Review

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Review

Brains Are Expensive, but Cognition Is Often Cheap

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Abstract

The fundamental premise that energy demands constrain neural computation has led to the widely held belief that cognitive activity is always metabolically costly. However, brain imaging and whole-body measurements in mammals demonstrate that solving cognitive tasks is typically accompanied by either a minimal increase of overall energy expenditure or no change at all. In this article, we review the relevant experimental evidence and describe why maintaining the resting state can be as costly as engaging in explicit tasks. Refraining from cognitive activity might often not be an efficient way to save energy, which has important implications for understanding the metabolic bases of brain function and behaviour. For example, the pervasiveness of non-instrumental activity (such as curiosity-driven exploration) can be readily explained from an evolutionary angle if reducing exploration does not result in significant decrease of metabolic costs. We propose that addressing the question of how different homeostatic mechanisms interact to keep the overall brain energy expenditure relatively steady will help to uncover the fundamental principles of neural computation.

Keywords: metabolism; cognitive effort; efficient coding; exploratory behaviors

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Introduction

One of the most ubiquitous assumptions in the neuroscience literature is that cognition is energetically expensive. Indeed, our brains consume around one fifth of the calories that we intake every day, much more than could be expected based on their mass [1]. This fact is often cited to support the conclusion that the cognitive activity that we engage in is very costly, and thus at some level must be useful – otherwise, the evolutionary pressure would not allow for such a waste of energy [2–4].

A clear example comes from the literature on exploratory behaviors and curiosity. This type of activity – seeking information for the sake of information, and not to obtain any external rewards – is typically considered a puzzle that requires further explanation [5,6]. A typical solution is to demonstrate that in the long run curiosity-driven exploration can increase the amount of food that the organism is able to gather (e.g., because it helps to develop smarter foraging strategies), even if in the short run it is often just a waste of energy [7–9]. If we agree that all cognition is costly, it seems to be an almost unavoidable conclusion.

In this paper we would like to question the original assumption and propose an alternative approach. We argue that although maintaining a brain is indeed costly, it does not mean that all cognitive activity requires spending a significant amount of additional energy. Quite the opposite, the experimental evidence indicates that at least some forms of cognition are extremely cheap. To be more precise, subjects engaged in cognitive tasks typically spend a similar amount of energy as subjects at rest. This counterintuitive finding becomes easier to understand when we realize that the mammalian brain is never truly at rest: most neurons continue to spend energy even in absence of any salient external stimuli. When we consider this, the assumption that any goal-directed cognitive activity is related to some fixed energetic cost – a cost that the organism would be able to otherwise avoid – becomes at least questionable. The goal of this paper is to deconstruct the assumption and briefly consider: if we reject it, what are the implications for neuroscience?

1. Brain uses similar amount of energy all the time

It is now textbook knowledge that although the human brain forms only 2% of the body mass, it consumes 20% of its energy [10,11]. During development this number is even higher – it peaks around the age of 5 years, when it reaches almost 45% of total energy expenditure [12]. Across mammalian species, proportionally larger brains correspond to higher basal metabolic rates [13], and human brains are exceptionally costly when compared to other primates [14,15]. There is no doubt that overall, brain is a very expensive organ.

It is much more difficult to measure how much energy is used by the brain to perform a particular cognitive task. Multiple studies attempted to do that using a relatively straightforward approach - measuring regional concentration of relevant metabolites during the task vs. at rest. Most typically, these experiments compared effects of visual stimulation (e.g., displaying lights on the screen) to a control condition (e.g., subjects had eyes closed). The reported results are surprisingly variable: some authors observed significant changes in concentration of glucose and/or high-energy phosphates [16–19], while others did not [20–23]. Other tasks - e.g., playing Tetris, verbal fluency or visual memory tests - often bring similarly inconclusive results [24–27].

This variability of results can be partially explained by what exactly was measured in a particular study. The regional consumption of oxygen and glucose (which traditionally were believed to be the only sources of brain energy) rarely changes more than 25% [28,29]. Concentration of lactate is much more variable [16,17,20,23,27,30,31] - some studies reported changes higher than 100% [30], while others no changes at all [21,32]. It was pointed out that because anaerobic production of ATP from lactate is very inefficient, the overall brain energy budget is probably much better reflected by the oxygen concentration [33]. When taken together, the data indicates that performing cognitive tasks increases regional brain energy expenditure by maximally 50% [33].

