The Journal of Experimental Biology 211, 1792-1804
Published by The Company of Biologists 2008
doi:10.1242/jeb.017574

Review

Energy limitation as a selective pressure on the evolution of sensory systems

Jeremy E. Niven[1,2,*] and Simon B. Laughlin[1]

[1]Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK and [2]Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, Panamá, República de Panamá

*Author for correspondence (e-mail: jen22@hermes.cam.ac.uk or nivenj@si.edu)

Accepted 2 April 2008

Summary

Evolution of animal morphology, physiology and behaviour is shaped by the selective pressures to which they are subject. Some selective pressures act to increase the benefits accrued whilst others act to reduce the costs incurred, affecting the cost/benefit ratio. Selective pressures therefore produce a trade-off between costs and benefits that ultimately influences the fitness of the whole organism. The nervous system has a unique position as the interface between morphology, physiology and behaviour; the final output of the nervous system is the behaviour of the animal, which is a product of both its morphology and physiology. The nervous system is under selective pressure to generate adaptive behaviour, but at the same time is subject to costs related to the amount of energy that it consumes. Characterising this trade-off between costs and benefits is essential to understanding the evolution of nervous systems, including our own. Within the nervous system, sensory systems are the most amenable to analysing costs and benefits, not only because their function can be more readily defined than that of many central brain regions and their benefits quantified in terms of their performance, but also because recent studies of sensory systems have begun to directly assess their energetic costs. Our review focuses on the visual system in particular, although the principles we discuss are equally applicable throughout the nervous system. Examples are taken from a wide range of sensory modalities in both vertebrates and invertebrates. We aim to place the studies we review into an evolutionary framework. We combine experimentally determined measures of energy consumption from whole retinas of rabbits and flies with intracellular measurements of energy consumption from single fly photoreceptors and recently constructed energy budgets for neural processing in rats to assess the contributions of various components to neuronal energy consumption. Taken together, these studies emphasize the high costs of maintaining neurons at rest and whilst signalling. A substantial proportion of neuronal energy consumption is related to the movements of ions across the neuronal cell membrane through ion channels, though other processes such as vesicle loading and transmitter recycling also consume energy. Many of the energetic costs within neurons are linked to $3Na^+/2K^+$ ATPase activity, which consumes energy to pump Na^+ and K^+ ions across the cell membrane and is essential for the maintenance of the resting potential and its restoration following signalling. Furthermore, recent studies in fly photoreceptors show that energetic costs can be related, *via* basic biophysical relationships, to their function. These findings emphasize that neurons are subject to a law of diminishing returns that severely penalizes excess functional capacity with increased energetic costs. The high energetic costs associated with neural tissue favour energy efficient coding and wiring schemes, which have been found in numerous sensory systems. We discuss the role of these efficient schemes in reducing the costs of information processing. Assessing evidence from a wide range of vertebrate and invertebrate examples, we show that reducing energy expenditure can account for many of the morphological features of sensory systems and has played a key role in their evolution.

Key words: sodium–potassium pump, metabolic rate, energy efficiency, information processing, sparse coding, ion channel, photoreceptor.

Introduction

The evolution of the accessory structures (e.g. lenses in the eye), peripheral receptors and regions of the central nervous system that together form sensory systems is often viewed solely in terms of the benefits they provide to an animal, i.e. information about the animal's internal and external environments. Sensory systems differ widely in their complexity and size, from clusters of G-protein coupled receptors for chemosensation in bacteria (Maddock and Shapiro, 1993) to the olfactory and gustatory systems of insects and vertebrates (for reviews, see Laurent, 2002; Shepherd et al., 2004), and from single receptors innervating insect mechanosensory hairs (e.g. French and Sanders, 1981), whose activity is processed locally (e.g. Burrows and Newland, 1993; Burrows and Newland, 1994), to vertebrate somatosensory systems (e.g. Penfield and Boldrey, 1937; Nelson et al., 1980). Extracting germane information from internal and external environments requires sensory receptors (with their accessory structures) to sample these environments and central circuits to analyse and interpret the incoming information. In the case of the very simplest organisms, the entire machinery for sensing the environment and acting upon it is found within the same cell, whereas at their most elaborate, for example the mammalian visual system, peripheral sensory structures may consist of millions of neurons, with even greater numbers of neurons involved in processing the information they obtain within the central nervous system. Irrespective of its size and complexity, however, the more reliable the information a sensory system can extract from the environment, the more accurate the decision making and motor control it facilitates.

Several studies have now shown that there are high energetic costs incurred by neural tissue, including that of sensory systems, both whilst processing information and at rest (Ames et al., 1992; Attwell and Laughlin, 2001; Lennie, 2003; Niven et al., 2003a; Nawroth et al., 2007; Niven et al., 2007). There are also likely to be considerable energetic costs associated with the development and carriage of nervous systems. Thus, nervous systems are subject to two conflicting selective pressures: the need to minimise energy consumption and also to generate adaptive behaviour under fluctuating environmental conditions. More specifically, in sensory systems there will be a trade-off between the energetic cost of a sensory structure encoding a particular sensory modality and the amount of reliable, germane information obtained.

Selective pressures to reduce energy consumption and improve behavioural performance can affect all levels of organization within an individual, from sub-cellular structures and single cells to brain regions and entire brains. Equally, these selective pressures can affect any life history stage. For example, a large visual system with high acuity may allow more accurate assessment of potential mates facilitating better mate choice, but at an energetic cost that may reduce individual fecundity. This emphasizes that information obtained by sensory systems must affect behaviour in a way that is beneficial to the individual or it will be selected against. Furthermore, these behaviours must ultimately be realized as increased fitness if they are to be selected (e.g. Krebs and Davies, 1993).

Thus, understanding how energy acts as a selective pressure on the evolution of sensory systems requires assessment not only of the relationship between energy and performance at the cellular and sub-cellular levels but also at the levels of sense organs, brain regions, entire brains and the entire organism. Although information about a particular sensory modality may be obtained by specific peripheral sense organs and processed, at least initially, by discrete brain regions, it is essential to consider the benefits and the costs, not only in the context of the specific neural circuits involved but also in the context of the whole organism. To determine the impact of energy as a selective pressure on the evolution of the nervous system it is important to know both how and when energy is expended within specific sensory systems or whole nervous systems, and what proportion of energy is consumed by these processes, relative to the energy budget of the whole organism.

Animal energy budgets

Sensory processing consumes a proportion of the total energy consumption of the nervous system and, therefore, is limited both by an animal's total energy budget and the distribution of energy costs throughout the nervous system. An animal's total energy consumption can be measured using its metabolic rate, of which there are several available measures (for reviews, see Hammond and Diamond, 1997; White and Seymour, 2003; Savage et al., 2004; Weibel et al., 2004; Nagy, 2005; Suarez and Darveau, 2005; Weibel and Hoppeler, 2005). An important consideration is which of these measures is most relevant to understanding the limitations on the energy available for sensory processing. Basal metabolic rates (BMRs) have been measured in vertebrates, as have resting metabolic rates (RMRs) in invertebrates (see Lovegrove, 2000; White and Seymour, 2003; Bokma, 2004; Savage et al., 2004; Niven and Scharlemann, 2005; Chown et al., 2007). They are composed of the energy requirements of various housekeeping functions such as protein synthesis, membrane turnover and maintenance of membrane potentials in a range of tissues and organs as well as oxygen transport and, in endotherms, the maintenance of body temperature. The peripheral and central nervous systems represent a significant component of the BMR or RMR in many animals. For example, in humans (*Homo sapiens*), although the brain is just 2% of the body mass it consumes approximately 20% of the BMR (Clarke and Sokoloff, 1999). Likewise, in blowflies (*Calliphora vicina*), the retina alone is estimated to consume approximately 8% of the resting metabolic rate (Howard et al., 1987). The high proportional energy consumption of neural tissue suggests that it may have a significant effect upon the overall BMR or RMR of an animal, but this is not supported by the empirical data; although in mammals the scaling exponent of absolute brain size and BMR with body mass is similar (Martin, 1981; Mink et al., 1981), plotting the deviation in brain size *versus* the deviation in BMR from their predicted scaling relationships with body mass reveals no correlation (McNab and Eisenberg, 1989) (but see Isler and van Schaik, 2006a) (Fig. 1). This would be expected if the energy consumption of neural tissue can be traded off against the energy consumption of other 'expensive tissues' such as kidney or gut. Indeed, trade-offs between brain and gut have been suggested to play an important role in the evolution of human and primate brain size (Aiello and Wheeler, 1995).

Animals do not necessarily spend large amounts of time at their BMR, however, and the field metabolic rate (FMR) (for a review, see Nagy, 2005), which is a measure of an animal's energy consumption when it is freely moving through its natural environment, is likely to be a more relevant measure to understanding the effects of energy on the evolution of the brain and sensory systems. As far as we are aware, no direct comparison of FMR and brain size is available, although the blood flow to, and oxygen uptake of, the brain has been measured in some mammals, including humans, during exercise. In humans, periods of exercise, when the skeletal muscles consume large amounts of oxygen, cause a reduction in the blood supply to most of the organs that contribute to the BMR such as the kidneys or liver; however, the blood supply to the brain remains relatively constant (Ide and Secher, 2000). For example, when cycling there is no change in global blood flow to the brain (Madsen et al., 1993). However, voluntary movements, such as hand movements, do evoke increased local blood flow to

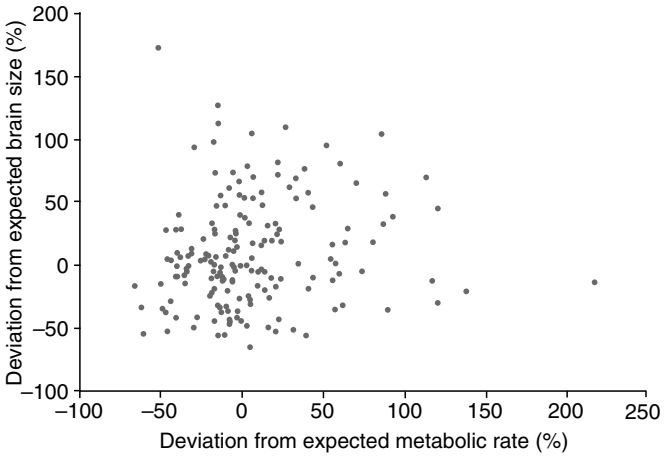

Fig. 1. The absence of a correlation between brain size and basal metabolic rate (BMR) in mammals. A plot of the percentage deviation from predicted brain size *versus* percentage deviation from predicted BMR in mammals reveals no correlation. This suggests that investment in the brain may be traded for other energetically cost tissues. Adapted from Striedter (Striedter, 2005); data from McNab and Eisenberg (McNab and Eisenberg, 1989).

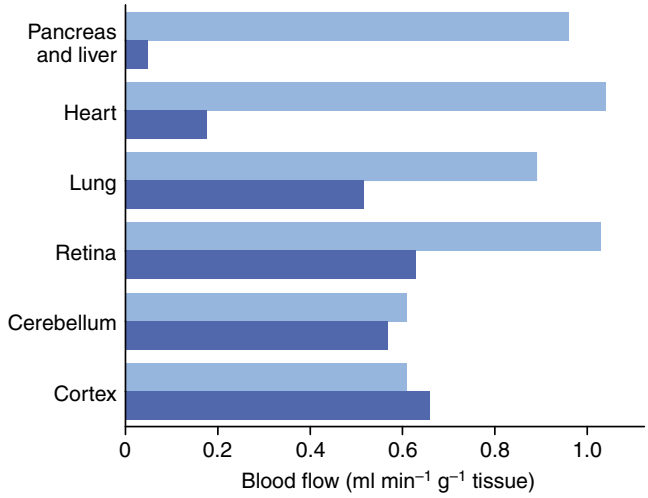

Fig. 2. Changes in the blood flow to major organs, the brain and retina in Weddell seals during diving. The normal blood flow (pale blue) and the blood flow during diving (dark blue) to the pancreas and liver, heart, lungs, retina, cerebellum and cortex. There is a substantial reduction in blood flow to the pancreas, liver and heart but not to the lungs, retina, cerebellum and cortex. Adapted from Schmidt-Nielsen (Schmidt-Nielsen, 1998); data from Zapol et al. (Zapol et al., 1979).

