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Corticocentric myopia: old bias in new cognitive sciences

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Traditionally, the cerebral cortex is seen to have the most important role in 'higher' functions of the brain, such as cognition and behavioral regulation, whereas subcortical structures are considered to have subservient or no roles in these functions. This article highlights the conceptual bias at the root of this corticocentric view of the human brain, and emphasizes its negative implications in current practices in the cognitive neurosciences. The aim of this article is to suggest that the 'corticocentric' view of the human brain is also a myopic view because it does not let us see that the 'higher' functions of the brain might in fact depend on the integrity of its 'lower' structures.

Introduction

In discussions about the neural basis of behavioral regulation, it is widely believed that during the course of brain evolution, the frontal lobes expanded disproportionately in humans to control the activity of lower subcortical structures and suppress instinctual desires, and thereby ensure a contextually appropriate behavior [1]. According to this traditional view, in a person with dysfunctional frontal lobes, when such inhibition fails, the lower brain regions are 'released' to act in their innate way and thus a 'disinhibited' behavior is generated.

Although there is certainly no doubt about the involvement of the cerebral cortex in cognitive functions and the involvement of the frontal lobes in behavioral regulation [2], the neuroanatomical basis of these higher functions of the brain has remained largely corticocentric, and the relationship between cortical and subcortical structures has been viewed in a linear, hierarchical and cortically dominant manner.

The aim of this opinion piece is to argue that the corticocentric view of brain organization is myopic because it does not let us see that the 'higher' functions of the brain are made possible by a reciprocal interconnection between cortical and subcortical structures rather than being localized only in the upper tip of the vertical neuroaxis.

In what follows, I argue that our corticocentric perspective is not rooted in the actual pattern of relationship between cortical and subcortical structures, but in the social and cultural bias and limited methodology of 19th century science that laid a suitable foundation for such a view of the human brain. I also demonstrate how this corticocentric perspective persists despite accumulating evidence against it.

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Historical background

Charles Darwin (1809–1882) [3], in his treatise entitled '*The Expression of the Emotions in Man and Animals*', argued that there are voluntary and involuntary centers in the brain and that involuntary actions are subject to partial suppression '*through the will*' [3].

Herbert Spencer (1820–1903) [4], one of the most influential philosophers of Queen Victoria's Britain, one of the most important proponent of Social-Darwinism, and the man who coined the notion of '*the survival of the fittest*', introduced the concept of 'evolution and dissolution in societies' [4]. According to Spencer, social hierarchy was not only justifiable but also a sign of highly evolved societies and a way to prevent social dissolution. For the survival of evolved societies, Spencer argued that it was necessary to legitimize a hierarchical governing structure and a sense of self-control to avoid the 'tragedies of the Reign of Terror' sweeping across Europe, especially in post-revolutionary France [4].

The British neurologist John Hughlings-Jackson (1835–1911), whose writings laid the foundations for the interpretation of many clinical conditions and still remain influential in contemporary neurology, psychiatry and clinical psychology, was influenced by Spencer. He had studied Spencer's work extensively and was in regular correspondence with him [5]. In his own words, Spencer was a man to whom he was '*under the deepest obligations*' [6]. In parallel with Spencer's notion of evolved hierarchical societies, Hughlings-Jackson advocated that the evolved human brain must also be organized in a hierarchical manner. He argued that in the course of brain evolution, new structures are added on top of old ones, and more importantly this 'adding on' of new structures in the human brain was, at the same time, a 'keeping down' of pre-existing structures. According to him, '*the higher nervous arrangements evolved out of the lower keep down those lower [arrangements], just as a government evolved out of a nation controls as well as directs that nation* [6] (p. 662).

The Jacksonian notion of disinhibition and hierarchical organization of the brain also influenced Sigmund Freud (1856–1939), who was a clinical neurologist by training and an admirer of Hughlings-Jackson [7]. Freud used a similarly hierarchical organization for the human psyche. The *id* was a protagonist playing the part of Jacksonian 'lower' structures whereas the *super-ego* was meant to 'keep down' the desires of the *id* and inhibit them from entering into consciousness. To Freud's credit, a third party, *ego,* maintained a balance between the higher and lower parties, and a blind suppression of *id* resulted in psychopathology.

