bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

An information-theoretic perspective on the costs of cognition

Zénon Alexandre*[1,2], Solopchuk Oleg[1,2], Pezzulo Giovanni[3]

[1]Institute of Neuroscience, Université catholique de Louvain, Brussels, Belgium

[2]Aquitaine Institute for Cognitive and Integrative Neuroscience, Université de Bordeaux, France

[3]Institute of Cognitive Sciences and Technologies, National Research Council, Via San Martino della Battaglia 44, 00185, Rome, Italy.

*Corresponding author:

Dr. Alexandre Zénon

E-mail: alexandre.zenon@u-bordeaux.fr

Current theories of cognitive effort provide either resource-based or motivation-based accounts of its cost. Despite the usefulness of these proposals, it remains unclear how to exactly quantify effort costs – or why certain tasks are more effortful than others. Here, we provide a novel perspective, based on the assumption that the brain constructs a probabilistic internal model of the world under efficient coding principles. We propose that effort cost is a function of the amount of information required to update the internal model to effectively solve a task. This novel theory naturally explains why some tasks – for example, unfamiliar or dual tasks – are costly and permits to precisely quantify these costs using information-theoretic measures. Finally, we argue that information costs translate into local metabolic costs – which sheds light on the adaptive value of cost-avoidance mechanisms (cognitive effort) in preventing the accumulation of local metabolic alterations over time.

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Keywords: cognitive effort, information theory, active inference, predictive coding, efficient coding, computational neuroscience

1. Introduction

Demanding cognitive tasks, such as mental arithmetic, are strongly aversive: we tend to avoid partaking in such tasks and they lead to unpleasant subjective feeling of mental exertion (Inzlicht et al., 2015). Various studies have revealed that we take into consideration a measure of cognitive cost or cognitive effort when deciding whether or not to engage in a task (Kool et al., 2010; Manohar et al., 2015; Schmidt et al., 2012; Westbrook et al., 2013; Westbrook and Braver, 2015). Furthermore, prolonged performance of demanding tasks leads to cognitive fatigue, which is characterized by a subjective dimension – i.e. feeling of exhaustion, impression of worsened ability and decreased willingness to engage in mental activities (Hockey, 2011; van der Linden et al., 2003) – and an objective dimension, with an actual decrease of task performance (Bailey et al., 2007; Tanaka, 2015; van der Linden et al., 2003). However, it is still unclear what is the origin of cognitive costs (i.e., what is costly about cognitive processing?), how to specify them quantitatively, and whether cognitive costs and cognitive fatigue have some adaptive value.

Previous characterizations of cognitive effort can be classified into two broad categories. First, effort can be framed as a consequence of resource limitations such as depletable metabolic precursors or interferences arising from shared uses of cognitive substrates (reviewed in Shenhav et al., 2017). Second, cognitive effort can be described as the phenomenological manifestation of the opportunity cost of engaging limited cognitive resources in demanding cognitive tasks (Kurzban et al., 2013). Here we advance a novel theoretical proposal that casts cognitive costs in terms of information-theoretic principles,

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

which allows us to provide quantitative predictions of task-specific cognitive costs and to bridge resource depletion and opportunity cost accounts of effort. The present framework highlights the relations between cognitive costs, the informational costs required to code a novel task or a policy to face it, and the ensuing metabolic costs of brain information processing. In this perspective, the brain is seen as a statistical machine that builds generative models of its environment and of the tasks it has to solve (Friston, 2010). To do this, it uses efficient coding mechanisms that try to minimize the information it needs to encode, given its current models, to perform accurately in a given task (Collell and Fauquet, 2015; Harremoës and Tishby, 2007; Laughlin, 2001; Sims, 2016; Wei and Stocker, 2015). By casting cognitive costs in terms of efficient information coding, this framework predicts that certain tasks - e.g., unfamiliar tasks or those that require counteracting natural biases (or default policies) - would be particularly costly, as they would require larger amounts of information to be coded. Importantly, these informational and cognitive costs have direct metabolic equivalents - in the sense that inefficient coding and large informational demands imply higher local metabolic costs, and accumulation of local metabolic alterations in the brain. Hence, ultimately, the avoidance of cognitive costs is an adaptive mechanism that prevents us from engaging in tasks that would imply high metabolic demands in the long run. The phenomenology associated to the costs of cognition - such as the fact that cognitively costly tasks have an associated subjective feeling of cognitive effort, and can lead to cognitive fatigue in the long run - can be understood within this adaptive framework that aims to minimize metabolic demands.

2. Efficient coding and cognitive costs: an example

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Efficient coding was initially described as a theory of redundancy reduction, according to which biological systems decorrelate sensory signals to avoid redundancy (Attneave, 1954; Barlow, 1961; Simoncelli and Olshausen, 2001). The theory has been successively extended to include other mechanisms through which neural coding adapts to the statistical structure of its environment (Simoncelli, 2003; Smith and Lewicki, 2006). One crucial aspect of efficient coding is the usage of an adaptive code, in which the cost for encoding each symbol is inversely proportional to its frequency in the environment - given the agent's model of the environment (Collell and Fauquet, 2015; Fairhall et al., 2001). As highlighted by Shannon's pioneering work, the minimal quantity of information necessary to encode a symbol in a message is equal to its negative log probability, or *surprisal* - which implies that under optimal encoding strategy, less likely, or less predictable events require more information (e.g. more bits in a computer memory) to be encoded. Clearly, for biological organisms, surprisal is a function of prior knowledge – as encoded in the organisms' internal model (Friston, 2010). Here we argue that the information cost associated with a task corresponds to how much an agent should *update its prior knowledge* in the light of novel evidence (which, in Bayesian terms would correspond to updating a prior distribution to form a posterior distribution); and this, in turn, depends on both the structure of the task (e.g., how many contingencies exist) and the agent's prior knowledge (e.g., what the agent already knows about the task).

In tasks that have clear stimulus-response association rules, determining such information costs is quite straightforward. Let's consider for example a digit-key association task, in which participants have to press the key that corresponds to the digit they see on the screen. If there are 4 possible digits and their probability distribution is uniform, the joint probability distribution prior to seeing the digit is the one shown in Figure 1 (left).

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

When participants see a digit on the screen, they have to update their prior distribution to a posterior distribution in which all the probability mass is in one stimulus-response association (i.e., one cell becomes 1 and all the other cells become zero, see Figure 1, right). This operation requires summing up the log probability of each possible stimulus-response combination (see below for a formal specification) - which, in this case, results in an information cost of –log(4). This approach has been used more than 60 years ago in a series of studies that resulted in the well-known Hick-Hyman law (Hick, 1952). In their seminal work, Hick and Hyman used various tasks in which the number of possible stimulus-response associations varied between 2 and 10. Their striking finding, replicated many times since, was that the reaction time in this task varies in linear proportion to the information cost. More recently, the metabolic activity (indexed by the BOLD signal) of brain regions that guided the decision was shown to vary also in proportion to information cost (Wu et al., 2017) - although the study did not systematically assess the quantitative relationships between information and metabolic costs.

This example suggests that in tasks like the digit-key association shown in Figure 1, which have a clear stimulus-response association matrix and in which the statistical structure is known, cognitive costs (CC) would be proportional to information costs (IC), or entropy of the stimulus-response matrix. In more formal terms:

$$CC \propto IC = -\sum_{s=1}^{n}\sum_{r=1}^{m} P(stim_s, resp_r) \times \log\left(P(stim_s, resp_r)\right)$$

When the statistical structure of the task is unknown and has to be learned, determining information cost requires considering an additional element: a measure of (Kullback-Leibler)

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

divergence D between the real task structure and the agent's current belief (or estimate) of such structure Q[1]:

$$IC = -\sum_{s=1}^{n}\sum_{r=1}^{m} P(stim_s, resp_r)\log\left(P(stim_s, resp_r)\right) + D_{KL}(Q||P)$$

with $D_{KL}(Q||P) = \sum_{i=1}^{n} Q(x_i)\log\left(\frac{Q(x_i)}{P(x_i)}\right)$

Intuitively, this formula implies that there would be an additional cost for performing a task whose statistical structure is still unknown. This information penalty is equal to the cost of learning the novel task contingency.

Understanding the mathematical details of these equations is not important. It is sufficient to consider that, first, we cast cognitive costs in terms of information costs required to engage in a task (e.g., encoding its contingencies and/or its structure); and second, that it is possible to use efficient coding principles to specify these information costs. In the next Section, we use these arguments to discuss what characteristics make cognitive tasks costly.

3. Predictions of the framework

We proposed an information-theoretic perspective that directly links cognitive costs to information costs (and metabolic costs, see below) that a participant incurs when engaging in a task. This framework predicts that certain kinds of tasks - those that have *many degrees of freedom*, are *unfamiliar*, necessitate to go *against natural biases*, have *variable statistical structure* or *low signal to noise ratios* - will lead to large subjective cognitive effort and will

[1] It is worth noting that the above example implies a massive lossy compression during stimuli perception, since all the information presented on the screen (>10^6 bits) is compacted into the few bits necessary to encode which of the possible digits is being presented. This sort of perceptual compression is outside the scope of this work; formal treatments of this problem rely on methods like the Blahut-Arimoto algorithm (Grau-Moya and Braun, 2015; Park and Pillow, 2017).

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

be perceived as aversive in virtue of the fact that they are demanding from an informational (efficient coding) perspective.

3.1 The costs of tasks that have many degrees of freedom

Tasks that have *many degrees of freedom*, or equivalently, a wide probability distribution of state-action combinations, are expected to be cognitively costly under our framework, as they imply low, widely spread prior probabilities - and thus significant information costs to update the priors (see Figure 2A). Arithmetic tasks, the N-back task, but also chess games or creative writing, which are well known for being cognitively demanding (Hess and Polt, 1964; Kellogg, 1987; Marshall, 2002; Westbrook and Braver, 2015) all assign a small prior probability mass for each possible decision and hence, lead to large divergence with the final posterior obtained when the choice has been made. Intuitively, this would be equivalent to having a very large matrix in Figure 1 (left), with the same, small probability in each cell - and an equally large matrix in Figure 1 (right) with only one cell encoding 1 and all the other cells encoding zero. Similarly, tasks that demand a deep contextualisation of the stimulus-response associations (e.g. learning to navigate in a complex maze) will lead to multidimensional prior distributions whose space can inflate very fast, leading also to fast increase in complexity.

