived from, basic principles as revealed by studies restricted to lower level substrates. Lower level organizational principles are conserved at higher levels of the neuraxis, but are elaborated and expanded at upper neuraxial levels [21]. Thus, we see greater integrative capacity, and

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Figure 3. (a) Hierarchical and (b) heterarchical structures, and the changes in functional properties across levels of organization. Lower level elements would include spinal reflexes while higher level elements would include neocortical structures such as the prefrontal cortex.
3.2. Multi-level perspectives

Explosive developments in neuroscience technologies, together with rapidly expanding information about neural processes at different scales of organization, are creating new opportunities for scientific investigations of the working human brain. Despite the increased sophistication and data yield from recent advances that make it possible to observe the operation of the brain at various levels of analysis, an atheoretical exploration alone is not likely to yield many discoveries of the working mind. It is simply too complex to understand the neural basis of specific mental processes without well-designed tasks that isolate those processes. Moreover, because of the emergent properties of complex organizations, it is unlikely that an understanding of higher level psychological processes can be satisfactorily derived from neurophysiology alone. Nor for that matter, by a restricted analysis of any single level of organization or function, whether it be psychological or neurobiological.

Some levels of analysis and description render relations more readily apparent and may be more optimal than others for characterizing specific relations. Although Beethoven’s Ninth Symphony could be described by the constituent frequencies and temporal patterns of the movement of atomic elements in the conductive medium, that would not be a short (nor particularly interesting) book. A more efficient appreciation, and one that better captures the aesthetics, would come through a description in terms of harmonics, musical style, the intent of the composer and its emotive content. Similarly, while an elegant dinner cuisine could be characterized by its chemical composition, even a chemist is more likely to use a food recipe than a chemical recipe in cooking. Because of the complexities of the phenomena and the problem of emergence, higher levels of analysis and description will be important in behavioural, cognitive and social neuroscience. At the same time, we have seen from the dead-end of behaviourism, which eschewed the contents and processes inside the ‘black box’. It was the cognitive science revolution and the subsequent rise of cognitive neuroscience that contributed to the view that psychological constructs must be tuned and evaluated by understandings of the organ that gives them rise. This is the essence of the cognitive neuroscience revolution as recognized by the presidential proclamation of the 1990s as the ‘Decade of the Brain’.

Although the understandings of brain–behaviour relations must be couched in the terms and constructs of biology, those terms and constructs will not likely be the extant biological constructs of today. Rather, biological understandings will need to be aligned and developed in the context of psychological findings (and vice versa), which will likely yield a rather different sounding biology from contemporary disciplines. Discoveries in epigenetics and their implications for understanding gene–behaviour relationships are a case in point.

Prior to the ready availability of computers in science, psychological studies were programmed by devices that implemented logic functions and other simple operations (AND/OR gates, inverters, switches, counters, timers, registers, etc.). Early versions of these devices were electromechanical, then transistor-based and ultimately implemented in integrated circuits. Because those devices had to be interconnected to be useful, programming entailed the explicit mapping of devices or functions and their interconnections. Much like Sherrington’s circuit analysis of spinal reflexes, explicit mappings—together with device rules and functions—constitute a sufficient description and accounting of the circuit processes and operations. Although brains are not like computers in many respects, a computer metaphor may be illustrative. With the development of complex computer systems, the logic-gate mentality for characterizing processes and operations is not efficient nor particularly helpful—at least for a programmer. More useful will be considerations of information flow, computational processing, decision systems, memory and constructs of that ilk. Such operations, of course, are all performed by semiconductor devices, but the low level implementations are handled by hardware and the software programming language, with its subroutines and primitives that can be called or invoked as the need arises without reference to the underlying implementations. Similarly, an efficient and meaningful description, model or theory of a complex psychological process is not likely to be cast in the terms and constructs of neurophysiology and synaptology, although those levels of analysis certainly apply. More useful theories will be based on a higher level of functional description, constrained and calibrated by knowledge of the underlying physiology. Indeed, those theories will almost surely also shape the development and refinement of physiological constructs and the way physiology is characterized.

For both the computer and the brain, reductionism may be possible, although not necessarily useful in all cases for all purposes. In fact, in some instances, it may be a clear hindrance to the extent to which eliminativist perspectives eschew studies of higher level psychological processes. In contrast, a calibrative reductionist approach may enhance knowledge and understanding of both higher level and lower level domains.