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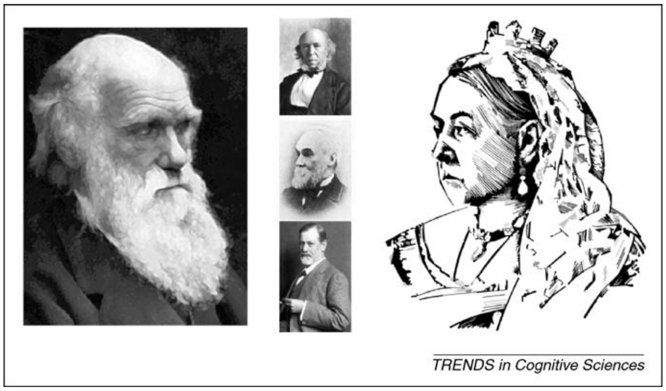

Figure 1. Social Darwinism, Victorian ethics and corticocentric myopia: the religious theme of Victorian ethics and the conceptual bias and methodological limitations of 19th century science created a suitable conceptual platform for the Social-Darwinistic ideas of Herbert Spencer to culminate in Hughlings-Jackson's writings about hierarchical organization in the brain and the dominance of the cerebral cortex over subcortical structures. Sigmund Freud sketched a similar hierarchical view of the human psyche. Queen Victoria (right); Charles Darwin (left); Herbert Spencer (top); John Hughlings-Jackson (center) and Sigmund Freud (bottom).

Spencer's Social-Darwinistic justification of hierarchies in the most evolved societies, and Hughlings-Jackson's notion of hierarchies in the most evolved brains, coincided in time with the peak of Queen Victoria's reign, during which moral views were framed in dichotomies such as good versus evil and free will versus basic instinct. In this dichotomous arrangement, based on the religious theme of Victorian ethics, the good should always dominate over the evil, and the power of free will should be able to shackle the beasts of basic instincts. According to Victorian ethics, every human being is able to inhibit sins from breaking out, that is, 'one shall do what is right' [8] (Figure 1).

It is beyond the scope of this article to provide a detailed historical analysis of the many complex facets of social life over the prolonged period of Queen Victoria's reign. Moreover, the earlier remarks are not intended to suggest that Victorian science was a blind and societally led process or that the religious theme of Victorian ethics determined the writings of Spencer or Hughlings-Jackson. Furthermore, the historical remarks are not intended to suggest that the roots of corticocentric bias were limited to the Victorian era and Britain. In fact, the roots of this bias can be traced back to pre-Victorian times and to countries outside England (see, for example, the writings of phrenologists such as Franz Joseph Gall, 1758–1828) [9]. Instead, the earlier remarks are meant to suggest that the conditions of the 19th century created a suitable ground where a hierarchical and dichotomous classification of the brain into a dominant cortex and a subservient subcortex could easily be incorporated into the influential writings of neurologists such as Hughlings-Jackson, whose writings have been represented in most textbooks of Neurology, and whose ideas continue to be influential today.

The corticocentric view of the brain was conceptualized at a time when knowledge of brain anatomy and physiology was extremely limited. Just to mention a few examples, Cajal had not yet proposed his doctrine of 'neuron'; Sherrington had not yet coined the term 'synapse'; Lewy had not discovered the Vagusstuff and neurotransmitters had not entered the vocabulary of Dale. Moreover, in the 19th century version of brain evolution, it was taken for granted that the nervous system is designed as a vertical neuroaxis with the most rostral structures being the most newly acquired ones. That is why the most rostral part of the brain was referred to as 'tele-encephalon', the region of the neuroaxis that was 'farthest' out in the evolutionary process [10]. Importantly, the frontal lobes were located at the tip of the telencephalon and thus represented the pinnacle of brain evolution. Based on the earlier work of pioneers such as Gall, Jean-Baptiste Bouillaud (1796–1881), S.A.E. Aubertin (1825–1893) and Pierre Paul Broca (1824–1880), the frontal lobes had already gained their 'frontline' status [11]. The frontal lobes were also seen as the pinnacle of the 'orthogenesis' of brain evolution – the belief that evolution has a linear and progressive pattern and the newest is the best [10]. Meanwhile, little attention was paid to the fact that several other structures of the nervous system were almost equally enlarged during the course of brain evolution: the inferior parietal lobule, the caudate nucleus of the basal ganglia, and the lateral hemispheres and dentate nucleus of the cerebellum, just to name a few. Moreover, in the 19th century, it was yet unknown that the proportional size of the frontal lobes is actually no different in humans than great apes [12].