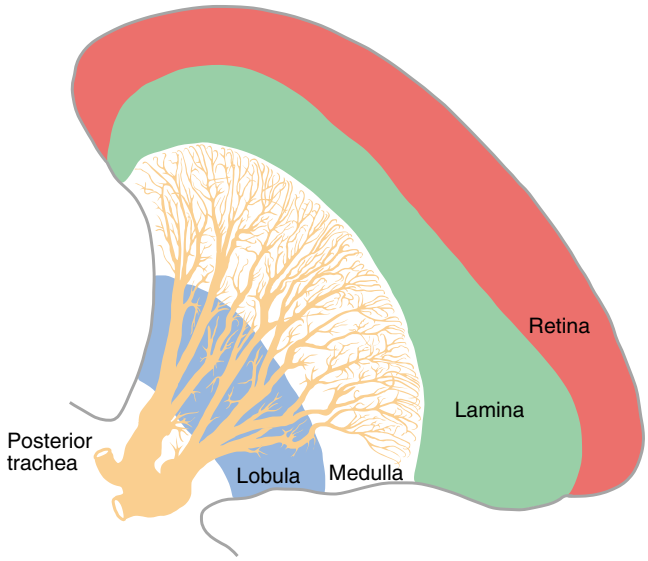

Fig. 3. Tracheoles supply oxygen to neural tissue in insects. A schematic of the right optic lobe of the desert locust (*Schistocerca gregaria*) viewed from the posterior surface showing the posterior trachea. This shows the dense ramifications of tracheoles necessary for oxygen supply within insect brains. Adapted from Burrows (Burrows, 1980).

cortical areas that receive sensory inputs as well as motor areas involved in execution (Raichle et al., 1976; Orgogozo and Larsen, 1979). This suggests that global blood flow to the brain is relatively constant, despite changes in regional blood flow. The relative constancy of global brain blood flow during behaviour is reinforced by data from Weddell seals (*Leptonychotes weddellii*), which whilst undertaking simulated dives, substantially reduce the blood flow to the heart, liver and pancreas and partially reduce the blood flow to the lungs and the retina, but not to the cortex or cerebellum (Fig. 2) (Zapol et al., 1979). This makes sense because during hunting sensory systems must continue to monitor the environment and the brain must continue to make decisions and execute motor patterns. The need for a constant supply of oxygen to the brain to maintain function is emphasized by the consequences of an interruption to the blood supply to the mammalian brain: a decrease in blood flow below critical levels can cause a 90% drop in ATP within 5 min (Erecinska and Silver, 2001). Thus, even short interruptions to the supply of oxygenated blood may lead to severe long-term functional consequences including swelling, lysis and ischemic cell death (for a review, see Lipton, 1999). The effects of a reduction in the amount of oxygen received by the brain can be observed in humans under hypoxic conditions, such as at high altitudes, where blood oxygen levels drop and both sensory and motor functions are severely impaired (Hornbein, 2001). To prevent such oxygen depletion the nervous systems of both vertebrates and insects are supplied with oxygen through dense networks of capillaries or tracheoles (Fig. 3), respectively. The neurons of some vertebrates such as the western painted turtle (*Chrysemys picta*), the common frog (*Rana temporaria*) and the crucian carp (*Cyprinus carpio*) have evolved to tolerate hypoxic or anoxic conditions (for reviews, see Lutz, 1992; Boutilier, 2001; Nilsson, 2001; Bickler and Donohoe, 2002). However, in both *C. picta* and *R. temporaria*, neural function is compromised under these conditions. However, neurons within the crucian carp brain remain active in anoxic conditions and continue to sense their environment and generate behaviour (Nilsson, 2001). Many invertebrates have remarkable tolerance under hypoxic or anoxic conditions, possibly due to their low metabolic rates in comparison to vertebrates (e.g. Niven and Scharlemann, 2005; Chown et al., 2007). However, there is little information about the effects of hypoxic/anoxic conditions upon invertebrate neurons, sensory systems or behaviour. Nevertheless, data from vertebrates clearly suggest that the sustained supply of oxygen to sensory systems and the brain has important implications for their evolution because nervous systems are a constant energy sink, consuming energy irrespective of whether they are at rest or active.

The energetic cost of neural tissue

There are numerous physiological processes within neural circuits that contribute to the overall costs of neural tissue: transduction, electrical signal transmission within the neuron and synaptic transmission (Fig. 4). For neurons that possess chemical synapses, these costs include the maintenance of concentration gradients for ions including Na^+, K^+, Ca^{2+}, H^+, Cl^- and HCO_3^- and potential differences across the cell membrane, the synthesis of neurotransmitter molecules, the loading of neurotransmitter molecules into vesicles, the docking of neurotransmitter vesicles at the pre-synaptic membrane and the breakdown or reuptake of neurotransmitter from the synaptic cleft. In addition, there are costs associated with the synthesis of macromolecules such as proteins and fatty acids.

The basic currency of energy within cells is the phosphate–phosphate bond of the adenosine triphosphate (ATP) molecule (for a review, see Alexander, 1999). In neurons, the energy released in breaking this bond is harnessed by the $3Na^+/2K^+$ ATPase, which exudes $3Na^+$ ions and admits $2K^+$ ions for each molecule of ATP that is converted to ADP, for the maintenance of the membrane potential (Skou, 1957; Post et al., 1972; Glynn, 1993). Numerous symporters and antiporters are coupled to the $3Na^+/2K^+$ ATPase, linking the movements of ions such as Ca^{2+}, Cl^- and HCO_3^- to the energy consumed by the $3Na^+/2K^+$ ATPase (Fig. 4). The potential and concentration gradients that drive the movements of ions through ion channels are also dependent upon the $3Na^+/2K^+$

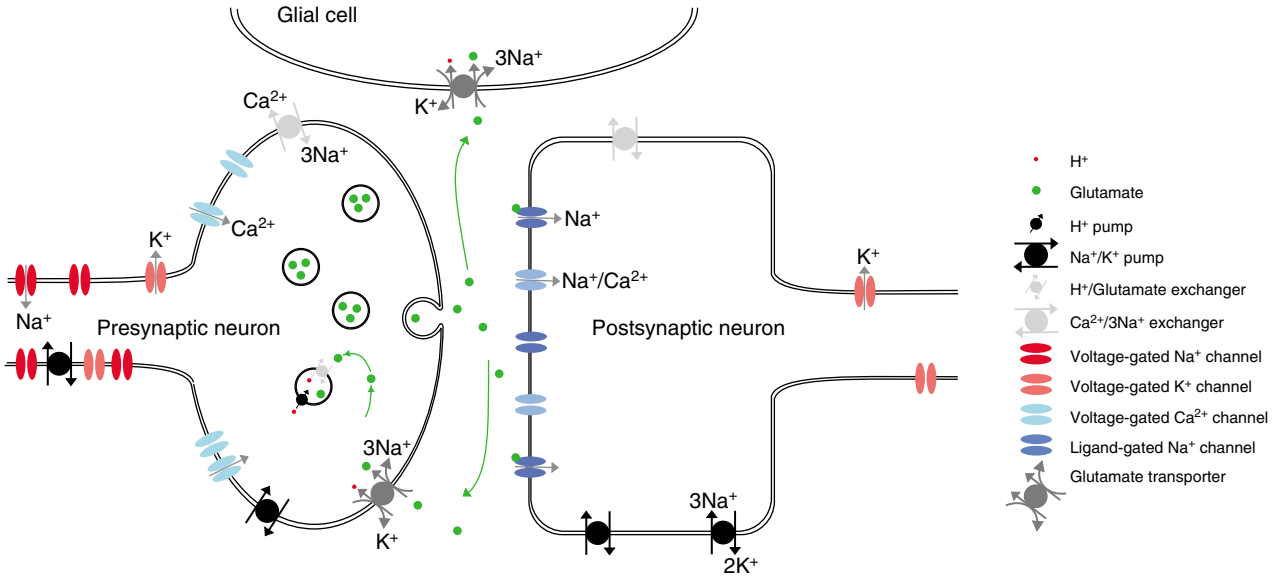

Fig. 4. A schematic diagram of a glutamatergic synapse showing many of the major sources of energy consumption. Movements of ions across the neuronal cell membrane account for a large proportion of the energy consumed. During transmission of the action potential along the axon, Na^+ and K^+ ions move through voltage-gated ion channels due to concentration gradients and potential differences across the membrane. When the action potential reaches a synapse, voltage-gated Ca^{2+} channels open, to admit Ca^{2+} ions and trigger the release of vesicles containing glutamate molecules. These glutamate molecules then bind to ligand-gated ion channels, which open admitting Na^+ molecules that depolarize the post-synaptic neuron. Glutamate in the synaptic cleft is transported into the presynaptic neuron or nearby glial cells by a glutamate co-transporter. Within the pre-synaptic neuron, glutamate molecules are transported into the synaptic vesicles by a glutamate/H^+ anti-porter. Almost all of these processes require the activity of two pumps, the $3Na^+/2K^+$ pump and the H^+ V-ATPase.

ATPase. Additionally, the V-ATPase, which transports one H^+ ion across the membrane for each molecule of ATP converted to ADP, is critically important to neurons (Harvey, 1992; Moriyana et al., 1992). The V-ATPase pumps H^+ ions into the lumen of synaptic vesicles, creating a concentration gradient and potential difference between the lumen and the surrounding cytoplasm that is used to drive the uptake of neurotransmitter molecules (Fig. 4).

Electrical models of single fly photoreceptors based upon intracellular measurements of their input resistance and membrane potential have been used to estimate the total energy consumption of the $3Na^+/2K^+$ ATPase within single neurons (Laughlin et al., 1998; Niven et al., 2003a; Niven et al., 2007). Comparison of the estimated ATP consumption from *Calliphora vicina* photoreceptors with estimates of the total costs derived from whole retina oxygen consumption measurements are remarkably similar (Laughlin et al., 1998; Pangršič et al., 2005; Niven et al., 2007). This suggests that, at least within photoreceptors, movements of ions across the neuronal cell membrane, which are driven by concentration gradients and potential differences maintained by the activity of the $3Na^+/2K^+$ ATPase, are the major energy cost.

Both electrical models of individual photoreceptors and oxygen measurements from whole retinas suggest that the energy consumption of neural tissue at rest is extremely high, e.g. rabbit (Ames et al., 1992), fly (Laughlin et al., 1998; Niven et al., 2003a; Niven et al., 2007; Pangršič et al., 2005). This high cost, even in the absence of any signalling, is due to the activity of the $3Na^+/2K^+$ ATPase, which is necessary for the maintenance of the resting potential (Niven et al., 2007). Comparison of signalling and resting costs in photoreceptors suggests that they are related, the resting costs being approximately 25% of the cost at the highest light levels (Fig. 5). Resting costs and signalling costs are probably related in all neurons (both spiking and non-spiking), although the precise relationship is likely to be different depending on the specific neural type.