4. CALIBRATIVE REDUCTIONISM

The construct of reductionism has taken many forms, but a common feature is that higher level or otherwise
complex systems can be understood in terms of (reduced to) the properties of lower level elements of which they are composed. Reductionism as a philosophical doctrine could be considered in an abstract sense, apart from any pragmatic reference. In science, however, it represents an important perspective on the relations between domains (physical versus mental) or levels of organization (e.g., molecular, cellular, tissue, organ, organ system, individual organism, social systems). Consequently, these constructs impact broadly on how we approach science and what constitutes a scientific explanation. The issue becomes especially acute for multi-level interdisciplinary approaches in the neurosciences, which seek to integrate information across disparate levels of organization and function, and associated levels of observation and analysis [11,24]. Neuroscience refers to the collection of disciplines concerned with the structure and function of the nervous system. The topic of study is sufficiently complex that it requires disparate basic, clinical and applied disciplines to cover the terrain. Within neuroscience are cross-cutting paradigms—general perspectives that underlie a range of theories and methodologies in the field. The fulcrum for some of these perspectives rests squarely under constituent structures at different levels of organization, whereas for others it falls under the broader domain of brain functions. Illustrative of the latter is behavioural neuroscience, in which the nervous system is viewed as an organ of sensation and response. Research representing this perspective tends to focus on topics such as learning, memory, motivation and homeostasis. Cognitive neuroscience emerged as a distinct functional perspective in which the brain is viewed as an information-processing organ, with a focus on topics such as attention, perception, representations, decision-making and reasoning. Social neuroscience represents yet another broad perspective, in which the emphasis is on functions related to the association or interactions of conspecifics (imagined or real)—and on the neural and hormonal mechanisms underlying these processes.

Philosophical positions on the relation between mental processes and physical or biological processes have been diverse, ranging from immaterialism, idealism or monistic idealism [25], which asserts that there is only, or that we can only know about, our subjective mental reality to eliminative materialism [26,27], which views the mind as a mere epiphenomenon or denies the existence of mental processes (cf. [28]). Both immaterialism and eliminative materialism could be considered essential denials of the mind–body problem, whereas others have argued that it is largely a measurement problem [29]. In contrast, emergentism maintains that combinations or interactions of lower level elements can give rise to novel (emergent) features or properties that may be irreducible [30]. Emergentism, however, does not necessarily imply a lack of reducibility. In its strong form (ontological emergence), the emergent features are considered not to be inherent in the lower level elements [31], whereas epistemological emergence might only reflect the fact that those features could not be ascertained by studying the lower level elements in isolation. It could be argued that features of the elements and combinatorial rules that become apparent only with studies of the aggregates are, nonetheless, properties and features of the elements. From a scientific perspective, however, this distinction has no pragmatic impact on the pursuit of scientific knowledge. In either case, studies of higher levels of organization are necessary. Recent attempts to deal with complex biological systems emphasize multi-level mechanistic approaches to understanding brain–behaviour relationships [11,32,33]. The present approach is in keeping with these perspectives. Calibrative reductionism represents a strategy, in the face of epistemological emergentism, to facilitate the pragmatic work of science.