Lastly, the relationship between the cerebral cortex and subcortical structures was defined on the basis of methodologically limited scientific observations. For instance, Charles Sherrington (1857–1952) [13] and Walter Cannon (1871–1945) [14] explored the physiological interrelationship between the cerebral cortex and subcortical structures in preparations where the spinal cord of cats was 'isolated' from the influence of the cerebral cortex. In these animals, 'decortication' or 'decerebration' invariably led to postural rigidity and hyperreflexia, and thus the findings seemed to be supportive of the Jacksonian notion that the cerebral cortex inhibits lower structures. However, in hindsight, we can see that the experiments on the functional relationship between the cortex and subcortex were primarily focused on the relationship between the cerebrum (not cerebral cortex) and the spinal cord (not subcortical structures in general). The cerebrum contains many subcortical structures such as the basal ganglia and the thalamus. The 'decortication' experiments were carried out using methods that we can now dismiss as too coarse. They simply could not allow one to deduce whether rigidity and hyperreflexia in 'decorticated' animals were only due to decortication rather than a lesion in other cerebral structures such as the basal ganglia [14].

These experiments, although futile in explaining the functional relationship between cortical and subcortical structures, led Sherrington to the discovery of inhibitory post-synaptic potential (IPSP) – taking the notion of disinhibition to a completely different level (i.e. the cellular level). Needless to say, the notion of disinhibition at the cellular level has remained undisputed and is scientifically well-grounded, but the leap from decerebrated cats to human cognition and behavior and the deduction from IPSPs at the cellular level to inhibition at the systems level remain unwarranted.

Corticocentric myopia in today's neurosciences

The text so far was intended to suggest that the notion of 'higher' versus 'lower' structures with the 'higher' inhibiting the 'lower' was based on a conceptual bias and the limitations of 19th century scientific methods, and thus seems to be outdated and problematic in its roots. In what follows, I argue that the same 19th century view of brain anatomy and function is still prevalent in today's cognitive neurosciences. More often than not, the hypotheses that are formulated or the explanations that are provided in many of the current scientific writings about human cognition and behavior still suffer from variable degrees of corticocentric myopia.

In clinical neurosciences, the problem is more prevalent than anywhere else. Inappropriate behavior in patients with neurological and psychiatric disorders is explained in the same 19th century terms: 'disinhibition' and 'release'. For instance, the phenomenon of inappropriate laughing or crying in patients with pseudobulbar affect is explained as the laughing and crying 'center' in the subcortex being disinhibited from a frontal inhibition [15] – as if the primary problem in these patients is lack of voluntary control of emotional behavior. As suggested elsewhere [16], this myopic view has prevented us from seeing the problem of pseudobulbar affect from a different perspective, namely as a condition in which the primary problem is a pathological 'generation' of a response rather than lack of voluntary 'control' to stop it once it is generated. Another example is the corticocentric bias in discussions of psychiatric problems in Huntington's disease. It has been argued that the psychiatric problems in these patients must be due to the thinning of the cortical gray matter as opposed to the pervasive degeneration of the basal ganglia [17]. The same applies to discussions of bladder dysfunction or hypertonia and hyper-reflexia in patients with spinal cord injury, all of which have been attributed to the problem of disinhibition and release (Box 1).

In non-clinical cognitive sciences, the problem of corticocentric myopia is still pervasive enough to raise concerns. Subcortical structures are rarely the focus of investigation, and if a change of activity is seen in a subcortical structure, authors might not even mention it in the discussion section of their papers (Box 2). A challenge for understanding the involvement of subcortical involvement in cognitive functions is that the majority of methods that have been developed in the last century are not suitable for the study of subcortical structures. For instance, electroencephalography or magnetoencephalography, near-infrared spectroscopy, optical imaging or transcranial magnetic stimulation cannot be used to unravel the mystery of subcortical structures even though they are very helpful tools otherwise.