To fully grasp the implications of this statement, one should not overlook the word ‘regional’. Most of the studies focus on the subset of brain regions which seem relevant for the task - e.g., if visual stimuli are employed, metabolism in the visual cortex is monitored [16–23]. Importantly, in such studies it is not unusual to observe that the increase in metabolic activity in some regions is accompanied by decrease in others [26,34]. There is now a large body of fMRI literature on ‘default mode network’ (DMN) - a subset of brain regions that typically *decreases* activity when subjects switch from rest to being focused on external stimuli [35]. There is also evidence that, at least for some tasks, this decrease of blood-oxygenation level indeed reflects lower metabolic activity [36,37]. Thus, the regional energy expenditure caused by cognitive tasks can be compensated by lower demands in other regions. Only a few studies reported how cognitive activity influenced the overall, whole-brain metabolic rate of glucose, and the results ranged from ~10% increase [38] to no significant effect at all [39,40].

Taken together, it is not surprising that most experts in the field seem to accept the same conclusion: **performing cognitive tasks increases whole-brain energy expenditure only to a moderate degree** [33,41,42], **typically by no more than 5%** [1,43–45]. On the level of the whole organism, this would correspond to spending overall 1% more energy than at rest. Such a small effect size could explain why many studies actually failed to detect any cognition-related metabolic changes within the brain [20–23].

2. On the whole-body level, cognitive activity is often cheap

As shown in the previous section, it is far from trivial to measure how much energy is spent by the brain to perform a certain cognitive task. An alternative strategy would be to instead measure the energy expenditure of the whole body. The advantage of this approach is that it ignores the possible compensations (by other brain regions or by alternative metabolic pathways), and instead looks at the net cost for the whole organism, including the cost of cognition-related movements. Because the absolute number of calories burnt by each subject can vary substantially (depending on their body mass, sex etc.), the overall energy expenditure is most commonly expressed as percentage increase relative to the state of lying in bed and doing nothing, more technically referred to as the basal metabolic rate.

A survey of different cognitive activities - such as reading, writing, studying and thinking - indicates that the whole-body measurements are as variable as the data on brain energy consumption, and range from 0 to 50% increase from basal metabolic rate [46,47]. That is much lower than any physical activities, which can increase the energy consumption by anywhere from 100% (for walking slowly or washing dishes) up to 1500% (running fast uphill, training combat sports) [47]. Of course, spending 50% more energy on a cognitive task would still be a substantial cost for the organism. However, to properly interpret this number, one should ask how much of this energy is actually consumed by the task itself, and how much by maintaining a certain posture. Subjects are typically asked to read while sitting, whereas basal metabolic rate is an estimation of how much energy is spent on just maintaining physiological functions at rest. When compared directly, reading while sitting consumes either the same amount of energy as just sitting, or is only minimally more expensive.[46] Indirect comparisons (i.e., looking at data from different studies) also indicate that cognitive tasks require a similar amount of energy as maintaining the posture (e.g., sitting at a desk) [47]. Thus, we can conclude that from the perspective of the whole organism, the main cost of cognitive activity is related to the postural changes, and not to the mental activity itself [48].

The evidence cited above contradicts a common wisdom that ‘thinking is hard work’ that requires a lot of calories. We will come back to the issue of what ‘hard work’ might actually mean in section 5, but for now we would like to focus only on its metabolic aspect. In pop-science, there is a widespread conviction that chess players burn 6000 kcal a day during the tournaments - at least twice more than an average person [49]. Although it is hard to trace down what was the origin of this idea, it might be related to observing that chess players can have very high momentary heart-rate, and extrapolating this parameter to the whole metabolism. When measured precisely under laboratory conditions, the energy spent by professionals during match is not significantly higher than at baseline (i.e., sitting and resting) [50]. Of course, that does not exclude the possibility that some chess players burn a lot of calories during the tournaments - which seems to be supported by anecdotal observations that they lose weight and eat more [49] - but it strongly suggests that the excess energy expenditure is related to other factors, such as high stress levels, and not to the cognitive activity *per se* [50]. We are not aware of any scientific evidence which would indicate that just through mental effort, people can spend several times more energy than at rest. To understand why there is no evidence for that (and plenty of evidence for the contrary), in the next section we would like to reflect on how energy expenditure is measured, and what it actually means for a mammalian subject to be ‘at rest’.