Recently, three energy budgets have been produced that attempt to divide the total energy consumption of neural tissue into its constituent components (Attwell and Laughlin, 2001; Lennie,

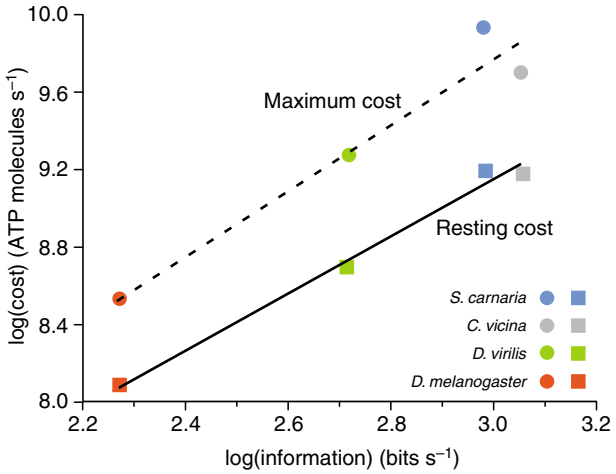

Fig. 5. Resting and maximum energy consumption of photoreceptors scales with their performance. Comparison of four homologous fly R1–6 photoreceptors from (smallest to largest): *Drosophila melanogaster*, *D. virilis*, *Calliphora vicina* and *Sarcophaga carnaria*. The largest photoreceptors are capable of transmitting more information but expend more energy at rest (squares; solid line) and whilst signalling (circles; broken line) than the smaller photoreceptors. This shows that neural performance is related to energy consumption at rest and whilst signalling. Adapted from Niven et al. (Niven et al., 2007).

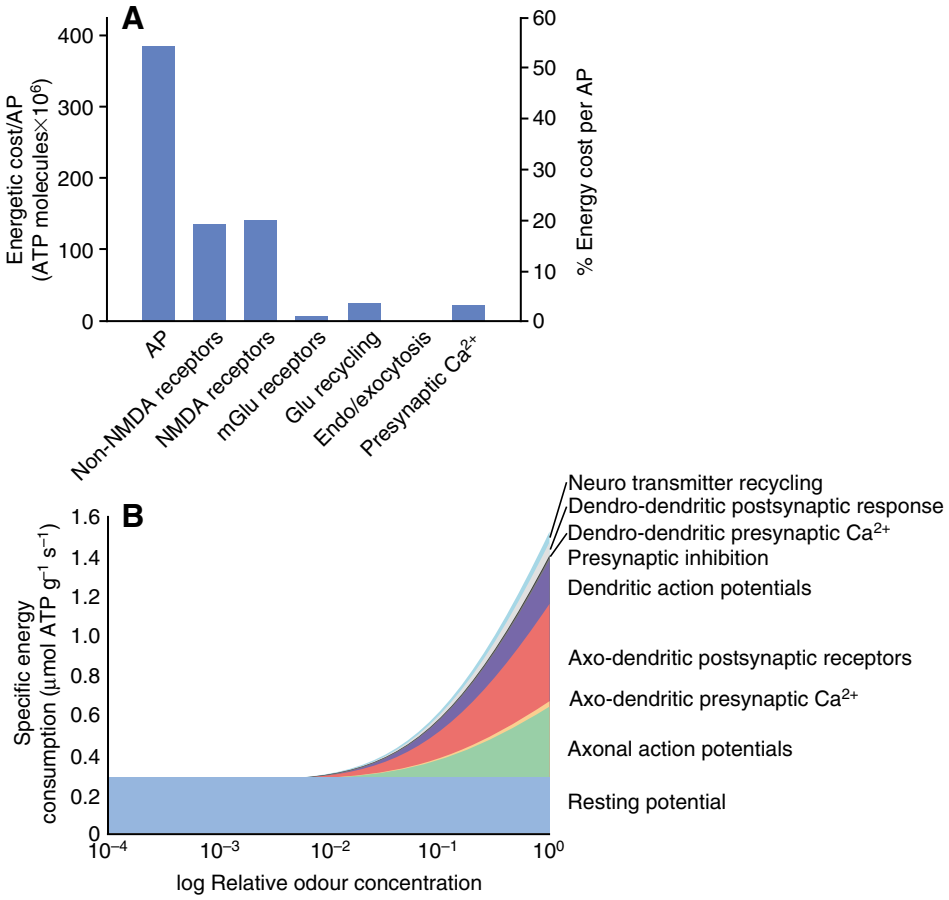

Fig. 6. Energy budgets break down the energetic costs of neural processing into its constituent components. (A) The energy consumption of the various neuronal components that contribute to the energy consumption of a single action potential (AP) and the events at a glutamateric synapse triggered by it in rat cortex. The AP itself consumes more than 50% of the total energy consumed. Other processes that also consume energy include the activation of NMDA, non-NMDA and metabotropic glutamate post-synaptic receptors, the recycling of glutamate and the entry of pre-synaptic Ca^{2+} ions that trigger vesicle release. Many of these processes can be linked to the activity of the sodium–potassium exchanger. (B) The energy consumption of various neural components within a rat olfactory glomerulus with one sniff per second as a function of odour concentration. The contributions of different components change with increasing odour concentration. The resting potential is the dominant cost at low odour concentrations but axonal action potentials, the activation of post-synaptic receptors and dendritic back-propagating action potentials consume substantial amounts of energy at higher concentrations. Adapted from Attwell and Laughlin (Attwell and Laughlin, 2001) and Nawroth et al. (Nawroth et al., 2007).

2003; Nawroth et al., 2007). For example, Attwell and Laughlin (Attwell and Laughlin, 2001) divide the energy consumption of a single action potential in rat grey matter into the voltage-gated currents producing the action potential, pre-synaptic Ca^{2+} entry at the synapse, the recycling of glutamate released into the synaptic cleft and loading of vesicles, vesicle endo- and exocytosis and the activation of post-synaptic receptors (NMDA, non-NMDA and mGluR) (Fig. 6A). The costs calculated for a single component are then multiplied by the total number of these components within the nervous system to give the total energy consumption. These energy budgets emphasize the high costs of maintaining the membrane potential at rest as well as the extremely high costs of action potential conduction. Indeed, within an active olfactory glomerulus the energetic costs were dominated by the demands of action potential transmission within the afferent olfactory neurons and their synaptic outputs, despite post-synaptic dendrites comprising at least half the total glomerular volume (Nawroth et al., 2007) (Fig. 6B). Other functions of neurons such as the loading of vesicles with glutamate and its recycling following release into the synaptic cleft constitute a relatively small proportion of these energy budgets (Attwell and Laughlin, 2001; Nawroth et al., 2007).

These studies emphasize that the movements of ions across the neuronal cell membrane at rest and whilst signalling are a major cost in both spiking and non-spiking neurons. The costs themselves are likely to differ between cell types depending on the input resistance at rest, the precise combinations and densities of ion channels in the membrane, the total membrane area, the number of output synapses and type of neurotransmitter they release.

The energetic cost of information processing

Whilst oxygen consumption and blood flow measurements, electrical circuit models and energy budgets can explain the mechanistic causes of the high energetic costs associated with single neurons, sensory processing regions or grey matter; they do not in themselves explain why such costs exist. To understand why specific components within the nervous system cost particular amounts of energy we need to understand the function of these components. Two particularly important factors that affect the energetic cost of neural information processing are noise and response speed, which determine the signal-to-noise ratio (SNR) and bandwidth, respectively (Laughlin, 2001; Niven et al., 2007). Noise in sensory systems is both intrinsic and extrinsic (for review, see Faisal et al., 2008). Extrinsic noise is derived from the sensory stimuli themselves, which because they are either quantum-mechanical or molecular in nature do not perfectly convey information about the environment (Hecht et al., 1942; Barlow et al., 1971; Berg and Purcell, 1977; Baylor et al., 1979; Lillywhite and Laughlin, 1979; Aho et al., 1988). Intrinsic noise occurs at all stages of sensory processing, including the transduction of the sensory stimulus into an electrical signal, the transmission of electrical signals within neurons and synaptic transmission of signals between neurons (Barlow, 1956; Katz and Miledi, 1970; Lillywhite and Laughlin, 1979; Aho et al., 1988; Mainen and Sejnowski, 1995; Berry et al., 1997; de Ruyter van Steveninck et al., 1997). One potential way to improve the SNR of single neurons is to increase their numbers of receptor molecules and ion channels (Weckström and Laughlin, 1995; Laughlin, 1996; Niven et al., 2003b; Vähäsöyrinki et al., 2006; Niven et al., 2007). However, each additional receptor that is

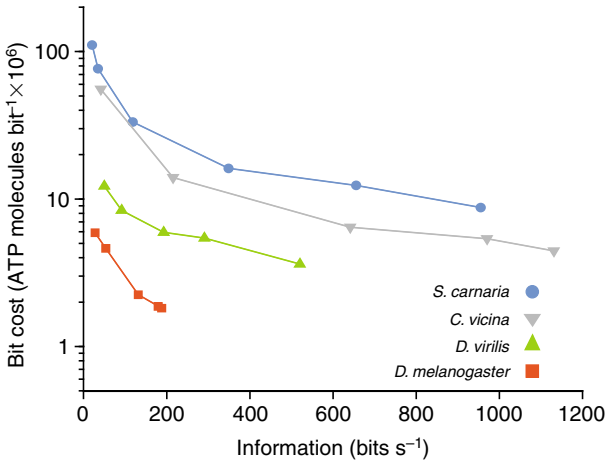

Fig. 7. A trade-off between energy efficiency and information coding in insect photoreceptors. The information rates (bits s^{-1}) *versus* the energy efficiency of information transmission (ATP molecules $bit^{-1}\times10^6$) of photoreceptors from four fly species (smallest to largest): *Drosophila melanogaster*, *D. virilis*, *Calliphora vicina* and *Sarcophaga carnaria*. Larger photoreceptors can transmit higher rates of information but are less energy efficient. Adapted from Niven et al. (Niven et al., 2007).

activated or ion channel that is opened consumes energy. Likewise, an improved SNR could be conveyed to postsynaptic neurons by releasing greater numbers of synaptic vesicles but each additional vesicle will consume more energy. At the circuit level, noise reduction can be produced by averaging the outputs of sensory receptors or neurons in space, time, or both. In the peripheral nervous system, averaging the signals from neighbouring receptors may eliminate noise to some extent if the noise in these receptors is uncorrelated. However, spatial averaging reduces the resolution with which the sensory receptors sample the environment, requiring an increase in receptor density to restore the resolution. Thus, averaging increases the energetic costs of sensory processing because greater numbers of neurons are required.

Increasing the number of receptors and ion channels in a neuron not only affects its SNR but also its bandwidth. In particular, increasing the density of ion channels will decrease the input resistance and the membrane time constant. However, greater densities of receptors and ion channels allow a greater flow of ions across the neuronal cell membrane during signalling that require the $3Na^+/2K^+$ ATPase to restore them after signalling. The bandwidth and SNR both contribute to the information rate. Recent comparative studies have explained the links between fly photoreceptor energy consumption and information rates through their bandwidth and SNR (Niven et al., 2007). In both small and large photoreceptors the cost of a unit of information (bit) drops as more is encoded (Fig. 7). This is due to the resting costs, which are divided by the amount of information encoded. Nevertheless, smaller photoreceptors are more efficient than their larger counterparts despite having lower information rates because their energetic costs are substantially lower (Niven et al., 2007).

Energy efficiency in sensory systems

Given the finite energy budgets of animals, the high energetic demands of sensory systems and the need for animals to generate adaptive behaviour, energy efficient solutions to the challenges faced by sensory systems should be strongly selected for during evolution. Energy efficiency, which leads to an increase in the ratio between the information encoded and the energy expended by sensory systems, can occur due to adaptations in their morphology, physiology, or both. Numerous examples of energy efficient strategies exist at all levels of neural organization, from the combinations of ion channels within single neurons (Niven et al., 2003a) and their size (Niven et al., 2007) to the coding of information within populations of neurons (Levy and Baxter, 1996; Baddeley et al., 1997; Vinje and Gallant, 2000; Perez-Orive et al., 2002; Hromádka et al., 2008) and computational maps (Chklovskii and Koulakov, 2004).