3.2 The costs of novel or unfamiliar tasks

A similar issue arises with *unfamiliar tasks*, that is, tasks in which the statistical structure of the sensory states, state transition probabilities (conditional on the performed actions) or action policies (e.g. sequences of motor actions) are poorly known (see Figure 2B). This lack

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

of knowledge of statistical properties of the task leads to non-optimal encoding and large information costs. As shortly discussed above, the extra cost to learn task structure can be formalized as the Kullback-Leibler divergence between the real probability distribution and the one assumed by the subject (given its imperfect knowledge). While the effect of novelty on cognitive effort seems intuitive, relatively little evidence exists on this relation. Yet, a few studies have showed that task effort decreases with training by measuring pupil size - which has been consistently found to index effort (Hyönä et al., 1995; Mykityshyn et al., 2002; Recarte and Nunes, 2000; Solopchuk et al., 2016). It is also interesting to note that training typically leads to decreased (not increased) brain activation (Solopchuk et al., 2017; Wiestler and Diedrichsen, 2013) - plausibly, by increased knowledge of task contingencies and the ensuing decrease of the metabolic costs to maintain the internal generative model.

3.3 The costs of counteracting priors or default policies

Our framework predicts also that tasks that require *counteracting deep priors* or *default policies* (e.g., self-control) would be particularly demanding (see Figure 2C). To understand why this is the case, it is necessary to extend our info-theoretic perspective beyond representational (internal coding) issues to also cover action selection - by appealing to the notion of active inference (Friston, 2010). Under the active inference framework, agents are equipped with hierarchical generative models and perform the kind of Bayesian inference described above; and have the general objective to minimize their free energy or, with some simplifications, their surprise - or the discrepancy between what they expect, based on their beliefs, and what they sense. Importantly, they can minimize their surprise in two ways: by changing their beliefs to make them more similar to what they sense about the world (i.e. perceptual processing) or by changing the world to make it more similar to their prior beliefs

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

(i.e. using actions to fulfil one's own expectations). This duality is possible if one considers that active inference agents are hierarchically organized. While hierarchically lower prior beliefs might faithfully adapt to the external world, hierarchically deeper priors would prescribe what states an agent should achieve by acting (Friston et al., 2012a; Pezzulo et al., 2015). These latter, deeper priors hence play the role of goals and motivational factors that are relatively less permeable to learning (i.e., in Bayesian terms, they have very high precision or inverse uncertainty) because they are key to survival. Indeed, a key statement of active inference is that biological agents need to minimize their long-term surprise in order to survive; if one thinks of these deep priors as describing the "good" states in an agent's ecological niche, minimizing surprise means that the agent should attempt to remain always close to these states. One example of deep (and perhaps hard-coded) prior is a homeostatic drive, such as the prior probability of body nutrients being within an acceptable physiological range. A discrepancy (prediction error) between such deep prior (e.g., be satiated) and the current interoceptive sensations (e.g., feeling hungry) would not lead to the revision of the prior - since the prior is largely impermeable in virtue of having high precision. Instead, the prediction error would steer a cascade of predictions about the conditions that might restore body nutrients (e.g., consuming food), which in turn would steer an adaptive policy or action sequence to fulfil these predictions (e.g., open the fridge and take some food). This formulation makes it apparent that a hungry active inference agent would assign a high probability to (predicted) states and policies associated to consuming food. Since efficient coding assumes that counteracting such high-probability states (or equivalently, pursuing low-probability states) has high information costs, any task that necessitates counteracting deep priors or their ensuing policies should lead to large information and cognitive costs. This explains the effortful nature of self-control (Kool et al., 2013), which consists precisely in going against natural biases, as investigated in the large, but still very controversial

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

literature on ego depletion (Hagger et al., 2016; Martin S. Hagger et al., 2010; Job et al., 2010; Kurzban et al., 2013; Muraven and Baumeister, 2000).

One can use similar arguments to explain why counteracting habits is so costly, too. Habitual behaviour is characterized by fast, automatic processing, low effort and lack of flexibility (Kahneman, 2011; Moors and De Houwer, 2006; Schneider and Chein, 2003). In hierarchical formulations of active inference, habits manifest themselves after overtraining, when (priors at) lower hierarchical layers acquire sufficient precision to become relatively impermeable to top-down influences from higher hierarchical levels (Pezzulo et al., 2015). Habits thus steer default responses to environmental stimuli and are largely inflexible and impermeable to long-term goals. This is because, with overtraining, the encoding of task-specific information follows so closely the statistical task structure that all the task-irrelevant information would get ignored. The ensuing cognitive processing does not need to engage higher hierarchical levels; hence, task processing would be extremely efficient but also crucially dependent on the particular task contingencies that have been learned. Expected stimuli, transitions and actions would have very large priors, and would therefore be encoded with minimal cost, while unexpected stimuli, transitions or actions would have very low prior probabilities and would therefore be very costly to encode. This would imply that a person following habitual policies would have lower costs to engage in familiar tasks but higher costs to engage in novel tasks. Intuitively, this impact of familiarity on cognitive cost could explain why novel environments (e.g. new places, new languages, new people, etc.) are generally described as being more fatiguing than familiar ones, while natural, familiar environments would have, on the contrary, restoring effects (Kaplan and Berman, 2010). The cognitive costs associated to (for example) the Stroop and the Simon tasks can be explained within the same framework, by considering that a preponderant habitual, but incorrect action interferes with the response

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

instructed by the stimulus. In incongruent conditions in the Stroop and the Simon tasks, the prior of the correct, instructed action remains lower compared to the priors associated to incorrect, habitual responses (Wang et al., 2016), thus implying a high cognitive cost. In other words, situations that systematically require encoding posteriors that differ greatly from the initial prior distributions, such as incongruent conditions in the Stroop or the Simon tasks will have comparatively larger complexity scores than congruent conditions for which posteriors conform nicely to the prior. The same arguments, based on strong (deep / homeostatic or shallow / habitual) priors can help understand the phenomenology associated to some pathological situations, such as Tourette syndrome and obsessive-compulsive disorders. These and other syndromes have been associated to strong priors that are, however, maladaptive and lead to inappropriate behaviour (Adams et al., 2013; Friston et al., 2014). Patients suffering from these disorders typically describe being able to overcome their (habitual) tics (Delorme et al., 2016) or compulsive behaviour but at the price of tremendous cognitive effort (Kawohl et al., 2009).

3.4 The costs of task switching and dual tasks

Another classic cause of cognitive effort is *task switching* (see Figure 2D). Changing from a task set to another is associated to a significant cost in performance, usually measured as an increased reaction time, is accompanied with a subjective cognitive effort cost and leads to cognitive fatigue (Apps et al., 2015; Borragán et al., 2017; Sohn et al., 2000; Wylie and Allport, 2000). This is explained in our framework by considering that after a switch from task A to task B, the learned statistical structure of task A would be initially used to encode sensory states, state transition probabilities and action contingencies of task B, thus leading to an additional information cost. The same arguments may apply in more mundane situations

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

in which one is required to switch continuously between multiple tasks (multi-tasking); or to dual-task situations, in which one has either to maintain a sophisticated internal model where the probability distribution span the contingencies of both tasks, or to rapidly and repeatedly switch between the tasks to be executed concurrently. Interestingly, our model makes the specific prediction that switching costs should be proportional to the Kullback-Leibler divergence between the probability distributions governing tasks A and B - or, at least, the subjects' estimates of these distributions. This prediction remains to be tested in future research.

3.5 The costs for controlling the rate of information processing and the role of arousal

Another task feature that is well known to affect cognitive cost is *signal to noise ratio* (see Figure 3). When the ratio between signal and noise in sensory data is low, performance decreases, pupil size increases and subjective cognitive effort increases (Manohar et al., 2015; Sarampalis et al., 2009; Zekveld et al., 2014). In predictive coding theories, low signal-to-noise ratio would automatically imply low sensory precision and an attenuated sensory sampling (because sensations are unreliable). However, when one is engaged in an important task, one would want to extract and use sensory information even if it is immersed in high noise - hence attempt to raise the signal-to-noise ratio. In turn, doing so would require up-regulating sensory sampling, or information rate, to counteract the default adjustments (down-regulations)[2]. However, in our framework that links informational and cognitive costs, this compensatory increase in information rate has an associated cognitive cost (and also a

[2] If information rate really adjusts to noise, it may be implemented as a trade-off between the metabolic cost associated to information rate and the behavioural cost of distortion (Alemi et al., 2017; Marzen and DeDeo, 2017; Still et al., 2012; van den Berg and Ma, 2017) rather than as a variation of information rate to keep distortion constant, since the latter mechanism would lead to prohibitive increase in information rate when noise is high. See also (Gold and Stocker, 2017; Sims, 2016) for a critical discussion of information rate adjustments in the brain.

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

metabolic cost, see Section 4). The adjustability of information rate evokes the concept of task engagement and the fact that motivational factors and reward incentives can influence task performance by putting high information rate at a premium (Camerer et al., 1999). This mechanism implies some cost-benefit computation to select the optimal trade-off between the cost of information rate and the value associated with performance (see Figure 3A-D), akin to many earlier models of effort-based decision making (Chong et al., 2017; Christie and Schrater, 2015; Rigoux and Guigon, 2012; Shenhav et al., 2013; Verguts et al., 2015).

At the neural level, the dynamical adjustments (up-regulations) of information rate as a function of sensory noise may depend on arousal. Arousal could be defined as a global brain state characterized by the amplitude of synchronized low-frequency oscillations and sensory responsiveness (McGinley et al., 2015) and is controlled by brainstem nuclei and neuromodulators such as noradrenaline and acetylcholine (Reimer et al., 2016). A large body of literature suggests that arousal modulates signal to noise ratio in cortical representations by sharpening tuning curves and increasing neural gain, thus improving the encoding of the most relevant information, at the expense of less salient or important data (Eldar et al., 2013; Mather et al., 2016; Servan-Schreiber et al., 1990). Arousal increases also the weight (or precision) of sensory inputs in updating internal models (Nassar et al., 2012). It increases with surprisal (Friedman et al., 1973; Lavín et al., 2014; O'Reilly et al., 2013; Preuschoff et al., 2011), precision-weighted prediction errors (Ferreira-Santos, 2016), uncertainty (Yu and Dayan, 2003), and large incentives (Kahneman and Peavler, 1969; Manohar and Husain, 2015). This body of evidence is compatible with the idea that in specific conditions, such as high-valued tasks, decreasing signal-to-noise ratio triggers arousal mechanisms that adjust

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

(up-regulate) information rate[3], in order to maintain performance. Interestingly, such dynamical adjustments may be indexed by pupil size, which tracks the level of arousal (Reimer et al., 2016). The reliable relations between arousal, cognitive workload and corresponding increases in pupil size (Beatty and Lucero-Wagoner, 2000) may be productively exploited to design experiments that track the dynamical adjustments of information rate.

