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Perspective

Cortical control of behavior and attention from an evolutionary perspective

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SUMMARY

For animals to survive, they must interact with their environment, taking in sensory information and making appropriate motor responses. Early on during vertebrate evolution, this was accomplished with neural circuits located mostly within the spinal cord and brainstem. As the cerebral cortex evolved, it provided additional and powerful advantages for assessing environmental cues and guiding appropriate responses. Importantly, the cerebral cortex was added onto an already functional nervous system. Moreover, every cortical area, including areas traditionally considered sensory, provides input to the subcortical motor structures that are bottlenecks for driving action. These facts have important ramifications for cognitive aspects of motor control. Here we consider the evolution of cortical mechanisms for attention from the perspective of having to work through these subcortical bottlenecks. From this perspective, many features of attention can be explained, including the preferential engagement of some cortical areas at the cost of disengagement from others to improve appropriate behavioral responses.

INTRODUCTION

Brain evolution is messy. It is not a process based on intelligent design but rather follows a path guided by stochastic mutation events. In this account, we focus on evolutionary constraints on the functioning of cortex. (For simplicity, when we refer to “cortex,” we mean “neocortex”; our views do not necessarily apply to paleocortex or archicortex.) Cortical evolution did not generally accompany removal of older (subcortical) circuits that had evolved to control behavior, and thus as cortex evolved, there was no evolution of a motor plant to which cortex has sole access, meaning that cortex must function through older motor control circuits, such as the midbrain and red nucleus (e.g., for access to tectospinal and rubrospinal control, among other examples). A rare exception restricted to Old World primates, including humans, is a limited direct projection from motor cortex to spinal motoneurons involved mostly in fine control of the fingers (Porter and Lemon, 1993; Lemon, 2008; Witham et al., 2016).

Here, we consider how this process constrains a number of features of cortical functioning. In particular, in our evolutionary history, many subcortical circuits evolved that served vital purposes, and even as new circuits, such as cortical ones, evolved, many and probably most of these older ones remain and continue to serve important functions. Indeed, as we emphasize below, without them, cortex would be pretty useless.

The result of these evolutionary processes is that, in its involvement in the control of behavior, cortex must interact and cooperate with these older subcortical circuits. This, in turn, leads to certain limitations in cortical functioning. One limitation relates to neuronal bases of attention. We argue here that, in addition to enhancement of corticofugal control of subcortical motor circuits from those areas involved in analyzing attended aspects of the environment (e.g., visual areas when attention is directed at visual stimuli), a major feature of attention is the suppression of such control from other areas. Because cortex must operate to control behavior via these subcortical centers, chaos would result if all cortical areas simultaneously tried to influence behavior. To avoid such chaos, a sort of filtering occurs that results in only certain areas of cortex able to dominate. This requirement of dealing with the subcortical bottleneck is what leads to appropriate areas of cortex showing enhanced corticofugal functioning, while in others, this is suppressed.

SUBCORTICAL INVOLVEMENT AND CONTROL OF BEHAVIOR

There are many examples of behaviors that do not involve cortex. Activities such as normal breathing, chewing gum, and climbing a familiar set of stairs are examples. These rely instead on central pattern generator circuits evolved at spinal and brainstem levels. (Our exposition hereafter concentrates on spinal control of body movements for simplicity, but similar arguments can be made for circuitry involved in eye, head, and neck movements.) Central pattern generators are earlier evolved spinal and brainstem circuits that subserve rhythmic behaviors such as swimming, walking, and breathing and can still function when isolated from higher control circuits residing in the brainstem and cortex. Figure 1A shows schematically how the central nervous system is arranged with regard to these central pattern generators in the lamprey, a popular animal model for studies of brain evolution that emerged more than 350 million years ago, as it is thought to have retained many of the features present

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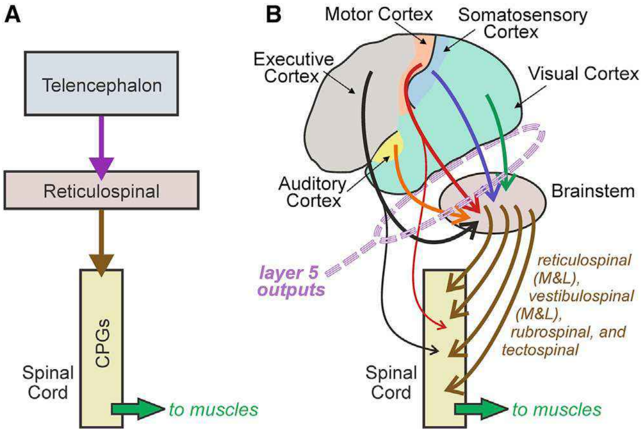

