Neuroscience and Biobehavioral Reviews 143 (2022) 104921

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Adaptively navigating affordance landscapes: How interactions between the superior colliculus and thalamus coordinate complex, adaptive behaviour

James M. Shine

Brain and Mind Centre, The University of Sydney, Sydney, Australia

ARTICLE INFO

Keywords:
superior colliculus
thalamus
pulvinar
mediodorsal
attractor
adapative

ABSTRACT

The thalamus plays a crucial role in higher-order emergent functions of the brain, including working memory, attention and conscious awareness. How this small subcortical structure supports these crucial capacities remains poorly understood. In this manuscript, I argue that the connections between the thalamus and the superior colliculus, along with their topological location within the broader systems-level circuitry of the brain, play a crucial role in shaping complex, adaptive dynamics. Through these connections, the superior colliculus is proposed to mediate conscious awareness of highly-valued sensory phenomena, and hence, to maximise the adaptive nature of subsequent actions engaged by the networks of the ventral tier of the thalamus. This perspective leads to multiple testable predictions that will shape research questions regarding the interactions between distributed systems supported by unique regions within the thalamus.

1. Introduction

The coordinated activity of billions of neurons in the human brain gives rise to a wide variety of different experiences and behaviours. A profound benefit of this organisation is that complex, adaptive behaviour can emerge from the massively parallel interactions between neurons in a manner that doesn't require a central operator (Eisenreich et al., 2017). As the nervous system expanded in size and complexity, there was a commensurate explosion in the number of possible ways that an animal could respond to subtle differences in context. Despite conferring major advantages (such as heightened adaptability to novel circumstances), this increase in nervous system complexity (Cisek, 2019) and the complexity of our external terrestrial environment (MacIver and Finlay, 2022; Mugan and MacIver, 2020) creates an inherent challenge: oftentimes what an animal needs simply isn't the most salient feature of the surrounding environment. For instance, if the machinery of the cerebral cortex is recruited by a maladaptive source (e.g., boosting a food signal when an animal is already satiated), an animals' behaviour can easily become decoupled from the things that the organism actually needs. To remedy this issue, a nervous system require processes for coordinating responses to opportunities as they present themselves (Redgrave et al., 1999), based on what an organism needs at a particular moment in time.

One way to solve this problem is to selectively augment the subset of neural activity that is of the most acute value to the organism. Without such a capacity, an organism with multiple options would constantly be pulled in different (and inevitably, irreconcilable) directions (Redgrave et al., 1999) – for instance, an animal that was simultaneously both hungry and afraid would attempt to both exploit a local food source and flee from a perceived predator in the same instant, creating a schism that is incompatible with life. So how might the mammalian nervous system get around this issue? There is ample evidence that the brain contains numerous mechanisms for non-linearly augmenting the activity and receptivity of specific subcircuits within the broader system of the brain (Desimone and Duncan, 1995). One popular argument suggests that the prefrontal regions of the cerebral cortex subserve these augmenting capacities (Miller and Cohen, 2001), however subcortical structures (i.e., those outside the telencephalon) also play prominent roles in driving behaviour, and also play a prominent role in augmenting specific neural activity patterns.

A paradigm example of such a subcortical structure is the superior colliculus (also known as the optic tectum in early vertebrates; Isa et al., 2021; Thompson et al., 2016). Sitting on the dorsal aspect of the brainstem, wedged between the thalamus and cerebellum, the superior colliculus is commonly associated with saccadic eye movements (May, 2006). However, the superior colliculus also maintains strong ascending

---

E-mail address: mac.shine@sydney.edu.au.

https://doi.org/10.1016/j.neubiorev.2022.104921
Received 4 April 2022; Received in revised form 8 September 2022; Accepted 8 September 2022

projections that connect the thalamus with the cerebral cortex and basal ganglia, integrating the structure within the context of global brain activity. For these reasons, it has been suggested that the colliculus acts to integrate sensory, motor and motivational signals into a coherent consensus that we experience as conscious awareness (Merker, 2007, 2013). Recent experiments in rodents have provided causal evidence directly linking the connections between the cerebral cortex, higher-order thalamus, striatum and superior colliculus to conscious perception (Takahashi et al., 2020). Specifically, inhibiting the descending axonal projections of layer V pyramidal neurons to both the thalamus and superior colliculus caused distinct impairments in the conscious perception of normally detectable stimuli. Thus, a key question arises: how do these distributed cortico-subcortical circuits work together in order to shape the contents of conscious awareness?

In this manuscript, I will outline a neuroanatomical circuit that integrates the superior colliculus, thalamus, basal ganglia and cerebral cortex in order to mediate complex, adaptive behaviour. Within this circuit, a critical role is played by the connections between the superficial and deep layers of the superior colliculus and the pulvinar and mediodorsal nucleus of the thalamus, respectively. The former circuit offers a natural means for augmenting an informationally-compressed subset of the neural activity processing visual inputs – i.e., for controlling the contents of visual conscious awareness. The latter circuit integrates value-based signals from the basal ganglia and hypothalamus in order to ensure that ongoing neural activity is shaped and constrained by an animal's motivational state. After reviewing the functional neuroanatomy of these two systems, I will then summarise key algorithmic features of the colliculo-thalamic circuitry by extending a previously-proposed attractor landscape framework (Shine, 2020) to consider the role played by the colliculus in yoking activity to a valued set of affordances that augment adaptive behaviour. Finally, I argue that, through their evolving interactions, the key components of these circuits distributed across the brain are ideally suited for shaping the contents of an animal's conscious awareness of the world around them.

2. Interactions between the superficial superior colliculus and inferior pulvinar

The superior colliculus first emerged in vertebrates around ~550 mya, around the time of the Cambrian explosion (Butler, 1994; Feinberg and Mallatt, 2013). While mostly known for its retinotopic organisation and association with saccadic eye movements (which are driven by structures in the deep layers of the superior colliculus; May, 2006), the neurons of the superficial superior colliculus are actually heavily inter-connected with a number of other structures, including the dorsal thalamus (Fig. 1), the ventromedial hypothalamus, the periaqueductal grey, and the zona incerta (Benavidez et al., 2021).

Most critical for the mechanisms described in this manuscript are the so-called "Wide-Field" cells of the superficial colliculus (Fig. 1; light blue), which receive a large glutamatergic input from PT-type pyramidal neurons, primarily from occipital cortex, but also presumably from the relatively sparse yet widespread projections from temporal, frontal and parietal cortices that innervate the superficial superior colliculus (Basso and May, 2017; Collins et al., 2005; Fries, 1984; May, 2006). The number of PT-type cells that project to the colliculus is far greater than the number of Wide-field cells, suggesting that these cells likely perform a dimensionality reduction, similar to the functions mediated by connections between the cerebral cortex and the striatum (Bar-Gad et al., 2003). Rather than projecting into the brainstem (like the much-studied neurons in the deep layers of the superior colliculus), the glutamatergic projections of Wide-Field cells instead ascend back into the brain where they form dense clusters that engulf the dendrites of glutamatergic neurons in the inferior section of the pulvinar nuclei in the posterior thalamus (Baizer et al., 1993; Basso and May, 2017; Gale and Murphy, 2018; Gharaei et al., 2020; Zhou et al., 2017). Investigations in primate thalamus suggest that these projections contact regions of the pulvinar that are distinct from those that receive the typical "driver-like" inputs from layer V PT-type pyramidal neurons in the occipital and temporal cortices (Rovo et al., 2012). This raises an interesting question: what are the characteristics of the ascending connections between the tectorecipient pulvinar and the cerebral cortex?

Projections from the thalamus to the cerebral cortex exist along a continuum that is blended in different proportions within individual nuclei across the thalamus. At one end are parvalbumin-staining "core" cells that project in a targeted fashion to granular layers of the cerebral cortex (Jones, 2001; Münkle et al., 2000; Shine, 2020), wherein they innervate both pyramidal cells and fast-spiking interneurons and promote high-frequency spiking activity (Jones, 2001). At the other end are calbindin-enriched "matrix" cells that project more diffusely to supragranular regions of the cerebral cortex that cross regional boundaries

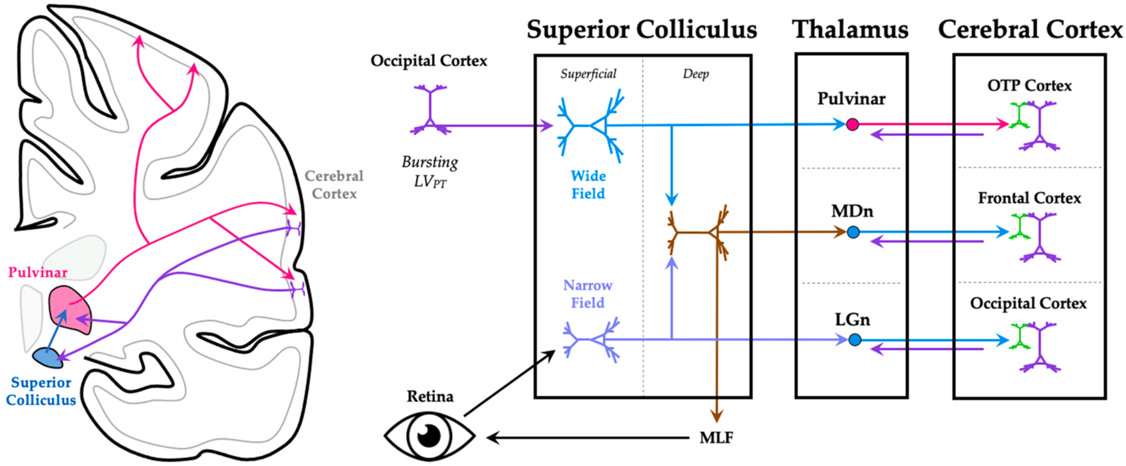

Fig. 1. A posterior cortico-subcortico-cortical circuit. Left – a coronal slice through a typical adult human brain, with a rough circuit diagram connecting layer V PT-type pyramidal neurons (purple) in the cerebral cortex (grey) with the superior colliculus (light blue) and the pulvinar (pink), which then projects back diffusely to the cerebral cortex. Right – a more refined diagram highlighting the key inputs and outputs of the different cells in the circuit: retinal inputs contact Narrow Field cells (lilac) and layer V PT-type neurons in the occipital cortex (purple) contact Wide Field cells (light blue) in the superficial ('visuo-sensory') superior colliculus, both of which then send projections to the deep ('motor') layers of the superior colliculus (Doubell et al., 2003; Huerta and Harting, 1984; May, 2006; Mooney et al., 1988) where they potentially innervate motor cells (brown) that in turn travel via the medial longitudinal fasciculus (MLF) to control the movements of the eye. The Narrow Field, Wide Field and Motor cells then project to the lateral geniculate (LGn), Mediodorsal (MDn) and Pulvinar nuclei of the thalamus, which in turn innervate the occipital, frontal and occipito-temporo-parietal (OTP) regions of the cerebral cortex.

(Jones, 2001; Münkle et al., 2000; Shine, 2020), and also to subcortical structures, such as the striatum and amygdala (Clascá et al., 2012). Interestingly, the pulvinar is known to contain cells that demonstrate connectivity profiles at both of these extremes (Batini et al., 1991; Gutierrez et al., 1995, 2000), as well as intermediate patterns that display both core- and matrix-like features (Clascá et al., 2012). Crucially, the tectorecipient pulvinar neurons display features suggesting of matrix-type nuclei, particularly in the inferior pulvinar regions that receive dense input from the colliculus (Zhou et al., 2017). This implies that any signals reaching the pulvinar are ultimately distributed to both subcortical structures, such as the striatum and amygdala (Day-Brown et al., 2010), and the cerebral cortex in a realtively diffuse fashion (Clascá et al., 2012; Harris et al., 2019; Jones, 2001; Roth et al., 2016). Through its dense connections with the occipital cortex (Basso and May, 2017; May, 2006; Shipp, 2003; Zhou et al., 2017, 2018), the inferior pulvinar nuclei are ideally placed to that re-expand the dimensionality of the thalamic signal (Luo, 2021), and also to coordinate interactions amongst pyramidal neurons in the posterior cerebral cortex (Fiebelkorn and Kastner, 2019; Kastner et al., 2020; Phillips et al., 2021; Saalmann et al., 2012; Sherman and Guillery, 2002). This in turn can help expediate the interactions that facilitate both predictive processing and pattern matching (Kanai et al., 2015; van Vugt et al., 2018). Evidence from primates suggests that pulvinar nuclei are also under the inhibitory control of the reticular nuclei and either the anterior pretectal nuclei or the zona incerta (Halassa and Acsády, 2016; Imura, 2007), which suggests that the patterns that ultimately return to the cerebral cortex are likely further modulated by the intrinsic circuitry of the diencephalon.

