

Review

The pulvinar as a hub of visual processing and cortical integration

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The pulvinar nucleus of the thalamus is a crucial component of the visual system and plays significant roles in sensory processing and cognitive integration. The pulvinar's extensive connectivity with cortical regions allows for bidirectional communication, contributing to the integration of sensory information across the visual hierarchy. Recent findings underscore the pulvinar's involvement in attentional modulation, feature binding, and predictive coding. In this review, we highlight recent advances in clarifying the pulvinar's circuitry and function. We discuss the contributions of the pulvinar to signal modulation across the global cortical network and place these findings within theoretical frameworks of cortical processing, particularly the global neuronal workspace (GNW) theory and predictive coding.

The transthalamic visual cortico-cortical pathways

When viewing an image, signals originating from the retina are transmitted through the lateral geniculate nucleus (LGN) of the thalamus to the primary visual cortex (V1) for local feature processing. Subsequently, information regarding the image characteristics is conveyed to hierarchically organized cortical areas, where progressively greater integration of biologically relevant patterns leads to appropriate behavioral responses [1]. Historically, visual perception was attributed solely to hierarchical cortico-cortical connections [2]. This corticocentric viewpoint has often overlooked the fact that the operations of the cortex are deeply intertwined with those of subcortical structures, including the basal ganglia, cerebellum, and thalamus. This complex interplay forms the basis of our cognitive abilities and behaviors. As depicted in [Figure 1](#), it is important to recognize that sensory information from lower cortical areas can be conveyed directly to higher-order cortical areas not only through cortico-cortical connections but also indirectly via cortico-thalamo-cortical projections, through **higher-order thalamic nuclei** (see [Glossary](#)). While the importance of these transthalamic cortical pathways involving higher-order thalamic nuclei has been acknowledged by several researchers, and notable advancements have been made in recent years, numerous questions regarding the involvement of these nuclei in cortical computations remain unanswered [3,4] and, regrettably, theories of sensory and cognitive integration often neglect the role of the transthalamic pathways. Evidence suggests that the pulvinar, a central higher-order thalamic nucleus, which is reciprocally linked to visual cortical areas and also to auditory, somatosensory, associative, and executive cortical regions, assumes a central role in regulating neuronal signal processing within and between cortices [5,6]. Further supporting this proposition, dysfunctions in transthalamic cortical communication via the pulvinar are linked to sensory deficits observed in conditions like autism, attention-deficit/hyperactivity disorder, and schizophrenia [7–9].

Reframing the pulvinar's role within theories that elucidate the integration and computation of diverse cortical signals is essential for a more comprehensive understanding of transthalamic pathways. This review begins with an overview of the visual pulvinar and its associated cortical network. We then delve into the pulvinar's key role in governing visual cortical processing,

Highlights

The thalamic pulvinar exhibits extensive reciprocal connections with the visual cortex. These connections provide alternative pathways for the transmission of signals between cortical neurons.

Although the precise roles of the pulvinar in vision are incompletely understood, research indicates that the pulvinar is involved in target selection among distractors, feature binding, and visual attention. Pulvinar dysfunctions have been associated with sensory deficits observed in individuals with schizophrenia.

Computational models suggest that the pulvinar plays a crucial role in establishing persistent activity within the cortical network by regulating the flow of information across visual cortical areas and the synchronization of their activity.

We highlight the organization of brain networks involving the pulvinar and propose a pivotal role for the pulvinar within the framework of cortical theories that aim to elucidate the processes of perception and cognitive integration.