The efficiency with which single neurons code information is critically dependent upon the biophysical properties of their membranes, such as the total surface area or the combinations of ion channels that they express, because the movement of ions across the membrane is the major energetic cost of neurons (Laughlin et al., 1998; Attwell and Laughlin, 2001; Niven et al., 2007). Numerous features of neurons such as their conduction velocity, time constants and space constants are dependent upon the combinations and densities of ion channels within the membrane (Hille, 2001).

The most obvious impact of ion channels upon the energy efficiency of single neurons is the generation of action potentials by voltage-gated sodium channels. A high density of voltage-gated sodium channels can support the production of action potentials, which are used to code information digitally. However, some neurons lack voltage-gated sodium channels (or a sufficient density of voltage-gated sodium channels) and code information as graded changes in membrane potential. These non-spiking neurons are found in the peripheral visual, auditory and vestibular systems of vertebrates (e.g. photoreceptors, bipolar cells and hair cells) and throughout the visual and mechanosensory systems of insects and crustaceans (e.g. photoreceptors, motion detector neurons, local non-spiking interneurons) (Tomita, 1965; Ripley et al., 1968; Autrum et al., 1970; Werblin and Dowling, 1969; Hagins et al., 1970; Harris et al., 1970; Kaneko, 1970; Burrows and Siegler, 1976; Yau et al., 1977). These neurons all transmit information to post-synaptic neurons as graded or analogue signals.

Simulations of large monopolar cells in the fly retina suggest that transmission of analogue information (graded potentials) is at least as costly per unit of information (measured in bits) as digital transmission (action potentials) but far more information can be transmitted per second using analogue coding (Laughlin et al., 1998). This suggests that many more spiking neurons are required to transmit a given amount of information per second. In this case, even if the cost per bit of information were the same with both coding schemes, digital coding would incur greater overall energy consumption because when no information is coded the resting potentials of a larger number of spiking neurons must be maintained. Thus, analogue coding is a more efficient solution to transmitting a given amount of information within a limited amount of time. However, graded potentials degrade over long distances and so there is a reduction in the reliability of the analogue signals being transmitted. Digital coding using action potentials also has the benefit of being able to threshold out synaptic noise, which may accumulate in networks due to synaptic transmission (Sarpeshkar, 1998; Laughlin et al., 2000). This reduction in reliability means that the relative energy efficiency of analogue *versus* digital coding drops as the distance information is to be transmitted increases. The greater efficiency of analogue coding over short distances and digital coding over longer distances suggests that the nervous system should use a mixture of the two schemes. Such hybrid coding schemes are indeed observed in neural circuits, which combine graded potentials (including postsynaptic potentials) and action potentials. Indeed, a

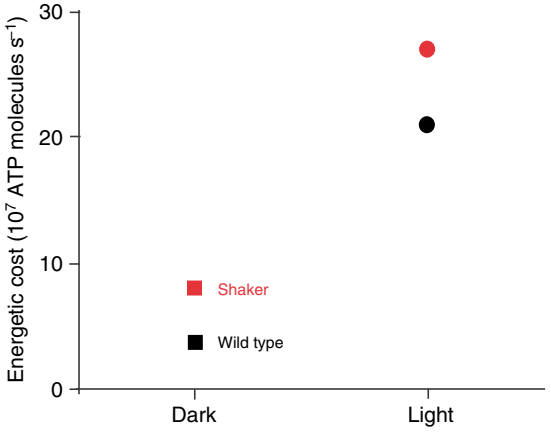

Fig. 8. Ion channels alter the relationship between energy consumption and information coding. *Drosophila melanogaster* photoreceptors from *Shaker* mutant flies, which lack functional *Shaker* K^+ channels (red), have an increased energetic cost at rest and whilst signalling when compared to wild-type photoreceptors (black). Adapted from Niven et al. (Niven et al., 2003a).

theoretical prediction of the optimal mixture of analogue and digital coding in electronic devices closely resembles that observed in cortical neurons (Sarpeshkar, 1998).

As well as influencing whether neurons code information as graded or action potentials, ion channels can also alter energy efficiency through their density and their activation/inactivation properties. For example, in *Drosophila melanogaster* photoreceptors, a considerable proportion of *Shaker* voltage-gated K^+ channels are activated at the steady-state resting potential, reducing the current-to-voltage gain (Niven et al., 2003b). Photoreceptors exposed to bright lights depolarize, inactivating the *Shaker* voltage-gated K^+ channels and increasing the current-to-voltage gain and improving the spread of the signal across the voltage range. The *Shaker* conductance incurs an energetic cost at rest, but not at more depolarized potentials when it is inactivated (Niven et al., 2003a; Niven et al., 2003b). In *Drosophila* mutant photoreceptors that lack the *Shaker* conductance, it is replaced with a leak conductance that restores the current-to-voltage gain at rest but it does not inactivate at more depolarized potentials (Niven et al., 2003b). This leak conductance incurs an energetic cost both at rest and at more depolarized potentials. Thus, photoreceptors experience a twofold cost associated with the loss of the *Shaker* channel, a drop in their information rate and an increase in their energy expenditure (Niven et al., 2003a; Niven et al., 2003b) (Fig. 8). More generally, altering the precise types of voltage-gated ion channels and their densities within a neuron will alter the relationship between energy consumption and information processing. Voltage-gated ion channels may increase the energy efficiency of information coding in neurons by altering the relationship between resting costs and signalling costs. For example, voltage-gated ion channels that activate at high voltages do not incur an energetic cost at rest. In spiking neurons, increasing the threshold potential would significantly reduce energy consumption because fewer action potentials would be initiated, although this will alter the information transmitted.

The properties of other classes of ion channels and metabotropic receptors may also alter the energy efficiency of information transmission in sensory receptors or at synapses. For example, several different receptor types, including AMPA, Kainate, NMDA and metabotropic glutamate receptors, are found on the post-synaptic membrane of glutamatergic synapses, which are found throughout vertebrate sensory systems. The AMPA receptors have evolved to activate and deactivate on millisecond timescales in response to glutamate, whereas NMDA and metabotropic glutamate receptors operate on longer timescales (Attwell and Gibb, 2005). It has been shown that energy consumption limits neuronal time constants and the millisecond timescale of AMPA receptors (Attwell and Gibb, 2005). It is suggested that the properties of the NMDA and metabotropic glutamate receptors are linked to their role as coincidence detectors and their involvement with synaptic plasticity. Altering the precise combination of AMPA, Kainate, NMDA and metabotropic glutamate receptors will alter the energetic cost of that particular synapse.

Energy efficiency can also be achieved by matching the filter properties of neuronal components to the signals they process (Laughlin, 1994; Laughlin, 2001; Niven et al., 2007). For example, insect photoreceptors have a region of photosensitive membrane, the rhabdom, and photoinsensitive membrane that filters the light-induced current generated by the rhabdom. The filter properties of the photoinsensitive membrane are determined by the combination and density of ion channels expressed by the photoreceptor (Vallet et al., 1992; Laughlin and Weckström, 1993; Laughlin, 1994; Weckström and Laughlin, 1995; Laughlin, 1996; Juusola et al., 2003; Niven et al., 2003b; Niven et al., 2004; Vähäsöyrinki et al., 2006). An ability to process information at frequencies beyond those necessary for the generation of adaptive behaviour (having excess bandwidth in the photosensitive filter) will be severely penalized by increased energetic costs over the entire signalling range and at rest (Niven et al., 2007). Indeed, the filter properties of the photoinsensitive membrane would be expected to be reduced to the absolute minimum necessary for maintaining function. Similarly, it has been suggested that the timescale of activation and deactivation of AMPA receptors at glutamatergic synapses is matched to the membrane time constants of neurons and, hence, their signalling speed (Attwell and Gibb, 2005).

Strategies to improve the energy efficiency of neural coding are not restricted to single neurons but can also occur within populations of neurons (Levy and Baxter, 1996; Vinje and Gallant, 2000; Balasubramanian et al., 2001; Willmore and Tolhurst, 2001; De Polavieja, 2002; Perez-Orive et al., 2002; Schreiber et al., 2002; Olshausen and Field, 2004; Hromádka et al., 2008). Energy efficiency within neural populations is still constrained by the properties of individual neurons, such as the relationship between the energetic cost of maintaining a neuron at rest and whilst signalling. This relationship is particularly important for sparse coding, an energy efficient coding strategy in which a small proportion of the neurons in a population represent information (for a review, see Olshausen and Field, 2004). The optimum proportion of neurons within a population is dependent upon the relationship between resting costs and signalling costs. High signalling costs and low resting costs will favour extremely sparse representations of information, so called ‘grandmother neuron’ codes in which a single event is associated with the activity of a single neuron (Attneave, 1954; Barlow, 1969), whereas higher fixed costs favour denser neural codes in which a greater number of neurons within a population are active (Levy and Baxter, 1996; Attwell and Laughlin, 2001) (Fig. 9). Studies in both vertebrates and invertebrates have shown that neural codes at higher levels of sensory systems, such as the primary visual cortex of primates, may be sparse (e.g. Vinje and Gallant, 2000; Perez-Orive et al., 2002; Hromádka et al., 2008).

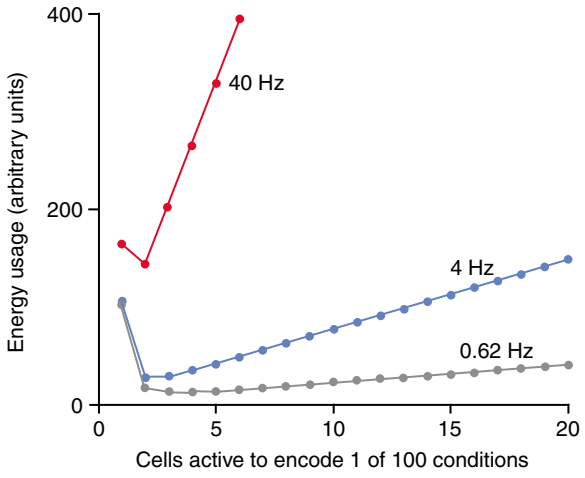

Fig. 9. Reducing energy consumption with distributed coding in spiking neurons. The energy requirements for encoding 1 of 100 conditions initially decrease but subsequently increase as the number of active neurons increases (for cells signalling with spike rates below 60 Hz). As the spike rate increases the region of the parameter space in which distributed coding is advantageous becomes smaller. Adapted from Attwell and Laughlin (Attwell and Laughlin, 2001).

Energy efficiency can also be achieved by the placement of components within nervous systems/sensory systems to minimize energetic costs by 'saving wire' (Cherniak, 1994; Cherniak, 1995). For example, the placement of brain regions with high interconnectivity adjacent to one another will reduce the total length of axons. This will reduce the amount of axonal membrane and the distance over which action potentials are transmitted. The placement of neural components at several levels of organization, from visual cortical areas to single neurons, has been shown to closely match the minimized wire length. For example, the interconnectivity of neurons within the cortex appears to minimize wiring volume (Chklovskii, 2004).

Although energy efficient coding strategies and component placements occur in many sensory systems, constraints also exist that prevent energy savings. Noise is a constraint both upon energy efficient coding and the minimization of wiring costs within the nervous system (Balasubramanian et al., 2001; De Polavieja, 2002; Faisal et al., 2005). For example, an optimum energy efficient code that maximizes the information coded by a given number of spikes (the Boltzmann distribution) predicts that neural spike rates should follow an exponential distribution. Populations of neurons encoding natural stimuli adhere to this prediction at high spike rates but not at low spike rates, which are used less often than predicted, because they are less reliable (Baddeley et al., 1997; Balasubramanian et al., 2001; Balasubramanian and Berry, 2002; De Polavieja, 2002). Functional constraints, such as timing or the positions of peripheral nerves, may also prevent the nervous system adopting energy efficient strategies (Chen et al., 2006; Kaiser and Hilgetag, 2006; Niven et al., 2008). These constraints limit the extent to which selective pressures on the nervous system to reduce energetic costs can affect the coding of information and the placement of components.