In addition to strong connections with the occipital cortex, recent anatomical tracing studies in rodents show that the inferior pulvinar is interconnected with regions in both the parietal and temporal lobes (Bennett et al., 2019; Phillips et al., 2019). Visual processes that recruit the temporal lobe are often classified as belonging to the 'what' pathway, as they are involved in classifying different objects and contexts. In contrast, neurons in the parietal lobe are variably described as belonging to the 'where' (Corbetta and Shulman, 2002) or 'when' (Battelli et al., 2007) pathway, in that they are more typically associated with increased firing based on the location of items, as the sequence in which items are presented, respectively. Within gradient-based frameworks (Margulies and Smallwood, 2017; Mesulam, 1998), these cortical regions are typically classified as heteromodal, in that they lie at the intersection between multiple different modalities: the parietal lobe lies at the intersection between visual and sensorimotor inputs (to occipital and post-central cortices, respectively), whereas the temporal lobe integrates auditory and visual input streams, with strong connections to structures important for declarative memory, such as the entorhinal cortex and hippocampus (Buzsáki, 2015). Together, these posterior cortical circuits are thought to be responsible for defining opportunities for action, which are also known as 'affordances' (Greeno, 1994; Pezzulo and Cisek, 2016). Thus, the superficial superior colliculus is ideally placed to broadcast a compressed signal to multiple regions of the subcortex and posterior cerebral cortex. In the next section, I suggest potential algorithmic benefits of this particular neuronal implementation scheme.

3. The putative algorithmic signature of the cortico-colliculo-pulvinar circuit

The pulvinar is interconnected with a wide range of both cortical and subcortical structures (Kanai et al., 2015; Shipp, 2003; Zhou et al., 2017), and is known to act as hub regions (Bell and Shine, 2016), particularly within the connections associated with the posterior regions of the cerebral cortex. Indeed, there is empirical evidence in macaque monkeys to suggest that the axonal projections of the pulvinar coordinate coupling between distributed regions across the cerebral cortex during the performance of attentionally-demanding tasks (Saalmann et al., 2012). These empirical results lend support to the hypothesis that broad features of cognition and attention depend crucially on the thalamus (Fiebelkorn and Kastner, 2019; Gottlieb, 2007; Halassa and Kastner, 2017), although there is consternation regarding precisely how this support manifests at the macroscopic scale of neuronal recordings. For instance, some researchers focus on the role of the pulvinar in mediating oscillatory 'coupling' between otherwise disconnected regions of the cortex, whereas others have argued for mechanisms that mediate cortical change through the alteration of neural gain (Bourgeois et al., 2020; Chou et al., 2020; de Souza et al., 2020; Phillips et al., 2021; Purushothaman et al., 2012; Zhou et al., 2016) – note that these mechanisms are not mutually exclusive. Irrespective of these details, the many synaptic steps between sensory inputs and parietotemporal cortex afford the system the opportunity to adaptively (Verbeke and Verguts, 2022) amplify the gain of specific combinations of input features (Salinas and Sejnowski, 2001). In this way, the pulvinar and parietotemporal cortices are well-suited to pragmatically "represent" (Pezzulo and Cisek, 2016) opportunities for action (i.e., Gibsonian affordances; Clark, 1999).

Neuroanatomically, the diffuse ascending connections of the inferior pulvinar typically innervate both deep and superficial layers of the cerebral cortex (Zhou et al., 2016), which is consistent with the known projection topologies of matrix-like thalamic nuclei (Clascá et al., 2012; Jones, 2001). This unique projection pattern provides the thalamic cells with the capacity to distribute activity across multiple regions in a manner that likely expands the dimensionality of the thalamic signal (Luo, 2021), while also facilitating patterns of burst-firing in the main output cell of the cerebral cortex – namely, thick-tufted PT-type pyramidal neurons (Harris and Shepherd, 2015). The functional importance of these cells is revealed by a unique feature of their anatomy: their cell bodies are grounded in the deep layers of the cortex, where they remain electrically isolated from their branching apical dendrites, which extend into the more superficial layers where they receive inputs from matrix thalamus (Moore et al., 2019; Rockland, 2019) and descending cortical inputs (Larkum, 2013). Layer V PT-type cells fire relatively sparsely while an animal is awake, driven by volleys of action potentials that arise from the core thalamus and lower layers of the cerebral cortex (Larkum, 2013). However, when relatively coincident inputs (i.e., within ~20msec of one another) contact both the basal (near the cell body) and apical dendrites (e.g., from higher regions of cortex (Harris and Shepherd, 2015), or via matrix thalamic inputs (Shepherd and Yamawaki, 2021)), these cells can transition into a powerful burst-firing mode (Larkum, 2013; Larkum et al., 1999). Recent empirical work has linked this mode with different states of consciousness (Aru et al., 2020; Suzuki and Larkum, 2020) and also with the contents of perceptual awareness (Takahashi et al., 2020). However the same studies also made a striking observation – if the subcortical projections of these cells to the higher-order thalamus and superior colliculus were blocked (via DREADDS-mediated inhibition), animals behaved as if they did not consciously perceive the whisker stimulation at all (Takahashi et al., 2020). In other words – the subcortical projections of layer V pyramidal neurons play a causal role in shaping conscious experience, although it bears mention that this role may simply relate to the fact that the subcortical regions in question merely afford the emergence of specific firing modes in their down-stream cortical targets. Either way, these results thus highlight a cortical mechanism for conscious awareness of whisker perturbations, but also demonstrate that this circuit depends critically on the interactions between the cortex, thalamus and superior colliculus.

Based on these empirical results (Takahashi et al., 2020) and the unique connectivity of the posterior circuitry, I propose that the connections between the superior colliculus, inferior pulvinar and posterior cerebral cortex fulfil a similar role for visual stimuli. Specifically, I propose that the pulvinar and colliculi act to filter ongoing cortical activity based on the environmental affordances available to an organism, such that the subset of cortical neurons firing in a particular temporal window amplifies specific features of the ongoing brain state in a way that is causally related to our perceptual experience. Previous work has hypothesised that burst-firing in layer V PT-type pyramidal neurons forms the basis of our conscious experience (Aru et al., 2019, 2020; Suzuki and Larkum, 2020; Takahashi et al., 2020). Within this framework, perceptual awareness can be conceptualised as the subset of bursting layer V PT-type pyramidal neurons (interconnected with the appropriate thalamo-collicular circuit; Takahashi et al., 2020) whose high-frequency activity patterns cause them to "pop out" from the ongoing firing activity of the rest of the brain. By becoming highly active within a particular window of time, this subset of neural activity is also in a privileged position to influence whichever activity pattern comes next in the sequence. In this way, the concept is highly reminiscent of the notion of "fame in the brain" (Dennett, 2001) or "pandemonium" (Selfridge, 1998), in which a unified, serial process (i.e., connections between LV_{PT}, SC and pulvinar) can be simultaneously supported alongside parallel processes (i.e., regular spiking in LV_{PT} and other cortical neurons), without the need for an external controller. In other words, the system can boost a particular subset of activity, while remaining susceptible to stimuli outside of conscious awareness in a manner that is reminiscent of the notion of quasi-criticality (Müller et al., 2020). Here, I extend these concepts to suggest a critical role for the sSC and inferior pulvinar in this process – namely, to shape the contents of conscious experience so that they are internally consistent (Fig. 2).

A key feature of the connections between the cerebral cortex, colliculus and pulvinar is that a large number of neurons in the cerebral cortex project to a smaller group of neurons in the superficial colliculus (Basso and May, 2017) – implying dimensionality reduction (Luo, 2021) – whereas the axons of pulvinar nuclei regularly branch out to contact multiple areas of the cerebral cortex (Clascá et al., 2012) – implying dimensionality expansion (Luo, 2021). Interestingly, similar patterns of dimensionality collapse and expansion are regularly employed within self-organising neuronal networks, such as the classical "neo-cognitron" model (Fukushima, 1980) or in more modern auto-encoder networks (Bank et al., 2021). In such networks, the reduction and expansion of nodes is thought to imbue neural networks with the ability to efficiently and automatically detect the most salient features in a given display, without the need for supervision (Schmidhuber, 2015), and in such a way that the network is forced to learn a compressed version of the input data. Through this unique filter, the cortico-collicular circuit would have the effect of promoting generalisation (only low-dimensional patterns can be propagated; Beiran et al., 2021) and selection (which would be further augmented by the divisive normalisation mechanisms mediated by the diffuse GABAergic projections of the reticular nucleus; John et al., 2018). By sifting ongoing cortical activity through a dimensionality-manipulating filter, colliculo-pulvinar circuits (Padmala, 2010; Wang et al., 2020; Wilke et al., 2009) are able to shape burst firing in layer V pyramidal neurons in the cerebral cortex, such that particular circuits become associated with the contents of conscious experience, as has been shown in mice (Takahashi et al., 2020).

Algorithmically, the circuit created by the colliculus, thalamus and cerebral cortex is reminiscent of a concept known as coherent information maximisation (Kay and Phillips, 2011), which occurs when the outputs of a system maximises the synergistic information between a set of inputs and a set of contextual modulators. In previous work (Phillips et al., 2018), it was argued that the logic of coherent information maximisation maps clearly onto the non-linear anatomical architecture of layer V PT-type pyramidal neurons – these neurons can be said to be maximising their information processing content when the synergy between an incoming signal (to basal dendrites) and the context (to apical dendrites) is high (i.e., there is no redundant information; Wibral et al., 2017). Extending this concept to incorporate the subcortex, I argue that the addition of a colliculo-pulvinar sub-circuit would act to boost both local (i.e., PT-type pyramidal neuron) and global (i.e., cortico-subcortical) coherent information (Fig. 2), such that any stimulus received by the visual system is processed in such a way that

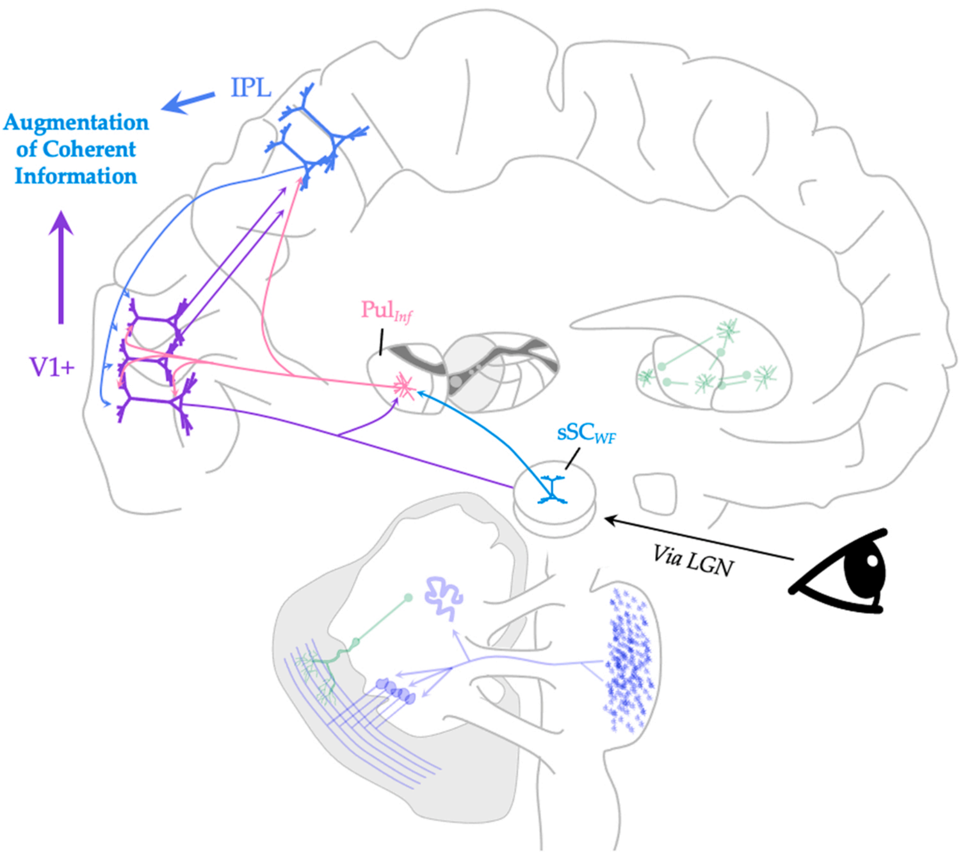

Fig. 2. The superficial superior colliculus connects with the pulvinar to augment coherent information. Following the reception of visual input from retina (via the LGN and primary visual cortex; V1), the wide-field cells of the superficial superior colliculus (sSC_{WF}) project to the inferior pulvinar (Pul_{Inf}), which then send diffuse connections to deep and superficial layers of visual cortex, as well as projections to other regions (Clascá et al., 2012). Pyramidal neurons with apical dendrites in V1 project back to both the pulvinar and sSC, completing a cortico-subcortical circuit that is proposed to augment the coherent information at the systems-level.

maximises the synergy between the inputs and the perceptual context in which it is perceived. There is compelling evidence to support the notion that interactions between higher-order and lower-order visual regions of the cerebral cortex are involved in this process (Lamme, 2006; van Vugt et al., 2018) – the algorithmic features of the colliculo-thalamic circuit will undoubtedly augment this capacity by collapsing the dimensionality of the information processed by the posterior cortex, effectively ensuring that the maximal amount of synergy is created between the inputs received and the potential categories that can be used to match the stimulus.