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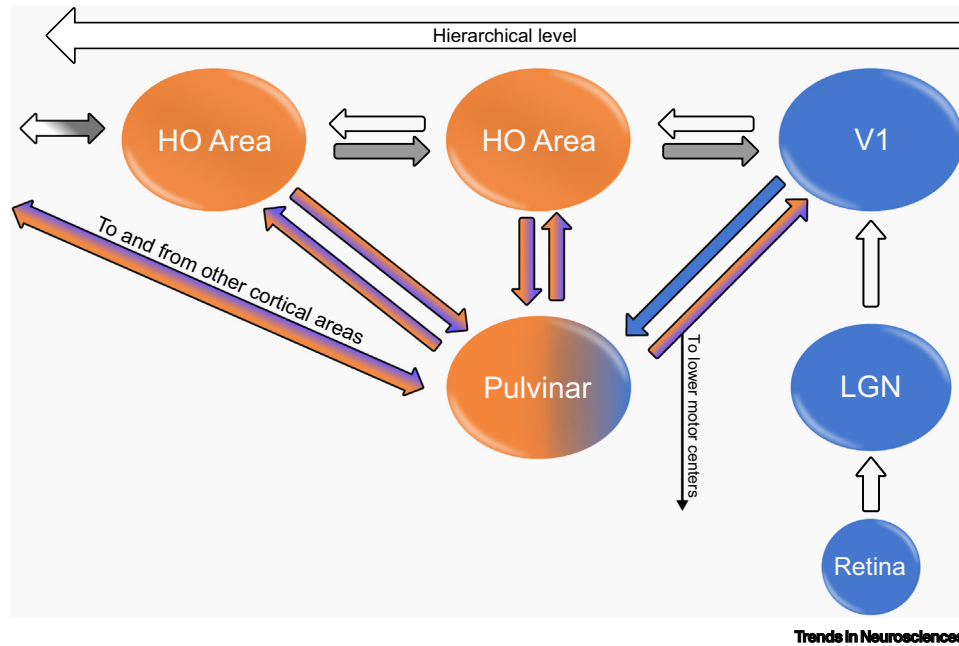


Figure 1. The transthalamic cortical visual pathways. Sensory signals from the retina are sent to the lateral geniculate nucleus (LGN) and then to the primary visual cortex (V1). V1 signals can be transmitted to higher-order visual cortical areas (HO) not only through cortico-cortical connections (white and gray arrows, representing feedforward and feedback projections, respectively) but also through the pulvinar, which mediates the transthalamic cortical communication between all areas of the visual cortex in the feedforward and feedback directions.

specifically its integration of visual and cognitive information across cortical areas. We pay special attention to cortical theories that aim to clarify perception and cognitive integration, such as the GNW theory and predictive coding frameworks.

Subdivisions and functional connectivity of the pulvinar

The pulvinar is situated above the dorsolateral posterior thalamus and extends along the medial border of the LGN. Throughout mammalian evolution, the pulvinar has grown and differentiated, mirroring changes in the neocortex (Box 1) [10]. Consequently, the pulvinar stands as the most prominent visual nucleus within the thalamus in higher-order mammals, including humans [11, 12]. The subsequent section delineates the anatomical subdivisions of the pulvinar in primates, cats, and rodents, emphasizing its multifaceted roles from sensory processing to motor control. Next, we introduce the concept of a dorso-ventral pulvinar gradient as a framework to better understand the functional diversity of the pulvinar.

Anatomical subdivisions in primates

Historically, in view of the pulvinar's intricate architecture in primates, this brain region was divided into three major subdivisions: the inferior pulvinar (PI), the lateral pulvinar (PL), and the medial pulvinar (PM) [13]. A contemporary naming system has refined pulvinar subdivisions based on its connection with early visual areas (Box 1) [14]. Thus, the PI and PL have been segmented further. The PI is subdivided into the posterior, middle, central medial, and central lateral subnuclei (PIp, PI_m, PI_{cm}, and PI_{cl}, respectively). While PIp, PI_m, and PI_{cm} primarily interface with the **dorsal visual stream**, PI_{cl} exhibits connections with the **ventral visual stream** [15]. The PL has been further categorized into two regions: the dorso-medial (PL_{dm}) and the ventro-lateral (PL_{vl}). While PL_{vl} is primarily linked to the superior colliculus (SC), V1, V2, and areas associated

Glossary

Alpha rhythm: rhythmic neural activity typically defined in humans within the 7.5–12.5 Hz range.

Asynchronous or synchronous neuronal activity: asynchronous activity in neural networks describes a regime with weak temporal correlations among neurons, whereas synchronous activity refers to a regime where temporal correlations are strong.