A complementary strategy to directly reducing the cost of processing information is to reduce the amount of predictable or redundant information within sensory systems (Atteneave, 1954; Barlow, 1961; Srinivasan et al., 1982). The most obvious source of predictable sensory information is the sensory feedback generated by motor activity. For example, limb movements can produce predictable mechanosensory feedback; however, it is the deviation from the expected sensory feedback that is essential for maintaining limb control and stability (Gossard et al., 1990; Gossard et al., 1991; Wolf and Burrows, 1995). An efference copy of the expected movements can be used to selectively gate-out the predictable sensory feedback and allow only the novel sensory feedback to be processed (Sillar and Skorupski, 1986; Bell and Grant, 1989; Gossard et al., 1990; Gossard et al., 1991; Wolf and Burrows, 1995; Li et al., 2002; Poulet and Hedwig, 2006). By reducing the number of predictable signals being processed, the overall energetic cost is reduced but not the total amount of information. For example, within the visual system, redundant information can arise because adjacent photoreceptors sample neighbouring points on natural scenes that are highly correlated (Atteneave, 1954; Barlow, 1961; Srinivasan et al., 1982). Again, eliminating redundant signals reduces the overall energetic cost but not the total information.

Is there a relationship between size, performance and energy consumption?

Many animals possess enlarged or elaborated sensory systems for the acquisition of a specific sensory modality. The elaboration of sensory structures is often correlated with behavioural and/or ecological specialization and improved performance in particular behavioural tasks. For example, the insectivores show considerable behavioural and ecological diversity and have sensory specializations in both the peripheral sense organs and cortical regions (for a review, see Catania, 2005). The East African hedgehog (*Atelerix albiventris*) possesses large eyes and ears as well as whiskers and microvibrissae that suggest they are generalists, not relying wholly on one specific sensory modality. This is reflected in the organization of their cortex, which contains large prominent auditory, somatosensory and visual areas (Fig. 10A). In contrast moles, and in particular the star-nosed mole (*Condylura cristata*), are specialized for a subterranean lifestyle with reduced eyes and a highly modified nose that contains 22 tactile appendages and a relatively enlarged cortical somatosensory representation (Fig. 10B). Ant species with more visual behaviour, likewise, show an enlargement of the optic lobes and mushroom body lip – brain regions associated with visual processing and possibly visual memory, respectively (Gronenberg and Hölldobler, 1999).

There is often an implicit assumption that relatively larger structures within sensory systems are associated with an increase in information processing and, consequently, improved behavioural performance. Relatively larger sensory structures may have greater numbers of neurons, neurons with a greater volume, or both. It also seems likely that relatively larger sensory structures will incur a greater absolute energetic cost. However, for most sensory systems, these relationships remain assumptions without empirical support. These relationships between information processing and energy consumption have been assessed in the fly retina (Niven et al., 2007). Comparison of different sized photoreceptors showed that the largest had substantially higher information rates than the smallest but also incurred substantially higher energetic costs, both at rest and whilst signalling (Fig. 7). Thus, information processing in the largest photoreceptors was less energy efficient than in their smaller counterparts. The largest photoreceptors were from flies with the greatest number of photoreceptors suggesting that, in this case, the largest retina had both the highest total energy consumption and processed the greatest quantity of information.

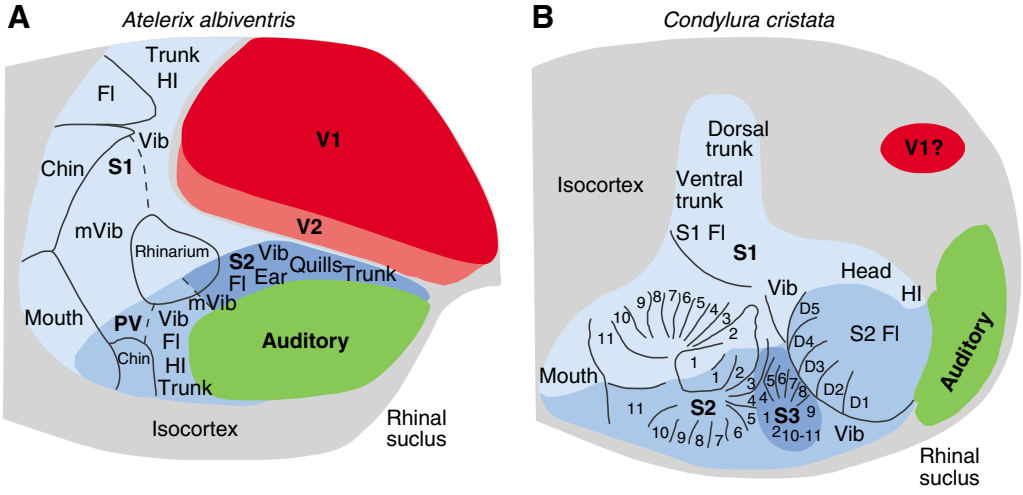

Fig. 10. A reduction in the size of visual cortical regions and an expansion in cortical regions associated with mechanosensory processing are associated with subterranean living. (A) The African hedgehog *Atelerix albiventris* lives above ground and has well developed visual (V) and auditory processing. (B) The star-nosed mole *Condylura cristata* is subterranean and has reduced visual (V) representation and an enlarged somatosensory representation. Adapted from Catania (Catania, 2005). See text for details.

Although similar relationships can be envisaged for other peripheral sensory structures, the relationship between information processing, energy consumption and the size of higher centres remains unclear. The efficacy of energy-efficient coding schemes can change with size (e.g. graded *versus* action potentials, sparse coding), making direct comparisons difficult. Thus, direct quantification of the energetic costs, performance and size of a particular sensory system is essential for understanding the cost–benefit trade-offs that have influenced its evolution. This is particularly important in comparisons of phylogenetically distant species, among which it is not reasonable to assume that a specific volume of neural tissue consumes similar amounts of energy. For example, elasmobranchs have a larger relative brain size when compared to teleost fish of the same body mass (Nilsson et al., 2000) (Fig. 11A). Early studies assumed that elasmobranch brains consumed considerably more energy than those of teleosts with similar body mass. However, measurements from elasmobranch and teleost neural tissue have shown that they have very different specific rates of energy consumption but that overall their brains consume similar amounts of energy (Fig. 11B,C).

Environmental influences on trade-offs between energy and performance

If the trade-off between the performance of sensory systems and their energetic costs has influenced their evolution, then under conditions in which the need to maintain performance in a particular sensory system is reduced, the sensory system itself should be reduced. Many animals living in environments in which information from a particular sensory modality is no longer useful, and is therefore under reduced selective pressure, do indeed show marked reductions in the size of structures associated with that modality. For example, the peripheral and central components of the visual systems of animals that live in caves or subterranean environments are often reduced or absent. Populations of the Mexican cave fish (*Astyanax mexicanus*) isolated in caves without light have undergone convergent eye loss at least three times within the last 1 million years, whereas populations that have lived continuously on the surface have retained their eyes (Fig. 12A) (Strecker et al., 2004; Wilkens, 2007; Borowsky, 2008; Niven, 2008a). Likewise, fish that live permanently in caves have relatively smaller visual processing regions in their brain compared to those that are found both in caves and on the surface (Fig. 12B) (Poulson and White, 1969). Blind mole rats (*Spalax ehrenbergi*) also show a marked reduction in eye size, the remaining structures being maintained subcutaneously for circadian rhythm generation (David-Gray et al., 1998). Like the star-nosed mole, blind mole rats have a reduced thalmocortical visual system and an expanded somatosensory representation associated with a subterranean lifestyle. In some cases, reductions in the volume of sensory processing regions can occur within individuals following the transition to a new environment. For example, virgin female ants (*Messor pergandei* or *Pogonomyrmex rugosus*) make mating flights before removing their wings and excavating a subterranean nest to found a new colony. Brain regions specifically associated with visual processing such as the medulla are reduced in volume in these mature mated ant queens relative to virgin female ants (Julian and Gronenberg, 2002).

The reductions of specific sensory structures and their associated brain regions also occur in animals living on islands (see Niven, 2005; Niven, 2007; Niven, 2008b). For example, a fossil bovid, *Myotragus balearicus*, found on two Mediterranean islands, has a reduced orbit and endocast volume relative to bovids found on

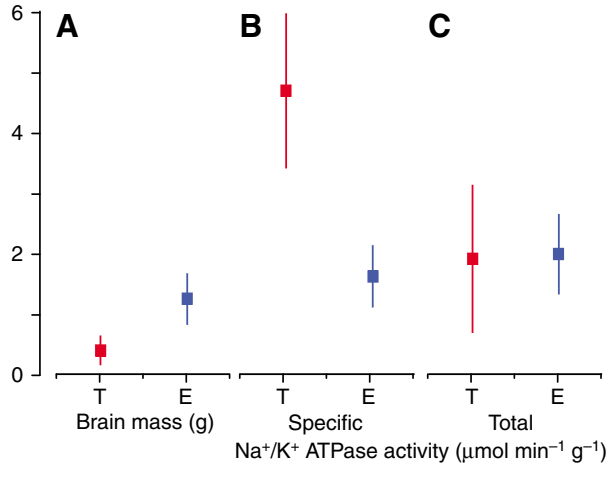

Fig. 11. The relative size of brains and brain regions is not a direct indicator of energy consumption. (A) The average brain mass of elasmobranch fishes (E, blue) weighing between 175 and 1250 g and teleost fishes (T, red) weighing between 222 and 1170 g. (B) The specific activity of the Na^+/K^+ ATPase (µmol min^{-1} g^{-1}). (C) The total brain Na^+/K^+ ATPase activity (µmol min^{-1}). Data from Nilsson et al. (Nilsson et al., 2000).

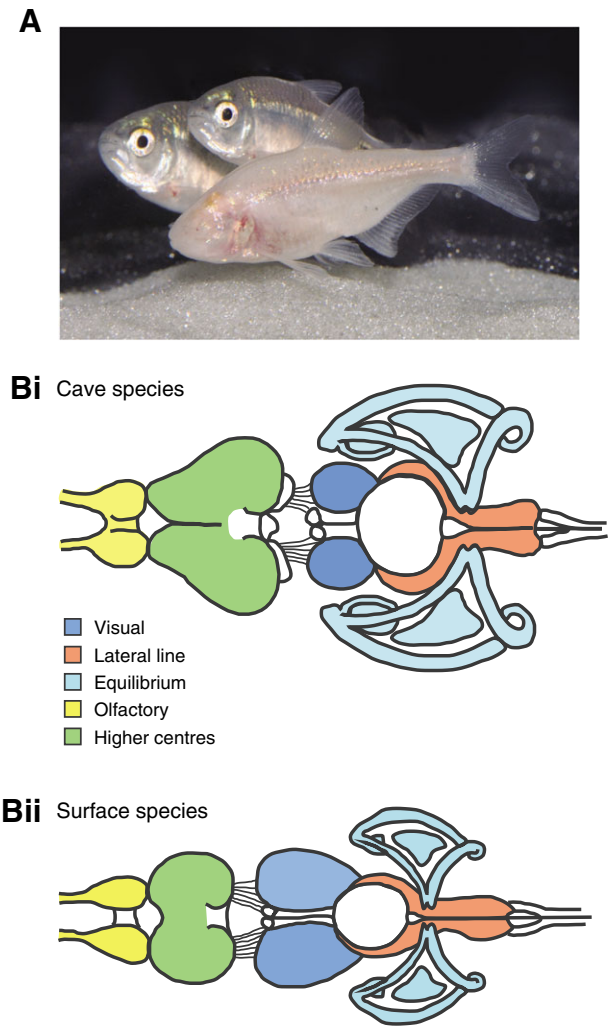

Fig. 12. Reduction of the retina and central regions of the visual system in cave fish. (A) Eye loss in cave populations of *Astyanax mexicanus* that have been isolated for approximately 1 million years. The photograph shows one eyeless cave fish (foreground) and two fish from closely related surface-dwelling populations. (B) Reduction in the relative size of the brain regions associated with visual processing in fish species living permanently in caves. (i) *Amblyopsis spelaea*, a fish species living exclusively in caves. (ii) *Chologaster agassizi*, a fish species occasionally found in caves but also in surface environments. Adapted from Poulson and White (Poulson and White, 1969). Photograph by R. Borowsky, reproduced with permission.

the mainland (Kohler and Moya-Sola, 2004) suggesting a reduction in visual processing due to a reduced need for vigilance in the absence of mainland predators on these islands (Kohler and Moya-Sola, 2004; Niven, 2005). Fruit flies (*Drosophila melanogaster*) bred under laboratory conditions do not require vision to locate food or mates reducing the selection pressure on the visual system (Fig. 13). These flies show an overall reduction in compound eye size and facet size that is related to their time in captivity (Tan et al., 2005).