Eliminativism (or eliminative materialism) in its strongest form admits of no psychological reality, and advocates the abandonment of such constructs—the ultimate form of reductionism to neuroscience. One problem with this perspective is that many interesting problems, with considerable personal and societal implications, revolve around psychological processes. To ‘reduce’ these to the language and concepts of neuroscience may not adequately capture the essence of the phenomena in question. A category error is likely, as there may not be a simple one-to-one mapping across domains. The identification of the brain mechanisms underlying specific psychological processes first requires the accurate specification of those processes. Psychological scientists are the experts in this specification and in creating protocols for isolating specific psychological processes in the human brain; so psychological scientists have a central role to play in this endeavour. As with behaviourism, however, an exclusive focus on a single level of analysis may not be optimal, as it may deprive the field of important constraints on theories or concepts that can come from alternative levels of analysis. One of the original goals of the field of artificial intelligence was to elucidate potential neural implementations of intelligent systems. The field drifted away from this goal and now is represented largely by the field of robotics, a discipline that in and of itself tells us little about the brain. The emerging approaches in computational neuroscience and network modelling, however, hold promise in this regard. Understanding how networks might function, especially when constrained by knowledge of neural processes may yield the kind of multi-level perspective that truly informs mind–body relations. Terms, concepts and theories of different disciplines often develop in relative isolation. Consequently, integration of information across levels of analysis may be challenging in view of potential category errors and the misalignment of concepts. The collection and description of data from different levels of analysis are not sufficient, however. The alignment of data and concepts is critical—a task that is advanced by the study of the aggregate to determine the properties, features and combinatorial rules of the elements that give rise to the properties of the aggregates. Such integration holds great promise for understanding the relations between neural systems and psychological processes. An integrative multi-level approach may hold the greatest promise, where the concepts and theories of distinct levels are calibrated by understandings from other levels of analysis. This may permit the
observations at one level of description or analysis to be related to those of lower levels, and vice versa. Optimally, this calibration would be a reciprocal, two-way process of multi-level alignments. An example comes from the oxytocin story mentioned earlier. Historically, oxytocin was considered a peripherally acting endocrine hormone with a role in the milk let-down reflex and in parturition. It was only with studies at the behavioural level that revealed its role in social processes and social cognition, and chasing down the underlying mechanisms informed the physiological role of oxytocin in the brain as well as the role of psychological states in the regulation of oxytocin secretion. Both social psychological and neuroendocrinological constructs required modification or reciprocal ‘calibration’ based on knowledge derived from another level of analysis. Another example comes from the pharmacological literature on amphetamine. Haber & Barchas [34] investigated the effects of amphetamine on primate social behaviour. No clear pattern emerged between the drug and placebo conditions until each primate’s position in the social hierarchy was considered. When this factor was taken into account, amphetamine was found to increase dominant behaviour in primates high in the social hierarchy and to increase submissive behaviour in primates low in the social hierarchy. This illustrates how the effects of drugs on behaviour can appear unreliable until the analysis is extended across levels of organization. A strictly physiological (or social) analysis, regardless of the sophistication of the measurement technology, may not have revealed the orderly relationship that existed.

Observations at the psychological or behavioural domain constitute much of the interesting grist for neuroscience. Of course, contemporary theories regarding psychological representations and processes are approximations that continue to evolve as new empirical data, methods and models are developed, and major questions remain about these representations and processes. Neuroscience perspectives may help clarify and constrain these efforts in the psychological domain, and vice versa. As such, the pursuit of such issues will contribute not only to a better understanding of the brain mechanisms underlying these processes, but also to the evolution of sophisticated psychological theories. In contrast to eliminativism, which seeks to abandon psychological explanations, calibrative reductionism seeks to mutually relate and align psychological concepts and understandings with lower level analyses, thereby enriching both. We term this approach calibrative reductionism because the alignment of terms and constructs across levels of organization and analysis permit observations at one level to be explicated in terms of a lower level of analysis. This goal may never be fully realized, of course, but it is a goal worth striving for. This perspective is also consistent with downward causation, as the multi-level approach embraces causal relations across levels in either direction. It might be argued that there are no true mappings between psychological and neural domains or constructs—that is, the mind–body problem will remain a problem [35]. The goal of calibrative reductionism is to maximize potential mappings, however, by a mutual calibration of constructs across levels of analysis. The resulting fields of psychology and biology may not resemble what we have today. Indeed, the distinction should become increasingly blurred.

5. A BRIEF SOCIAL NEUROSCIENCE PERSPECTIVE

The methods used during the twentieth century to explore the nature of the human mind were largely insensitive to social emergent organizations and to the remarkable capacities that the evolution of the hierarchical structure of the human nervous system made possible [21,36] (see also [37]). A new approach termed social neuroscience represents a new development in which evolutionary theory, genetics and the neurosciences are all brought to bear in the study of the human mind [5] (see review by Cacioppo et al. [10]). Social species are so characterized because they form organizations that extend beyond the individual. The goal of social neuroscience is to investigate the biological mechanisms that underlie these social structures, processes and behaviour, and the influences between social and neural structures and processes. This new perspective has spawned new metaphors for the mind, as well (e.g. the Internet rather than the solitary computer). From the perspective of social neuroscience, the human brain is the organ of the mind, but understanding the mind and its capacities cannot be limited to the study of events within the cranial vault alone [10,38]. Social neuroscience is challenging because it necessitates the integration of multiple levels, as in calibrative reductionism.