3. Brains are active even at rest

All the studies cited so far share a fundamental assumption: that to measure the costs of a cognitive activity, one should compare it to some baseline state. Although there is nothing wrong with this approach, we should not forget that what happens during baseline will significantly change the interpretation of a study. For example, reading can seem costly when compared to the basal metabolic rate, but not when the control condition involves sitting at a desk. Similarly, when measuring energy expenditure related to vision, researchers are faced with a dilemma: should they compare it to looking at an empty screen [26,34] or to keeping eyes completely closed [19,21,23,32]?

A quick reflection on these two examples reveals a fundamental difference between motor and neuronal activity. The former can be ceased almost completely: at rest most of skeletal muscles are largely relaxed, which reduces their oxygen consumption as much as 70 times compared to intense exercise [51]. The brain, on the other hand, is constantly involved in maintaining homeostasis – keeping heart beating, hormones flowing at sustainable concentrations, and respiratory tracts not obscured. Obviously, none of those processes are stopped during baseline periods. A similar argument can be also applied to functions traditionally recognized as more 'sensory' or 'cognitive'. The experimenter might ask us to close our eyes, but even then we perceive the amount of light getting through eyelids. We cannot voluntarily stop hearing sounds or feeling textures on our skin. Similarly, when asked to stop thinking about a cognitive task, we do not turn off our consciousness, but rather let the mind wander freely, which activates imagination, memory etc [52].

The argument that mammalian brains are active even at rest is supported also by physiological data. Although it is still not entirely clear which aspects of brain activity are the most energy consuming - e.g., intracellular signalling, protein synthesis or maintaining resting potentials [33] - there is no doubt that to keep cells alive, none of them can be simply stopped. Hypothetically, spiking seems to be the best candidate for saving energy: if the function of a neuron is to signal a particular stimulus, it could completely stop firing in absence of the target. But in reality, this almost never happens - even in early sensory areas most neurons remain some level of baseline firing regardless of the conditions [53]. It was recently demonstrated that such 'spontaneous' spikes are probably necessary to avoid accumulation of reactive oxygen species, which otherwise would become toxic for the cells [54]. Even if mice are food deprived, the number of spikes in their visual cortex remains the same, and instead some energy is saved by putting less strict constraints on maintaining steady resting potentials [55].

Taken together, the data suggests that mammalian neurons perform their signalling functions within relatively narrow metabolic margins. Obviously, they can increase or decrease activity in response to stimuli, but only within some limits - breaking of which could result in cell death [54]. Off note, these physiological limits can be shifted - for example, during hibernation [56] - but not in the time range of initiating a single cognitive task. In the next section we will consider the implications of these findings.

4. What are the implications for understanding cognition?

So far we have demonstrated that, although maintaining a brain is extremely expensive, performing cognitive tasks is often cheap. The argument was supported by three kinds of evidence: a) measurements of brain energy expenditure b) measurements of whole-body energy expenditure c) demonstrating that brains remain highly active also during baseline state (i.e., at rest). If our reasoning is correct, what are the implications for understanding cognition?

First and foremost: **refraining from cognitive activity is often not a good way to save energy**. For example, solving a crossword might be considered energetically expensive, in the sense that it requires activating semantic memory systems, emitting spikes, producing neurotransmitters etc. But when we consider an alternative, just sitting in front of the crossword will not save a huge amount of energy: it will activate different brain systems (such as the default mode network), while all the 'background' neuronal activity will be continued anyway. In this sense, solving a crossword is extremely cheap. As we demonstrated, the assumption that all cognitive activity is related to some significant energetic cost is not supported by empirical data. Our interpretation of this finding is that maintaining the baseline state is often similarly costly as performing the cognitive task itself. In other words, spending energy by the brain is simply unavoidable.