3.6 Summary so far

To summarize, we have offered a unitary perspective that may explain many experimental findings on cognitive effort and fatigue - by appealing to the fact that specific kinds of tasks that are known to be cognitively costly, such as novel tasks or those that require counteracting habitual policies or switching contingencies, all have high informational costs associated to encoding or revising probability distributions within the generative models that support task performance. Equipped with this formalization of cognitive costs, we can now turn to the question of what are their possible adaptive roles. We propose that cognitive costs are proxies that the brain uses to prevent local metabolic alterations to occur. For example, in order to decide whether or not to engage in a task, the brain might consider its current level of cognitive fatigue and/or the predicted cognitive costs associated to the task - in order to prevent future local metabolic alterations. The idea that cognitive and metabolic costs are associated is not novel (Laughlin et al., 1998). However, our theory indicates that there is a quantitative relation between the *informational* costs of a task (as defined above) and its associated metabolic demands. Discussing this relation is the topic of the next section.

[3] In turn, since arousal is associated with diminished processing of less salient data, it also leads to an opportunity cost, with a down-regulation of exploratory or housekeeping processes (Kurzban et al., 2013; Raichle, 2010) - which also connects our framework to the opportunity cost view on cognitive effort (Kurzban, 2016).

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

4. Cognitive costs and metabolic costs: metabolic consequences of neural activity

Information processing requires energy expenditure (Landauer, 1996; Sengupta et al., 2013; Still et al., 2012). The relation between informational and metabolic costs was central in early theories of efficient coding (Atick, 1992; Attneave, 1954; Barlow, 1961; Borst and Theunissen, 1999; Niven and Laughlin, 2008), which assumed that neural responses, carrying large metabolic costs, impose a constraint on brain information processing capacity. Under this framework, the brain attempts to maximize the amount of (mutual) information it processes, given this fixed capacity limit. More recent approaches have relaxed this principle by using different measures of efficiency, and by considering energetic demand as a cost rather than as a fixed constraint (Denève et al., 2017; Ortega and Braun, 2013; Park and Pillow, 2017; Sengupta et al., 2013). This last, subtle modification opens the door to cost-benefit adjustments of the kind exposed above (see Figure 3), which allow metabolic costs to be adjusted as a function of demands in performance (Marzen and DeDeo, 2017; Park and Pillow, 2017; Sims, 2016).

Numerous pieces of evidence exist in favour of brain reliance on efficient coding, even though most are indirect and qualitative. Low-level vision and audition show data filtering properties and neural codes that are closely similar to predictions issued from efficient coding models (Borst and Theunissen, 1999; Gutnisky and Dragoi, 2008; Laughlin, 2001; Olshausen and Field, 2004; Sharpee et al., 2006; Smith and Lewicki, 2006). Predictability leads to diminished brain activation (Auksztulewicz and Friston, 2016; Bell et al., 2016; Carreiras et al., 2009; Garrido et al., 2013; Lieder et al., 2013; Mars et al., 2008; Meyniel et al., 2016; Overath et al., 2007; Wacongne et al., 2012) and pupil responses (Friedman et al., 1973), but increases reliability of encoding (Kok et al., 2012), in agreement with the idea that

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

predictable stimuli, carrying little information, are encoded more economically. Along the same line, decreased brain activation following training (Chen and Wise, 1995; Solopchuk et al., 2017; Toni et al., 1998; Wiestler and Diedrichsen, 2013) suggests that training decreases metabolic cost by allowing learners to leverage task statistics to optimize brain representations, while increasing the quantity of information being processed.

Given the fundamental link between information processing and metabolic demands, the observation that global cerebral energy consumption does not vary between resting and active conditions may appear surprising (Sokoloff, 2009; Sokoloff et al., 1955). Blood delivers glucose and oxygen to brain in excess of demand, such that in physiological conditions (i.e. in absence of hypoxia or hypoglycaemia), the availability of energetic precursors is not a limiting factor to cognitive activity (Brown and Ransom, 2014). However, total blood delivery to the brain is a constant that cannot be upregulated in response to cognitive demand (Brown and Ransom, 2014). Therefore, the cost of cognitive activity can hardly be explained by the need to curb total energetic consumption. It is noteworthy, however, that despite this lack of change in global energetic demand of the brain, global glucose intake increases in the brain during cognitive activity (Volkow et al., 2008). This utilization of glucose in excess of oxygen consumption is referred to as aerobic glycolysis (Vaishnavi et al., 2010). It is modulated by arousal (Dienel and Cruz, 2016) and while the function of aerobic glycolysis remains debated, it may be linked to cortical plasticity (Goyal et al., 2014) and the replenishment of glutamate and GABA reserves (Hertz and Chen, 2017a). This increased glucose demand during active behaviour has justified resource depletion theories of cognitive effort, according to which glucose is the main resource that puts a constraint on cognitive activity (Gailliot et al., 2007). This theory, and the experimental evidence on which it is based, have been put under increased criticism recently (Hagger et al., 2016; Martin S Hagger et al., 2010; Kurzban et al., 2013). Here we consider an alternate view on the link between

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

cognitive cost and metabolic activity, based on the idea that metabolic cost should be understood as a local rather than a global phenomenon.

Astrocytes contain important stocks of glycogen (Benarroch, 2010). These glycogen stores are mobilized during sensory stimulation (Dienel and Cruz, 2006), intense physical exercise (Matsui et al., 2017) or encoding in long-term memory (Hertz and Chen, 2017b). The rate of degradation of glycogen, or glycogenolysis, rises 6–50-fold above resting-state values during neural activity (Dienel and Cruz, 2014) and is under the control of arousal (Gibbs, 2015). Blocking the degradation of glycogen leads to dramatic increases in glucose consumption, indicating that in normal conditions, glycogen is an important source of energy supply during neural activity, and that its lack can be compensated by glucose mobilization, but supposedly with an associated loss of efficiency (Dienel and Cruz, 2014). Blocking the production of glycogen-derived lactate has dramatic consequences on memory formation and physical endurance (Gibbs, 2015; Matsui et al., 2017). Also, glycogen levels fall during daytime, or sleep deprivation and are replenished during sleep (Kong et al., 2002). Finally, de novo synthesis of glutamate depends also on glycogenolysis (Hertz and Chen, 2017b). Therefore, it seems plausible that sustained local neural activity could lead to the *local* depletion of glycogen reserves, which could be responsible for the feeling of cognitive fatigue that follows prolonged mental demands (Christie and Schrater, 2015). It is worth pointing out that glycogenolysis in human primary visual cortex showed no detectable changes after visual stimulation (Öz et al., 2007). This finding appears to contradict the hypothesis of a link between glycogen reserves and fatigue but the interpretation of this negative result remains debated, in part because of the limited sensitivity of the measurement technique used in this study (DiNuzzo et al., 2012).

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Another link between metabolic and cognitive (and informational) costs emerges when considering the role of arousal in adjusting information rate, as discussed earlier. This increased informational demand plausibly corresponds to commensurate surges in energy mobilization. Arousal appears to increase the metabolic mobilization orchestrated by astrocytes in response to neural activity (O'Donnell et al., 2012; Paukert et al., 2014), including glycogen reserves (Hertz and Zielke, 2004; O'Donnell et al., 2012), while also restricting glymphatic circulation, thus limiting the capacity of the brain to eliminate potentially harmful metabolites (Xie et al., 2013). Interestingly, although arousal is a global phenomenon, its effect in cortex is believed to be restricted to active regions (Mather et al., 2016). Increased arousal would thus lead to increased metabolic rate in these active regions, while dampening activation in already less active background structures (Mather et al., 2016). This suggests that – even though global energetic brain expenditure may remain constant across task and rest conditions (Sokoloff, 2009) and increased metabolic costs in specific brain regions may entail decreased demands in other regions (Fox and Raichle, 2007) - cognitive effort and fatigue may be the consequence of *local* rather than global metabolic demands[4].

If engaging in cognitive tasks produces cognitive fatigue and ultimately depletes local metabolic resources, how are these restored? Cerebral housekeeping is assumed to be one of the main functions of sleep (Tononi and Cirelli, 2014; Xie et al., 2013). The necessity to shut down cerebral activity periodically entails that metabolic steady-state cannot be maintained

[4] Since effort and fatigue are both global phenomena, they should result from some form of integration of the local alterations. This integration should be nonlinear and convex, such that the marginal cost of increasing metabolic activity increases with metabolic activity. Short of that, the cost of local metabolic activity in one region of the brain could be compensated by decreased activity in other brain regions. Discussing the neural substrate of this integration is outside the scope of the present work but anterior cingulate cortex and anterior insula should be considered as potential hubs for such integration (Engström et al., 2013).

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

during continuous periods of brain activity (Tononi and Cirelli, 2014). This rest-dependent housekeeping activity may include the replenishment of protein stocks, of presynaptic calcium, of astrocytic glycogen (Kong et al., 2002), the recycling of membranes, the resting of mitochondria (Tononi and Cirelli, 2014), the replenishment of glutamate vesicles (Tani et al., 2014) or the clearance of the extracellular space (Xie et al., 2013). Some authors have proposed that the accumulation of these deviations from metabolic steady-state could lead cortical regions to enter a local sleep mode, characterized by slow-wave synchronization and associated with disturbed processing capacity (Siclari and Tononi, 2017). Going back to the issue of anaerobic glycolysis, the excess utilization of glucose during intense brain activity could lead to the accumulation of intermediate metabolic pools, which would be converted to their final metabolic destination only during periods of rest or sleep (Madsen et al., 1999). These deviations from steady-state, local sleep modes and accumulation of intermediate metabolites could be accelerated locally when engaging in demanding tasks, eventually leading to fatigue.

Finally, the severity of the behavioural effects associated with local metabolic alterations could depend on the affected brain regions. On the one hand, sensory cortices encompass large area, with topographic organization, in which processing of different input features or spatial locations leads to activations of different cortical regions. Prolonged execution of spatially constrained task leads to local neural alterations (Mednick et al., 2005), and decline in performance that remains limited to the stimulated location (Mednick et al., 2002). Such alterations are easy to compensate. On the other hand, the multiple demand system is an ensemble of brain areas engaged in a large variety of tasks (Fedorenko et al., 2013), including in interoceptive processing (Kleckner et al., 2017), i.e. in adapting behaviour to ensure physiological needs, a function essential to survival. Thus, local metabolic depletion within this network may have more adverse behavioural consequences (and presumably more severe

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

effort and fatigue phenomenology), bridging our theory with the opportunity cost view on mental effort (Kurzban et al., 2013).

In sum, we have argued that information processing leads to quantifiable metabolic costs, in the form of glycogen depletion, accumulation of latent metabolic processes, or local sleep modes, whose consequences would remain largely confined to the neural tissue involved during the task. These local metabolic changes are arousal-dependent, and their consequences could vary in severity as a function of the affected brain region. We propose that effort is the phenomenological consequence of an adaptive mechanism that drives us away from behaviours that are anticipated to worsen these local alterations.