Figure 1. Schematic view of two evolutionary stages of vertebrate central nervous system

(A) Central nervous system of the lamprey, the most primitive living vertebrate and thus likely representative of early vertebrate species. Here, the central nervous system is dominated largely by limited supraspinal control of central pattern generators (CPGs; for swimming behavior, etc.). Redrawn from Grillner (2003), Stuart (2007), and Suryanarayana et al. (2017).

(B) Later mammalian evolutionary stage, showing human example. Here, cortical control of lower motor centers has evolved. Note that cortex must operate via layer 5 projections to centers evolved in (A) with additional subcortical supraspinal control centers also appearing. Many of the circuits that evolved in (A) remain functional in (B).

in the first vertebrates, which emerged about 500 million years ago (Kumar and Hedges, 1998; Grillner, 2003; Xu et al., 2016; Suryanarayana et al., 2017). Central pattern generators in the lamprey spinal cord mostly initiate rhythmic swimming movements and are controlled by descending supraspinal circuits that appear to be largely homologous to the mammalian reticulospinal pathway; these supraspinal pathways, in turn, could be controlled by descending inputs from primitive telencephalic structures.

The existence and functionality of these older circuits have been known since the pioneering work of Sherrington (1906). For example, when the spinal cord of a cat is surgically separated from descending brainstem and cortical control, the animal can exhibit coordinated limb movements (Eidelberg et al., 1980; Rossignol et al., 2000; Hultborn and Nielsen, 2007), and even when a transection is made at thoracic levels, isolating spinal control of the lower limbs, these limbs can exhibit such movements (Rossignol and Bouyer, 2004). When a cat is rendered decerebrate by a transection at brainstem levels that removes all descending cortical projections but retains brainstem inputs, the animal can exhibit even more coordinated stepping behaviors (Grillner and Wallén, 1985; Whelan, 1996; Duysens and Van de Crommert, 1998). This shows the functionality of various projections from supraspinal centers in activating relevant spinal circuitry, as the higher the brainstem transection, the more supraspinal circuitry is spared. Thus, a higher transection allows more complex behavior in the experimental animals. These examples illustrate many features of neuronal substrates of behavior that can function independently of cortical control.

Furthermore, many aspects of sensory perception also appear to function without cortex. A classic example is the Sprague effect, in which cats without visual cortex can detect and locate novel visual stimuli on the basis of functioning of the superior colliculus (Sprague, 1966). This ability to detect stimuli strictly with subcortical circuits has also been extended to the auditory and somatosensory systems (Lomber et al., 2007; Hong et al., 2018). Note that the remaining ability of experimental animals to detect stimuli after cortical removal depends on subcortical structures such as the superior colliculus, and these structures have likely been directly or indirectly deafferented by the cortical lesions, suggesting that their contribution to sensation in intact subjects may be even more significant.

The main point here is that during pre-mammalian vertebrate evolution, brainstem centers formed the capacity for quite effective sensorimotor processing, typically reaching maximum effectiveness in evolution of circuits involving midbrain structures such as the optic tectum, which is the homolog of the mammalian superior colliculus, although older and simpler telencephalic structures also exist in primitive vertebrates such as the lamprey (Herman et al., 2018; Krauzlis et al., 2018; Gharaei et al., 2020; Basso et al., 2021). Many and perhaps all of these older circuits remain viable and in use in mammalian brains. Perhaps the most obvious example is spinal circuitry, which evolved with the first vertebrates about 500 million years ago, and much of this circuitry remains intact and functional in our central nervous systems. In fact, the cortex could not operate without these older but still viable brainstem and spinal circuits.