A key challenge that might be levied at this account is that conscious awareness clearly extends to features outside of our visual experience. To clarify, I am not arguing that the colliculo-pulvinar bottleneck outlined above is responsible for consciousness per se, but rather that the colliculo-pulvinar circuitry is ideally placed (topologically) to facilitate an adaptive signal boost in the cortical circuits connected to inputs from the retina – that is, the circuit is simply an effective means for winning the evolving battle for “fame” in the visual brain. Perhaps a somewhat counterintuitive implication that arises from this framework is that, during visual processing, even the retina is involved in the conscious experience of a particular visual image. Importantly, there’s no a priori reason that other circuits can’t be involved in the most famous coalition – some circuits are just more well-suited to winning the battle for conscious access. Along these lines, I predict that other structures with similar topological properties to the colliculo-pulvinar circuit will also mediate the conscious perception of which information streams the circuits process. For instance, the basal ganglia is well known to follow a similar dimensionality reduction/expansion motif (Bar-Gad et al., 2003; Wilson, 2013), as are the connections between the cerebral cortex and matrix thalamic nuclei (Jones, 2001; Shine, 2020). It is also entirely possible that some of these circuits may not ultimately arise to level of conscious awareness, nor outcompete other salient sensorimotor affordances that might happen to co-occur with a salient visual input, or that pathology may induce states, such as aphantasia (Keogh and Pearson, 2018) or blind-sight (Kinoshita et al., 2019), in which subjects can act on information without necessarily having a perceptual experience.

Along these lines, there are multiple distinct neural mechanisms that can ultimately lead to the augmentation of a ‘famous’ coalition of active regions in the brain. Based on their discovery through psychological and cognitive neuroscience tasks, many of these mechanisms have distinct names that don’t necessarily capture the crucial similarities (and dissimilarities) regarding their neural implementation (Buzsáki, 2020; Hommel et al., 2019). For instance, rather than selectively boosting a particular signal, it is also possible to cause a set of neurons to stand out from the background activity by silencing firing in the broader population – a process known as divisive normalisation (Reynolds and Heeger, 2009). Although there are numerous mechanisms for this effect in the brain, one prominent process is enacted by the loop created between CT-type pyramidal neurons, the core nuclei of the thalamus and the GABAergic reticular nucleus (John et al., 2018). The prominent overlap between the neurons in this circuit and the layer V pyramidal neuron mechanism described in this paper offers a parsimonious explanation for the observation that focussed attention and conscious awareness can be made to dissociate under specific experimental conditions (Koch and Tsuchiya, 2007). From the perspective outlined here, focussed attention likely arises from a divisive normalisation process enacted by the loop created between CT-type pyramidal neurons, core nuclei of the thalamus and the GABAergic reticular nucleus (John et al., 2018). In contrast, conscious awareness is proposed to arise from a selective gain enhancement imbued by cortico-colliculo-thalamo-cortical loops (Takahashi et al., 2020). The anatomical overlap of these two mechanisms helps to explain why they are often considered synonymous. For instance, the processes that win an attentional battle are overwhelmingly likely to enter into conscious awareness (Cohen et al., 2012), however many highly adaptive behaviours don’t require conscious awareness in order to confer adaptive benefit (Shea and Frith, 2016). This perspective also helps to explain important experimental results, such as the fact that reversible lesions of the superior colliculus impair awareness while leaving cortical activity patterns intact (Krauzlis et al., 2013), as well as the well-known blind-sight syndrome (Phillips, 2021), in which individuals with occipital cortex lesions can still respond to visual inputs (likely via colliculo-pulvinar pathways; Isa and Yoshida, 2021; Kinoshita et al., 2019) and for whom full site can be restored by disinhibiting the colliculus (the so-called ‘Sprague’ effect; Merker, 2007), at least in animal models of the disorder.

4. The deep superior colliculus and the shaping of adaptive network dynamics

While the capacity to augment the activity of neurons in the cerebral cortex according to their internal consistency clearly has adaptive benefits, the computational elegance of this circuit comes with a price – namely, that the system will naturally identify the most salient aspects of an input stream (Itti and Koch, 2000), irrespective of whether they are relevant to the organism. In many instances, the needs of an organism are not directly reflected in the properties of the natural world – predators (and prey) are experts at camouflage (Stevens and Merilaita, 2011), and food isn’t always present precisely when you are hungry. Others have described this as the difference between a *salience map* (Fecteau and Munoz, 2006; Itti and Koch, 2000) – what is present in the world – and a *priority map* (Bourgeois et al., 2020) – what an animal wants at a particular time. Unfortunately, what you need isn’t always what is available to you – in other words, salience maps don’t always coincide with priority maps (Bourgeois et al., 2020; Redgrave et al., 1999). Recent evidence suggests a critical role for the SC in mediating between *priority* and *salience* maps during the processing of natural scenes (White et al., 2017).

Fortunately, natural selection has imbued the colliculo-thalamic circuit with an elegant solution to this problem. As described elegantly by Merker (2007), the superior colliculus is heavily interconnected with a number of neural valuation systems whose activity is well-known to reflect the motivational- or goal-state of the organism. For instance, there is evidence that the deep layers of the superior colliculus integrate inputs from the ventromedial hypothalamus (Benavidez et al., 2021) and the periaqueductal grey (Benavidez et al., 2021), which are both prominently involved in the mediation of brain states as a function of organismal needs and energy balance (Williams et al., 2001). Importantly, the influence that an animals’ motivational state has over the colliculus does not occur directly via the superficial colliculo-pulvinar circuits described above, but rather through changing other systems in the brain, such as producing saccadic eye movements to new, informative locations in the surrounding environment (Foley et al., 2017; Friston et al., 2012), or by boosting the gain of frontal cortical regions through the engagement of the mediodorsal thalamic nucleus (Basso and May, 2017; Fine and Hayden, 2022; Mitchell, 2015) that ultimately bias ongoing information processing in critical ways.

To mediate these adaptive capacities, the colliculus, pulvinar and cerebral cortex are all strongly interconnected with another set of key subcortical structures that tracks changes in motivation and value: the basal ganglia. The superficial SC sends glutamatergic projections to the subthalamic nucleus (Coizet et al., 2009) and both the dopaminergic pars compacta and GABAergic pars reticularis subregions within the substantia nigra (McHaffie et al., 2005). In addition, the matrix thalamic nuclei in the inferior pulvinar that are the targets of superficial SC inputs (Benavidez et al., 2021; Day-Brown et al., 2010, p.; Redgrave, 2010) also project strongly to the striatum (Smith et al., 2004, 2014), wherein they contact both spiny projection neurons (Smith et al., 2004) and tonically-active cholinergic interneurons (Galvan and Smith, 2011), as well as cortical projections that target the striatum (Zhou et al., 2018), suggesting an important role for these posterior circuits in engaging the basal ganglia. Furthermore, there is evidence that the colliculus is interconnected with the amygdala (Wei et al., 2015; Zhou et al., 2018), which is thought to involve a circuit very similar to a corticostriatal loop, albeit with GABAergic control over the hypothalamus and brainstem (John et al., 2016; Puelles and Rubenstein, 2015). Through these interactions, value signals can be conveyed to the colliculus (Hikosaka and Isoda, 2010), however their influence is better suited for shaping saccadic eye movements and ascending projections to the frontal cortices (via the mediodorsal thalamic nucleus; Mitchell, 2015) than for shaping processing in the posterior cortices (Basso and May, 2017).

The topology of the thalamic projections of the deep layers of the SC is distinct from those in the superficial layers. Rather than targeting matrix nuclei within the pulvinar (as is the case with sSC), glutamatergic projections from the dSC instead innervate core-like nuclei in the mediodorsal nucleus (MDn), which in turn project to the frontal eye fields in the frontal cortex (which, in turn, re-innervate the dSC; Matsumoto et al., 2018). Importantly, the MDn receives inputs from multiple different subcortical regions – the basal ganglia, cerebellum and dSC – that each contact different subnuclei within the MDn (*magnocellular/densocellular, parvocellular* and *pars multiforms*, respectively; Mitchell, 2015; Prevosto and Sommer, 2013; Sommer, 2003; Fig. 3). Importantly, each of these sub-nuclei is densely interconnected with pyramidal neurons in different regions of the frontal cortex. The magnocellular nuclei, which receive GABAergic inhibitory innervation from the basal ganglia (Mitchell, 2015; Sommer, 2003) and central amygdala (Mitchell, 2015; Mitchell and Chakraborty, 2013) innervate supragranular layers of orbitofrontal and rostral cingulate regions, where they make contact with the apical dendrites of deep pyramidal neurons and VIP+ interneurons (Anastasiades et al., 2021), which have been associated with volitional control in rodent sensory cortex (Yu et al., 2019). The cerebellum innervates parvocellular MD*pc*, which then projects to middle layers of granular dorsolateral prefrontal cortex (Houk and Wise, 1995; Preuss and Wise, 2022), wherein it transmits anticipatory signals associated with the corollary discharges of previously-active layer V PT-type pyramidal neurons (Montgomery and Perks, 2019; Prevosto and Sommer, 2013; Shine, 2020). Finally, the small *pars multiforms* region in MDn receives corollary discharges from dSC (Sommer and Wurtz, 2002, 2006) and projects to the frontal and parietal eye fields in order to prepare the cortex for the effects of saccadic eye movements.

The deep layers of the superior colliculus are also linked to motor-based structures that help to augment adaptive behaviour (Basso and May, 2017). The most prominent such circuit controls visual saccades, which are rapid, jerky movements that align the fovea with the most informative aspect of an external display. It’s long been known that neurons with their cell bodies in the deep structures of the superior colliculus descend via the medial longitudinal fasciculus (MLF; Fig. 1) to innervate the cranial nerves (III, IV and VI) that then control the contraction and relaxation of the extra-ocular muscles, thus moving the eye. By yoking this system to the posterior circuits of the pulvinar and superficial colliculus, the occulomotor system is ideally placed to create rapid saccadic movements to the locations of highest potential information content (Foley et al., 2017; Friston et al., 2012). Interestingly, our perceptual awareness of visual movement is typically absent during saccadic eye movements – a phenomenon known as saccadic suppression (Krekelberg, 2010; Ross et al., 2001). Though there are likely other neural circuits involved (Idrees et al., 2020), there are a number of features of the internal circuitry of the superior colliculus that could also support saccadic suppression. Specifically, every time the eyes saccade following the activity of deep layers of the superior colliculus, local GABAergic circuits are recruited that ascend back to the superficial