5. Conclusions and relations to alternative views

The phenomenology of cognitive cost and cognitive effort - in terms of subjective feeling of exhaustion experienced when performing a cognitive task and its associated task-avoidance - is relatively well known. Yet, several aspects of the problem of the costs of cognition are currently debated, including the specification of what is costly in cognitive processing, how to quantify these costs and what is their adaptive value.

We have defended a view that starts from the idea that, if the brain encodes information in accordance with the principles of efficient coding, then cognitive cost should be a function of the information cost required to encode and perform the task (using generative models). We have used this theory to explain the cognitive costs associated to (for example) novel or complex tasks, showing that it can provide a unitary perspective on several experimental findings in the literature. Furthermore, we have discussed how cognitive effort (i.e., the

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

subjective feeling associated to performing costly tasks) and cognitive fatigue that ensue from long-term engagement in costly tasks can be considered as adaptive mechanisms that prevent individuals from performing activities that may have adverse consequences in the long run, i.e., activities that imply huge local metabolic demands. In this perspective, difficult cognitive tasks are avoided because they entail an expected loss of long-term utility (caused by potential increases of local metabolic demands).

Our perspective is coherent with several recent theories, which proposed that task avoidance stems from the (optimal) choice between potential policies while accounting for their respective cost. In this framework, cognitive effort is assumed to depend on the degree to which the task depends on cognitive control (Shenhav et al., 2017, 2013). The present work is in continuity with these earlier proposals as it relies on optimality principles and describes cognitive effort as a cost, which discounts the expected utility of a given course of actions (Apps et al., 2015; Chong et al., 2017; Manohar et al., 2015; Westbrook and Braver, 2015). However, our proposal departs from these theories as it addresses more directly the question of the *causes* of cognitive cost - and casts them in terms of information principles. In particular, the present framework attributes costs to general informational aspects of cognitive processing, rather than specifically to cognitive control. What determines cognitive cost is the amount of information to be processed and tasks involving cognitive control may be more costly in general because they typically require large informational loads (Fan, 2014) on the multiple demand system (Wu et al., 2017).

Another related proposal addresses cognitive effort from a normative perspective, in which apparently maladaptive states (cognitive fatigue) constitute the adaptive response of an optimal controller that has (or feels having) low self-efficacy and limited control over one's

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

own environment, similar to learned helplessness in the animal learning literature (Stephan et al., 2016). Although we have not addressed the long-term consequences of being exposed to complex cognitive tasks, our model would be coherent with this proposal in assuming that prolonged expectations of poor outcomes, or poor control, would crystallize task-avoidance behaviour. In other words, an agent whose local metabolic resources are frequently depleted, could develop an adaptive task aversion, manifested, for example, as chronic fatigue syndrome.

It is also worth noting that challenging cognitive activity is not always experienced as aversive but may be even sought for (Cacioppo et al., 1984). Idling or engaging in repetitive, monotonous tasks can be also unpleasant (Nakamura and Csikszentmihalyi, 2002). This seeking of effortful activities, in apparent contradiction with our framework, can be explained by the mediating influence of intrinsic motivation. Complex tasks need mastery, and intrinsic motivation appears to depend in large part on the feeling of competence and autonomy, i.e. the feeling of being capable of performing a task, despite its difficulty (Ryan and Deci, 2000) - and in the active inference setting, on the necessity to improve one's internal models (Friston et al., 2017). Pathologies like depression are characterized by increased task aversion (Salamone et al., 2016), fatigue-induced performance decline can be counteracted by self-affirmation (Job et al., 2010; Schmeichel and Vohs, 2009) and people report enjoying challenging tasks even when controlling for perceived expertise (Abuhamdeh and Csikszentmihalyi, 2012). Intrinsic motivation has been associated to anterior insula (Arsalidou et al., 2017; Lee et al., 2012; Wager and Barrett, 2004), an interoceptive brain area, suggesting that motivation to perform a task stems from our belief that its performance would lead eventually to positive effects on interoceptive states. This connects to the "dark room" problem evoked in the context of active inference, in which minimization of free

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

energy and cognitive effort seem to predict that agents should seek the absence of interaction with the environment in order to suppress information cost altogether. However, because of the aforementioned deep priors of maintaining interoceptive states within ranges compatible with survival (Friston et al., 2012b), this putative preference for null information cost is overtaken by interoceptive needs (in terms of both homeostatic imperatives and intrinsic motivation), which leads naturally to exploratory behaviour, targeted to resolve uncertainty about future states of the world (Friston et al., 2015). In other words, improving one's internal model to minimize surprise in the future can compensate the short-term costs of investing effort in the present moment. Spontaneous engagement in demanding tasks would therefore depend on the cost-benefit comparison between immediate informational and metabolic costs and future needs, mediated by mechanisms of exploration, model learning or intrinsic motivation that are part and parcel of active inference (or free energy minimization; Friston et al., 2017). We believe that neuroimaging studies on mental fatigue will be particularly helpful to disentangle the contribution of local brain metabolism and intrinsic motivation to task aversiveness.

In sum, we have provided a novel view on cognitive effort costs, based on principles of efficient coding and active inference. While supported by previous experimental evidence, it makes specific quantitative predictions, which will be an exciting venue of future research.

Acknowledgements

This work was supported by Fonds de la Recherche Scientifique (FNRS–FDP), Fondation Médicale Reine Elisabeth (FMRE), the Fondation Louvain and IdEx Bordeaux.

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

References

Abuhamdeh, S., Csikszentmihalyi, M., 2012. The Importance of Challenge for the Enjoyment of Intrinsically Motivated, Goal-Directed Activities. Personal. Soc. Psychol. Bull. 38, 317–330. doi:10.1177/0146167211427147

Adams, R.A., Stephan, K.E., Brown, H.R., Frith, C.D., Friston, K.J., 2013. The Computational Anatomy of Psychosis. Front. Psychiatry 4. doi:10.3389/fpsyt.2013.00047

Alemi, A., Machens, C., Denève, S., Slotine, J.-J., 2017. Learning arbitrary dynamics in efficient, balanced spiking networks using local plasticity rules.

Apps, M.A.J., Grima, L.L., Manohar, S., Husain, M., 2015. The role of cognitive effort in subjective reward devaluation and risky decision-making. Sci. Rep. 5, 16880. doi:10.1038/srep16880

Arsalidou, M., Pawliw-Levac, M., Sadeghi, M., Pascual-Leone, J., 2017. Brain areas associated with numbers and calculations in children: Meta-analyses of fMRI studies. Dev. Cogn. Neurosci. doi:10.1016/j.dcn.2017.08.002

Atick, J., 1992. Could information theory provide an ecological theory of sensory processing? Netw. Comput. Neural Syst. 3, 213–251. doi:10.1088/0954-898X/3/2/009

Attneave, F., 1954. Some informational aspects of visual perception. Psychol. Rev. 61, 183–193.

Auksztulewicz, R., Friston, K., 2016. Repetition suppression and its contextual determinants in predictive coding. Cortex 80, 125–140. doi:10.1016/j.cortex.2015.11.024

Bailey, A., Channon, S., Beaumont, J.G., 2007. The relationship between subjective fatigue and cognitive fatigue in advanced multiple sclerosis. Mult. Scler. J. 13, 73–80. doi:10.1177/1352458506071162

Barlow, H.B., 1961. Possible principles underlying the transformation of sensory messages. Sens. Commun. 217–234.

Beatty, J., Lucero-Wagoner, B., 2000. The pupillary system. Handb. Psychophysiol. 142–162.

Bell, A.H., Summerfield, C., Morin, E.L., Malecek, N.J., Ungerleider, L.G., 2016. Encoding of Stimulus Probability in Macaque Inferior Temporal Cortex. Curr. Biol. 26, 2280–2290. doi:10.1016/j.cub.2016.07.007

Benarroch, E.E., 2010. Glycogen metabolism: Metabolic coupling between astrocytes and neurons. Neurology 74, 919–923. doi:10.1212/WNL.0b013e3181d3e44b

Borragán, G., Slama, H., Bartolomei, M., Peigneux, P., 2017. Cognitive fatigue: A Time-based Resource-sharing account. Cortex 89, 71–84. doi:10.1016/j.cortex.2017.01.023

Borst, A., Theunissen, F.E., 1999. Information theory and neural coding. Nat. Neurosci. 2, 947–57. doi:10.1038/14731

Brown, A.M., Ransom, B.R., 2014. Astrocyte glycogen as an emergency fuel under conditions of glucose deprivation or intense neural activity. Metab. Brain Dis. 30, 233–239. doi:10.1007/s11011-014-9588-2

Cacioppo, J.T., Petty, R.E., Kao, C.F., 1984. The efficient assessment of need for cognition. J. Pers. Assess. 48, 306–307. doi:10.1207/s15327752jpa4803_13

Camerer, C.F., Hogarth, R.M., Budescu, D. V., Eckel, C., 1999. The Effects of Financial Incentives in Experiments: A Review and Capital-Labor-Production Framework, in: Elicitation of Preferences. pp. 7–48. doi:10.1007/978-94-017-1406-8_2

Carreiras, M., Riba, J., Vergara, M., Heldmann, M., Münte, T.F., 2009. Syllable congruency and word frequency effects on brain activation. Hum. Brain Mapp. 30, 3079–3088. doi:10.1002/hbm.20730

Chalk, M., Seitz, A.R., Series, P., 2010. Rapidly learned stimulus expectations alter perception of motion. J. Vis. 10, 2–2. doi:10.1167/10.8.2

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Chen, L.L., Wise, S.P., 1995. Neuronal activity in the supplementary eye field during acquisition of conditional oculomotor associations. J Neurophysiol 73, 1101–1121. doi:10.1016/S0896-6273(00)80658-3

Chong, T.T.J., Apps, M., Giehl, K., Sillence, A., Grima, L.L., Husain, M., 2017. Neurocomputational mechanisms underlying subjective valuation of effort costs. PLoS Biol. 15. doi:10.1371/journal.pbio.1002598

Christie, S.T., Schrater, P., 2015. Cognitive cost as dynamic allocation of energetic resources. Front. Neurosci. 9, 1–15. doi:10.3389/fnins.2015.00289

Collell, G., Fauquet, J., 2015. Brain activity and cognition: a connection from thermodynamics and information theory. Front. Psychol. 6, 818. doi:10.3389/fpsyg.2015.00818

Delorme, C., Salvador, A., Valabrègue, R., Roze, E., Palminteri, S., Vidailhet, M., De Wit, S., Robbins, T., Hartmann, A., Worbe, Y., 2016. Enhanced habit formation in Gilles de la Tourette syndrome. Brain 139, 605–615. doi:10.1093/brain/awv307