These reductions or losses of sensory structures in numerous independent lineages suggest that there is an advantage to the loss of sensory structures in environments in which they cannot provide information, implying that they represent a cost. An alternative explanation may be that in the absence of selection pressure to retain

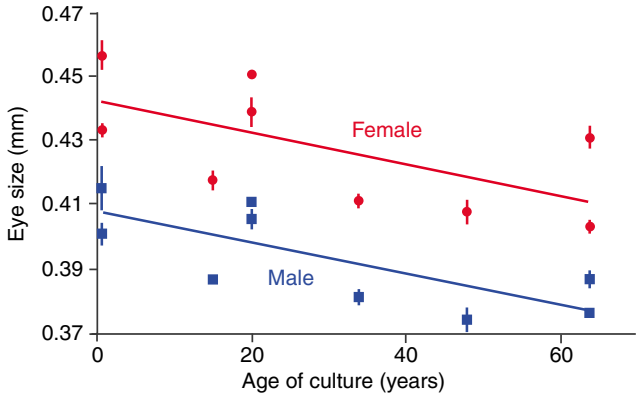

Fig. 13. Length of time in culture causes a reduction in eye size in *Drosophila melanogaster*. Changes in absolute eye size with the number of years in culture. Blue indicates measurements from male flies and red indicates measurements from female flies. Error bars indicate one standard deviation. Adapted from Tan et al. (Tan et al., 2005).

sensory structures they are lost through disuse, not because of their cost, as proposed by Darwin (Darwin, 1859):

> "*As it is difficult to imagine that the eyes, though useless, could be in any way injurious to animals living in darkness, their loss may be attributed to disuse.*"

As we discussed above, however, neural tissue is energetically expensive both to use and to maintain (Ames et al., 1992; Nilsson, 1996; Attwell and Laughlin, 2001; Lennie, 2003; Niven et al., 2003a; Nawroth et al., 2007; Niven et al., 2007). Thus, in the case of subterranean vertebrates and invertebrates, maintaining the retina and central visual processing regions would incur considerable energetic costs, even in the dark. This suggests that the reduction of peripheral and central visual structures is indeed due, at least in part, to their high energetic costs. The high energetic costs of maintaining and using neural structures should influence the evolution of both central and peripheral structures irrespective of the particular sensory modality. Indeed, these high energetic demands should favour the reduction of peripheral and central structures associated with a particular sensory modality to a functional minimum (Niven et al., 2007). However, the strength of the selective pressure for reduced energetic costs of sensory systems will depend critically upon the precise environmental circumstances in which a specific animal finds itself (Niven, 2005; Niven, 2007; Niven, 2008a; Niven, 2008b). For example, animals living in caves or on islands are often extremely energy limited, increasing the need for energy saving by reducing sensory structures to a functional minimum.

Trade-offs between sensory systems

The limited energy budgets of animals coupled with the high energetic costs of the brain have led to the suggestion that the additional energy invested in the development, maintenance and use accompanying an expansion in brain size is traded off against a reduction in the size of another energetically expensive tissue. Aiello and Wheeler proposed that during primate evolution the expansion of the brain relative to body mass was accompanied by a relative reduction in gut size: the expensive-tissue hypothesis (Aiello and Wheeler, 1995). A similar correlation has also been found in teleost fish (Kaufman et al., 2003). However, more recent tests of this theory

in birds and bats have failed to find strong support for a trade-off between brain size and gut size (Jones and MacLarnon, 2004; Isler and van Schaik, 2006b). For example, in birds pectoral muscle mass is negatively correlated with brain size, suggesting a trade-off, whilst reproductive costs are positively correlated (Isler and van Schaik, 2006b). One possibility suggested is that species with larger brains are better able to provision their offspring (Isler and van Schaik, 2006b).

A further implication of the expensive-tissue hypothesis is that a reduction in brain size relative to body could accompany increased energy usage by another tissue/organ. For example, some ant queens use their energy stores to produce the initial workers within their colony. The provisioning of eggs requires large amounts of energy and queens use additional energy gained from the breakdown of flight muscles and possibly from visual processing structures for reproduction (Hölldobler and Wilson, 1990; Julian and Gronenberg, 2002).

Trade-offs may also occur between sensory systems, the increase in the volume of peripheral sense organs or central sensory processing regions in one modality being accompanied by a reduction in another sensory modality. For example, as mentioned above, both the star-nosed mole and the blind mole rat have reduced a thalmocortical visual system and an expanded somatosensory representation (Cooper et al., 1993; Catania, 2005). Numerous examples of enhanced somatosensory systems in animals with reduced visual systems also occur in both vertebrates and invertebrates that inhabit cave systems. These trade-offs between different sensory modalities may be important because they may not affect the total energetic cost of sensory processing within the brain substantially and, therefore, do not necessarily affect energetic demands. However, the expansion or reduction of peripheral or central sensory processing structures may be limited by the extent to which regions within the brain can evolve independently (mosaic evolution) (Finlay and Darlington, 1995; Barton and Harvey, 2000; Striedter, 2005). Within the mammalian cortex, however, substantial developmental plasticity can occur with sensory processing regions being co-opted for different sensory modalities depending on experience, including trauma (for a review, see Krubitzer and Kaas, 2006). Such plasticity between different sensory modalities within the cortex may be particularly important because it facilitates rapid adaptation to novel environmental circumstances without substantially affecting the total energetic cost of sensory processing within the brain.

Conclusions

Energy consumption affects all aspects of animal life from cellular metabolism and muscle contraction to growth and foraging (Alexander, 1999). Yet despite early studies on energy metabolism in neural tissue (e.g. Kety, 1957), the impact of energy consumption upon the evolution of nervous systems has only recently begun to be generally appreciated (Laughlin, 2001). Recent studies have made substantial advances in relating the energy consumption of neural tissue to neural function. Together these studies show that there are high energetic costs associated with the nervous system both at rest and whilst neurons are signalling (Laughlin et al., 1998; Attwell and Laughlin, 2001; Niven et al., 2007). Crucially for the evolution of the nervous system, and in particular sensory systems, these costs are incurred even during activity. Thus, animals pay an energetic cost associated with nervous system irrespective of the demands of other tissues such as skeletal muscle.

Evidence from fly photoreceptors suggests that the energetic costs incurred by neurons at rest are linked to their energetic costs whilst signalling by basic biophysical relationships (Niven et al., 2007). Thus neural function, and therefore the production of adaptive behaviour, is linked to neural energy consumption. Excess signal processing capacity in sensory systems is severely penalized by increased energetic costs producing a Law of Diminishing Returns. The precise relationship between energy consumption and signalling is likely to depend on the specific neuronal type; these relationships can be adjusted by the specific combinations of ion channels, and possibly synaptic inputs, within the neuronal cell membrane. Numerous strategies for reducing the costs incurred by the sensory systems have been found in both insect and vertebrate sensory systems (e.g. Vinje and Gallant, 2000; Perez-Orive et al., 2002; Niven et al., 2003a; Niven et al., 2003b; Hromádka et al., 2008). These strategies aim to reduce the energetic costs within sensory systems by filtering out predictable inputs to sensory systems, reducing the amount of redundant information that is encoded and representing this information more efficiently.

Energy limitations appear to have affected the evolution of sensory systems, causing trade-offs between sensory systems encoding different modalities. The effects of energy limitation appear to be especially obvious in animals living in on islands or in caves, which tend to be energy-limited environments (Kohler and Moya-Sola, 2004; Niven, 2007; Borowsky, 2008; Niven, 2008a; Niven, 2008b). For these animals, reductions or complete losses of visual structures are relatively common and appear to confirm the penalty for excess capacity found at the level of single neurons.

The acquisition of sensory information for many modalities, including vision, requires muscular movements that are largely ignored by most analyses of energy consumption within sensory systems. For example, eye and/or head movements are essential in both mammals and insects for obtaining certain types of visual information, such as parallax. Active senses such echolocation in bats and electrosensation in fish also depend on motor activity to generate the initial signal. The energetic costs associated with this muscle activity may be substantial and will further increase our estimates of the costs of sensory systems.

We would like to thank John Douglass, Biswa Sengupta and Bill Wcislo for comments. This study was supported by the Royal Society (J.E.N.), the BBSRC (S.B.L.) and the Frank Levinson Family Foundation to the STRI Laboratory of Behavior and Evolutionary Neurobiology (J.E.N.).

References

Aho, A. C., Donner, K., Hyden, C., Larsen, L. O. and Reuter, T. (1988). Low retinal noise in animals with low body temperature allows high visual sensitivity. *Nature* **334**, 348-350.

Aiello, L. C. and Wheeler, P. (1995). The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. *Curr. Anthropol.* **36**, 199-221.

Alexander, R. M. (1999). *Energy for Animal Life*. Oxford: Oxford University Press.

Ames, A., Li, Y. Y., Heher, E. C. and Kimble, C. R. (1992). Energy-metabolism of rabbit retina as related to function-high cost of Na^+ transport. *J. Neurosci.* **12**, 840-853.

Attneave, F. (1954). Some informational aspects of visual perception. *Psychol. Rev.* **61**, 183-193.

Attwell, D. and Gibb, A. (2005). Neuroenergetics and the kinetic design of excitatory synapses. *Nat. Rev. Neurosci.* **6**, 841-849.

Attwell, D. and Laughlin, S. B. (2001). An energy budget for signaling in the grey matter of the brain. *J. Cereb. Blood Flow Metab.* **21**, 1133-1145.

Autrum, H., Zettler, F. and Järvilahto, M. (1970). Postsynaptic potentials from a single monopolar neuron of ganglion opticum I of blowfly *Calliphora*. *Z. Vergl. Physiol.* **70**, 414-424.

Baddeley, R., Abbott, L. F., Booth, M. C. A., Sengpiel, F., Freeman, T., Wakeman, E. A. and Rolls, E. T. (1997). Responses of neurons in primary and inferior temporal visual cortices to natural scenes. *Proc. R. Soc. Lond. B Biol. Sci.* **264**, 1775-1783.

Balasubramanian, V. and Berry, M. J. (2002). A test of metabolically efficient coding in the retina. *Network* **13**, 531-552.

Balasubramanian, V., Kimber, D. and Berry, M. J. (2001). Metabolically efficient information processing. *Neural Comput.* **13**, 799-815.

Barlow, H. B. (1956). Retinal noise and absolute threshold. *J. Opt. Soc. Am.* **46**, 634-639.

Barlow, H. B. (1961). Possible principles underlying the transformation of sensory messages. In *Sensory Communication* (ed. W. A. Rosenblith), pp. 217-234. Cambridge, MA: MIT Press.