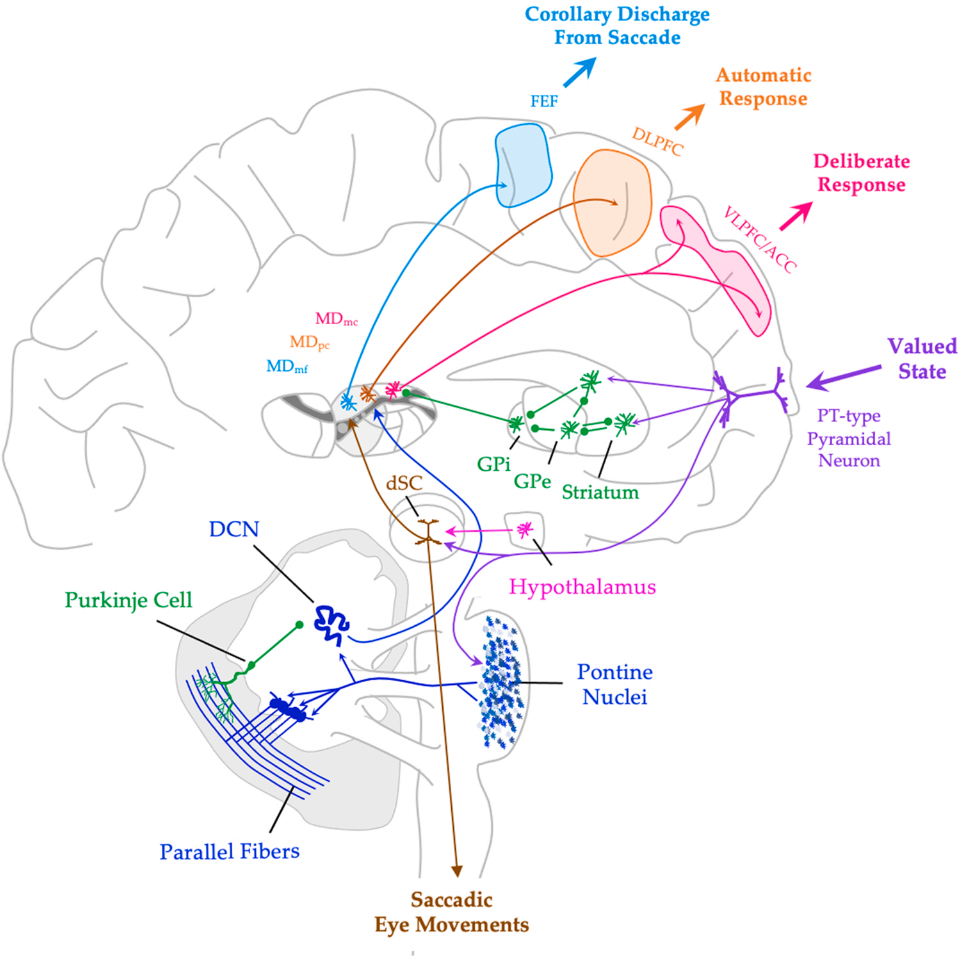

Fig. 3. Adaptive paths through mediodorsal nucleus. Different subregions within the mediodorsal nucleus of the thalamus (MDn) receive inputs from distinct subcortical circuits: the *pars multiforms* ($\mathrm{MD}_{\mathrm{mf}}$) nucleus receives glutamatergic drive from the deep layers of the superior colliculus (dSC, brown), which then project to the frontal eye fields (FEF), where they convey corollary discharge information regarding saccadic eye movements (light blue); the *parvocellular* ($\mathrm{MD}_{\mathrm{pc}}$) nucleus receives glutamatergic drive from the deep cerebellar nuclei (DCN, blue) and projects to granular prefrontal cortex (DLPFC) where it drives feedforward activity and relatively automatic responses; and the *magnocellular* ($\mathrm{MD}_{\mathrm{mc}}$) nucleus receives GABAergic inputs from the globus pallidus (green) and projects to ventromedial prefrontal cortex (vmPFC) and anterior cingulate cortex (ACC), where it controls deliberate actions. In the presence of a change in brain state (hypothalamus, orange) and other changes in neuromodulatory tone (not shown), these circuits can differentially impact how an animal responds to the opportunities for action (i.e., affordances) present in the environment. Note that there are numerous inputs from the cerebral cortex to the MD thalamus that are not represented in this figure for sake of visual clarity.

layers of the colliculus, wherein they inhibit the projections of wide-field cells to the inferior pulvinar (Basso and May, 2017; Isa et al., 2021). This mechanism has clear adaptive benefits (e.g., noisy inputs are inhibited while shifting the target of your vision), and has also been shown to arise as a side-effect of efficient sensorimotor processing (Crevecoeur and Kording, 2017).

5. Interactions between the colliculus and thalamus shape adaptive behaviour

The implications for this separation of salience augmentation and motivational signalling is important for promoting adaptive behaviour. By ensuring that neural activity reflecting the most motivationally salient subset of options available to an animal obtains a privileged position in the functional neural hierarchy, animals are essentially reducing the amount of evidence required to enact a particular decision. Consider how different a buffet looks to someone who is hungry compared to someone who has recently eaten: in the former case, the sights and smells associated with food seem to flood our conscious experience, whereas in the latter (particularly if one has over-indulged), the mere sight of food can trigger a bout of dyspepsia. In other words, the information that ‘shows up’ to an animal out of the background of sensory bombardment that it faces on a moment-to-moment basis is not the many different affordances (Pezzulo and Cisek, 2016) present in the environment per se (they of course define the ways in which an animal can interact with an object in the environment (Greeno, 1994)), but how the affordances are valued, based on the animals current motivational state.

Fig. 4 offers a simple example of this capacity in action. At baseline, the brain will likely process the most salient feature of an external scene (e.g., a loud football game on the screen). However, if one becomes hungry (blue) or thirsty (orange-red), the change in state can be communicated by the hypothalamus to the superior colliculus, which can then shift the focus of the eyes to the valued stimulus, or facilitate frontally-mediated brain states that coordinate potential options for navigating towards the valued items. Once the stimuli are within the scope of the visual system, the colliculus can bias the signals in the pulvinar that mediate activity in the parietal and temporal cortices, such that the less salient features of the world can be augmented and hence, reach conscious awareness. Similarly, if one thinks of an idea relating to an ongoing project (light orange), the need to jot down the thought can bias the system to notice a pen and paper that were otherwise ignored on the table in front of you. In this way, the colliculo-pulvinar-cortical circuit is proposed to boost the salience of visual patterns as a function of need, such that actions can be taken on the features in the world that the animal prioritises, and not simply those that are the most salient. Importantly, this capacity is not necessarily unique to the superior colliculus – other circuits identified as important for promoting conscious awareness also have connections with regions that convey valuation signals. In addition, the olfactory cortex maintains close direct connections with the hypothalamus (Gascuel et al., 2012), which may explain why we are still conscious of smells and tastes despite the lack of connections between the olfactory cortex and primary thalamic relays (Courtiol and Wilson, 2015).

6. Adaptively navigating the affordance landscape

The complexity and massive dimensionality of the neural interactions within the brain can make it challenging to conceptualise the consequences of specific topological features of the nervous system, each of which interact with (and hence, constrain) one another. In previous work (Shine, 2020), I argued that a beneficial means for conceptualising the inherently dynamic and distributed patterns that characterise adaptive brain activity is to consider the systems’ flow on a dynamically evolving attractor landscape (Fig. 5). Attractors represent idealised states towards which the evolving activity of the brain flows over time – as if the brain state was a ball rolling over a hilly landscape, pulled only by the force of gravity (Müller et al., 2021; Rabinovich et al., 2008). The topography of the landscape defines the rules that govern how the state of the brain changes over time: imagine a collection of balls (representing, say, distinct layer V PT-type cortical pyramidal neurons) that roll into valleys (i.e., attractors that might represent appetitive affordances), but are blocked by ridges (i.e., aversive affordances). The natural flow of the balls around the landscape thus offers an intuitive means for conceptualising the emergent systems-level activity of the brain (Shine, 2020), but crucially also links directly to the

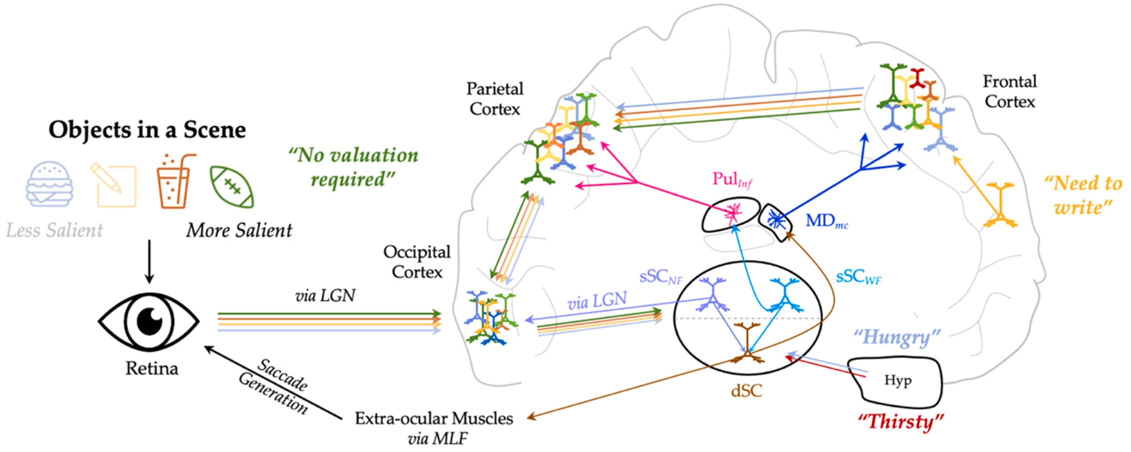

Fig. 4. A putative mechanism for collicular-pulvinar-mediated signal amplification. Imagine a crowded sports bar, in which different items have more (or less) salience (top right) – the most salient images in the scene (e.g., the football game on the screen; green) may not align with an individuals’ evolving needs, however they need not value the game (strange as it may seem) for it to enter their awareness. If they are hungry (blue) or thirsty (dark orange), then connections from the medial hypothalamus can act to amplify the cortico-collicular patterns, indirectly via the deep superior colliculus [dSC] to magnocellular mediodorsal nucleus [MD*mc*] pathways that amplify neurons in the frontal cortex. Through intra-cortical connections to the parietal cortex, these patterns can boost the patterns that pragmatically “represent” how the signals associated with either food (blue) or drinks (dark orange). Alternatively, if a more abstract goal emerges (e.g., the need to write down an exciting idea; caramel), then a separate circuit might drive the frontal cortex, and in turn prime the parietal lobe to boost the signals associated with writing implements. Once the amplification has taken place, the cortical patterns responsible for acting on the opportunities that are present (i.e., the valued affordances) can be enacted, leading to actions that will accomplish the specific goal. Key: sSC_{NF} – narrow field cells of superficial superior colliculus; $\mathrm{sSC}_{\mathrm{WF}}$ – wide field cells of superficial superior colliculus; Pul_{Inf} – inferior pulvinar; LGN – lateral geniculate nucleus; Hyp – hypothalamus.

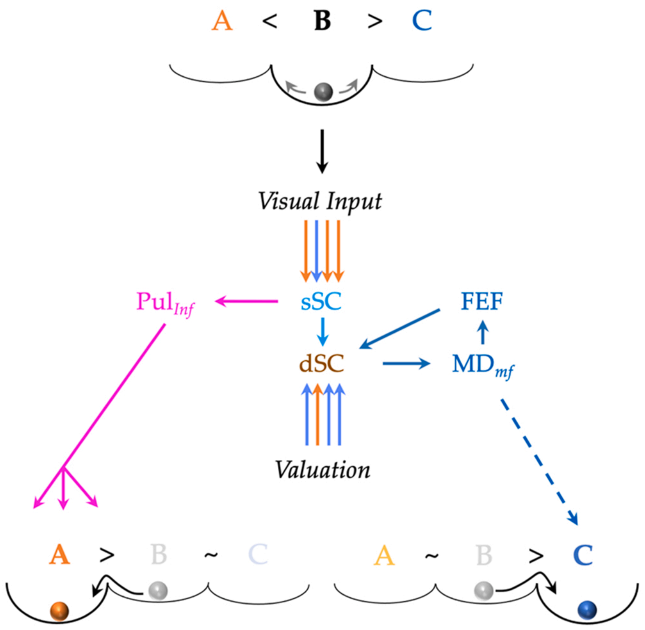

Fig. 5. How the superior colliculus alters the topography of the attractor landscape. Distributed neural activity can be conceptualised as a ball rolling along a hilly landscape. Here, I demonstrate the hypothesised impact of the superior colliculus and its thalamic connections on the topography of the landscape. Imagine a brain at rest, with the intrinsic dynamics of posterior cortical pyramidal cells confined to attractor B (top panel). Following a visual input with stronger salience for A (orange) then C (blue), the visual inputs to the superficial superior colliculus (sSC; light blue) will drive matrix thalamic cells in the inferior pulvinar (Pul$_{Inf}$; pink), which then augment the depth of the attractor representing object A (left). If the animal prefers C to A, then a valuation signal will contact the deep superior colliculus (dSC; dark blue), which will then, via the *multiforms* subdivision of the mediodorsal nucleus (MD$_{mf}$), recruit the frontal eye fields (FEF) in the cerebral cortex to shift the focus of the sSC (i.e., to option C). In this way, the dSC can only indirectly change the depth of the attractor for option C (dotted blue line).

mathematical principles used to model the spatiotemporal dynamics of neuronal populations (Rabinovich et al., 2008; Shine, 2020).