Denève, S., Alemi, A., Bourdoukan, R., 2017. The Brain as an Efficient and Robust Adaptive Learner. Neuron. doi:10.1016/j.neuron.2017.05.016

Dienel, G.A., Cruz, N.F., 2016. Aerobic glycolysis during brain activation: adrenergic regulation and influence of norepinephrine on astrocytic metabolism. J. Neurochem. 14–52. doi:10.1111/jnc.13630

Dienel, G.A., Cruz, N.F., 2014. Contributions of glycogen to astrocytic energetics during brain activation. Metab. Brain Dis. 30, 281–298. doi:10.1007/s11011-014-9493-8

Dienel, G.A., Cruz, N.F., 2006. Astrocyte activation in working brain: Energy supplied by minor substrates. Neurochem. Int. 48, 586–595. doi:10.1016/j.neuint.2006.01.004

DiNuzzo, M., Mangia, S., Maraviglia, B., Giove, F., 2012. The role of astrocytic glycogen in supporting the energetics of neuronal activity. Neurochem. Res. 37, 2432–2438. doi:10.1007/s11064-012-0802-5

Eldar, E., Cohen, J.D., Niv, Y., 2013. The effects of neural gain on attention and learning. Nat. Neurosci. 16, 1146–1153. doi:10.1038/nn.3428

Engström, M., Landtblom, A.-M., Karlsson, T., 2013. Brain and effort: brain activation and effort-related working memory in healthy participants and patients with working memory deficits. Front. Hum. Neurosci. 7, 140. doi:10.3389/fnhum.2013.00140

Fairhall, A.L., Lewen, G.D., Bialek, W., de Ruyter van Steveninck, R.R., 2001. Efficiency and ambiguity in an adaptive neural code. Nature 412, 787–792. doi:10.1038/35090500

Fan, J., 2014. An information theory account of cognitive control. Front. Hum. Neurosci. 8. doi:10.3389/fnhum.2014.00680

Fedorenko, E., Duncan, J., Kanwisher, N., 2013. Broad domain generality in focal regions of frontal and parietal cortex. Proc. Natl. Acad. Sci. U. S. A. 110, 16616–21. doi:10.1073/pnas.1315235110

Ferreira-Santos, F., 2016. The role of arousal in predictive coding. Behav. Brain Sci. 39, e207. doi:10.1017/S0140525X15001788

Fox, M.D., Raichle, M.E., 2007. Spontaneous fluctuations in brain activity observed with functional magnetic resonance imaging. Nat. Rev. Neurosci. 8, 700–711. doi:10.1038/nrn2201

Friedman, D., Hakerem, G., Sutton, S., Fleiss, J.L., 1973. Effect of stimulus uncertainty on the pupillary dilation response and the vertex evoked potential. Electroencephalogr. Clin. Neurophysiol. 34, 475–484. doi:10.1016/0013-4694(73)90065-5

Friston, K., 2010. The free-energy principle: a unified brain theory? Nat. Rev. Neurosci. 11, 127–138. doi:10.1038/nrn2787

Friston, K., Adams, R., Montague, R., 2012a. What is value-accumulated reward or evidence? Front. Neurorobot. doi:10.3389/fnbot.2012.00011

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Friston, K., Rigoli, F., Ognibene, D., Mathys, C., Fitzgerald, T., Pezzulo, G., 2015. Active inference and epistemic value. Cogn. Neurosci. 6, 187–224. doi:10.1080/17588928.2015.1020053

Friston, K., Thornton, C., Clark, A., 2012b. Free-energy minimization and the dark-room problem. Front. Psychol. 3, 130. doi:10.3389/fpsyg.2012.00130

Friston, K.J., Lin, M., Frith, C.D., Pezzulo, G., Hobson, J.A., Ondobaka, S., 2017. Active Inference, Curiosity and Insight. Neural Comput. 1–51. doi:10.1162/neco_a_00999

Friston, K.J., Stephan, K.E., Montague, R., Dolan, R.J., 2014. Computational psychiatry: the brain as a phantastic organ. The Lancet Psychiatry 1, 148–158. doi:10.1016/S2215-0366(14)70275-5

Gailliot, M.T., Baumeister, R.F., DeWall, C.N., Maner, J.K., Plant, E.A., Tice, D.M., Brewer, L.E., Schmeichel, B.J., 2007. Self-control relies on glucose as a limited energy source: Willpower is more than a metaphor. J. Pers. Soc. Psychol. 92, 325–336. doi:10.1037/0022-3514.92.2.325

Garrido, M.I., Sahani, M., Dolan, R.J., 2013. Outlier Responses Reflect Sensitivity to Statistical Structure in the Human Brain. PLoS Comput. Biol. 9. doi:10.1371/journal.pcbi.1002999

Gibbs, M.E., 2015. Role of Glycogenolysis in Memory and Learning: Regulation by Noradrenaline, Serotonin and ATP. Front. Integr. Neurosci. 9, 70. doi:10.3389/fnint.2015.00070

Gold, J.I., Stocker, A.A., 2017. Visual Decision-Making in an Uncertain and Dynamic World. Annu. Rev. Vis. Sci. 3, annurev-vision-111815-114511. doi:10.1146/annurev-vision-111815-114511

Goyal, M.S., Hawrylycz, M., Miller, J.A., Snyder, A.Z., Raichle, M.E., 2014. Aerobic glycolysis in the human brain is associated with development and neotenous gene expression. Cell Metab. 19, 49–57. doi:10.1016/j.cmet.2013.11.020

Grau-Moya, J., Braun, D. ~A., 2015. Adaptive information-theoretic bounded rational decision-making with parametric priors. ArXiv e-prints.

Gutnisky, D.A., Dragoi, V., 2008. Adaptive coding of visual information in neural populations. Nature 452, 220–224. doi:10.1038/nature06563

Hagger, M.S., Chatzisarantis, N.L.D., Alberts, H., Anggono, C.O., Batailler, C., Birt, A.R., Brand, R., Brandt, M.J., Brewer, G., Bruyneel, S., Calvillo, D.P., Campbell, W.K., Cannon, P.R., Carlucci, M., Carruth, N.P., Cheung, T., Crowell, A., De Ridder, D.T.D., Dewitte, S., Elson, M., Evans, J.R., Fay, B.A., Fennis, B.M., Finley, A., Francis, Z., Heise, E., Hoemann, H., Inzlicht, M., Koole, S.L., Koppel, L., Kroese, F., Lange, F., Lau, K., Lynch, B.P., Martijn, C., Merckelbach, H., Mills, N. V., Michirev, A., Miyake, A., Mosser, A.E., Muise, M., Muller, D., Muzi, M., Nalis, D., Nurwanti, R., Otgaar, H., Philipp, M.C., Primoceri, P., Rentzsch, K., Ringos, L., Schlinkert, C., Schmeichel, B.J., Schoch, S.F., Schrama, M., Schütz, A., Stamos, A., Tinghög, G., Ullrich, J., vanDellen, M., Wimbarti, S., Wolff, W., Yusainy, C., Zerhouni, O., Zwienenberg, M., 2016. A Multilab Preregistered Replication of the Ego-Depletion Effect. Perspect. Psychol. Sci. 11, 546–573. doi:10.1177/1745691616652873

Hagger, M.S., Wood, C., Stiff, C., Chatzisarantis, N.L.D., 2010. Ego depletion and the strength model of self-control: A meta-analysis. Psychol. Bull. 136, 495–525. doi:10.1037/a0019486

Hagger, M.S., Wood, C., Stiff, C., Chatzisarantis, N.L.D., 2010. Ego depletion and the strength model of self-control: a meta-analysis. Psychol. Bull. 136, 495–525. doi:10.1037/a0019486

Harremoës, P., Tishby, N., 2007. The information bottleneck revisited or how to choose a good distortion measure, in: IEEE International Symposium on Information Theory -

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Proceedings. pp. 566–570. doi:10.1109/ISIT.2007.4557285
Hertz, L., Chen, Y., 2017a. Integration between Glycolysis and Glutamate-Glutamine Cycle Flux May Explain Preferential Glycolytic Increase during Brain Activation, Requiring Glutamate. Front. Integr. Neurosci. 11, 18. doi:10.3389/fnint.2017.00018
Hertz, L., Chen, Y., 2017b. Glycogenolysis, an astrocyte-specific reaction, is essential for both astrocytic and neuronal activities involved in learning. Neuroscience. doi:10.1016/j.neuroscience.2017.06.025
Hertz, L., Zielke, H.R., 2004. Astrocytic control of glutamatergic activity: Astrocytes as stars of the show. Trends Neurosci. 27, 735–743. doi:10.1016/j.tins.2004.10.008
Hess, E.H., Polt, J.M., 1964. Pupil Size in Relation to Mental Activity during Simple Problem-Solving. Science (80-.). 143, 1190–1192.
Hick, W.., 1952. On the rate of gain of information. Q. J. Exp. Psychol. 4, 11–26. doi:10.1080/17470215208416600
Hockey, G.R.J., 2011. A Motivational Control Theory of Cognitive Fatigue. Cogn. fatigue Multidiscip. Perspect. Curr. Res. Futur. Appl. 167–187. doi:10.1037/12343-008
Hyönä, J., Tommola, J., Alaja, A.-M., 1995. Pupil Dilation as a Measure of Processing Load in Simultaneous Interpretation and Other Language Tasks. Q. J. Exp. Psychol. Sect. A 48, 598–612. doi:10.1080/14640749508401407
Inzlicht, M., Bartholow, B.D., Hirsh, J.B., 2015. Emotional foundations of cognitive control. Trends Cogn. Sci. doi:10.1016/j.tics.2015.01.004
Job, V., Dweck, C.S., Walton, G.M., 2010. Ego depletion-is it all in your head? Implicit theories about willpower affect self-regulation. Psychol. Sci. 21, 1686–1693. doi:10.1177/0956797610384745
Kahneman, D., 2011. Thinking , Fast and Slow (Abstract), Book. doi:10.1007/s13398-014-0173-7.2
Kahneman, D., Peavler, W.S., 1969. Incentive effects and pupillary changes in association learning. J. Exp. Psychol. 79, 312–318. doi:10.1037/h0026912
Kaplan, S., Berman, M.G., 2010. Directed Attention as a Common Resource for Executive Functioning and Self-Regulation. Perspect. Psychol. Sci. 5, 43–57. doi:10.1177/1745691609356784
Kawohl, W., Bruhl, A., Krowatschek, G., Ketteler, D., Herwig, U., 2009. Functional magnetic resonance imaging of tics and tic suppression in Gilles de la Tourette syndrome. World J Biol Psychiatry 10, 567–570. doi:10.1080/15622970802118356
Kellogg, R.T., 1987. Effects of topic knowledge on the allocation of processing time and cognitive effort to writing processes. Mem. Cognit. 15, 256–266. doi:10.3758/BF03197724
Kleckner, I.R., Zhang, J., Touroutoglou, A., Chanes, L., Xia, C., Simmons, W.K., Quigley, K.S., Dickerson, B.C., Feldman Barrett, L., 2017. Evidence for a large-scale brain system supporting allostasis and interoception in humans. Nat. Hum. Behav. 1, 69. doi:10.1038/s41562-017-0069
Kok, P., Jehee, J.F.M., de Lange, F.P., 2012. Less Is More: Expectation Sharpens Representations in the Primary Visual Cortex. Neuron 75, 265–270. doi:10.1016/j.neuron.2012.04.034
Kong, J., Shepel, P.N., Holden, C.P., Mackiewicz, M., Pack, A.I., Geiger, J.D., 2002. Brain glycogen decreases with increased periods of wakefulness: implications for homeostatic drive to sleep. J. Neurosci. 22, 5581–7. doi:20026500
Kool, W., McGuire, J.T., Rosen, Z.B., Botvinick, M.M., 2010. Decision making and the avoidance of cognitive demand. J. Exp. Psychol. Gen. 139, 665–682.
Kool, W., McGuire, J.T., Wang, G.J., Botvinick, M.M., 2013. Neural and Behavioral Evidence for an Intrinsic Cost of Self-Control. PLoS One 8, 1–6.