One possible objection against this line of reasoning would be that cognitive activity rarely happens entirely in our heads, and energy could be saved through restraining from movement. For example, doing a crossword requires not only sitting, but also handwriting, scratching one's head etc. To some extent we agree with this objection, in the sense that accompanying motor activity for sure puts bigger energetic constraints on cognition than the act of thinking itself. But that is exactly why - in order to learn how a murder mystery ends - most of us are willing to turn book pages, but not to walk to the town where the author lives. Many movements accompanying cognitive activity do not require high force and are extremely brief. A good example comes from orienting: when presented with novel stimuli, animals often turn their sensory organs and whole bodies towards them. But even these short movements usually disappear after a few trials - if the stimulus stops being surprising, the animals do not waste energy on continuing exploration.[6] Additionally, it is not obvious to what extent energy could be saved by ceasing *all* movements for long periods of time [57]. For mammals, remaining absolutely still for more than a few minutes is actually rather difficult [58,59] and may potentially lead to minor problems with muscle stiffness [60], thermoregulation [61], tissue damage [62] etc.

If we accept these arguments, the fact that animals willingly engage in cognitive activity without any expectations for reward is no longer paradoxical. If neuronal (and, to lesser degree, motor) activity cannot be easily stopped, the rational thing to do is to direct it in a way that would maximize the acquisition of novel information. **We propose that curiosity-motivated exploration is typically not a waste of energy, but on the contrary - a way to optimize energy expenditure that would happen anyway.** From the evolutionary perspective, this would mean that the selection pressure on refraining from gathering new information is very weak. Quite the contrary, some positive pressure might be expected: computational models consistently demonstrate that in reward-seeking tasks, implementing curiosity vastly improves learning, especially if the rewards available in the environment are sparse [6]. In conclusion, curiosity might be an energetically cheap adaptation, which would explain why all the species studied so far do show some form of novelty-triggered exploratory behaviors. A similar argument can be easily applied to other forms of cognitive activity without a clear function: games, puzzles etc.

5. ‘Cheap’ is not the same as ‘free’

Because the proposed approach might seem to contradict some well-established findings, in the following section we would like to clarify our position. In particular, we will present how our claims can be reconciled with several popular views on the costs of cognition.

a) Some forms of cognition might be more expensive than others

As we demonstrated, many studies failed to detect significant increase in energy expenditure caused by cognitive activity. However, that does not imply that such an increase *never* happens - some particular forms of cognitive activity are probably more costly than others. For example, a recent study found that presentation of highly unpredictable visual stimuli can increase regional cerebral oxygen metabolism by around 10%, as compared to easily predictable ones [29]. Similarly, longitudinal experiments indicate that the highest energy expenditure is typically registered during learning a completely new skill, and can drop to baseline levels after training [63]. Developmentally, brains consume proportionally much more energy in children than in adults, which is probably related to creating - and then pruning - many new synaptic connections [12].

Taken together, the data supports the conclusion that - although cognitive activity is generally much cheaper than movement - some forms of cognition might be more costly than others. The best candidates for high-energy demanding tasks are the ones that require a high level of structural neuroplasticity [64]. However, more research is needed to establish what is the upper-bound of task-related energy consumption, and which factors make a cognitive task metabolically more expensive.

b) Brains are highly optimized

Intuitively, our proposal might seem to contradict some normative theories, which assume that almost every aspect of brain functioning is metabolically optimized throughout evolution [65]. If cognition is cheap, maybe there is no need to optimize anything that brains do? In our opinion, quite the opposite is true: cognition is cheap because many aspects of brain anatomy and physiology are already highly optimized.

Multiple examples from the literature - e.g., regarding synaptic efficiency [66], long-range wiring [67], or sparsity of single-neuron responses [68], just to name a few - clearly demonstrate that many solutions adapted by the nervous system utilize as little energy as possible to carry out their function. In other words, it is possible (and often required for survival) to save significant amounts of energy through selecting some design principles over others. What we propose is that once this highly optimized machinery is present, refraining from using it is typically not a good way to save energy, at least not within the constraints imposed by the mammalian brain. As a result, the selection pressure regarding brain structure is probably much higher than the selection regarding how eagerly animals engage in cognitive activity. However, one should keep in mind that this argument takes into account only energy expenditure per se, and not other potential costs for the organism. Such alternative costs will be briefly discussed in the next section.