Different connectivity patterns can have distinct effects on the topography of the attractor landscape. In previous work, different subcortical organisational wiring rules were argued to suggest novel ways in which the attractor landscape could change over time: the high-dimensional, anticipatory nature of the cerebellar circuitry should naturally create grooves in the attractor landscape that can be followed without conscious access; whereas the low-dimensional circuitry of the basal ganglia should instead force the system into a serial-processing mode, albeit with some constrained variability induced by the relatively diffuse supragranular projections of the matrix thalamic nuclei (Shine, 2020). Similarly, the presence (or absence) of different neuromodulatory neurotransmitters has been argued to alter the shape of the attractor landscape, making it more easy (or difficult) to transition into new states over time (Munn et al., 2021). Based on the connectivity profiles highlighted in this manuscript, what kinds of processing regimes might the connections between the superior colliculus and the thalamus impose on the dynamic evolution of the attractor landscape?

Rather than changing the shape of the attractor landscape, the evidence reviewed here suggests that the crucial role employed by the colliculus, pulvinar and posterior cerebral cortex (and hence, visual conscious awareness) is to ensure that an animal's behaviour is highly adaptive, from moment-to-moment, across all manner of contexts. That is, that the ball rolls around the attractor landscape in a coherent way that is shaped and constrained by the potential available options (i.e., affordances) that also matter to the animal (i.e., have inherent value, given the current state of the system) (Fig. 5). Without such a circuit, behaviour would likely be more divergent (e.g., an animal could attempt to eat and sleep at the same time, raising the risk of choking) and less context-specific (e.g., an animal may run towards a predator, rather than away from them) – i.e., far less adaptive. In addition, without a tecto-thalamic system, there is also a greater chance for actions to be driven by basic features of the visual input that are highly *salient* (e.g., the most obvious feature of a scene), rather than by the opportunity that best aligns with the inherent *priorities* required by the animal (e.g., identifying and augmenting the faint smell of food when hungry). There are of course likely to be many features of developed nervous systems that help to achieve these capacities, however the argument here is that the circuit connecting the colliculus, pulvinar and posterior cerebral cortex in the mammalian brain is particularly well-suited for such a task.

The computational features of the different circuits in Fig. 5 are argued to all work synergistically in order to provide actions that are fit to an animals' current evolving needs. In other words, the distributed circuits in the brain all work in tandem to shape adaptive behaviour. For instance, if an animal becomes hungry, assuming activity in the vmPFC signals that its sensible to forage for food (Daw et al., 2006), hypothalamic signals can begin to prime activity in the dSC (Fig. 5, brown), which in turn can cause saccadic shifts (via the MLF; Fig. 1) and preparatory activity in the frontal eye fields that might reorient the animal to the new location under the focus of the fovea (Fig. 5, light blue; Kopec et al., 2015). The location of saccades has been shown to be associated with priority maps in the parietal cortex that represent areas of maximal potential information gain at particular saccadic locations (Foley et al., 2017; Friston et al., 2012). Once the new location has been oriented to the focus of visual input, the sSC/pulvinar circuit can boost the gain of signals that also coincide with the needs of the animal (Fig. 5). The affordances offered by these signals can then feed into frontal circuits that control action, irrespective of whether the actions are concrete (e.g., the movement of a particular limb) or more abstract (search in the fridge or cupboard for food; Badre and Nee, 2018). In each case, any action taken (expressed via populations of bursting layer V PT-type pyramidal neurons) will cause efference copies to be sent to both the pontine nuclei (Kratochwil et al., 2017; Fig. 4, dark blue) and striatum (Reiner et al., 2010; Fig. 4, pink). From there, the internal computations within the cerebellum and basal ganglia can influence the next coalition of cortical pyramidal neurons in the search for food – if there is a relatively fast, automatic way to solve the problem at hand, the cerebellum will rapidly suggest it, whereas if more deliberate, focussed volitional search is required, the basal ganglia is more suited to mediating these effects (Shine, 2020). In short, the unique topological interconnections between specialist regions around the brain work in concert to mediate adaptive behaviour – and conscious awareness – across multiple spatial and temporal scales.

From this perspective, it is interesting to consider what happens in the brain when during the performance of highly trained skills and habits (e.g., driving a car on a familiar road) that effectively play out relatively automatically – i.e., without the need for ongoing conscious awareness (Shine and Shine, 2014). What is it that keeps these processes from reaching the threshold for awareness? A parsimonious explanation is that, while the contexts that trigger these processes do initially reach the criteria for conscious awareness, different architectures in the brain specialised for mnemonic functions – e.g., the cerebellum (D'Angelo and Casali, 2013) and hippocampus (O'Reilly et al., 2014), both of which greatly expand the dimensionality of their input streams (Billings et al., 2014; Cayco-Gajic and Silver, 2019) – ultimately allow the coordinated patterns required for their effective execution to unfurl relatively rapidly over time. That is, they don't allow the brain state to dwell in a particular attractor for long before moving to the next attractor (Rabinovich et al., 2008). This suggests that, for a stimulus (or internal brain state) to ascend to the level of awareness that we notice, a further constraint needs to be satisfied – namely, the brain state needs to be protracted and retained over time (O'Callaghan et al., 2021; Whyte and

Smith, 2020). This temporal protraction affords further combination and interaction with other evolving brain states, as well as constraints over more quickly evolving brain states – i.e., for the benefits of neuronal 'fame' to be realised. Similar arguments could help to explain why we often act in response to high-salience items – either those that occur extremely quickly (Wang et al., 2020; such as a car swerving into our lane) or high-salience items (such as the shape of a snake; Maior et al., 2011, 2012; Van Le et al., 2013)) – before we are consciously aware of them. It's not like the items in these examples are not identifiable from the background – it's simply the case that there are adaptive processes at play that don't allow the brain to dwell on augmenting the signals prior to mediating evasive actions. This mechanism thus provides a parsimonious explanation for why the colliculo-pulvinar circuit can be both crucial for visual awareness, but also involved in rapid responses to potentially threatening situations (Pessoa and Adolphs, 2010).

Finally, this mechanism helps to explain an otherwise puzzling feature of many studies of consciousness: the expansion of the cerebral cortex is a relatively recent phylogenetic event (Cisek, 2019), whereas behavioural signatures of conscious awareness and sentience can be traced back ~500 million years to the time of the Cambrian explosion (Feinberg and Mallatt, 2013), just after the evolution of the modern architecture of the eye (Parker, 2004). I have argued here that the basic circuits linking the colliculus, pulvinar, hypothalamus, basal ganglia and cerebral cortex support a highly adaptive brain state in which highly valued individual features of the visual world can be caused to stand out from the rest of the activity in the brain. Importantly, this capacity would only be augmented by the broad expansion of the brain and related cognitive repertoire that coincided with the transition from an aquatic to a terrestrial environment (Mugan and MacIver, 2020), and also with the capacity to hold information over longer and longer timescales (a feature characteristic of associative regions of the cerebral cortex; Honey et al., 2012). Irrespective of these augmented features of awareness, it is overwhelmingly likely that the capacity of conscious awareness – which is argued to align with the ability to selectively augment requisite neural activity – is heavily reliant on a set of neuroanatomical structures that lie outside the cerebral cortex. The process model argued for here provides a plausible, testable mechanism for mediating the benefits of conscious awareness in the brain – namely, coordinated bursting of layer V PT-type pyramidal neurons.

7. Conclusion

In this manuscript, I have summarised a unique feature of the connections between the posterior cerebral cortex, superficial superior colliculus, pulvinar and hypothalamus that is proposed to instantiate an amplification of sensory signals that mediates the contents of visuoperceptual conscious experience. By performing a combined dimensionality reduction and expansion on ongoing activity patterns in the cerebral cortex, the colliculo-pulvinar circuit acts to automatically amplify the most salient features in a given scene, which in turn will likely integrate with other key amplifying capacities of the deep layers of the cerebral cortex (Zolnik et al., 2020), the claustrum (Smith et al., 2019) and the ascending arousal system (Munn et al., 2021; Shine et al., 2019, 2021; Wainstein et al., 2022) to shape and constrain the brain's state as it evolves over time (Shine, 2020). By integrating this circuit with valuation signals from the hypothalamus, the superior colliculus can act to ensure that the augmented signals are those that represent the most pressing needs of the animal. In this way, the posterior subcortical circuitry is proposed to constrain the evolution of the current brain state to the most valued affordances available to the animal. This functional neuroanatomical feature is argued to mediate the highly adaptive nature of conscious awareness. The consistency of these architecture features across massive swathes of the evolutionary landscape, from humans (Krauzlis et al., 2013), to monkeys (Crapse et al., 2018), rodents (Takahashi et al., 2020), fish (Isa et al., 2021), lamprey (Saitoh et al., 2007) and even insects Barron and Klein, 2016), suggests that the capacity for subjective awareness is a common feature of complex living systems, however the idiosyncratic features of these systems also warrants caution. Future work that carefully compares these capacities across taxa are of critical importance for our burgeoning understanding of how the brain supports conscious experience.

Funding

JMS was supported by the National Health and Medical Research Council and the University of Sydney.

Data availability

No data was used for the research described in the article.

Acknowledgements

I would like thank Karthik Srinivasan, Yohan John and Jaan Aru for thoughtful feedback on an earlier version of the manuscript.

References

Anastasiades, P.G., Collins, D.P., Carter, A.G., 2021. Mediodorsal and ventromedial thalamus engage distinct L1 circuits in the prefrontal cortex. Neuron 109, 314–330. https://doi.org/10.1016/j.neuron.2020.10.031.

Aru, J., Suzuki, M., Larkum, M.E., 2020. Cellular mechanisms of conscious processing. Trends Cogn. Sci. 24, 814–825. https://doi.org/10.1016/j.tics.2020.07.006.

Aru, J., Suzuki, M., Rutiku, R., Larkum, M.E., Bachmann, T., 2019. Coupling the state and contents of consciousness. Front. Syst. Neurosci. 13, 43. https://doi.org/10.3389/fnsys.2019.00043.

Badre, D., Nee, D.E., 2018. Frontal cortex and the hierarchical control of behavior. Trends Cogn. Sci. 22, 170–188. https://doi.org/10.1016/j.tics.2017.11.005.

Baizer, J.S., Desimone, R., Ungerleider, L.G., 1993. Comparison of subcortical connections of inferior temporal and posterior parietal cortex in monkeys. Vis. Neurosci. 10, 59–72. https://doi.org/10.1017/S0952523800003229.

Bank, D., Koenigstein, N., Giryes, R., 2021. Autoencoders. arXiv:2003.05991 [cs, stat] https://doi.org/10.48550/arXiv.2003.05991.

Bar-Gad, I., Morris, G., Bergman, H., 2003. Information processing, dimensionality reduction and reinforcement learning in the basal ganglia. Prog. Neurobiol. 71, 439–473.

Barron, A.B., Klein, C., 2016. What insects can tell us about the origins of consciousness. Proc. Natl. Acad. Sci. USA 113, 4900–4908. https://doi.org/10.1073/pnas.1520084113.

Basso, M.A., May, P.J., 2017. Circuits for action and cognition: a view from the superior colliculus. Annu. Rev. Vis. Sci. 3, 197–226. https://doi.org/10.1146/annurev-vision-102016-061234.

Batini, C., Guegan, M., Palestini, M., Thomasset, M., 1991. The immunocytochemical distribution of calbindin-D28k and parvalbumin in identified neurons of the pulvinar-lateralis posterior complex of the cat. Neurosci. Lett. 130, 203–207. https://doi.org/10.1016/0304-3940(91)90397-C.

Battelli, L., Pascual-Leone, A., Cavanagh, P., 2007. The 'when' pathway of the right parietal lobe. Trends Cogn. Sci. 11, 204–210. https://doi.org/10.1016/j.tics.2007.03.001.

Beiran, M., Meirhaeghe, N., Sohn, H., Jazayeri, M., Ostojic, S., 2021. Parametric control of flexible timing through low-dimensional neural manifolds (preprint). Neuroscience. https://doi.org/10.1101/2021.11.08.467806.

Bell, P.T., Shine, J.M., 2016. Subcortical contributions to large-scale network communication. Neurosci. Biobehav. Rev. 71, 313–322.