Beta rhythm: rhythmic neural activity typically defined in humans within the 12.5–30 Hz range.

Dorsal visual stream: the dorsal stream, or 'where/how' pathway, originates in the striate cortex, extending to the parietal lobe for spatial and motion awareness.

Feedforward and feedback processing: feedforward processing refers to flow of neural information through hierarchical levels of processing, from low level to higher levels, whereas feedback processing is the reverse flow from higher to lower levels, enabling top-down modulation of activity.

Firing rate coding: in firing rate coding, the intensity of a stimulus is encoded by the frequency or rate of neuronal action potentials. Excitatory neurons typically increase firing rates for stronger stimuli; inhibitory neurons decrease firing rates, modulating neural network activity.

Fleeting memory: also known as sensory memory, it is the initial stage of memory processing that briefly stores incoming sensory information in its original form before it is further processed.

Gamma rhythm: rhythmic neural activity typically defined in humans within the 25–70 Hz range.

Higher-order thalamic nucleus: unlike first-order nuclei, which primarily receive their driving input from the sensory organs, higher-order thalamic nuclei receive their primary driving signals from cortical areas.

Subliminal visual stimulus: typically refers to a brief and low-energy visual stimulation that the observer does not consciously perceive.

Temporal coding: a mode of neuronal communication that relies on the precise timing of action potentials or inter-spike intervals for encoding information.

Theta rhythm: rhythmic neural activity typically defined in humans within the 4–7.5 Hz range.

V4: a cortical visual area of the ventral pathway that integrates feature

Box 1. Evolutionary expansion of the pulvinar in primates: functional nuances and the role of vGLUTs

The primate pulvinar exhibits two prime distinctions from other species: the expansion of PM, and the proliferation of the ventral subunits, PI and PLvl (Figure I). PM, as highlighted by recent research, functions as a multisensory hub, crucial for sensory–motor integration, eye–hand coordination, and potentially conveying complex emotional cues to the amygdala [8,16]. In contrast, PI and PL, which have evolved into at least five subdivisions, enhance the relay from sources such as V1 and V2, retina, and SC to both dorsal and ventral visual streams in the cortex [13–15]. For instance, Plcm and Plp primarily interact with regions around the medial temporal area (MT) and receive direct projections from SC, and Plm, receiving extra projections from the retina, has a direct link with MT [12,15,39,116,118]. A potential driving factor behind the evolution of ventral subdivisions might be the migration of neurons from the SC to the retinofugal pathway. For context, 85–90% of rodent retinal cells project to the SC [119], but only about 50% in cats (26% from temporal retina) [120] and 10% in primates do so [121]. Such migrations illustrate the balance between retinal and SC projections into the caudal pulvinar, influencing the evolution of the PI and the emergence of the MT complex [118,122]. Collectively, these changes in the pulvinar allow for intricate interactions with the cortex, accommodating high-level neural integration, as seen with PM, and specialized visual perception tasks, as seen with PI and PL.

The newly discovered subdivisions of PL and PI exhibit distinctive protein staining patterns and varied connections, revealing diverse interactions with visual cortical areas and a range of functions [14]. A significant example of this complexity is the divergent roles of vesicular glutamate transporters, vGLUT1 and vGLUT2, essential markers for delineating functionally distinct territories within the visual pulvinar and for understanding the dynamics of thalamocortical neurons and their inputs. Extensive studies have investigated the unique roles of vGLUT1 and vGLUT2 across diverse species, uncovering their subtle functionalities within the visual pulvinar [123]. Initially, vGLUT1 was associated with modulatory projections and vGLUT2 with driving projections [124]. However, this initial dichotomy has proven to be more nuanced. For instance, in macaques, driver corticopulvinar projections from layer 5 pyramidal cells are enriched with vGLUT1, while vGLUT2 defines subcortical terminal areas [12]. These areas may be crucial for relaying information from the retina and SC to the neocortex. These interspecies variations stress transporters' adaptive roles in visual processing, showing the balance in neural and synaptic functions across diverse contexts.

processing and visual attention, situated at intermediate levels of the visual cortical hierarchy.