Beyond myopia: the brain's actual architecture

The problem with corticocentrism is not the problem of hierarchies in the brain or the argument that cortical regions such as the frontal lobes are important for cognition and behavioral regulation even through inhibition. In fact, there is overwhelming evidence that supports these propositions (see, for example, Ref. [18]). Nor is the problem about localizing functions to cortical as opposed to subcortical structures. It would be equally troubling if we tried to localize functions to subcortical structures only. In reality, there is no cortex versus basal ganglia divide. One does not exist without the other, and there is only an interlinked network of corticostriatal loops – as many

Box 1. Corticocentrism in clinical neurosciences

The problem of increased tone (hypertonia) in patients with lesions above the spinal cord is often considered to be a prime example for cortical disinhibition. At least two lines of clinical evidence suggest that the notion of disinhibition is too simplistic to explain this clinical phenomenon. First, there is evidence that the increased muscle tone is not due to decortication, as Sherrington [13] and Cannon [14] argued, but more because of lesions along the extrapyramidal tracts originating from the basal ganglia and the brainstem (see, for example, Refs [53,54]). Second, clinicians know that acute lesions in the brain (including the frontal lobes and motor cortices) cause severe paralysis and loss, rather than an increase, of muscle tone. Only when the injury is sustained for a long time, hypertonia emerges, and more importantly, it emerges in some, but not all, muscles. Only the tone of flexors in the upper and extensors in the lower limb will be increased. With this pattern, hip and knee extensors become rigid and lock the hip and knee joints so that the affected leg becomes an extended (straightened) as a stable piece of rod to walk on. Equally interesting is the pattern of hypertonia in the affected arm. The affected arm becomes hyperflexed,that is, rotated inward (adducted) in the shoulder joint and bent (flexed) in the elbow (so that the arm is brought closer to the axis of gravity), and flexors of the wrist and fingers will turn the affected hand into a functional hook. Although hypertonia in the arm flexors ensures that a monkey can still use the affected arm to hang from a tree, hypertonia in the leg extensors ensures that a patient can still use the affected leg to walk on. As it is widely taught in medical schools, this selective pattern of hypertonia is evolutionarily advantageous: hypertonia reflects a more complex reorganization within the central nervous system (to help survival) rather than a simple release of the spinal cord from cortical inhibition.

Box 2. Corticocentric trend in current neurosciences

The following is an attempt to provide a semi-quantitative measure of the corticocentric bias in current neuroscience research. I reviewed 100 papers published in 2008 in the fields of decision-making and language (please see Supplementary Materials 1 (decision-making) and 2 (language) for detailed information on how these papers were selected). This review revealed the following trends (see Table I): (i) the cerebral cortex is the focus of the overwhelming majority of studies, and only rarely do authors focus on the role of subcortical structures in cognitive functions; (ii) ~30% of studies use methods that are solely, or mostly, designed for the study of the cerebral cortex and not suitable for the study of subcortical structures and (iii) importantly, in a large number of papers, especially in the domain of language, findings from subcortical structures were reported in tables and/or result sections of articles, but never discussed.

Table I. Degree of Corticocentrism in current Neurosciences

	Language (50 papers)	Decision making (50 papers)
Subcortex[a] could be the focus of study[b]	36/50 (72%)	35/50 (70%)
Subcortex was the focus of study	5/36 (14%)	3/35 (9%)
Subcortical findings were reported	18/36 (50%)	23/35 (66%)
and not discussed	9/18 (50%)	5/23 (22%)
and discussed	9/18 (50%)	18/23 (78%)

[a]See Figure 2 in main text for the working definition of 'subcortex'.
[b]Subcortex could not be the focus of study for those papers that employed a methodology that is not suitable for the study of subcortical structures (e.g. EEG, MEG, etc.).