Benavidez, N.L., Bienkowski, M.S., Zhu, M., Garcia, L.H., Fayzullina, M., Gao, L., Bowman, I., Gou, L., Khanjani, N., Cotter, K.R., Korobkova, L., Becerra, M., Cao, C., Song, M.Y., Zhang, B., Yamashita, S., Tugangui, A.J., Zingg, B., Rose, K., Lo, D., Foster, N.N., Boesen, T., Mun, H.-S., Aquino, S., Wickersham, I.R., Ascoli, G.A., Hintiryan, H., Dong, H.-W., 2021. Organization of the inputs and outputs of the mouse superior colliculus. Nat. Commun. 12, 4004. https://doi.org/10.1038/s41467-021-24241-2.

Bennett, C., Gale, S.D., Garrett, M.E., Newton, M.L., Callaway, E.M., Murphy, G.J., Olsen, S.R., 2019. Higher-order thalamic circuits channel parallel streams of visual information in mice. Neuron 102, 477–492. https://doi.org/10.1016/j.neuron.2019.02.010.

Billings, G., Piasini, E., Lőrincz, A., Nusser, Z., Silver, R.A., 2014. Network structure within the cerebellar input layer enables lossless sparse encoding. Neuron 83, 960–974. https://doi.org/10.1016/j.neuron.2014.07.020.

Bourgeois, A., Guedj, C., Carrera, E., Vuilleumier, P., 2020. Pulvino-cortical interaction: an integrative role in the control of attention. Neurosci. Biobehav. Rev. 111, 104–113. https://doi.org/10.1016/j.neubiorev.2020.01.005.

Butler, A.B., 1994. The evolution of the dorsal pallium in the telencephalon of amniotes: cladistic analysis and a new hypothesis. Brain Res. Rev. 19, 66–101. https://doi.org/10.1016/0165-0173(94)90004-3.

Buzsáki, G., 2015. Hippocampal sharp wave-ripple: a cognitive biomarker for episodic memory and planning. Hippocampus 25, 1073–1188.

Buzsáki, G., 2020. The brain–cognitive behavior problem: a retrospective. eNeuro 7. https://doi.org/10.1523/ENEURO.0069–20.2020 (ENEURO.0069–20.2020).

Cayco-Gajic, N.A., Silver, R.A., 2019. Re-evaluating circuit mechanisms underlying pattern separation. Neuron 101, 584–602. https://doi.org/10.1016/j.neuron.2019.01.044.

Chou, X., Fang, Q., Yan, L., Zhong, W., Peng, B., Li, H., Wei, J., Tao, H.W., Zhang, L.I., 2020. Contextual and cross-modality modulation of auditory cortical processing through pulvinar mediated suppression. eLife 9, e54157. https://doi.org/10.7554/eLife.54157.

Cisek, P., 2019. Resynthesizing behavior through phylogenetic refinement. Atten., Percept. Psychophys. 26, 535.

Clark, A., 1999. An embodied cognitive science. Trends Cogn. Sci. 3, 345–351. https://doi.org/10.1016/S1364-6613(99)01361-3.

Clascá, F., Rubio-Garrido, P., Jabaudon, D., 2012. Unveiling the diversity of thalamocortical neuron subtypes. Eur. J. Neurosci. 35, 1524–1532.

Cohen, M.A., Cavanagh, P., Chun, M.M., Nakayama, K., 2012. The attentional requirements of consciousness. Trends Cogn. Sci. 16, 411–417. https://doi.org/10.1016/j.tics.2012.06.013.

Coizet, V., Graham, J.H., Moss, J., Bolam, J.P., Savasta, M., McHaffie, J.G., Redgrave, P., Overton, P.G., 2009. Short-latency visual input to the subthalamic nucleus is provided by the midbrain superior colliculus. J. Neurosci. 29, 5701–5709. https://doi.org/10.1523/JNEUROSCI.0247-09.2009.

Collins, C.E., Lyon, D.C., Kaas, J.H., 2005. Distribution across cortical areas of neurons projecting to the superior colliculus in new world monkeys. Anat. Rec. 285A, 619–627. https://doi.org/10.1002/ar.a.20207.

Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. Nat. Rev. Neurosci. 3, 201–215. https://doi.org/10.1038/nrn755.

Courtiol, E., Wilson, D.A., 2015. The olfactory thalamus: unanswered questions about the role of the mediodorsal thalamic nucleus in olfaction. Front. Neural Circuits 9. https://doi.org/10.3389/fncir.2015.00049.

Crapse, T.B., Lau, H., Basso, M.A., 2018. A role for the superior colliculus in decision criteria. Neuron 97, 181–194. https://doi.org/10.1016/j.neuron.2017.12.006.

Crevecoeur, F., Kording, K.P., 2017. Saccadic suppression as a perceptual consequence of efficient sensorimotor estimation. eLife 6, e25073. https://doi.org/10.7554/eLife.25073.

D'Angelo, E., Casali, S., 2013. Seeking a unified framework for cerebellar function and dysfunction: from circuit operations to cognition. Front. Neural Circuits 6. https://doi.org/10.3389/fncir.2012.00116.

Daw, N.D., O'Doherty, J.P., Dayan, P., Seymour, B., Dolan, R.J., 2006. Cortical substrates for exploratory decisions in humans. Nature 441, 876–879. https://doi.org/10.1038/nature04766.

Day-Brown, J.D., Wei, H., Chomsung, R.D., Petry, H.M., Bickford, M.E., 2010. Pulvinar projections to the striatum and amygdala in the tree shrew. Front. Neuroanat. 4 https://doi.org/10.3389/fnana.2010.00143.

Dennett, D., 2001. Are we explaining consciousness yet? Cognition 79, 221–237. https://doi.org/10.1016/S0010-0277(00)00130-X.

Desimone, R., Duncan, J., 1995. Neural mechanisms of selective visual attention. Annu. Rev. Neurosci. 18, 193–222. https://doi.org/10.1146/annurev.ne.18.030195.001205.

Doubell, T.P., Skaliora, I., Baron, J., King, A.J., 2003. Functional connectivity between the superficial and deeper layers of the superior colliculus: an anatomical substrate for sensorimotor integration. J. Neurosci. 23, 6596–6607. https://doi.org/10.1523/JNEUROSCI.23-16-06596.2003.

Eisenreich, B.R., Akaishi, R., Hayden, B.Y., 2017. Control without controllers: toward a distributed neuroscience of executive control. J. Cogn. Neurosci. 29, 1684–1698.

Fecteau, J., Munoz, D., 2006. Salience, relevance, and firing: a priority map for target selection. Trends Cogn. Sci. 10, 382–390. https://doi.org/10.1016/j.tics.2006.06.011.

Feinberg, T.E., Mallatt, J., 2013. The evolutionary and genetic origins of consciousness in the Cambrian Period over 500 million years ago. Front. Psychol. 4 https://doi.org/10.3389/fpsyg.2013.00667.

Fiebelkorn, I.C., Kastner, S., 2019. A rhythmic theory of attention. Trends Cogn. Sci. 23, 87–101. https://doi.org/10.1016/j.tics.2018.11.009.

Fine, J.M., Hayden, B.Y., 2022. The whole prefrontal cortex is premotor cortex. Philos. Trans. R. Soc. B 377, 20200524. https://doi.org/10.1098/rstb.2020.0524.

Foley, N.C., Kelly, S.P., Mhatre, H., Lopes, M., Gottlieb, J., 2017. Parietal neurons encode expected gains in instrumental information. Proc. Natl. Acad. Sci. USA 114, E3315–E3323. https://doi.org/10.1073/pnas.1613844114.

Fries, W., 1984. Cortical projections to the superior colliculus in the macaque monkey: a retrograde study using horseradish peroxidase. J. Comp. Neurol. 230, 55–76. https://doi.org/10.1002/cne.902300106.

Friston, K., Adams, R.A., Perrinet, L., Breakspear, M., 2012. Perceptions as hypotheses: saccades as experiments. Front. Psychol. 3 https://doi.org/10.3389/fpsyg.2012.00151.

Fukushima, K., 1980. Neocognitron: a self-organizing neural network model for a mechanism of pattern recognition unaffected by shift in position. Biol. Cybern. 36, 193–202. https://doi.org/10.1007/BF00344251.

Gale, S.D., Murphy, G.J., 2018. Distinct cell types in the superficial superior colliculus project to the dorsal lateral geniculate and lateral posterior thalamic nuclei. J. Neurophysiol. 120, 1286–1292. https://doi.org/10.1152/jn.00248.2018.

Galvan, A., Smith, Y., 2011. The primate thalamostriatal systems: anatomical organization, functional roles and possible involvement in Parkinson's disease. Basal Ganglia 1, 179–189. https://doi.org/10.1016/j.baga.2011.09.001.

Gascuel, J., Lemoine, A., Rigault, C., Datiche, F., Benani, A., Penicaud, L., Lopez-Mascaraque, L., 2012. Hypothalamus-olfactory system crosstalk: orexin A immunostaining in mice. Front. Neuroanat. 6 https://doi.org/10.3389/fnana.2012.00044.

Gharaei, S., Honnuraiah, S., Arabzadeh, E., Stuart, G.J., 2020. Superior colliculus modulates cortical coding of somatosensory information. Nat. Commun. 11, 1693. https://doi.org/10.1038/s41467-020-15443-1.

Gottlieb, J., 2007. From thought to action: the parietal cortex as a bridge between perception, action, and cognition. Neuron 53, 9–16. https://doi.org/10.1016/j.neuron.2006.12.009.

Greeno, J.G., 1994. Gibson's affordances. Psychol. Rev. 101, 336–342. https://doi.org/10.1037/0033-295X.101.2.336.

Gutierrez, C., Yaun, A., Cusick, C.G., 1995. Neurochemical subdivisions of the inferior pulvinar in macaque monkeys. J. Comp. Neurol. 363, 545–562. https://doi.org/10.1002/cne.903630404.

Gutierrez, C., Cola, M.G., Seltzer, B., Cusick, C., 2000. Neurochemical and connectional organization of the dorsal pulvinar complex in monkeys. J. Comp. Neurol. 419, 61–86 https://doi.org/10.1002/(SICI)1096-9861(20000327)419:1<61::AID-CNE4>3.0.CO;2-I.

Halassa, M.M., Acsády, L., 2016. Thalamic inhibition: diverse sources, diverse scales. Trends Neurosci. 39, 680–693.

Halassa, M.M., Kastner, S., 2017. Thalamic functions in distributed cognitive control. Nat. Neurosci. 20, 1669–1679.

Harris, J.A., Mihalas, S., Hirokawa, K.E., Whitesell, J.D., Choi, H., Bernard, A., Bohn, P., Caldejon, S., Casal, L., Cho, A., Feiner, A., Feng, D., Gaudreault, N., Gerfen, C.R., Graddis, N., Groblewski, P.A., Henry, A.M., Ho, A., Howard, R., Knox, J.E., Kuan, L., Kuang, X., Lecoq, J., Lesnar, P., Li, Y., Luviano, J., McConoughey, S., Mortrud, M.T., Naeemi, M., Ng, L., Oh, S.W., Ouellette, B., Shen, E., Sorensen, S.A., Wakeman, W., Wang, Q., Wang, Y., Williford, A., Phillips, J.W., Jones, A.R., Koch, C., Zeng, H., 2019. Hierarchical organization of cortical and thalamic connectivity. Nature 575, 195–202. https://doi.org/10.1038/s41586-019-1716-z.

Harris, K.D., Shepherd, G.M.G., 2015. The neocortical circuit: themes and variations. Nat. Neurosci. 18, 170–181.

Hikosaka, O., Isoda, M., 2010. Switching from automatic to controlled behavior: cortico-basal ganglia mechanisms. Trends Cogn. Sci. 14, 154–161.

Hommel, B., Chapman, C.S., Cisek, P., Neyedli, H.F., Song, J.-H., Welsh, T.N., 2019. No one knows what attention is. Atten. Percept. Psychophys. 81, 2288–2303. https://doi.org/10.3758/s13414-019-01846-w.

Honey, C.J., Thesen, T., Donner, T.H., Silbert, L.J., Carlson, C.E., Devinsky, O., Doyle, W.K., Rubin, N., Heeger, D.J., Hasson, U., 2012. Slow cortical dynamics and the accumulation of information over long timescales. Neuron 76, 423–434. https://doi.org/10.1016/j.neuron.2012.08.011.

Houk, J.C., Wise, S.P., 1995. Distributed modular architectures linking basal ganglia, cerebellum, and cerebral cortex: their role in planning and controlling action. Cereb. Cortex 5, 95–110.

Huerta, M.F., Harting, J.K., 1984. Connectional organization of the superior colliculus. Trends Neurosci. 7, 286–289. https://doi.org/10.1016/S0166-2236(84)80197-6.