Ventral visual stream: the ventral stream, the 'what' pathway, also starts in the striate cortex but leads to the temporal lobe, focusing on object and face recognition.

Winner-take-all: in the context of neural networks, winner-take-all is a competitive neural mechanism where only a specific subset of neurons fire in response to a particular input.

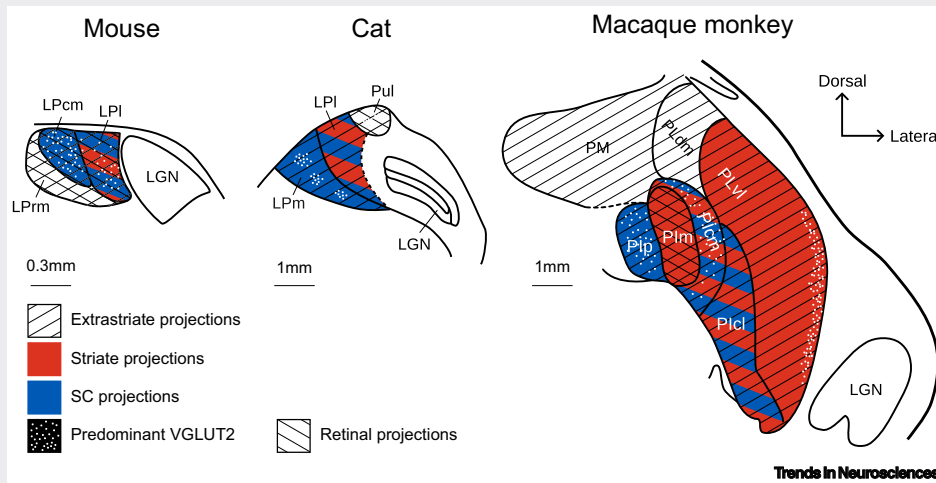


Figure I. This figure illustrates the distinctive pulvinar subdivisions present in mice, cats, and macaques, their vGLUT2 expression, and a general view of their cortical and subcortical inputs. In mice, the subdivisions of the lateral posterior nucleus (LP, homolog of pulvinar) are as follows: LPcm, caudal medial LP; Pl, lateral LP; LPm, rostral medial LP. In cats, the main subdivisions of the LP-pulvinar complex are designated as: LPl, lateral LP; LPm, medial LP; Pul, the pulvinar nuclei proper. In macaques, a more complex structure is observed, including: Plcm, central medial inferior pulvinar; Plcl, central lateral inferior pulvinar; Plp, posterior inferior pulvinar; Plpl, posterior lateral inferior pulvinar; PLvl, ventrolateral lateral pulvinar; Pldm, dorsomedial lateral pulvinar; PM, medial pulvinar. Please note the prominent increase in the most dorsal subunit, PM, and the proliferation of subunits devoted specifically to visual processing in macaques, illustrating the advanced and specialized nature of the primate pulvinar relative to other species. Mice, cat, and macaque schematics are based on [12,23,125], [19,20,22,98,107,124,126,127], and [12–15], respectively. Abbreviations: LGN, lateral geniculate nucleus; SC, superior colliculus.

with the ventral visual stream, PLdm is more associated with regions that are part of the dorsal visual stream [16]. Finally, the PM has two specialized subdivisions [5,17]. Its lateral division involves extensive visual processing, connecting with areas such as the LGN, V1, V2, dorsal and ventral stream cortical areas, and the SC. In contrast, PM's medial division is linked to auditory and motor-related regions, signifying a broader range of functions (see later and [Box 1](#)) [8].

Comparative perspectives: cats and rodents

In cats, the pulvinar manifests as the lateral-posterior (LP)/pulvinar complex, with the lateral and medial portions of the LP nucleus (LPI and LPm, respectively), and the pulvinar proper [18]. While the LPI has a unique feature of direct projections from the striate cortex or V1 [18,19], both LPI and LPm receive dense recipient extrastriate projections. However, LPm is the main recipient of SC projections, with LPI having a small tectorecipient zone [20,21]. Additionally, the pulvinar proper receives primarily retinal inputs [22]. The relationship between subnuclei and dorsal/ventral cortical streams in cats remains largely unknown. In rodents, the pulvinar is notably smaller and more homogeneous than in higher mammals [23]. Nevertheless, recent research found distinct subdivisions with unique cortical inputs in rodents, implying specialized subregions [24].