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

doi:10.1371/journal.pone.0072626
Kurzban, R., 2016. The sense of effort. Curr. Opin. Psychol. 7, 67–70. doi:10.1016/j.copsyc.2015.08.003
Kurzban, R., Duckworth, A., Kable, J.W., Myers, J., 2013. An opportunity cost model of subjective effort and task performance. Behav. Brain Sci. 36, 661–679. doi:10.1017/S0140525X12003196
Landauer, R., 1996. Minimal Energy Requirements in Communication. Science (80-.). 272, 1914–1918. doi:10.1126/science.272.5270.1914
Laughlin, S.B., 2001. Energy as a constraint on the coding and processing of sensory information. Curr. Opin. Neurobiol. 11, 475–480. doi:10.1016/S0959-4388(00)00237-3
Laughlin, S.B., de Ruyter Van Steveninck, R.R., Anderson, J.C., 1998. The metabolic cost of neural information. Nat. Neurosci. 1, 36–41. doi:10.1038/236
Lavín, C., San Martín, R., Rosales Jubal, E., 2014. Pupil dilation signals uncertainty and surprise in a learning gambling task. Front. Behav. Neurosci. 7. doi:10.3389/fnbeh.2013.00218
Lee, W., Reeve, J., Xue, Y., Xiong, J., 2012. Neural differences between intrinsic reasons for doing versus extrinsic reasons for doing: An fMRI study. Neurosci. Res. 73, 68–72. doi:10.1016/j.neures.2012.02.010
Lieder, F., Daunizeau, J., Garrido, M.I., Friston, K.J., Stephan, K.E., 2013. Modelling Trial-by-Trial Changes in the Mismatch Negativity. PLoS Comput. Biol. 9. doi:10.1371/journal.pcbi.1002911
Madsen, P.L., Cruz, N.F., Sokoloff, L., Dienel, G. a, 1999. Cerebral oxygen/glucose ratio is low during sensory stimulation and rises above normal during recovery: excess glucose consumption during stimulation is not accounted for by lactate efflux from or accumulation in brain tissue. J. Cereb. Blood Flow Metab. 19, 393–400. doi:10.1097/00004647-199904000-00005
Manohar, S.G., Chong, T.T.J., Apps, M.A.J., Batla, A., Stamelou, M., Jarman, P.R., Bhatia, K.P., Husain, M., 2015. Reward Pays the Cost of Noise Reduction in Motor and Cognitive Control. Curr. Biol. 25, 1707–1716. doi:10.1016/j.cub.2015.05.038
Manohar, S.G., Husain, M., 2015. Reduced pupillary reward sensitivity in Parkinson's disease. npj Park. Dis. 1, 15026. doi:10.1038/npjparkd.2015.26
Mars, R.B., Debener, S., Gladwin, T.E., Harrison, L.M., Haggard, P., Rothwell, J.C., Bestmann, S., 2008. Trial-by-Trial Fluctuations in the Event-Related Electroencephalogram Reflect Dynamic Changes in the Degree of Surprise. J. Neurosci. 28, 12539–12545. doi:10.1523/JNEUROSCI.2925-08.2008
Marshall, S.P., 2002. The Index of Cognitive Activity: measuring cognitive workload. Proc. IEEE 7th Conf. Hum. Factors Power Plants 5–9. doi:10.1109/HFPP.2002.1042860
Marzen, S.E., DeDeo, S., 2017. The evolution of lossy compression. R. Soc. Interface 14, 1–10. doi:10.1098/rsif.2017.0166
Mather, M., Clewett, D., Sakaki, M., Harley, C.W., 2016. Norepinephrine ignites local hotspots of neuronal excitation: How arousal amplifies selectivity in perception and memory. Behav. Brain Sci. 39, e200. doi:10.1017/S0140525X15000667
Matsui, T., Omuro, H., Liu, Y.-F., Soya, M., Shima, T., McEwen, B.S., Soya, H., 2017. Astrocytic glycogen-derived lactate fuels the brain during exhaustive exercise to maintain endurance capacity. Proc. Natl. Acad. Sci. 114, 6358–6363. doi:10.1073/pnas.1702739114
McGinley, M.J., David, S. V., McCormick, D.A., 2015. Cortical Membrane Potential Signature of Optimal States for Sensory Signal Detection. Neuron 87, 179–192. doi:10.1016/j.neuron.2015.05.038
Mednick, S.C., Arman, a C., Boynton, G.M., 2005. The time course and specificity of

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

perceptual deterioration. Proc. Natl. Acad. Sci. U. S. A. 102, 3881–3885. doi:10.1073/pnas.0407866102

Mednick, S.C., Nakayama, K., Cantero, J.L., Atienza, M., Levin, A.A., Pathak, N., Stickgold, R., 2002. The restorative effect of naps on perceptual deterioration. Nat. Neurosci. 5, 677. doi:10.1038/nn864

Meyniel, F., Maheu, M., Dehaene, S., 2016. Human Inferences about Sequences: A Minimal Transition Probability Model. PLoS Comput. Biol. 12. doi:10.1371/journal.pcbi.1005260

Mischel, W., 2014. The Marshmallow Test: Mastering self-control, The Marshmallow Test: Mastering self-control. doi:10.1038/scientificamerican0914-92c

Moors, A., De Houwer, J., 2006. Automaticity: A Theoretical and Conceptual Analysis. Psychol. Bull. 132, 297–326. doi:10.1037/0033-2909.132.2.297

Muraven, M., Baumeister, R.F., 2000. Self-Regulation and Depletion of Limited Resources□: Does Self-Control Resemble a Muscle□? Psychol. Bull. 126, 247–259. doi:10.1037//0033-2909.126.2.247

Mykityshyn, A.L., Fisk, A.D., Rogers, W. a, 2002. Learning to use a home medical device: Mediating age-related differences with training. Hum. Factors 44, 354–364. doi:10.1518/0018720024497727

Nakamura, J., Csikszentmihalyi, M., 2002. The Concept of Flow Optimal Experience and Its Role in Development. Handb. Posit. Psychol. 89–105. doi:10.1007/978-94-017-9088-8_16

Nassar, M.R., Rumsey, K.M., Wilson, R.C., Parikh, K., Heasly, B., Gold, J.I., 2012. Rational regulation of learning dynamics by pupil-linked arousal systems. Nat. Neurosci. 15, 1040–1046. doi:10.1038/nn.3130

Niven, J.E., Laughlin, S.B., 2008. Energy limitation as a selective pressure on the evolution of sensory systems. J. Exp. Biol. 211, 1792–1804. doi:10.1242/jeb.017574

O'Donnell, J., Zeppenfeld, D., McConnell, E., Pena, S., Nedergaard, M., 2012. Norepinephrine: A neuromodulator that boosts the function of multiple cell types to optimize CNS performance. Neurochem. Res. 37, 2496–2512. doi:10.1007/s11064-012-0818-x

O'Reilly, J.X., Schüffelgen, U., Cuell, S.F., Behrens, T.E.J., Mars, R.B., Rushworth, M.F.S., 2013. Dissociable effects of surprise and model update in parietal and anterior cingulate cortex. Proc. Natl. Acad. Sci. U. S. A. 110, E3660--9. doi:10.1073/pnas.1305373110

Olshausen, B.A., Field, D.J., 2004. Sparse coding of sensory inputs. Curr. Opin. Neurobiol. doi:10.1016/j.conb.2004.07.007

Ortega, P.A., Braun, D.A., 2013. Thermodynamics as a theory of decision-making with information-processing costs Subject Areas□: Author for correspondence□: Proc. R. Soc. A Math. Phys. Eng. Sci. 469, 20120683–20120683. doi:10.1098/rspa.2012.0683

Overath, T., Cusack, R., Kumar, S., Von Kriegstein, K., Warren, J.D., Grube, M., Carlyon, R.P., Griffiths, T.D., 2007. An information theoretic characterisation of auditory encoding. PLoS Biol. 5, 2723–2732. doi:10.1371/journal.pbio.0050288

Öz, G., Seaquist, E.R., Kumar, A., Criego, A.B., Benedict, L.E., Rao, J.P., Henry, P.-G., Van De Moortele, P.-F., Gruetter, R., 2007. Human brain glycogen content and metabolism: implications on its role in brain energy metabolism. Am. J. Physiol. Metab. 292, E946–E951. doi:10.1152/ajpendo.00424.2006.