INTEGRATION OF THE NEW CORTEX WITH THE OLD BRAIN: LAYER 5 CORTICOFUGAL PROJECTIONS

The cortex, for all of its complex circuitry and computational power, would be unable to affect behavior if not for its subcortical projections that access these older motor circuits. As noted, most of these subcortical motor targets are in the brainstem and involve centers for supraspinal control, such as the midbrain for the tectospinal tract and the red nucleus for the rubrospinal tract, but some layer 5 axons also innervate the spinal cord (Kuypers and Lawrence, 1967; Giuffrida et al., 1991; Kita and Kita, 2012; Economo et al., 2018; Prasad et al., 2020). These links between cortex and behavior involve layer 5 corticofugal projections. The only other source of subcortical projection arises from a population of layer 6 cells: some innervate thalamus and others the claustrum, but of great importance in the context of this perspective, in no case do these innervate obvious subcortical motor centers (Sherman and Guillery, 2013; Sherman, 2016; Usrey and Sherman, 2019). It is also worth noting that cells in layers 5 and 6 that project subcortically rarely project to other cortical areas, and vice versa (Petrof et al., 2012). Some further details on differences between layer 5 and 6 corticofugal projections are provided below. It is the layer 5 cells that innervate numerous subcortical motor centers (Deschênes et al., 1994; Bourassa and Deschênes, 1995; Bourassa et al., 1995; Kita and Kita, 2012; Prasad et al., 2020) and thus appear to be the effective route whereby cortex influences behavior. Figure 1 places this in an evolutionary perspective and illustrates the point that, without these layer 5 corticofugal projections, cortex would be unable to influence behavior (Figure 1B).

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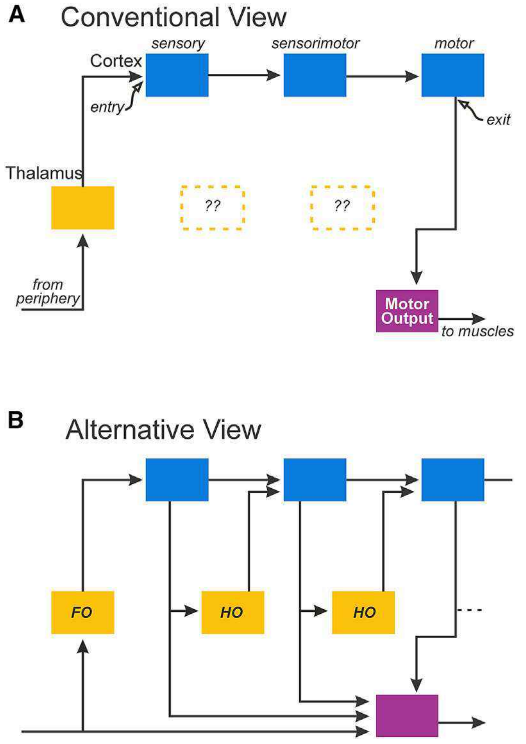

Figure 2. Two views of thalamocortical function

(A) Conventional view. Once information reaches cortex, it is processed up a hierarchy of cortical areas, passing through various sensory, sensorimotor, and motor levels before reaching an executive level from which a motor command is initiated. Thus there is a single entry and exit point for cortical processing. Such processing suggests no function for most of thalamus, indicated here by question marks.

(B) Alternative view. Here, every cortical area has a layer 5 projection that innervates motor subcortical regions, and via branching axons, also innervates the thalamic nuclei (indicated by question marks in A) to initiate transthalamic cortico-cortical communication. Although not shown, the strength of the cortical drive to subcortical motor centers is likely not the same across the cortical hierarchy; for instance, it may get stronger higher in the hierarchy. Further details in text. FO, first order thalamus; HO, higher order thalamus.

Three features of these layer 5 projections bear further emphasis. First, layer 5 corticofugal cells represent only 5% of all neurons in motor cortex of the mouse (Zhang et al., 2020). Although this percentage may vary across areas and species, it very likely is a small percentage throughout cortex. This may be seen as a bottleneck for cortical control of behavior. It also implies that there are not enough cortical output neurons to recreate all of the complex circuitry needed to establish the vast and flexible array of behaviors of which we are capable.