Dorso-ventral pulvinar gradient

One of the main challenges in the study of pulvinar physiology is that its functions in sensory processing are sometimes inconsistent with its anatomical subdivisions [25,26]. Despite the complexities that arise from the pulvinar's anatomical subdivisions, the pulvinar exhibits a dorso-ventral functional gradient, which emulates a hierarchical continuum of brain functions from basic perception to advanced cognitive processing [5]. In primates, the ventral pulvinar, often referred to as the 'visual pulvinar', includes the anatomically defined PI and PLvl, both of which are intricately connected to occipital and temporal cortices [16]. Specialized connectivity shapes pulvinar's receptive fields, which bear a striking resemblance to those of visual cortical neurons. Research in both cats and monkeys has shown that many pulvinar receptive fields are binocularly selective and sensitive to retinal disparity [27]. Additionally, they respond to essential image features like orientation and motion direction [20,28]. Further studies revealed that pulvinar neurons in cats and humans also encode higher-order visual processes, such as discerning the direction of complex visual stimuli like moving plaids and random dot kinematograms [29–31]. Moreover, a coarse retinotopic organization has been identified in the lateral and inferior primate pulvinar subdivisions [32,33], as well as in the main subdivisions of the LP-pulvinar in cats [20,34]. Conversely, the dorsal pulvinar of primates, consisting of the PLdm and PM, aligns more with higher-order cognitive processes [16]. It is functionally connected to frontal, parietal, and cingulate cortices and is essential for attentional control (e.g., goal-directed eye movements) and other advanced cognitive functions [14,16,35]. For example, dorsal pulvinar, like PM, processes fear-eliciting stimuli like images of snakes through its connectivity with the amygdala [36,37]. This conserved behavior may underlie phenomena like 'affective blindsight', which relies less on corticothalamic or thalamocortical connectivity and more of a PM-driven event [26,38,39]. In sum, the pulvinar's dorso-ventral functional gradient serves as a unifying framework that encompasses its diverse functions, ranging from basic visual processing to advanced cognitive functions [20,27–32,36,37,40,41].

Unveiling the complexity of cortex–thalamus interactions: an integrated examination of a driver/modulator framework

Anatomical characteristics of axon terminals

It is noteworthy that a neuron in the primary visual cortex is only one thalamic synapse away from neurons in higher-order areas, thanks to the pulvinar. According to the 'driver/modulator' framework [42], cortical inputs are conceptualized to belong to one of two categories: modulators and drivers (type 1 and type 2 terminals) [43,44]. Type 1 terminals, with small round terminals, thin

axons, and long, thin branches, may adjust or modify the ongoing firing of recipient neurons, through metabotropic receptors [45]. Conversely, type 2 terminals are characterized by large round terminals, large caliber axons with clustered endings [18]. They define the target cell's receptive field using fast ionotropic receptors [45,46]. Cortico-thalamic projections to pulvinar neurons exhibit a mix of these two terminal types, but their relative proportion varies across the visual cortical hierarchy [47]. Neurons in early visual cortical areas have a higher proportion of type 2 terminals, while those in higher processing levels send more type 1 terminals [18]. This organizational scheme suggests that early visual areas like V1 send driver signals to form basic visual maps in the pulvinar, whereas higher-order visual cortical areas primarily modulate pulvinar neuron activity. The driver/modulator framework is not immutable. Atypical axon terminals with driver-like properties (type 3) have been discovered in collicular neurons that project to the pulvinar [45]. These may play a vital role in transmitting information about eye fixation and saccades to the cortex [48]. Little is known about the morphology of the reverse connections, the thalamocortical projections from the pulvinar, and their variations across cortical hierarchy. Addressing this knowledge gap would be essential for a comprehensive understanding of the pulvinar-cortical network and its functional implications.