Park, I.M., Pillow, J.W., 2017. Bayesian Efficient Coding. bioRxiv. doi:10.1101/178418

Paukert, M., Agarwal, A., Cha, J., Doze, V.A., Kang, J.U., Bergles, D.E., 2014. Norepinephrine controls astroglial responsiveness to local circuit activity. Neuron 82, 1263–1270. doi:10.1016/j.neuron.2014.04.038

Pezzulo, G., Rigoli, F., Friston, K., 2015. Active Inference, homeostatic regulation and

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

adaptive behavioural control. Prog. Neurobiol. doi:10.1016/j.pneurobio.2015.09.001
Preuschoff, K., 't Hart, B.M., Einhäuser, W., 2011. Pupil dilation signals surprise: Evidence for noradrenaline's role in decision making. Front. Neurosci. 1–12. doi:10.3389/fnins.2011.00115
Raichle, M.E., 2010. Two views of brain function. Trends Cogn. Sci. doi:10.1016/j.tics.2010.01.008
Recarte, M.A., Nunes, L.M., 2000. Effects of verbal and spatial-imagery tasks on eye fixations while driving. J. Exp. Psychol. Appl. 6, 31–43. doi:10.1037/1076-898X.6.1.31
Reimer, J., Mcginley, M.J., Liu, Y., Rodenkirch, C., Wang, Q., Mccormick, D.A., Tolias, A.S., 2016. Pupil fluctuations track rapid changes in adrenergic and cholinergic activity in cortex. Nat. Publ. Gr. 7, 1–7. doi:10.1038/ncomms13289
Rigoux, L., Guigon, E., 2012. A Model of Reward- and Effort-Based Optimal Decision Making and Motor Control. PLoS Comput. Biol. 8, e1002716.
Ryan, R.M., Deci, E.L., 2000. Self-determination theory and the facilitation of intrinsic motivation, social development, and well-being. Am. Psychol. 55, 68–78. doi:10.1037/0003-066X.55.1.68
Salamone, J.D., Yohn, S.E., López-Cruz, L., San Miguel, N., Correa, M., 2016. Activational and effort-related aspects of motivation: neural mechanisms and implications for psychopathology. Brain 139, 1325–1347. doi:10.1093/brain/aww050
Sarampalis, A., Kalluri, S., Edwards, B., Hafter, E., 2009. Objective Measures of Listening Effort: Effects of Background Noise and Noise Reduction. J. Speech Lang. Hear. Res. 52, 1230. doi:10.1044/1092-4388(2009/08-0111)
Schmeichel, B.J., Vohs, K., 2009. Self-affirmation and self-control: Affirming core values counteracts ego depletion. J. Pers. Soc. Psychol. 96, 770–782. doi:10.1037/a0014635
Schmidt, L., Lebreton, M., Cléry-Melin, M.-L., Daunizeau, J., Pessiglione, M., 2012. Neural mechanisms underlying motivation of mental versus physical effort. PLoS Biol. 10, e1001266.
Schneider, W., Chein, J.M., 2003. Controlled & automatic processing: Behavior, theory, and biological mechanisms. Cogn. Sci. doi:10.1016/S0364-0213(03)00011-9
Sengupta, B., Stemmler, M.B., Friston, K.J., 2013. Information and Efficiency in the Nervous System-A Synthesis. PLoS Comput. Biol. doi:10.1371/journal.pcbi.1003157
Servan-Schreiber, D., Printz, H., Cohen, J.D., 1990. A network model of catecholamine effects: gain, signal-to-noise ratio, and behavior. Science (80-.). 249, 892–895. doi:10.1126/science.2392679
Sharpee, T.O., Sugihara, H., Kurgansky, A. V., Rebrik, S.P., Stryker, M.P., Miller, K.D., 2006. Adaptive filtering enhances information transmission in visual cortex. Nature 439, 936–942. doi:10.1038/nature04519
Shenhav, A., Botvinick, M., Cohen, J., 2013. The expected value of control: An integrative theory of anterior cingulate cortex function. Neuron 79, 217–240. doi:10.1016/j.neuron.2013.07.007
Shenhav, A., Musslick, S., Lieder, F., Kool, W., Griffiths, T.L., Cohen, J.D., Botvinick, M.M., 2017. Toward a Rational and Mechanistic Account of Mental Effort. Annu. Rev. Neurosci. 40, 99–124. doi:10.1146/annurev-neuro-072116-031526
Siclari, F., Tononi, G., 2017. Local aspects of sleep and wakefulness. Curr. Opin. Neurobiol. 44, 222–227. doi:10.1016/j.conb.2017.05.008
Simoncelli, E.P., 2003. Vision and the statistics of the visual environment. Curr. Opin. Neurobiol. doi:10.1016/S0959-4388(03)00047-3
Simoncelli, E.P., Olshausen, B.A., 2001. Natural image statistics and neural representation. Annu Rev Neurosci 24, 1193–1216. doi:10.1146/annurev.neuro.24.1.1193
Sims, C.R., 2016. Rate-distortion theory and human perception. Cognition 152, 181–198.

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

doi:10.1016/j.cognition.2016.03.020
Smith, E.C., Lewicki, M.S., 2006. Efficient auditory coding. Nature 439, 978–982. doi:10.1038/nature04485
Sohn, M.H., Ursu, S., Anderson, J.R., Stenger, V.A., Carter, C.S., 2000. The role of prefrontal cortex and posterior parietal cortex in task switching. Proc. Natl. Acad. Sci. U. S. A. 97, 13448–53. doi:10.1073/pnas.240460497
Sokoloff, L., 2009. Local cerebral energy metabolism: its relationships to local functional activity and blood flow. Cereb. Vasc. smooth muscle its Control.
Sokoloff, L., Mangold, R., Wechsler, R.L., Kenney, C., Kety, S.S., 1955. The effect of mental arithmetic on cerebral circulation and metabolism. J. Clin. Invest. 34, 1101–1108. doi:10.1172/JCI103159
Solopchuk, O., Alamia, A., Dricot, L., Duque, J., Zénon, A., 2017. cTBS disruption of the supplementary motor area perturbs cortical sequence representation but not behavioural performance. Neuroimage 163. doi:10.1016/j.neuroimage.2017.09.013
Solopchuk, O., Alamia, A., Olivier, E., Zénon, A., 2016. Chunking improves symbolic sequence processing and relies on working memory gating mechanisms. Learn. Mem. 23. doi:10.1101/lm.041277.115
Stephan, K.E., Manjaly, Z.M., Mathys, C.D., Weber, L.A.E., Paliwal, S., Gard, T., Tittgemeyer, M., Fleming, S.M., Haker, H., Seth, A.K., Petzschner, F.H., 2016. Allostatic Self-efficacy: A Metacognitive Theory of Dyshomeostasis-Induced Fatigue and Depression. Front. Hum. Neurosci. 10. doi:10.3389/fnhum.2016.00550
Still, S., Sivak, D.A., Bell, A.J., Crooks, G.E., 2012. Thermodynamics of prediction. Phys. Rev. Lett. 109, 1–5. doi:10.1103/PhysRevLett.109.120604
Tanaka, M., 2015. Effects of Mental Fatigue on Brain Activity and Cognitive Performance: A Magnetoencephalography Study. Anat. Physiol. s4. doi:10.4172/2161-0940.S4-002
Tani, H., Dulla, C.G., Farzampour, Z., Taylor-Weiner, A., Huguenard, J.R., Reimer, R.J., 2014. A local glutamate-glutamine cycle sustains synaptic excitatory transmitter release. Neuron 81, 888–900. doi:10.1016/j.neuron.2013.12.026
Toni, I., Krams, M., Turner, R., Passingham, R.E., 1998. The time course of changes during motor sequence learning: a whole-brain fMRI study. Neuroimage 8, 50–61. doi:10.1006/nimg.1998.0349
Tononi, G., Cirelli, C., 2014. Sleep and the Price of Plasticity: From Synaptic and Cellular Homeostasis to Memory Consolidation and Integration. Neuron 81, 12–34. doi:10.1016/j.neuron.2013.12.025
Vaishnavi, S.N., Vlassenko, A.G., Rundle, M.M., Snyder, A.Z., Mintun, M.A., Raichle, M.E., 2010. Regional aerobic glycolysis in the human brain. Proc. Natl. Acad. Sci. 107, 17757–17762. doi:10.1073/pnas.1010459107
van den Berg, R., Ma, W.J., 2017. A rational theory of set size effects in working memory and attention. bioRxiv.
van der Linden, D., Frese, M., Meijman, T.F., 2003. Mental fatigue and the control of cognitive processes: effects on perseveration and planning. Acta Psychol. (Amst). 113, 45–65.
Verguts, T., Vassena, E., Silvetti, M., 2015. Adaptive effort investment in cognitive and physical tasks: a neurocomputational model. Front. Behav. Neurosci. 9, 57. doi:10.3389/fnbeh.2015.00057
Volkow, N.D., Fowler, J.S., Wang, G.J., Telang, F., Logan, J., Wong, C., Ma, J., Pradhan, K., Benveniste, H., Swanson, J.M., 2008. Methylphenidate decreased the amount of glucose needed by the brain to perform a cognitive task. PLoS One 3. doi:10.1371/journal.pone.0002017
Wacongne, C., Changeux, J.-P., Dehaene, S., 2012. A Neuronal Model of Predictive Coding

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Accounting for the Mismatch Negativity. J. Neurosci. 32, 3665–3678. doi:10.1523/JNEUROSCI.5003-11.2012

Wager, T.D., Barrett, L.F., 2004. From affect to control: Functional specialization of the insula in motivation and regulation. Emotion 129, 2865. doi:http://dx.doi.org/10.1101/102368

Wang, C., Trongnetrpunya, A., Samuel, I.B.H., Ding, M., Kluger, B.M., 2016. Compensatory Neural Activity in Response to Cognitive Fatigue. J. Neurosci. 36, 3919–24. doi:10.1523/JNEUROSCI.3652-15.2016

Wei, X.-X., Stocker, A.A., 2015. A Bayesian observer model constrained by efficient coding can explain "anti-Bayesian" percepts. Nat. Neurosci. 18, 1509–1517. doi:10.1038/nn.4105

Westbrook, A., Braver, T.S., 2015. Cognitive effort: A neuroeconomic approach. Cogn. Affect. Behav. Neurosci. 15, 395–415. doi:10.3758/s13415-015-0334-y

Westbrook, A., Kester, D., Braver, T.S., 2013. What Is the Subjective Cost of Cognitive Effort? Load, Trait, and Aging Effects Revealed by Economic Preference. PLoS One 8, e68210. doi:10.1371/journal.pone.0068210

Wiestler, T., Diedrichsen, J., 2013. Skill learning strengthens cortical representations of motor sequences. Elife 2013. doi:10.7554/eLife.00801

Wu, T., Dufford, A.J., Egan, L.J., Mackie, M.-A., Chen, C., Yuan, C., Chen, C., Li, X., Liu, X., Hof, P.R., Fan, J., 2017. Hick–Hyman Law is Mediated by the Cognitive Control Network in the Brain. Cereb. Cortex 1–16. doi:10.1093/cercor/bhx127

Wylie, G., Allport, A., 2000. Task switching and the measurement of "switch costs". Psychol. Res. 63, 212–233. doi:10.1007/s004269900003

Xie, L., Kang, H., Xu, Q., Chen, M.J., Liao, Y., Thiyagarajan, M., O'Donnell, J., Christensen, D.J., Nicholson, C., Iliff, J.J., Takano, T., Deane, R., Nedergaard, M., Xie, L., Kang, H., Xu, Q., Chen, M.J., Liao, Y., Thiyagarajan, M., Donnell, J.O., Christensen, D.J., Nicholson, C., Iliff, J.J., Takano, T., Deane, R., Nedergaard, M., 2013. Sleep Drives Metabolite Clearance from the Adult Brain. Science (80-.). 373, 373–377. doi:10.1126/science.1241224

Yu, A.J., Dayan, P., 2003. Expected and unexpected uncertainty: ACh and NE in the neocortex. Adv. neural Inf. Process. … 15, 157–164. doi:citeulike-article-id:496920

Zekveld, A.A., Heslenfeld, D.J., Johnsrude, I.S., Versfeld, N.J., Kramer, S.E., 2014. The eye as a window to the listening brain: Neural correlates of pupil size as a measure of cognitive listening load. Neuroimage 101, 76–86. doi:10.1016/j.neuroimage.2014.06.069

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Figure legends

Figure 1. Left: Prior joint probability distribution of stimuli and responses in a simple digit-key association task, before seeing the to-be-pressed digit on the screen. Right: Posterior joint probability distribution, after seeing the to-be-pressed digit.