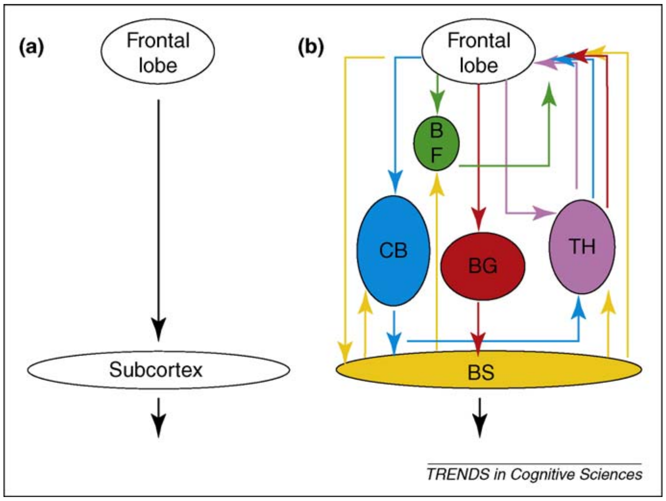

Figure 2. The cortex and subcortex: cortical and subcortical structures have traditionally been considered two dichotomous sets of structures ordered in a hierarchical relationship in which the cerebral cortex, such as the frontal lobe, dominates over subcortical structures **(a)**. Contrary to this linear and hierarchical view, the pattern of neuroanatomical connectivity in the brain suggests that there are reciprocal relationships between the frontal lobes and many subcortical structures such the basal forebrain (BF), basal ganglia (BG), the cerebellum (CB), the thalamus (TH) and the brainstem (BS) **(b)**. Many of the subcortical inputs to the frontal lobes are relayed by the thalamus, whereas projections from the brainstem monoaminergic nuclei and basal forebrain often target cortical structures directly. The function of the frontal lobes in behavioral regulation must therefore be seen in the context of its reciprocal interrelationship with many subcortical structures. Please note that 'subcortex' refers to the subcortical white matter, the basal forebrain nuclei, the basal ganglia, the diencephalic structures such as the thalamus and hypothalamus, the cerebellum and the brainstem. Not included are the claustrum and amygdala because there is evidence that, except for the central nucleus of amygdala, for the most part, these two structures stem from the same pallial progenitors as the cerebral cortex [52].

pioneering neuroscientists have already proposed (for a review see Ref. [19]).

The main problem with corticocentrism is the lack of appreciation of the reciprocal connectivity between cortical and subcortical structures. The problem is to see the relationship between cortical and subcortical structures in a one-way linear manner, and almost always in a top-down and hierarchical manner: from the cerebral cortex to the subcortex (Figure 2a). In reality, the actual pattern of connectivity between a given cortical region and subcortical structures is far more reciprocal (Figure 2b).

From a purely anatomical standpoint, it is obvious that the relationship between the cerebral cortex and subcortical structures is reciprocal rather than one-way linear. Telencephalic regions, such as the frontal lobes, are themselves under the influence of strong afferents originating from many subcortical structures. Powerful ascending pathways target cortical structures from the basal forebrain, the basal ganglia, the hypothalamus, the cerebellum and the brainstem, either directly or through the thalamus (Figure 3). In addition, the thalamus influences the operation of the cerebral cortex through mutually reciprocal loops.

Given the anatomical map of reciprocal interrelationship between subcortical and cortical structures, one might ask if the 'dominance' of the cerebral cortex over subcortical structures can ever be justified. Based on neuroanatomical data alone, one could expect that the functions of a given cortical area, such as the frontal lobe, would be severely impaired by lesions along the ascending pathways from the