Barlow, H. B. (1969). Pattern recognition and the responses of sensory neurons. *Ann. N. Y. Acad. Sci.* **156**, 872-881.
Barlow, H. B., Levick, W. R. and Yoon, M. (1971). Responses to single quanta of light in retinal ganglion cells. *Vision Res.* **11**, 87-101.
Barton, R. A. and Harvey, P. H. (2000). Mosaic evolution of brain structure in mammals. *Nature* **405**, 1055-1058.
Baylor, D. A., Lamb, T. D. and Yau, K.-W. (1979). Responses of retinal rods to single photons. *J. Physiol. Lond.* **288**, 613-634.
Bell, C. C. and Grant, K. (1989). Corollary discharge inhibition and preservation of temporal information in a sensory nucleus of Mormyrid electric fish. *J. Neurosci.* **9**, 1029-1044.
Berg, H. C. and Purcell, E. M. (1977). Physics of chemoreception. *Biophys. J.* **20**, 193-219.
Berry, M. J., Warland, D. K. and Meister, M. (1997). The structure and precision of retinal spike trains. *Proc. Natl. Acad. Sci. USA* **94**, 5411-5416.
Bickler, P. E. and Donohoe, P. H. (2002). Adaptive responses of vertebrate neurons to hypoxia. *J. Exp. Biol.* **205**, 3579-3586.
Bokma, F. (2004). Evidence against universal metabolic allometry. *Funct. Ecol.* **18**, 184-187.
Borowsky, R. (2008). Restoring sight in blind cavefish. *Curr. Biol.* **18**, R23-R24.
Boutilier, R. G. (2001). Mechanisms of cell survival in hypoxia and hypothermia. *J. Exp. Biol.* **204**, 3171-3181.
Burrows, M. (1980). The tracheal supply to the central nervous system of the locust. *Proc. R. Soc. Lond. B Biol. Sci.* **207**, 63-78.
Burrows, M. and Newland, P. L. (1993). Correlation between the receptive fields of locust interneurons, their dendritic morphology, and the central projections of mechanosensory neurons. *J. Comp. Neurol.* **329**, 412-426.
Burrows, M. and Newland, P. L. (1994). Convergence of mechanosensory afferents from different classes of exteroceptors onto spiking local interneurons in the locust. *J. Neurosci.* **14**, 3341-3350.
Burrows, M. and Siegler, M. V. S. (1976). Transmission without spikes between locust interneurones and motoneurones. *Nature* **262**, 222-224.
Catania, K. C. (2005). Evolution of sensory specializations in insectivores. *Anat. Rec. A Discov. Mol. Cell. Evol. Biol.* **287**, 1038-1050.
Chen, B. L., Hall, D. H. and Chklovskii, D. B. (2006). Wiring optimization can relate neuronal structure and function. *Proc. Natl. Acad. Sci. USA* **103**, 4723-4728.
Cherniak, C. (1994). Component placement optimization in the brain. *J. Neurosci.* **14**, 2418-2427.
Cherniak, C. (1995). Neural component placement. *Trends Neurosci.* **18**, 522-527.
Chklovskii, D. B. (2004). Synaptic connectivity and neuronal morphology: viewpoint two sides of the same coin. *Neuron* **43**, 609-617.
Chklovskii, D. B. and Koulakov, A. A. (2004). Maps in the brain: what can we learn from them? *Annu. Rev. Neurosci.* **27**, 369-392.
Chown, S. L., Marais, E., Terblanche, J. S., Klok, C. J., Lighton, J. R. B. and Blackburn, T. M. (2007). Scaling of insect metabolic rate is inconsistent with the nutrient supply network model. *Funct. Ecol.* **21**, 282-290.
Clarke, J. B. and Sokoloff, L. (1999). Circulation and energy metabolism of the brain. In *Basic Neurochemistry*, 6th edn (ed. G. J. Siegel, B.W. Agranoff, R. W. Albers, S. K. Fisher and M. D. Uhler), pp. 637-669. Philadelphia: Lippincott-Raven.
Cooper, H. M., Herbin, M. and Nevo, E. (1993). Visual system of a naturally microphthalmic mammal: the blind mole rat, *Spalax ehrenbergi*. *J. Comp. Neurol.* **328**, 313-350.
Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection, or The Preservation of Favoured Races in the Struggle for Life*. London: John Murray.
David-Gray, Z. K., Janssen, J. W. H., DeGrip, W. J., Nevo, E. and Foster, R. G. (1998). Light detection in a 'blind' mammal. *Nat. Neurosci.* **8**, 655-656.
De Polavieja, G. G. (2002). Errors drive the evolution of biological signalling to costly codes. *J. Theor. Biol.* **214**, 657-664.
de Ruyter van Steveninck, R. R., Lewen, G. D., Strong, S. P., Koberle, R. and Bialek, W. (1997). Reproducibility and variability in neural spike trains. *Science* **275**, 1805-1808.
Erecinska, M. and Silver, I. A. (2001). Tissue oxygen tension and brain sensitivity to hypoxia. *Respir. Physiol.* **128**, 263-276.
Faisal, A. A., White, J. A. and Laughlin, S. B. (2005). Ion-channel noise places limits on the miniaturization of the brain's wiring. *Curr. Biol.* **15**, 1143-1149.
Faisal, A. A., Selen, L. P. J. and Wolpert, D. M. (2008). Noise in the nervous system. *Nat. Rev. Neurosci.* **9**, 292-303.
Finlay, B. L. and Darlington, R. B. (1995). Linked regularities in the development and evolution of mammalian brains. *Science* **268**, 1578-1584.
French, A. S. and Sanders, E. J. (1981). The mechanosensory apparatus of the femoral tactile spine of the cockroach, *Periplaneta americana*. *Cell Tissue Res.* **219**, 53-68.
Glynn, I. M. (1993). Annual review prize lecture. 'All hands to the sodium pump'. *J. Physiol. Lond.* **462**, 1-30.
Gossard, J.-P., Cabelguen, J.-M. and Rossignol, S. (1990). Phase-dependent modulation of primary afferent depolarization in single cutaneous primary afferents evoked by peripheral stimulation during fictive locomotion in the cat. *Brain Res.*, **537**, 14-23.
Gossard, J.-P., Cabelguen, J.-M. and Rossignol, S. (1991). An intracellular study of muscle primary afferents during fictive locomotion in the cat. *J. Neurophysiol.*, **65**, 914-926.
Gronenberg, W. and Hölldobler, B. (1999). Morphologic representation of visual and antennal information in the ant brain. *J. Comp. Neurol.* **412**, 229-240.
Hagins, W. A., Penn, R. D. and Yoshikami, S. (1970). Dark current and photocurrent in retinal rods. *Biophys. J.* **10**, 380-412.
Hammond, K. A. and Diamond, J. (1997). Maximal sustained energy budgets in humans and animals. *Nature* **386**, 457-462.
Harris, G. G., Frischkopf, L. S. and Flock, Å. (1970). Receptor potentials from hair cells of the lateral line. *Science* **167**, 76-79.
Harvey, W. R. (1992). Physiology of V-ATPases. *J. Exp. Biol.* **172**, 1-17.
Hecht, S., Shlaer, S. and Pirenne, M. H. (1942). Energy, quanta, and vision. *J. Gen. Physiol.* **25**, 819-840.
Hille, B. (2001). *Ion Channels of Excitable Membranes* (3rd edn). Sunderland, MA: Sinauer Associates.
Hölldobler, B. and Wilson, E. O. (1990). *The Ants*. Cambridge, MA: Harvard University Press.
Hornbein, T. F. (2001). The high altitude brain. *J. Exp. Biol.* **204**, 3129-3132.
Howard, J., Blakeslee, B. and Laughlin, S. B. (1987). The intracellular pupil mechanism and photoreceptor signal-noise ratios in the fly *Lucilia cuprina*. *Proc. R. Soc. Lond. B Biol. Sci.* **231**, 415-435.
Hromádka, T., Deweese, M. R. and Zador, A. M. (2008). Sparse representation of sounds in the unanesthetized auditory cortex. *PloS Biol.* **6**, e16.
Ide, K. and Secher, N. H. (2000). Cerebral blood flow and metabolism during exercise. *Prog. Neurobiol.* **61**, 397-414.
Isler, K. and van Schaik, C. P. (2006a). Metabolic costs of brain size evolution. *Biol. Lett.* **2**, 557-560.
Isler, K. and van Schaik, C. P. (2006b). Costs of encephalization: the energy trade-off hypothesis in birds. *J. Hum. Evol.* **51**, 228-243.
Jones, K. E. and MacLarnon, A. M. (2004). Affording larger brains: testing hypotheses of mammalian brain evolution in bats. *Am. Nat.* **164**, E20-E31.
Julian, G. E. and Gronenberg, W. (2002). Reduction of brain volume correlates with behavioral changes in queen ants. *Brain Behav. Evol.* **60**, 152-164.
Juusola, M., Niven, J. E. and French, A. S. (2003). *Shaker* K^+ channels contribute early nonlinear amplification to the light response in *Drosophila* photoreceptors. *J. Neurophysiol.* **90**, 2014-2021.
Kaiser, M. and Hilgetag, C. C. (2006). Nonoptimal component placement, but short processing paths, due to long-distance projections in neural systems. *PLoS Comput. Biol.* **2**, 805-815.
Kaneko, A. (1970). Physiological and morphological identification of horizontal, bipolar, and amacrine cells in the goldfish retina. *J. Physiol. Lond.* **207**, 623-633.
Katz, B. and Miledi, R. (1970). Membrane noise produced by acetylcholine. *Nature* **226**, 962-963.
Kaufman, J. A., Hladik, C. M. and Pasquet, P. (2003). Discussion on the expensive-tissue hypothesis: independent support from highly encephalized fish. *Curr. Anthropol.* **44**, 705-707.
Kety, S. S. (1957). The general metabolism of the brain *in vivo*. In *Metabolism of the Nervous System* (ed. D. Richter), pp. 221-237. London: Pergamon.
Kohler, M. and Moya-Sola, S. (2004). Reduction of brain and sense organs in the fossil insular bovid Myotragus. *Brain Behav. Evol.* **63**, 125-140.
Krebs, J. R. and Davies, N. B. (1993). *An Introduction to Behavioural Ecology*. Oxford: Blackwell Science.
Krubitzer, L. and Kaas, J. H. (2006). The evolution of the neocortex in mammals: how is phenotypic diversity generated? *Curr. Opin. Neurobiol.* **15**, 444-453.
Laughlin, S. B. (1994). Matching coding, circuits, cells, and molecules to signals: general-principles of retinal design in the flys eye. *Prog. Retin. Eye Res.* **13**, 165-196.
Laughlin, S. B. (1996). Matched filtering by a photoreceptor membrane. *Vision Res.* **36**, 1529-1541.
Laughlin, S. B. (2001). Energy as a constraint on the coding and processing of sensory information. *Curr. Opin. Neurobiol.* **11**, 475-480.
Laughlin, S. B. and Weckström, M. (1993). Fast and slow photoreceptors: a comparative study of the functional diversity of coding and conductances in the diptera. *J. Comp. Physiol. A* **172**, 593-609.
Laughlin, S. B., van Steveninck, R. R. D. and Anderson, J. C. (1998). The metabolic cost of neural information. *Nat. Neurosci.* **1**, 36-41.
Laughlin, S. B., Anderson, J. C., O'Carroll, D. C. and De Ruyter van Steveninck, R. R. (2000). Coding efficiency and the metabolic cost of sensory and neural information. In *Information Theory and the Brain* (ed. R. Baddeley, P. Hancock and P. Foldiak), pp. 41-61. Cambridge: Cambridge University Press.
Laurent, G. (2002). Olfactory network dynamics and the coding of multidimensional signals. *Nat. Rev. Neurosci.* **3**, 884-895.
Lennie, P. (2003). The cost of cortical computation. *Curr. Biol.* **13**, 493-497.
Levy, W. B. and Baxter, R. A. (1996). Energy efficient neural codes. *Neural Comput.* **8**, 531-543.
Li, W.-C., Soffe, S. R. and Roberts, A. (2002). Spinal inhibitory neurons that modulate cutaneous sensory pathways during locomotion in a simple vertebrate. *J. Neurosci.* **22**, 10924-10934.
Lillywhite, P. G. and Laughlin, S. B. (1979). Transducer noise in a photoreceptor. *Nature* **277**, 569-557.
Lipton, P. (1999). Ischemic cell death in brain neurons. *Physiol. Rev.* **79**, 1431-1568.
Lovegrove, B. G. (2000). The zoogeography of mammalian basal metabolic rate. *Am. Nat.* **156**, 201-219.
Lutz, P. L. (1992). Mechanisms for anoxic survival in the vertebrate brain. *Annu. Rev. Physiol.* **54**, 601-618.
Maddock, J. R. and Shapiro, L. (1993). Polar location of the chemoreceptor complex in the *Escherichia coli* cell. *Science* **259**, 1717-1723.
Madsen, P. L., Sperling, B. K., Warming, T., Schmidt, J. F., Secher, N. H., Wildschiødtz, G., Holm, S. and Lassen, N. A. (1993). Middle cerebral artery blood velocity and cerebral blood flow and O_2 uptake during dynamic exercise. *J. Appl. Physiol.* **74**, 245-250.
Mainen, Z. F. and Sejnowski, T. J. (1995). Reliability of spike timing in neocortical neurons. *Science* **268**, 1503-1506.
Martin, R. D. (1981). Relative brain size and basal metabolic-rate in terrestrial vertebrates. *Nature* **293**, 57-60.
McNab, B. K. and Eisenberg, J. F. (1989). Brain size and its relation to the rate of metabolism in mammals. *Am. Nat.* **133**, 157-167.
Mink, J. W., Blumenschine, R. J. and Adams, D. B. (1981). Ratio of central nervous system to body metabolism in vertebrates: its constancy and functional basis. *Am. J. Physiol.* **241**, R203-R212.