Figure 2. Illustration of four task types that are commonly associated with large informational demands. A: Schematic illustration of the probability distribution of different chess moves. The large size of the state-action space leads to small prior probabilities for all options. The informational cost associated with the selection of the final choice is shown as a thick blue line, and can be quantified as $-\log(P_0)$, with P0 being the prior probability associated with the move actually chosen (see main text). B. Example of the difference in information cost between learned and unknown task contingencies. The example is inspired from (Chalk et al., 2010) where subjects learn to perform a motion discrimination task in which motion direction is distributed non-uniformly. C. The marshmallow test is an example of a task requiring to counteract deep priors (Mischel, 2014). Children are told that they will receive 2 marshmallows if they don't eat the one in front of them. The prior (and/or default policy) associated to consumption of high carbohydrate food is skewed in favour of immediate consumption, explaining why restraining from eating the marshmallow requires self-control and effort. D. Switching between two tasks requires to update the state-action transition probabilities. The cost associated to this change can be quantified as the Kullback-Leibler divergence between the corresponding probability distributions. See main text for further explanation of these and other cases.

Figure 3. Adjustment of information rate as a function of noise levels. A. Schematic relationship between information rate and distortion in a sensory discrimination task in two conditions of noise levels. Distortion is a measure of error rate (i.e. reciprocal of

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

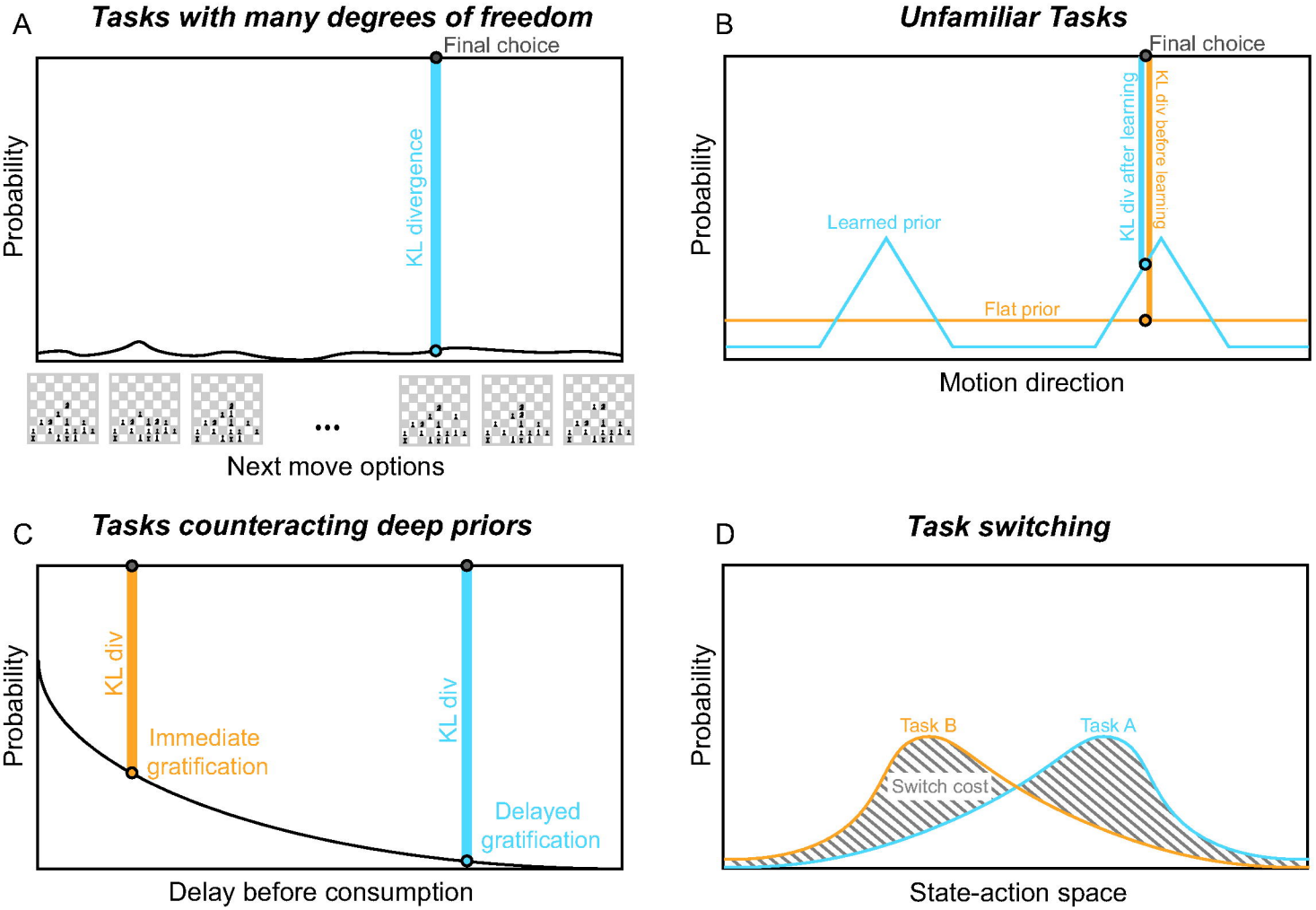
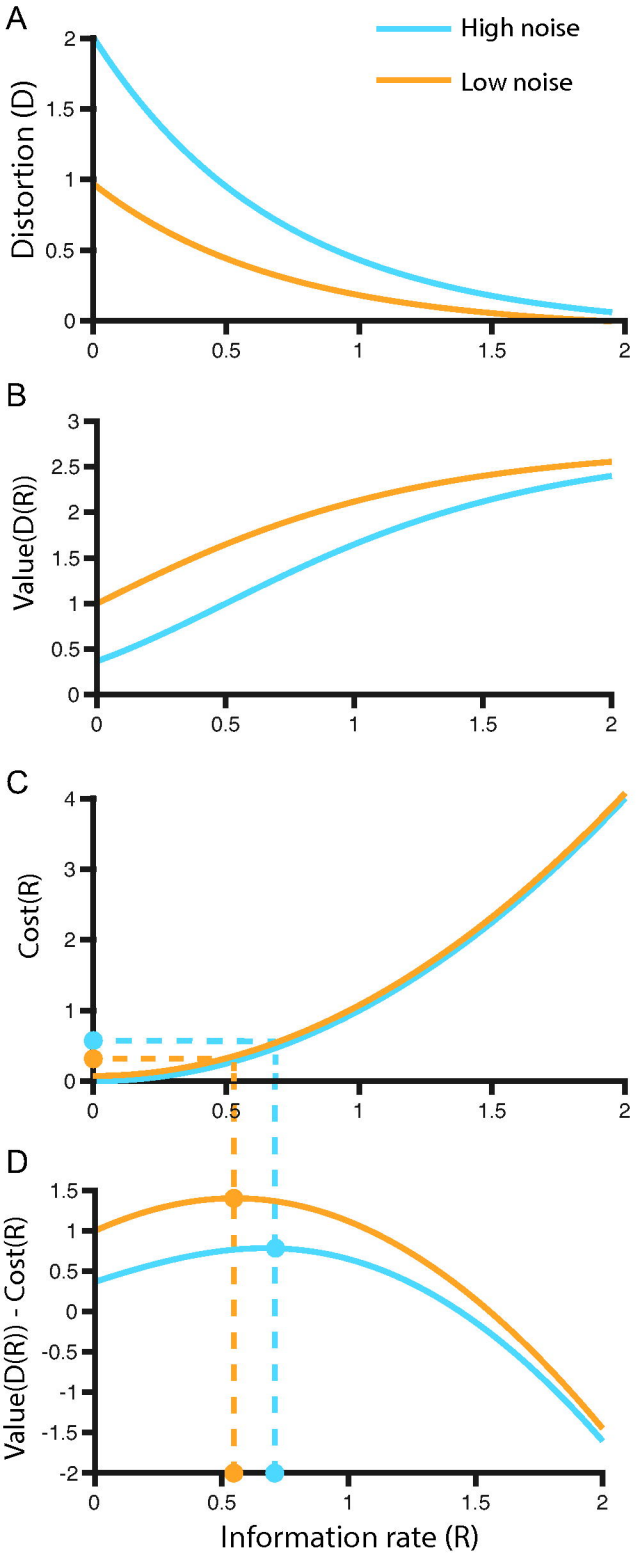
performance). Assuming distortion is quantified as the mean-squared error and the signal follows Gaussian distribution with variance σ^2: $\mathrm{D}(\mathrm{R}) = \frac{\sigma^2}{2^{2\mathrm{R}}}$. B. Value associated to distortion as a function of information rate in the 2 noise level conditions (arbitrary concave function: $\mathrm{Value}\big(\mathrm{D}(\mathrm{R})\big) = \mathrm{e}^{1-\mathrm{D}(\mathrm{R})}$). C. Cost function of information rate. This cost function is independent of the noise condition, leading to overlapping curves. An arbitrary convex function was chosen: $\mathrm{Cost}(\mathrm{R}) = \mathrm{R}^2$. The dashed lines indicate the cost corresponding to the optimal information rates in both conditions. D. Net value, corresponding to the value associated to distortion levels, to which the cost of information rate is subtracted. The optimal trade-off between distortion and information rate should be the one associated with maximal net value, as shown with the dashed line on the plot.

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Response \ Stimulus	1	2	3	4
D	1/4	0	0	0
C	0	1/4	0	0
B	0	0	1/4	0
A	0	0	0	1/4

Response \ Stimulus	1	2	3	4
D	0	0	0	0
C	0	1	0	0
B	0	0	0	0
A	0	0	0	0

bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.



bioRxiv preprint doi: https://doi.org/10.1101/208280; this version posted October 25, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.