c) There are other costs of cognition than energy

So far, we have used the word 'cost' as a synonym for energy expenditure. But engaging in cognitive activity can be related also to other types of costs: being exposed to predators, losing opportunities for obtaining food or decreasing attractiveness for potential mates. In this sense, cognition could be indeed expensive. Exploration of novel environments almost certainly increases the risk of encountering a predator, yet animals still do that, even when satiated [69]. Similarly, there is strong evidence that both humans and other animals often sacrifice some rewards in exchange for novel (yet materially useless) information.[6]

These examples illustrate that, even when metabolically cheap, curiosity-motivated exploration can go against short-term economic utility and thus require an evolutionary explanation in terms of costs and benefits. Such analysis is beyond the scope of this paper, but some solutions have been already proposed in the literature, and typically indicate that exploration is especially beneficial in unpredictable and reward-sparse environments [6,7,69,70].

d) Cognition is sometimes related to high subjective effort

What we propose might seem to contradict at least one common intuition: that cognitive activity is hard work. If our argumentation is correct, solving differential equations burns a similar amount of calories as watching reality TV - yet subjectively, one seems much more energy-consuming than the other. It is well documented that people avoid engaging in activities that require high cognitive load [71]. Additionally, it was reported that the mental fatigue caused by demanding cognitive tasks (especially the ones requiring prolonged self-control) can be reversed simply through consuming glucose.[72] These findings inspired some psychologists to propose something exactly opposite to our claim: that effortful cognition leads to 'ego-depletion', caused by running out of glucose resources [72,73]. How can we explain the contradiction between this approach and our proposal?

Firstly, the positive effect of glucose on cognitive performance could not be replicated [74] (and recently it was questioned whether the 'ego-depletion' paradigm actually works [75]). Secondly - even if the effect would eventually turn out to be real - it was noted that the decreases of glucose level observed after cognitive activity are much smaller than the amounts needed to improve subjects performance, which suggests an indirect mechanism of action [42,76]. Thirdly, the resource depletion approach was created not to explain cognitive activity in general, but only cases that require extensive self-control - which might impose special metabolic demands (see section 5a).

Taken together, the evidence indicates that the phenomenon of mental effort requires a much more nuanced explanation than simple depletion of resources. Such alternative explanations were already proposed. On the psychological level, they usually frame mental effort as a motivational process, which signals that shifting activity might be more beneficial than sticking to current tasks [77–79]. On the neuronal level, it was recently demonstrated that prolonged cognitive activity leads to accumulation of glutamate in the prefrontal (but not visual) cortex [80]. The authors proposed that mental fatigue might result from difficulties in keeping the level of this neurotransmitter under non-toxic boundaries. Both types of explanations are consistent with our approach.

e) Cognition might be not equally cheap for every species

A careful reader might have noticed that so far, when speaking about metabolic constraints on brain functions, we were often referring to the *mammalian* brain. One reason for that is most of the data on the topic comes from experiments conducted either on humans or laboratory rodents. The second, less trivial reason is that it remains an open question whether our argument is applicable to other animal groups.

There is comprehensive evidence that in insects, forming long-term memory can decrease the chance of producing healthy offspring and even surviving under food scarcity (for review, see [64]). Because such a form of learning requires costly protein synthesis, these results were interpreted as evidence for depletion of energetic resources. Although we are not aware of any direct experimental comparisons, it is possible that for insects cognitive activity is related to proportionally higher energy expenditure than for mammals.

Another interesting example comes from reptiles, which - unlike mammals - can refrain from any movements for long periods of time [81]. Because they are ectothermic (colloquially: 'cold-blooded') animals, such inactivity can decrease the temperature of their bodies [82], which typically is related to slowing down metabolism [83] and reduction of neuronal firing rates [84]. Thus, it is not unreasonable to hypothesise that in reptiles and other ectotherms refraining from cognitive activity - such as curiosity-driven exploration - might be a good way to save energy. If true, exploratory drive in reptiles compared to mammals could be not only lower, but also regulated differently by food availability. Unfortunately, these predictions remain speculative, as we are not aware of any studies that would directly test them.

The most important implication of this brief comparative analysis is that in some species, cognitive inactivity could potentially result in saving substantial amounts of energy. However, more experimental research is needed to directly estimate how much the costs of cognitive activity (e.g., learning) varies between animal groups.