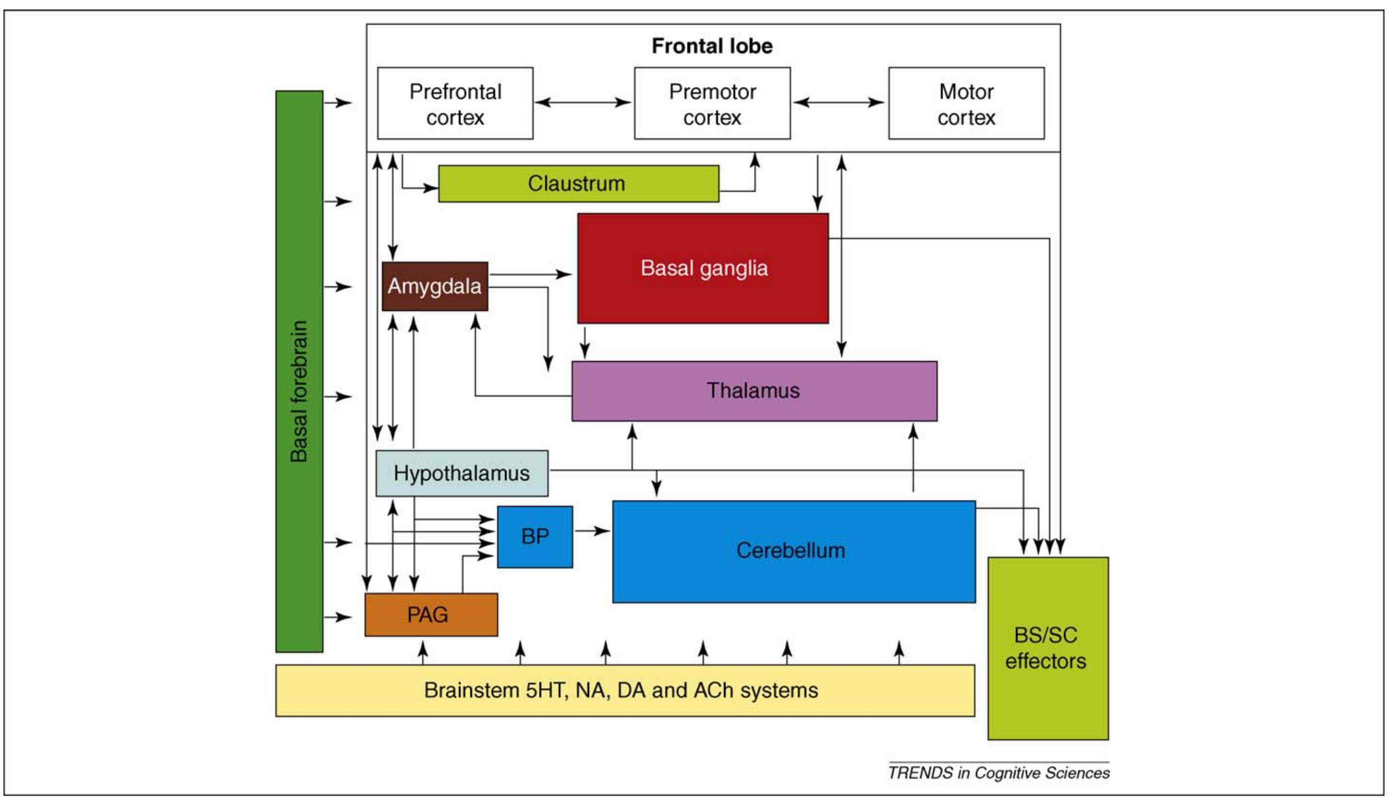

Figure 3. Beyond the cerebral cortex. Behavioral output structures in the brainstem and spinal cord (BS/SC effectors) are part of a complex system that includes the frontal lobe and many other non-cortical structures. Although the contribution of each one of these structures remains to be determined, their pattern of anatomical interconnections suggests that the role of the frontal lobes in regulating human behavior must be viewed in the context of its reciprocal relationship with many subcortical structures. Abbreviations: BP, basis pontis; PAG, periaqueductal gray; 5HT, serotonergic; NA, noradrenergic; DA, dopaminergic; Ach, cholinergic systems.

subcortical structures. In other words, the so-called 'higher' functions of the brain might in fact depend on signals from subcortical to cortical structures rather than the other way around.

In agreement with the anatomical proposal suggested earlier, a substantial number of studies in the past 30 years have highlighted the importance of the relationship between subcortical and cortical areas placing the 'higher' brain functions in the loops operating between the cortical areas and 'lower' subcortical structures such as the basal ganglia [20–31]; the basal forebrain [32–34]; the thalamus [35–38]; the cerebellum [39–43] and the brainstem dopaminergic and noradrenergic systems [43–49]. This evidence ranges from the involvement of basal ganglia structures in cognitive flexibility, language (syntax) and reward-based associative learning to the involvement of basal forebrain cholinergic systems in learning and memory and the brainstem in vigilance, attention, emotion and consciousness.

Concluding remarks

Currently we do not have sufficient knowledge about the mode of subcortical involvement in cognition and behavioral regulation. In fact, we know very little about the role of subcortical structures in these 'higher' functions, precisely because a significant proportion of current research does not see beyond the cerebral cortex. It seems as if the new cognitive sciences still suffer from the same old Victorian bias. In the 19th century era, Darwin's doctrine of evolution was incorporated into a Social-Darwinistic framework and the superiority of the most evolved cerebral cortex was seen to parallel the superiority of the fittest in hierarchical societies. In those days, humans were considered to be strictly different from animals because of their voluntary inhibition of instinctual desires by virtue of rationality and pure reason. However, the times have changed. We have recently begun to acknowledge the biological roots of our core human values, such as empathy, sense of fairness and culture, in other animals [50,51]. In the years to come, we will no longer need an artificial separation of the 'higher' from the 'lower' – we can see them together as parts of the same system because one does not exist without the other.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.tics.2009.04.008.

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