Moriyana, Y., Maeda, M. and Futai, M. (1992). The role of V-ATPase in neuronal and endocrine systems. *J. Exp. Biol.* **172**, 171-178.
Nagy, K. A. (2005). Field metabolic rate and body size. *J. Exp. Biol.* **208**, 1621-1625.
Nawroth, J. C., Greer, C. A., Chen, W. R., Laughlin, S. B. and Shepherd, G. M. (2007). An energy budget for the olfactory glomerulus. *J. Neurosci.* **27**, 9790-9800.
Nelson, R. J., Sur, M., Felleman, D. J. and Kaas, J. H. (1980). Representations of the body surface in postcentral parietal cortex of *Macaca fascicularis*. *J. Comp. Neurol.* **192**, 611-643.
Nilsson, G. E. (1996). Brain and body oxygen requirements of *Gnathonemus petersii*, a fish with an exceptionally large brain. *J. Exp. Biol.* **199**, 603-607.
Nilsson, G. E. (2001). Surviving anoxia with the brain turned on. *News Physiol. Sci.* **16**, 217-221.
Nilsson, G. E., Routley, M. H. and Renshaw, G. M. C. (2000). Low mass-specific brain Na^+/K^+-ATPase activity in elasmobranch compared to teleost fishes: implications for the large brain size of elasmobranchs. *Proc. R. Soc. Lond. B Biol. Sci.* **267**, 1335-1339.
Niven, J. E. (2005). Brain evolution: getting better all the time? *Curr. Biol.* **15**, R624-R626.
Niven, J. E. (2007). Brains, islands and evolution: breaking all the rules. *Trends Ecol. Evol.* **22**, 57-59.
Niven, J. E. (2008a). Evolution: convergent eye losses in fishy circumstances. *Curr. Biol.* **18**, R27-R29.
Niven, J. E. (2008b). Response to Köhler et al.: impossible arguments about possible species? *Trends Ecol. Evol.* **23**, 8-9.
Niven, J. E. and Scharlemann, J. P. W. (2005). Do insect metabolic rates at rest and during flight scale with body mass? *Biol. Lett.* **1**, 346-349.
Niven, J. E., Vähäsöyrinki, M. and Juusola, M. (2003a). *Shaker* K^+-channels are predicted to reduce the metabolic cost of neural information in *Drosophila* photoreceptors. *Proc. R. Soc. Lond. B Biol. Sci.* **270**, S58-S61.
Niven, J. E., Vähäsöyrinki, M., Kauranen, M., Hardie, R. C., Juusola, M. and Weckström, M. (2003b). The contribution of *Shaker* K^+ channels to the information capacity of *Drosophila* photoreceptors. *Nature* **421**, 630-634.
Niven, J. E., Vähäsöyrinki, M., Juusola, M. and French, A. S. (2004). Interactions between light-induced currents, voltage-gated currents, and input signal properties in *Drosophila* photoreceptors. *J. Neurophysiol.* **91**, 2696-2706.
Niven, J. E., Anderson, J. C. and Laughlin, S. B. (2007). Fly photoreceptors demonstrate energy-information trade-offs in neural coding. *PLoS Biol.* **5**, 828-840.
Niven, J. E., Graham, C. M. and Burrows, M. (2008). Diversity and evolution of the insect ventral nerve cord. *Annu. Rev. Entomol.* **53**, 253-271.
Olshausen, B. A. and Field, D. J. (2004). Sparse coding of sensory inputs. *Curr. Opin. Neurobiol.* **14**, 481-487.
Orgogozo, J. M. and Larsen, B. (1979). Activation of the supplementary motor area during voluntary movement in man suggests it works as a supramotor area. *Science* **206**, 847-850.
Pangršič, T., Stušek, P., Belušič, G. and Zupančič, G. (2005). Light dependence of oxygen consumption by blowfly eyes recorded with a magnetic diver balance. *J. Comp. Physiol. A* **191**, 75-84.
Penfield, W. and Boldrey, E. (1937). Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. *Brain* **60**, 389-443.
Perez-Orive, J., Mazor, O., Turner, G. C., Cassenaer, S., Wilson, R. I. and Laurent, G. (2002). Oscillations and sparsening of odor representations in the mushroom body. *Science* **297**, 359-365.
Post, R. L., Hegyvary, C. and Kume, S. (1972). Activation by adenosine triphosphate in the phosphorylation kinetics of sodium and potassium ion transport adenosine triphosphatase. *J. Biol. Chem.* **247**, 6530-6540.
Poulet, J. F. A. and Hedwig, B. (2006). New insights into corollary discharges mediated by identified neural pathways. *Trends Neurosci.* **30**, 14-21.
Poulson, T. L. and White, W. B. (1969). The cave environment. *Science* **165**, 971-981.
Raichle, M. E., Grubb, R. L., Gado, M. H., Eichling, J. O. and Terpogossian, M. M. (1976). Correlation between regional cerebral blood-flow and oxidative metabolism. *Arch. Neurol.* **33**, 523-526.
Ripley, S. H., Bush, B. M. H. and Roberts, A. (1968). Crab muscle receptor which responds without impulses. *Nature* **218**, 1170-1171.
Sarpeshkar, R. (1998). Analog versus digital: extrapolating from electronics to neurobiology. *Neural Comput.* **10**, 1601-1638.
Savage, V. M., Gillooly, J. F., Woodruff, W. H., West, G. B., Allen, A. P., Enquist, B. J. and J. H. B. (2004). The predominance of quarter-power scaling in biology. *Funct. Ecol.* **18**, 257-282.
Schmidt-Nielsen, K. (1997). *Animal Physiology: Adaptation and Environment* (5th edn), pp. 607. Cambridge: CUP.
Schreiber, S., Machens, C. K., Herz, A. V. M. and Laughlin, S. B. (2002). Energy-efficient coding with discrete stochastic events. *Neural Comput.* **14**, 1323-1346.
Shepherd, G. M., Chen, W. R. and Greer, C. (2004). Olfactory bulb. In *The Synaptic Organization of the Brain*, 5th edn (ed. G. M. Shepherd), pp. 165-216. New York: Oxford University Press.
Sillar, K. T. and Skorupski, P. (1986). Central input to primary afferent neurones in crayfish, *Pacifastacus leniusculus* is correlated with rhythmic output of thoracic ganglia. *J. Neurophysiol.* **55**, 678-688.
Skou, J. C. (1957). The influence of some cations on an adenosine triphosphatase from peripheral nerves. *Biochim. Biophys. Acta* **1000**, 439-446.
Srinivasan, M. V., Laughlin, S. B. and Dubs, A. (1982). Predictive coding: a fresh view of inhibition in the retina. *Proc. R. Soc. Lond. B Biol. Sci.* **216**, 427-459.
Strecker, U., Faúndez, V. H. and Wilkens, H. (2004). Phylogeography of surface and cave *Astyanax* (Teleostei) from Central and North America from cytochrome b sequence data. *Mol. Phylogenet. Evol.* **33**, 469-481.
Striedter, G. F. (2005). *Principles of Brain Evolution*. Sunderland, MA: Sinauer Associates.
Suarez, R. K. and Darveau, C. A. (2005). Multi-level regulation and metabolic scaling. *J. Exp. Biol.* **208**, 1627-1634.
Tan, S. J., Amos, W. and Laughlin, S. B. (2005). Captivity selects for smaller eyes. *Curr. Biol.* **15**, R540-R542.
Tomita, T. (1965). Electrophysiological study of the mechanisms subserving color coding in the fish retina. *Cold Spring Harb. Symp. Quant. Biol.* **30**, 559-566.
Vähäsöyrinki, M., Niven, J. E., Hardie, R. C., Weckström, M. and Juusola, M. (2006). Robustness of neural coding in *Drosophila* photoreceptors in the absence of slow delayed rectifier K^+ channels. *J. Neurosci.* **26**, 2652-2660.
Vallet, A. M., Coles, J. A., Eilbeck, J. C. and Scott, A. C. (1992). Membrane conductances involved in amplification of small signals by sodium channels in photoreceptors of the drone Honey Bee. *J. Physiol. Lond.* **456**, 303-324.
Vinje, W. E. and Gallant, J. L. (2000). Sparse coding and decorrelation in primary visual cortex during natural vision. *Science* **287**, 1273-1276.
Weckström, M. and Laughlin, S. B. (1995). Visual ecology and voltage-gated ion channels in insect photoreceptors. *Trends Neurosci.* **18**, 17-21.
Weibel, E. R. and Hoppeler, H. (2005). Exercise-induced maximal metabolic rate scales with muscle aerobic capacity. *J. Exp. Biol.* **208**, 1635-1644.
Weibel, E. R., Bacigalupe, L. D., Schmitt, B. and Hoppeler, H. (2004). Allometric scaling of maximal metabolic rate in mammals: muscle aerobic capacity as determinant factor. *Respir. Physiol. Neurobiol.* **140**, 115-132.
Werblin, F. S. and Dowling, J. E. (1969). Organization of the retina of the mudpuppy, *Necturus maculosus*. II. Intracellular recording. *J. Neurophysiol.* **32**, 339-355.
White, C. R. and Seymour, R. S. (2003). Mammalian basal metabolic rate is proportional to body mass(2/3). *Proc. Natl. Acad. Sci. USA* **100**, 4046-4049.
Wilkens, H. (2007). Regressive evolution: ontogeny and genetics of cavefish eye rudimentation. *Biol. J. Linn. Soc. Lond.* **92**, 287-296.
Willmore, B. and Tolhurst, D. J. (2001). Characterizing the sparseness of neural codes. *Network* **12**, 255-270.
Wolf, H. and Burrows, M. (1995). Proprioceptive sensory neurons of a locust leg receive rhythmic presynaptic inhibition during walking. *J. Neurosci.* **15**, 5623-5636.
Yau, K.-W., Lamb, T. D. and Baylor, D. A. (1977). Light-induced fluctuations in membrane current of single toad rod outer segments. *Nature* **269**, 78-80.
Zapol, W. M., Liggins, G. C., Schneider, R. C., Qvist, J., Snider, M. T., Creasy, R. K. and Hochachka, P. W. (1979). Regional blood-flow during simulated diving in the conscious Weddell Seal. *J. Appl. Physiol.* **47**, 968-973.