Idrees, S., Baumann, M.P., Franke, F., Münch, T.A., Hafed, Z.M., 2020. Perceptual saccadic suppression starts in the retina. Nat. Commun. 11, 1977. https://doi.org/10.1038/s41467-020-15890-w.

Imura, K., 2007. Giant neurons in the macaque pulvinar: a distinct relay subpopulation. Front. Neuroanat. 1 https://doi.org/10.3389/neuro.05.002.2007.

Isa, T., Yoshida, M., 2021. Neural mechanism of blindsight in a Macaque model. Neuroscience 469, 138–161. https://doi.org/10.1016/j.neuroscience.2021.06.022.

Isa, T., Marquez-Legorreta, E., Grillner, S., Scott, E.K., 2021. The tectum/superior colliculus as the vertebrate solution for spatial sensory integration and action. Curr. Biol. 31, R741–R762. https://doi.org/10.1016/j.cub.2021.04.001.

Itti, L., Koch, C., 2000. A saliency-based search mechanism for overt and covert shifts of visual attention. Vis. Res. 40, 1489–1506. https://doi.org/10.1016/S0042-6989(99)00163-7.

John, Y.J., Zikopoulos, B., Bullock, D., Barbas, H., 2016. The emotional gatekeeper: a computational model of attentional selection and suppression through the pathway from the amygdala to the inhibitory thalamic reticular nucleus. PLOS Comput. Biol. 12, e1004722 https://doi.org/10.1371/journal.pcbi.1004722.

John, Y.J., Zikopoulos, B., Bullock, D., Barbas, H., 2018. Visual attention deficits in schizophrenia can arise from inhibitory dysfunction in thalamus or cortex. Comput. Psychiatry 2, 223. https://doi.org/10.1162/CPSY_a_00023.

Jones, E.G., 2001. The thalamic matrix and thalamocortical synchrony. Trends Neurosci. 24, 595–601.

Kanai, R., Komura, Y., Shipp, S., 2015. Cerebral hierarchies: predictive processing, precision and the pulvinar. Philos. Trans. R. Soc. Lond. Ser. B, Biol. Sci. 370, 20140169.

Kastner, S., Fiebelkorn, I.C., Eradath, M.K., 2020. Dynamic pulvino-cortical interactions in the primate attention network. Curr. Opin. Neurobiol. 65, 10–19. https://doi.org/10.1016/j.conb.2020.08.002.

Kay, J.W., Phillips, W.A., 2011. Coherent infomax as a computational goal for neural systems. Bull. Math. Biol. 73, 344–372. https://doi.org/10.1007/s11538-010-9564-x.

Keogh, R., Pearson, J., 2018. The blind mind: no sensory visual imagery in aphantasia. Cortex 105, 53–60. https://doi.org/10.1016/j.cortex.2017.10.012.

Kinoshita, M., Kato, R., Isa, K., Kobayashi, K., Kobayashi, K., Onoe, H., Isa, T., 2019. Dissecting the circuit for blindsight to reveal the critical role of pulvinar and superior colliculus. Nat. Commun. 10, 135. https://doi.org/10.1038/s41467-018-08058-0.

Koch, C., Tsuchiya, N., 2007. Attention and consciousness: two distinct brain processes. Trends Cogn. Sci. 11, 16–22. https://doi.org/10.1016/j.tics.2006.10.012.

Kopec, C.D., Erlich, J.C., Brunton, B.W., Deisseroth, K., Brody, C.D., 2015. Cortical and subcortical contributions to short-term memory for orienting movements. Neuron 88, 367–377. https://doi.org/10.1016/j.neuron.2015.08.033.

Kratochwil, C.F., Maheshwari, U., Rijli, F.M., 2017. The long journey of pontine nuclei neurons: from rhombic lip to cortico-ponto-cerebellar circuitry. Front. Neural Circuits 11, 33.

Krauzlis, R.J., Lovejoy, L.P., Zénon, A., 2013. Superior colliculus and visual spatial attention. Annu. Rev. Neurosci. 36, 165–182. https://doi.org/10.1146/annurev-neuro-062012-170249.

Krekelberg, B., 2010. Saccadic suppression. Curr. Biol. 20, R228–R229. https://doi.org/10.1016/j.cub.2009.12.018.

Lamme, V.A.F., 2006. Towards a true neural stance on consciousness. Trends Cogn. Sci. 10, 494–501. https://doi.org/10.1016/j.tics.2006.09.001.

Larkum, M., 2013. A cellular mechanism for cortical associations: an organizing principle for the cerebral cortex. Trends Neurosci. 36, 141–151. https://doi.org/10.1016/j.tins.2012.11.006.

Larkum, M.E., Zhu, J.J., Sakmann, B., 1999. A new cellular mechanism for coupling inputs arriving at different cortical layers. Nature 398, 338–341. https://doi.org/10.1038/18686.

Luo, L., 2021. Architectures of neuronal circuits. Science 373, eabg7285. https://doi.org/10.1126/science.abg7285.

MacIver, M.A., Finlay, B.L., 2022. The neuroecology of the water-to-land transition and the evolution of the vertebrate brain. Philos. Trans. R. Soc. B 377, 20200523. https://doi.org/10.1098/rstb.2020.0523.

Maior, R.S., Hori, E., Uribe, C.E., Saletti, P.G., Ono, T., Nishijo, H., Tomaz, C., 2012. A role for the superior colliculus in the modulation of threat responsiveness in primates: toward the ontogenesis of the social brain. Rev. Neurosci. 23 https://doi.org/10.1515/revneuro-2012-0055.

Maior, R.S., Hori, E., Barros, M., Teixeira, D.S., Tavares, M.C.H., Ono, T., Nishijo, H., Tomaz, C., 2011. Superior colliculus lesions impair threat responsiveness in infant capuchin monkeys. Neurosci. Lett. 504, 257–260. https://doi.org/10.1016/j.neulet.2011.09.042.

Margulies, D.S., Smallwood, J., 2017. Converging evidence for the role of transmodal cortex in cognition. Proc. Natl. Acad. Sci. USA 114, 12641–12643.

Matsumoto, M., Inoue, K., Takada, M., 2018. Causal role of neural signals transmitted from the frontal eye field to the superior colliculus in saccade generation. Front. Neural Circuits 12, 69. https://doi.org/10.3389/fncir.2018.00069.

May, P.J., 2006. The mammalian superior colliculus: laminar structure and connections. In: Progress in Brain Research. Elsevier, pp. 321–378. 〈https://doi.org/10.1016/S0079-6123(05)51011-2〉.

McHaffie, J., Stanford, T., Stein, B., Coizet, V., Redgrave, P., 2005. Subcortical loops through the basal ganglia. Trends Neurosci. 28, 401–407.

Merker, B., 2007. Consciousness without a cerebral cortex: A challenge for neuroscience and medicine. Behav. Brain Sci. 30, 63–81. https://doi.org/10.1017/S0140525X07000891.

Merker, B., 2013. The efference cascade, consciousness, and its self: naturalizing the first person pivot of action control. Front. Psychol. 4 https://doi.org/10.3389/fpsyg.2013.00501.

Mesulam, M.M., 1998. From sensation to cognition. Brain: J. Neurol. 121 (Pt 6), 1013–1052.

Miller, E.K., Cohen, J.D., 2001. An integrative theory of prefrontal cortex function. Annu. Rev. Neurosci. 24, 167–202. https://doi.org/10.1146/annurev.neuro.24.1.167.

Mitchell, A.S., 2015. The mediodorsal thalamus as a higher order thalamic relay nucleus important for learning and decision-making. Neurosci. Biobehav. Rev. 54, 76–88. https://doi.org/10.1016/j.neubiorev.2015.03.001.

Mitchell, A.S., Chakraborty, S., 2013. What does the mediodorsal thalamus do. Front. Syst. Neurosci. 7 https://doi.org/10.3389/fnsys.2013.00037.

Montgomery, J., Perks, K., 2019. Understanding cerebellum in vertebrate neuroethology: From sensing in sharks and electric fish to motor sequences in movement and birdsong. Behav. Neurosci. 133, 267–281.

Mooney, R., Nikoletseas, M., Hess, P., Allen, Z., Lewin, A., Rhoades, R., 1988. The projection from the superficial to the deep layers of the superior colliculus: an intracellular horseradish peroxidase injection study in the hamster. J. Neurosci. 8, 1384–1399. https://doi.org/10.1523/JNEUROSCI.08-04-01384.1988.

Moore, B., Li, K., Kaas, J.H., Liao, C.-C., Boal, A.M., Mavity-Hudson, J., Casagrande, V., 2019. Cortical projections to the two retinotopic maps of primate pulvinar are distinct. J. Comp. Neurol. 527, 577–588. https://doi.org/10.1002/cne.24515.

Mugan, U., MacIver, M.A., 2020. Spatial planning with long visual range benefits escape from visual predators in complex naturalistic environments. Nat. Commun. 11, 3057. https://doi.org/10.1038/s41467-020-16102-1.

Müller, E.J., Munn, B.R., Shine, J.M., 2020. Diffuse neural coupling mediates complex network dynamics through the formation of quasi-critical brain states. Nat. Commun. 11, 6337. https://doi.org/10.1038/s41467-020-19716-7.

Müller, E.J., Munn, B.R., Mohr, H., Ruge, H., Shine, J.M., 2021. Brain state kinematics and the trajectory of task performance improvement. NeuroImage 243, 118510.

Münkle, M.C., Waldvogel, H.J., Faull, R.L., 2000. The distribution of calbindin, calretinin and parvalbumin immunoreactivity in the human thalamus. J. Chem. Neuroanat. 19, 155–173.

Munn, B.R., Müller, E.J., Wainstein, G., Shine, J.M., 2021. The ascending arousal system shapes neural dynamics to mediate awareness of cognitive states. Nat. Commun. 12, 6016. https://doi.org/10.1038/s41467-021-26268-x.

O'Callaghan, C., Walpola, I.C., Shine, J.M., 2021. Neuromodulation of the mind-wandering brain state: the interaction between neuromodulatory tone, sharp wave-ripples and spontaneous thought. Philos. Trans. R. Soc. B 376, 20190699. https://doi.org/10.1098/rstb.2019.0699.

O'Reilly, R.C., Bhattacharyya, R., Howard, M.D., 2014. Complementary learning systems. Cogn. Sci. 38, 1229–1248.

Padmala, S., 2010. Pulvinar and affective significance: responses track moment-to-moment stimulus visibility. Front. Hum. Neurosci. 4 https://doi.org/10.3389/fnhum.2010.00064.

Parker, A., 2004. In the Blink of an Eye. Basic Books, New York.

Pessoa, L., Adolphs, R., 2010. Emotion processing and the amygdala: from a "low road" to "many roads" of evaluating biological significance. Nat. Rev. Neurosci. 11, 773–782. https://doi.org/10.1038/nrn2920.

Pezzulo, G., Cisek, P., 2016. Navigating the affordance landscape: feedback control as a process model of behavior and cognition. Trends Cogn. Sci. 20, 414–424.

Phillips, I., 2021. Blindsight is qualitatively degraded conscious vision. Psychol. Rev. 128, 558–584. https://doi.org/10.1037/rev0000254.

Phillips, J.M., Kambi, N.A., Redinbaugh, M.J., Mohanta, S., Saalmann, Y.B., 2021. Disentangling the influences of multiple thalamic nuclei on prefrontal cortex and cognitive control. Neurosci. Biobehav Rev. 128, 487–510. https://doi.org/10.1016/j.neubiorev.2021.06.042.

Phillips, J.W., Schulmann, A., Hara, E., Winnubst, J., Liu, C., Valakh, V., Wang, L., Shields, B.C., Korff, W., Chandrashekar, J., Lemire, A.L., Mensh, B., Dudman, J.T., Nelson, S.B., Hantman, A.W., 2019. A repeated molecular architecture across thalamic pathways. Nat. Neurosci. 22, 1925–1935.

Phillips, W.A., Bachmann, T., Storm, J.F., 2018. Apical function in neocortical pyramidal cells: a common pathway by which general anesthetics can affect mental state. Front. Neural Circuits 12, 50. https://doi.org/10.3389/fncir.2018.00050.

Preuss, T.M., Wise, S.P., 2022. Evolution of prefrontal cortex. Neuropsychopharmacol 47, 3–19. https://doi.org/10.1038/s41386-021-01076-5.

Prevosto, V., Sommer, M.A., 2013. Cognitive control of movement via the cerebellar-recipient thalamus. Front. Syst. Neurosci. 7, 56.