Second, it is of interest that every cortical area so far tested, including the primary sensory cortices, has such layer 5 projections, and these do innervate subcortical motor centers (Deschênes et al., 1994; Bourassa and Deschênes, 1995; Bourassa et al., 1995; Prasad et al., 2020). The fact that primary sensory cortices have a layer 5 projection to motor centers implies that these cortical areas have a fairly direct motor function. This is consistent with our understanding of evolution: any time a new sensory process evolves, it will have no survival value if it lacks a fairly immediate motor output. Thus, the idea that cortical "sensorimotor" processing involves initial inputs from a sensory nucleus (such as lateral geniculate nucleus input to primary visual cortex) and then ascends cortical hierarchies until an "executive" motor region is reached for a motor response to a new sensory input seems incongruous. Nonetheless, this remains the common "textbook" view of sensorimotor processing and is shown in Figure 2A. Figure 2A may be an example of an "intelligent design" for cortical processing but seems an unlikely result of evolution. Figure 2B contrasts this with the view presented here. That is, although there are numerous differences documented among cortical areas, including those commonly designated "motor" or "sensory," all cortical areas have a motor output; this includes those typically thought to be primary sensory areas, and thus the idea that some areas are strictly "sensory" and others "motor" (or even "association") is misleading. We thus suggest that reference to "sensory cortex" and "motor cortex" be reconsidered.

Furthermore, this pattern of layer 5 outputs throughout cortex seems necessary to provide a sufficiently large ensemble to facilitate and broaden the repertoire of cortical control of behavior, because the 5% or so of layer 5 outputs from what is normally considered to be motor cortex alone seems to be too small a number. It thus follows that the 5% of overall layer 5 projections is presumably enough output channels to select the combinations of older, established circuitry through which cortex acts.

Third, among the targets of these layer 5 projections, the superior colliculus stands out, because it is the subcortical motor structure to which every cortical area so far studied for this feature projects (Deschênes et al., 1994; Bourassa and Deschênes, 1995; Bourassa et al., 1995; Kita and Kita, 2012; Economo et al., 2018; Prasad et al., 2020). This makes sense, again, from an evolutionary perspective. That is, the midbrain tectum (the homolog of the superior colliculus) in nonmammalian vertebrates appears to be the most extensively evolved subcortical sensorimotor structure, providing for the most flexible responses to the environment for these animals. Not only does the tectospinal tract provide for control of bodily movements, but tectal outputs also help control head and eye movements. One way to look at how cortex exerts its control over behavior by activating appropriate subcortical motor centers is that these centers have evolved circuitry to initiate and control a number of complex behaviors, and by operating through these centers, cortex does not have to "reinvent the wheel" and create the detailed innervation patterns onto motoneurons in order to initiate and control complex behaviors. The process is like a computer program that can be built on different combinations of subroutines without having to provide the detailed instructions of all the subroutines each time.

BRANCHING OF LAYER 5 CORTICOFUGAL AXONS

A ubiquitous feature of layer 5 corticofugal axons is that they branch extensively, so that each innervates multiple targets (Bourassa and Deschênes, 1995; Bourassa et al., 1995; Kita and Kita, 2012; Economo et al., 2018). The branching means that an exact copy of a message is transmitted from one neuron to multiple targets (Cox et al., 2000; Raastad and Shepherd, 2003); the result may vary at different target cells because of differences in synaptic properties among the targets of the

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branched axon, but arguably, the best way to ensure that an exact copy of a message is transmitted from one neuron to multiple targets is via such a branching axon.

Furthermore, a common target of these layer 5 axons is thalamus, specifically higher order thalamus, which is the substrate for transthalamic, cortico-thalamo-cortical communication streams (Sherman and Guillery, 2013; Sherman, 2016). As noted, layer 6 cells also innervate thalamus, but there is an important distinction between the thalamic input from layer 6 and that from layer 5 (reviewed in Sherman and Guillery, 2013; Sherman, 2016; Usrey and Sherman, 2019). Layer 6 inputs to thalamus subserve a modulatory function and thus are not thought to provide information to be relayed back to cortex, whereas layer 5 inputs have driver properties and are thought to provide information for thalamocortical relay, which suggests that these transthalamic routes represent information streams organized in parallel with direct corticocortical connections (Sherman and Guillery, 1998; Theyel et al., 2010; Sherman and Guillery, 2013).