Conclusions

In this paper, we deconstructed the assumption that every cognitive act is associated with some significant energetic cost. Firstly, we demonstrated that empirical data does not support this claim, and many forms of cognitive activity increase energy expenditure either minimally or not at all. Secondly, we discussed how mammalian brains remain highly metabolically active even when the organisms are not engaged in any explicit cognitive task. Thirdly, we presented the main implication of our claims: engaging spontaneously in cognitive activity (such as curiosity-driven exploration or play) is not necessarily paradoxical, because in many cases, refraining from it would probably not significantly reduce energy consumption.

Speaking more broadly, our goal was to demonstrate that two separate assumptions about brain energy expenditure should not be confounded. There is solid evidence that maintaining a brain is energetically costly, and that many features of neuronal architecture were optimized to minimize this expenditure. However, that does not imply that every instance of using the brain is also costly - such a conclusion is a fallacy resulting from mixing different levels of analysis.

Clearly, identifying a dubious assumption is not yet an explanation, and simply opens new questions. Intuitively, it seems that rapid switching to a baseline, energy-saving state would be a useful adaptation, so why do mammals not do that? Does the constrained energy expenditure offer any computational advantages - for example, would it improve AI systems? And most importantly: how the steady expenditure is achieved by the brain? We propose that answering these questions will require expanding and integrating at least three areas of research.

Firstly, because most neuroscience experiments are task-based, it is not very well understood what the energy is spent on during periods typically classified as ‘baseline’. Both human and non-human subjects almost constantly produce uninstructed movements (such as blinking, changing breathing rate, fidgeting etc.), and only recently it was recognized that these behaviors have profound impact on neuronal activity [85]. Additionally, most circuits maintain some degree of spontaneous activity even in absence of overt movements [54,86,87]. A lot more experimental work is needed to characterize what processes contribute to such spontaneous activity and what is their metabolic cost and function.

Secondly, the metabolic cost of neuronal activity is limited by processes not related to cognition per se. There are multiple basic constraints - on biochemical [88], physiological [54] or vascular [89] level - that make it simply impossible for cells to function outside of a predefined metabolic range.

Only some of these constraints are specific to the brain, but neurons, not being able to store significant amounts of energy, might be particularly susceptible to them [54]. For example, under physiological conditions mammalian brains use only up to 40% of the oxygen available in the blood (compared to 95% in skeletal muscles), and it was proposed that this number is strictly limited by capillary density [89]. Understanding such basic constraints is critical for explaining how metabolism interacts with information processing.

Thirdly, brains implement many top-down regulatory mechanisms which could directly limit the energetic cost of solving cognitive tasks. For example, activity of large functional networks is anticorrelated (when the action-mode network is activated, the default-mode network becomes less active), which strongly suggests that long-range connectivity is calibrated to keep the overall activity levels relatively constant [90,91]. It was even proposed that brains prospectively monitor the cost of ongoing computations, which allows to avoid the most expensive operations [42]. Similar compensations can be observed also on whole-body level (in the context of physical activity), which is famously illustrated by the fact that hunter-gatherers spend daily the same amount of energy as white-collar workers [92]. Although the underlying mechanism is still poorly understood, it probably involves reducing the activity of reproductive and immune systems, as well as possibly diminishing frequency of non-essential movements (e.g., fidgeting) [93,94]. These examples strongly suggest that energy is spent on cognition not purely reactively, but can be dynamically redistributed between different systems, consistently with the notion of allostasis [95].

Unfortunately, the three areas of research discussed above are currently largely separated. In our opinion there is a great need to integrate them and, optimally, test their predictions against each other. The case presented in our paper illustrates that explaining metabolic aspects of cognition will require a quite nuanced theoretical approach. In particular, we argue that the simplistic account of brain energy expenditure - which assumes that each cognitive operation is completed in exchange for a fixed cost - is generally misleading. No matter what we do, the energy is used by the brain primarily to maintain homeostasis, and what we conventionally label as cognitive activity can happen only within the limits set by this process. That is why, to explain how cognition is influenced by metabolism, it will be required to go beyond the logic of information processing and study the multi-level constraints imposed on neuronal activity by homeostatic regulation.

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