Puelles, L., Rubenstein, J.L.R., 2015. A new scenario of hypothalamic organization: rationale of new hypotheses introduced in the updated prosomeric model. Front. Neuroanat. 9, 27.

Purushothaman, G., Marion, R., Li, K., Casagrande, V.A., 2012. Gating and control of primary visual cortex by pulvinar. Nat. Neurosci. 15, 905–912. https://doi.org/10.1038/nn.3106.

Rabinovich, M.I., Huerta, R., Varona, P., Afraimovich, V.S., 2008. Transient cognitive dynamics, metastability, and decision making. PLOS Comput. Biol. 4, e1000072.

Redgrave, P., 2010. Interactions between the midbrain superior colliculus and the basal ganglia. Front. Neuroanat. 4 https://doi.org/10.3389/fnana.2010.00132.

Redgrave, P., Prescott, T.J., Gurney, K., 1999. The basal ganglia: a vertebrate solution to the selection problem. Neuroscience 89, 1009–1023. https://doi.org/10.1016/S0306-4522(98)00319-4.

Reiner, A., Hart, N.M., Lei, W., Deng, Y., 2010. Corticostriatal projection neurons – dichotomous types and dichotomous functions. Front. Neuroanat. 4, 142. https://doi.org/10.3389/fnana.2010.00142.

Reynolds, J.H., Heeger, D.J., 2009. The normalization model of attention. Neuron 61, 168–185. https://doi.org/10.1016/j.neuron.2009.01.002.

Rockland, K.S., 2019. Distinctive spatial and laminar organization of single axons from lateral pulvinar in the Macaque. Vision 4, 1. https://doi.org/10.3390/vision4010001.

Ross, J., Morrone, M.C., Goldberg, M.E., Burr, D.C., 2001. Changes in visual perception at the time of saccades. Trends Neurosci. 24, 113–121. https://doi.org/10.1016/s0166-2236(00)01685-4.

Roth, M.M., Dahmen, J.C., Muir, D.R., Imhof, F., Martini, F.J., Hofer, S.B., 2016. Thalamic nuclei convey diverse contextual information to layer 1 of visual cortex. Nat. Neurosci. 19, 299–307. https://doi.org/10.1038/nn.4197.

Rovo, Z., Ulbert, I., Acsady, L., 2012. Drivers of the primate thalamus. J. Neurosci. 32, 17894–17908. https://doi.org/10.1523/JNEUROSCI.2815-12.2012.

Saalmann, Y.B., Pinsk, M.A., Wang, L., Li, X., Kastner, S., 2012. The pulvinar regulates information transmission between cortical areas based on attention demands. Science 337, 753–756.

Saitoh, K., Ménard, A., Grillner, S., 2007. Tectal control of locomotion, steering, and eye movements in lamprey. J. Neurophysiol. 97, 3093–3108. https://doi.org/10.1152/jn.00639.2006.

Salinas, E., Sejnowski, T.J., 2001. Book review: gain modulation in the central nervous system: where behavior, neurophysiology, and computation meet. Neuroscientist 7, 430–440. https://doi.org/10.1177/107385840100700512.

Schmidhuber, J., 2015. Deep learning in neural networks: an overview. Neural Netw. 61, 85–117. https://doi.org/10.1016/j.neunet.2014.09.003.

Selfridge, O.G., 1998. Pandemonium: a paradigm for learning, in: Neurocomputing: Foundations of Research. A Bradford Book. MIT Press, pp. 115–122. https://dl.acm.org/doi/book/10.5555/65669.

Shea, N., Frith, C.D., 2016. Dual-process theories and consciousness: the case for 'Type Zero' cognition: Table 1. niw005 Neurosci. Conscious 2016. https://doi.org/10.1093/nc/niw005.

Shepherd, G.M.G., Yamawaki, N., 2021. Untangling the cortico-thalamo-cortical loop: cellular pieces of a knotty circuit puzzle. Nat. Rev. Neurosci. https://doi.org/10.1038/s41583-021-00459-3.

Sherman, S.M., Guillery, R.W., 2002. The role of the thalamus in the flow of information to the cortex. Philos. Trans. R. Soc. Lond. B 357, 1695–1708. https://doi.org/10.1098/rstb.2002.1161.

Shine, J.M., 2020. The thalamus integrates the macrosystems of the brain to facilitate complex, adaptive brain network dynamics. Prog. Neurobiol., 101951 https://doi.org/10.1016/j.pneurobio.2020.101951.

Shine, J.M., Shine, R., 2014. Delegation to automaticity: the driving force for cognitive evolution? Front. Neurosci. 8.

Shine, J.M., Müller, E.J., Munn, B., Cabral, J., Moran, R.J., Breakspear, M., 2021. Computational models link cellular mechanisms of neuromodulation to large-scale neural dynamics. Nat. Neurosci. 24, 765–776. https://doi.org/10.1038/s41593-021-00824-6.

Shine, J.M., Breakspear, M., Bell, P.T., Ehgoetz Martens, K.A., Shine, R., Koyejo, O., Sporns, O., Poldrack, R.A., 2019. Human cognition involves the dynamic integration of neural activity and neuromodulatory systems. Nat. Neurosci. 22, 289–296. https://doi.org/10.1038/s41593-018-0312-0.

Shipp, S., 2003. The functional logic of cortico–pulvinar connections. Philos. Trans. R. Soc. Lond. B 358, 1605–1624. https://doi.org/10.1098/rstb.2002.1213.

Smith, J.B., Watson, G.D.R., Liang, Z., Liu, Y., Zhang, N., Alloway, K.D., 2019. A role for the claustrum in salience processing. Front. Neuroanat. 13, 64. https://doi.org/10.3389/fnana.2019.00064.

Smith, Y., Raju, D.V., Pare, J.-F., Sidibe, M., 2004. The thalamostriatal system: a highly specific network of the basal ganglia circuitry. Trends Neurosci. 27, 520–527.

Smith, Y., Galvan, A., Ellender, T.J., Doig, N., Villalba, R.M., Huerta-Ocampo, I., Wichmann, T., Bolam, J.P., 2014. The thalamostriatal system in normal and diseased states. Front. Syst. Neurosci. 8 https://doi.org/10.3389/fnsys.2014.00005.

Sommer, M.A., 2003. The role of the thalamus in motor control. Curr. Opin. Neurobiol. 13, 663–670. https://doi.org/10.1016/j.conb.2003.10.014.

Sommer, M.A., Wurtz, R.H., 2002. A pathway in primate brain for internal monitoring of movements. Science 296, 1480–1482. https://doi.org/10.1126/science.1069590.

Sommer, M.A., Wurtz, R.H., 2006. Influence of the thalamus on spatial visual processing in frontal cortex. Nature 444, 374–377. https://doi.org/10.1038/nature05279.

de Souza, B.O.F., Cortes, N., Casanova, C., 2020. Pulvinar modulates contrast responses in the visual cortex as a function of cortical hierarchy. Cereb. Cortex 30, 1068–1086. https://doi.org/10.1093/cercor/bhz149.

Stevens, M., Merilaita, S. (Eds.), 2011. Animal Camouflage: Mechanisms and Function. Cambridge University Press, Cambridge, UK; New York.

Suzuki, M., Larkum, M.E., 2020. General anesthesia decouples cortical pyramidal neurons. Cell 180, 666–676. https://doi.org/10.1016/j.cell.2020.01.024.

Takahashi, N., Ebner, C., Sigl-Glöckner, J., Moberg, S., Nierwetberg, S., Larkum, M.E., 2020. Active dendritic currents gate descending cortical outputs in perception. Nat. Neurosci. https://doi.org/10.1038/s41593-020-0677-8.

Thompson, A.W., Vanwalleghem, G.C., Heap, L.A., Scott, E.K., 2016. Functional profiles of visual-, auditory-, and water flow-responsive neurons in the zebrafish tectum. Curr. Biol. 26, 743–754. https://doi.org/10.1016/j.cub.2016.01.041.

Van Le, Q., Isbell, L.A., Matsumoto, J., Nguyen, M., Hori, E., Maior, R.S., Tomaz, C., Tran, A.H., Ono, T., Nishijo, H., 2013. Pulvinar neurons reveal neurobiological evidence of past selection for rapid detection of snakes. Proc. Natl. Acad. Sci. USA 110, 19000–19005. https://doi.org/10.1073/pnas.1312648110.

Verbeke, P., Verguts, T., 2022. Using top-down modulation to optimally balance shared versus separated task representations. Neural Netw. 146, 256–271. https://doi.org/10.1016/j.neunet.2021.11.030.

van Vugt, B., Dagnino, B., Vartak, D., Safaai, H., Panzeri, S., Dehaene, S., Roelfsema, P.R., 2018. The threshold for conscious report: signal loss and response bias in visual and frontal cortex. Science 360, 537–542. https://doi.org/10.1126/science.aar7186.

Wainstein, G., Müller, E.J., Taylor, N., Munn, B., Shine, J.M., 2022. The role of the locus coeruleus in shaping adaptive cortical melodies. Trends Cogn. Sci. 26, 527–538. https://doi.org/10.1016/j.tics.2022.03.006.

Wang, L., McAlonan, K., Goldstein, S., Gerfen, C.R., Krauzlis, R.J., 2020. A causal role for mouse superior colliculus in visual perceptual decision-making. J. Neurosci. 40, 3768–3782. https://doi.org/10.1523/JNEUROSCI.2642-19.2020.

Wei, P., Liu, N., Zhang, Z., Liu, X., Tang, Y., He, X., Wu, B., Zhou, Z., Liu, Y., Li, J., Zhang, Y., Zhou, X., Xu, L., Chen, L., Bi, G., Hu, X., Xu, F., Wang, L., 2015. Processing of visually evoked innate fear by a non-canonical thalamic pathway. Nat. Commun. 6, 6756. https://doi.org/10.1038/ncomms7756.

White, B.J., Berg, D.J., Kan, J.Y., Marino, R.A., Itti, L., Munoz, D.P., 2017. Superior colliculus neurons encode a visual saliency map during free viewing of natural dynamic video. Nat. Commun. 8, 14263. https://doi.org/10.1038/ncomms14263.

Whyte, C.J., Smith, R., 2020. The predictive global neuronal workspace: a formal active inference model of visual consciousness (preprint). Neuroscience. https://doi.org/10.1101/2020.02.11.944611.

Wibral, M., Priesemann, V., Kay, J.W., Lizier, J.T., Phillips, W.A., 2017. Partial information decomposition as a unified approach to the specification of neural goal functions. Brain Cogn. 112, 25–38.

Wilke, M., Mueller, K.-M., Leopold, D.A., 2009. Neural activity in the visual thalamus reflects perceptual suppression. Proc. Natl. Acad. Sci. USA 106, 9465–9470. https://doi.org/10.1073/pnas.0900714106.

Williams, G., Bing, C., Cai, X.J., Harrold, J.A., King, P.J., Liu, X.H., 2001. The hypothalamus and the control of energy homeostasis. Physiol. Behav. 74, 683–701. https://doi.org/10.1016/S0031-9384(01)00612-6.

Wilson, C.J., 2013. Active decorrelation in the basal ganglia. Neuroscience 250, 467–482.

Yu, J., Hu, H., Agmon, A., Svoboda, K., 2019. Recruitment of GABAergic interneurons in the barrel cortex during active tactile behavior. Neuron 104, 412–427. https://doi.org/10.1016/j.neuron.2019.07.027.

Zhou, H., Schafer, R.J., Desimone, R., 2016. Pulvinar-cortex interactions in vision and attention. Neuron 89, 209–220. https://doi.org/10.1016/j.neuron.2015.11.034.

Zhou, N., Maire, P.S., Masterson, S.P., Bickford, M.E., 2017. The mouse pulvinar nucleus: organization of the tectorecipient zones. Vis. Neurosci. 34, E011 https://doi.org/10.1017/S0952523817000050.

Zhou, N., Masterson, S.P., Damron, J.K., Guido, W., Bickford, M.E., 2018. The mouse pulvinar nucleus links the lateral extrastriate cortex, striatum, and amygdala. J. Neurosci. 38, 347–362. https://doi.org/10.1523/JNEUROSCI.1279-17.2017.

Zolnik, T.A., Ledderose, J., Toumazou, M., Trimbuch, T., Oram, T., Rosenmund, C., Eickholt, B.J., Sachdev, R.N.S., Larkum, M.E., 2020. Layer 6b is driven by intracortical long-range projection neurons. Cell Rep. 30, 3492–3505. https://doi.org/10.1016/j.celrep.2020.02.044.