Therefore, because of both the driving properties of layer 5 inputs to thalamus and also because of the branching, the messages relayed through thalamus in these transthalamic circuits are often exact copies of messages sent by cortex to motor centers. Such a copy may be considered an efference copy (or, perhaps, a corollary discharge; Crapse and Sommer, 2008) of motor instructions initiated by cortex, and this has led to the suggestion that part of the functional significance of transthalamic processing is the dissemination of efference copies (Sherman and Guillery, 2013;Sherman, 2016).

There are two key provisos to this idea of efference copies via transthalamic pathways. First, the pattern of action potentials sent along an axon can be considered the message that the axon transmits to its target neurons. Such a singular message may be read quite differently by different postsynaptic cells or circuits: some may read it as an efference copy, whereas others may read it in a very different context, such as relevant to a sensory stimulus, to a working memory, and so forth. Second, although it appears that all or nearly all layer 5 axons that innervate thalamus branch to innervate extrathalamic targets as well, the converse is not the case: many layer 5 axons innervate multiple subcortical targets but not thalamus (Economo et al., 2018). This raises the possibility that many motor commands initiated by cortex are not represented by transthalamic efference copies.

ATTENTION FROM THE PERSPECTIVE OF EVOLUTION AND LAYER 5 CORTICOFUGAL PROJECTIONS

The subject of attention has long been a focus for investigation in neuroscience. The above account of cortex operating through layer 5 outputs as depicted by Figure 2B has implications for attentional mechanisms. Corticothalamic projections from layer 6 can also play a role in attentional mechanisms by affecting thalamocortical functioning (e.g., McAlonan et al., 2008; Briggs et al., 2013). However, these layer 6 projections do not have any direct access to subcortical motor centers; we emphasize that it is the layer 5 corticofugal pathways that do strongly affect behavior and thus create the very need for cortical attentional processes. Indeed, from this perspective, we suggest that certain dogmatic concepts concerning the neuronal basis of attention should be reconsidered.

Current views of attention

A detailed discussion of attention is beyond the scope of this account, and many excellent reviews on the subject are available (Desimone and Duncan, 1995; Reynolds and Chelazzi, 2004; Maunsell and Treue, 2006; Petersen and Posner, 2012; Nobre et al., 2014). Most suggested neuronal mechanisms underlying attention involve bottom-up and/or top-down circuits that enable a cortical region to enhance processing of the attended object (Desimone and Duncan, 1995; Awh et al., 2012). Such mechanisms so far identified, among others, include enhanced responses to attended stimuli (Maunsell and Treue, 2006; Lee and Maunsell, 2010; Mineault et al., 2016; Suzuki et al., 2019), fewer noise correlations in firing among neurons in the attending circuit (Cohen and Maunsell, 2009), synchronization among neurons within the same cortical region (Womelsdorf et al., 2006), coherent, rhythmic neuronal firing across cortical areas (Fries, 2005; Chalk et al., 2010; Miller and Buschman, 2013; Suzuki et al., 2019; Fiebelkorn and Kastner, 2019), and enhancement of thalamocortical synaptic efficacy (Briggs et al., 2013).

A brief account of ideas regarding these mechanisms of attention follows. Attention is generally regarded as a cognitive process that underlies one's ability to direct processing resources to behaviorally relevant environmental events. This process improves stimulus detection and discrimination and speeds up reaction times for appropriate behavioral responses. Attention is often viewed as a spotlight, which implies it involves limited parts of the neuraxis; it is thus a limited resource that must be apportioned flexibly and under cognitive control. Because it is viewed as a cognitive process, neuronal substrates of attention allocation are frequently viewed as residing solely within cortex (but see below).

Why does attention reduce cognitive abilities to unattended objects?

The usual explanation for attentional mechanisms is that they enable our brains to respond fairly exclusively to environmental events of particular importance to our survival. For instance, a rabbit traveling through a grassy field might focus attention with vision on the lookout for hovering hawks. However, attention comes at a price, because that rabbit, by spotlighting visual stimuli, may be less responsive to auditory cues that could indicate a fox on the hunt. Even within vision there is a likely price to be paid: by concentrating where hawks fly on upper visual fields, the rabbit might miss detecting the fox in its lower visual field. In this sense, attention is a zero-sum game: resources devoted to some neuronal circuits impoverish others.

This raises a generally ignored question: given the extensive cortical circuitry subserving its enormous computational power, why cannot all areas of cortex function in an attentive-like mode so that the rabbit can be maximally sensitive to all sensory stimuli simultaneously? We believe that an evolutionary perspective offers a plausible answer to that question.