A notable example of the multiple representation of function arises from the evolutionary development and elaboration of social processes. Parenting in some species may involve little more than fertilization and the laying of eggs. With the advanced brain development of mammals, and the requisite body systems for effective expressions of brain operations (advanced sensory and motor systems), a more protracted social parenting period becomes necessary for offspring to survive. The establishment of adult social groups confers survival advantage in defence against predators, acquisition of food and division of labour. At low levels of the neuraxis, one sees the representation of basic, primitive social contact mechanisms. Grasping and sucking reflexes, together with the constitutionally endowed contact comfort reactions demonstrated by Harry Harlow in early developmental studies, all serve to establish and maintain contact with and derive nutrients from the mother. Another important set of evolutionary developments are those associated with social signalling. The survival advantage from social behaviours had a causal impact on the evolution of increasingly sophisticated, genetically determined, emotional and communicative neural systems [39]. Separation distress and associated vocal signalling is an important mechanism to maintain social contact with the parent. Vocalizations in many species are likely to simply reflect internal states, rather than communicative intent, but the reflexive and motivational systems
triggered by vocal signals confer considerable adaptive advantages. Evidence indicates that non-human primate vocalization may in fact be produced with communicative intent, but it is only in humans that one sees the development and elaboration of language and the sophisticated levels of communication and social interaction it allows.

It is interesting in this regard that human social processes were once thought to have been incidental to learning and cognition, whereas the social complexities and demands of primate species are now thought to have contributed to the evolution of the neocortex and various aspects of human cognition. The social brain hypothesis posits that the social complexities and demands of primate species contributed to the rapid increase in neocortical connectivity and intelligence. Warfare among ancestral hunter–gatherers appears to have contributed to group selection for human social behaviors, especially altruistic behaviors. Moreover, deducing better ways to find food, avoid perils and navigate territories has adaptive value for large mammals, but the complexities of these ecological demands are no match for the complexities of social living (especially in hostile between-group social environments), which include; recognizing ingroup and outgroup members; learning by social observation; recognizing the shifting status of friends and foes; anticipating and coordinating efforts between two or more individuals; using language to communicate, reason, teach and deceive others; orchestrating relationships, ranging from pair bonds and families to friends, bands and coalitions; navigating complex social hierarchies, social norms and cultural developments; subjugating self-interests to the interests of the pair bond or social group in exchange for the possibility of long-term benefits for oneself or one’s group; recruiting support to sanction individuals who violate group norms; and doing all this across time frames that stretch from the distant past to multiple possible future. Consistent with this reasoning, human toddlers and chimpanzees have similar cognitive skills for engaging the physical world but toddlers have more sophisticated cognitive skills than chimpanzees for engaging the social world; cross-species comparisons have revealed that the evolution of large and metabolically expensive brains is more closely associated with social than ecological demands of primate species contributed to the rapid increase in neocortical connectivity and intelligence. Warfare among ancestral hunter–gatherers appears to have contributed to group selection for human social behaviors, especially altruistic behaviors. Moreover, deducing better ways to find food, avoid perils and navigate territories has adaptive value for large mammals, but the complexities of these ecological demands are no match for the complexities of social living (especially in hostile between-group social environments), which include; recognizing ingroup and outgroup members; learning by social observation; recognizing the shifting status of friends and foes; anticipating and coordinating efforts between two or more individuals; using language to communicate, reason, teach and deceive others; orchestrating relationships, ranging from pair bonds and families to friends, bands and coalitions; navigating complex social hierarchies, social norms and cultural developments; subjugating self-interests to the interests of the pair bond or social group in exchange for the possibility of long-term benefits for oneself or one’s group; recruiting support to sanction individuals who violate group norms; and doing all this across time frames that stretch from the distant past to multiple possible future. Consistent with this reasoning, human toddlers have more sophisticated cognitive skills than chimpanzees for engaging the social world; cross-species comparisons have revealed that the evolution of large and metabolically expensive brains is more closely associated with social than ecological demands of primate species contributed to the rapid increase in neocortical connectivity and intelligence.

6. CONCLUSION

In the hierarchy of levels of organization from the subatomic to the atomic to the molecular to the cellular to the tissue to the organ and to the organism, the next level concerns the relations among organisms. This is the subject matter of the field of social neuroscience, which studies among the most complex neurobehavioral processes and systems, and is a discipline that pursues multi-level research across the broadest range of levels of organization. Consequently, issues of reductionism and emergence in complex systems are particularly acute in this area. The calibrative reductionistic approach outlined earlier is consistent with epistemological emergentism, but seeks rapprochement with a reductionistic perspective via a mutual calibration of concepts and theories across higher level and lower level systems and disciplines. The ultimate understandings of social neuroscience will not likely be expressed in the language of contemporary sciences, at either a psychological or a biological level. This approach does not advocate efforts to unilaterally cast higher level phenomena in terms of extant lower level elements and processes, as the latter are necessarily suboptimal and incomplete. Rather, multi-level interdisciplinary understandings may optimally arise through a process where distinct levels of analysis reciprocally inform and calibrate knowledge and theories of the other level, which is the specific focus of the field of social neuroscience.

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