As noted above, cortex evolved subsequently to and then in parallel with the evolution of lower motor circuits, mostly in the brainstem but also some in the spinal cord. In the process, cortex evolved access to these lower motor centers through layer 5 corticofugal pathways. Most important and as has been stressed above, the *only* way cortex can influence behavior is by

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operating through these layer 5 outputs that activate the older motor centers in the brainstem and spinal cord (Figure 2B). In this regard, these subcortical motor centers are a bottleneck through which cortex must operate.

This presents a real and generally unappreciated problem. We asked above why all of cortex cannot always engage its impressive analytic powers to evaluate the entire environment, involving all sensory systems. The point is that attention comes with a real cost in that it causes our brain to relatively ignore much of the goings on in our environment, and this can be seen as counterproductive to survival. As evolution works to maximize survival of the species, at least through the period of reproduction, there must be a good reason for this cost of attention.

We suggest the answer to this conundrum is as follows. If as suggested above, every cortical area operated at maximum capacity to turn its inputs into layer 5 motor commands, these would all compete for control through subcortical intermediaries, and chaos would likely ensue. It follows that there must be some selective process that ensures that the cortical areas engaged in evaluating environmental events deemed most important, or most crucial to survival, are preferentially permitted to control subcortical motor centers. This is where attention comes in and may even be regarded as a new, operational definition of attention itself. Somehow, via bottom-up or top-down neuronal processing (Desimone and Duncan, 1995; Awh et al., 2012), the appropriate cortical region or regions engage, and their layer 5 corticofugal projections act to dominate subcortical motor regions. The implication that follows is that other cortical areas (and their layer 5 outputs) dealing with less critical environmental events are suppressed, but experimental evidence for this is currently lacking.

Attention is not just cortical

As mentioned above, attention is generally regarded as a cognitive process, which strongly implies purely cortical substrates. As a result, the vast majority of studies on attention are concerned only with cortical contributions thereof. However, an evolutionary perspective suggests a more complex view with significant subcortical contributions to attention. Just as attention seems necessary to ensure that the appropriate cortical regions take control of behavior, more primitive species had to deal with the very same problem and did so without cortex (i.e., neocortex). Even in primitive vertebrates there would be multiple brainstem centers that could produce behaviors in the form of activating various incompatible central pattern generators, and for a given environmental set of circumstances, survival would often require that the appropriate set of such generators was activated. That is, like mammalian cortex, higher subcortical centers, such as the midbrain tectal area, also had to operate through older supraspinal and spinal centers, and the same problem as suggested above had to be overcome: that is, to avoid chaos, something like attentional mechanisms would be required to filter out inappropriate midbrain centers from controlling behavior.

A clear example of subcortical involvement in attention is that of the superior colliculus (reviewed in Krauzlis et al., 2013; Basso and May, 2017; Krauzlis et al., 2018; Basso et al., 2021). As noted above, the Sprague effect (Sprague, 1966) is an early example of how neuronal circuitry involving the superior colliculus acting independently of cortex in cats can direct attention to novel sensory stimuli (Sprague and Meikle, 1965; Lomber et al., 2007; Hong et al., 2018). Furthermore, muscimol inactivation of the superior colliculus in monkeys interferes with the ability of the animals to maintain attention to visual objects (Lovejoy and Krauzlis, 2010).

As mentioned above, there is also evidence for involvement of the thalamus in attentional mechanisms (Halassa and Kastner, 2017; Usrey and Kastner, 2020). Whereas the thalamus is, strictly speaking, a subcortical structure, it is so intimately associated with cortex that it seems pointless to regard its functioning in any way separate from cortical functioning. We thus instead emphasize the involvement of nonthalamic subcortical structures, such as the superior colliculus, in attention.

One general rule of evolution of our nervous system is that these older circuits are not discarded as newer ones evolve, and these older circuits continue to function. For example, the optic tectum of the primitive vertebrate, the lamprey, is involved in attentional mechanisms (Suzuki et al., 2019), and this structure is the homolog of the mammalian superior colliculus, which, as noted, remains involved in attentional mechanisms. It thus seems likely that attentional mechanisms in our brains are not limited to cortical circuitry but involve older, subcortical circuits as well, and these all must operate in a coordinated fashion. They remain operational, even if they may be considered noncognitive because of their subcortical placement.

This raises another interesting possibility. As we have noted above, evolution is messy and leaves mammalian brains with circuits at different levels that operate to control behavior. Also as noted, subcortical circuits for attention remain, and thus, it follows that these must work in harmony with cortical ones. For instance, imagine we are walking through the woods on an unfamiliar path with a friend with whom we are carrying on a conversation. We might consciously attend to the conversation (the cortical part), but subcortical centers are ‘‘attending’’ to the path to make sure we do not trip over a root (e.g., we make saccades three to five times per second that we do not consciously evoke in order to scan the environment). This would mean that attention is not simply a single, peremptory cortical process but involves cortical and subcortical processes that work together in harmony to control appropriate behavior.

CONCLUSIONS

We have argued that the evolutionary history of our brains places certain constraints on the functioning of the cerebral cortex, constraints that have not had much consideration to date. It seems that once an evolved neuronal circuit proves valuable in enhancing survivability, it typically remains. Further evolutionary progress involves building upon these older, useful circuits rather than completely replacing them by newer, improved models. Replacement might be a strategy used by an intelligent designer to keep things more orderly, but that is not the way of evolution. In any case, the result is that many older, useful spinal and brainstem circuits remain operational as cortex evolved in mammals.

The main result of having a structure, cortex, with such powerful computational properties means that it is able to provide a richer and more flexible range of motor responses to environmental challenges, all of which clearly enhances survivability.

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However, as emphasized above, cortex did not evolve complete with circuitry that allows direct control of motoneurons, and so instead must operate through the many older subcortical circuits previously evolved to control behavior. This represents a bottleneck through which cortex must operate. Furthermore, the *only* cortical access to this bottleneck is via its projections from a subset of layer 5 neurons found in every cortical area.

This presents a problem: this bottleneck has many potential inputs vying to take control of each of the multiple subcortical circuits. This includes both layer 5 inputs from different cortical areas as well as various older subcortical inputs. To avoid chaos, there must be mechanisms in place to ensure that the correct circuits control the final motor pathways so that the best response to any environmental challenge is evoked. This same selection process exists as well for purely subcortical circuits that also have evolved to control behavior in what can be viewed as subcortical attentional processes, and the possibility exists that several of these may be in play with or without cortical attentional processes to control complex behaviors.

This selection process is what we recognize as attention. From a cortical perspective, this means that only the subset of areas most urgently needed to relate to environmental events at that time are able to influence or control behavior via their layer 5 outputs; the implication is that, in other cortical areas, layer 5 outputs either are suppressed in cortex or their effectiveness in subcortical targets is reduced. The cost of this process is that other cortical areas are relatively disengaged from control of behavior, which explains why we cannot use all of the vast computational power of all of our cortex all of the time. Furthermore, for much behavior, as noted above, cortex is not involved. However, even without cortex, the same selection process for appropriate supraspinal centers to dominate behavior is needed, again to avoid chaos. And, as noted above, there is considerable evidence for subcortical mechanisms of attention.

All of this challenges common views of attention, which is usually seen through a corticocentric lens. That is, attention is usually viewed as a cognitive process that, because of limited cortical resources, concentrates these for certain cortical areas to dominate behavioral responses to environmental events. We emphasize that the process of evolution has resulted in circuitry that limits cortical control of behavior, forcing it to operate through a bottleneck of subcortical structures, which, in turn, requires a selection process that enables only some cortical areas to operate effectively. In other words, the resource limitation is not cortical circuitry per se but rather the bottleneck through which corticofugal control of behavior must operate because of the limitation of few layer 5 outputs that can effectively control subcortical motor structures.

This perspective emphasizes the scaling down of cortical functioning in areas not involved in addition to enhancing function in involved areas. This also challenges the notion that attention is necessarily a cognitive process. We normally associate cognition with cortical activity, and as such, subcortical processes involving attention would not be cognitive processes. Attention becomes a cognitive process only when cortical circuits are recruited to control behavior.

An alternative way to consider attention is from the perspective of the selection process whereby the appropriate subcortical or cortical circuits are brought into play to provide the best response to any environmental challenge at any given time. All of the other results described for attention can be seen as a logical and predictable consequence of this process.

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