The distinction between drivers and modulators has also been made based on the laminar organization of thalamocortical and corticothalamic projections. For bottom-up projections, the prevailing view suggests that thalamic terminals ending in layer 4 act as drivers, while those ending in layer 1 serve as modulators [49]. In top-down projections, layer 5 cortical cells provide driver signals, whereas layer 6 cells transmit modulatory signals. This holds true for the LGN, which targets layer 4 in V1 and receives feedback modulatory signals from layer 6 [50]. While it is generally accepted that pulvinar neurons in primates and cats receive driver inputs from V1 [51,52], and in turn send modulatory signals to layer 1 [53,54], it is still unknown if corticothalamic pathways involving higher-order areas and the pulvinar conform with the driver/modulator framework, despite recent findings of hierarchical anatomical organization of cortico-pulvinar projections in cats [18]. Addressing this issue is especially challenging since pulvinar axon terminals or cortical cell bodies are generally not restricted to a single cortical layer [55,56].

Functional characteristics of axons terminals

Drivers and modulators can be classified based on the input–output transfer of the neuronal responses. Modulator effects are categorized as either multiplicative or divisive (nonlinear gain control), while drivers act through additive or subtractive changes (linear gain control) [57,58]. Studies in rats have demonstrated that type 1 and type 2 corticothalamic terminals from V1 exhibit short-term facilitation and depression in excitatory postsynaptic potentials, respectively [59]. Expanding on this, the driver/modulator framework can indirectly correspond to the anatomical organization of the cortical visual hierarchy. Such a connection supports a unique type of communication throughout the hierarchy, deeply rooted in the inherent rhythmicity delineated in the local field potential (LFP) of neurons. In primates, feedforward connections are associated with high-frequency rhythms (gamma oscillations, >30 Hz), while feedback connections are linked to low-frequency oscillations (alpha and beta oscillations, 7–30 Hz) [60–62].

In cats and monkeys, findings from neuronal inactivation studies align with corticothalamic anatomical features. Silencing V1, for instance, abolishes visual responses in most pulvinar neurons in cats and monkeys [51,52], underscoring the notion of V1 as a driver of pulvinar activity. Conversely, considering our previous anatomical discussion, higher-order cortical areas are believed to primarily modulate pulvinar activity. However, further investigation is required since, in cats, higher-order areas are necessary to drive pattern-motion neurons in the pulvinar [30]. Similarly, limited information is available about the pulvinar's impact on cortical neurons in the visual hierarchy.

In primates, deactivating the PL notably reduces activity in V1's supragranular layers [54]. In cats, the primary effect of LPI inactivation on V1 neurons is a slight decrease in response gain [53], corroborating previous findings obtained through optical brain imaging in the same species [63]. In contrast, LPI inactivation leads to a substantial increase in response gain in most neurons in area 21a (putative homolog of area **V4** in primates), with a few cells exhibiting contrast gain changes [53]. Similarly, in *Cebus* monkeys, PL inactivation intensifies response amplitude in area V2 [64]. Collectively, these studies, while relatively limited, confirm that the pulvinar can influence processing across the visual cortex mainly by modulating neuronal activity, thus suggesting its role in controlling the flow of information throughout the visual cortex.

The pulvinar's dual role in visual attention and neural communication

Understanding the precise role of the pulvinar is a challenging task due to its unique anatomical-functional architecture. This thalamic region has been implicated in various processes and readers are encouraged to refer to previous reviews that describe the potential functions associated with the pulvinar [3,65–67]. In the next paragraphs, we will examine two prominent roles debated in the literature, relevant to the subsequent discussion on theoretical models.

Modulating visual attention

For decades, the pulvinar has been recognized as a modulator of visual attention. Early studies in monkeys suggested that neurons involved in attention tasks were primarily found in the dorsal pulvinar (i.e., in PLdm) [68,69]. Deactivating PLdm shifted visual attention and affected the motivation to reach and grasp objects, mirroring perceptual neglect symptoms. Subsequent investigations utilizing brain imaging and psychophysical techniques in both healthy and brain-damaged individuals reinforced the pulvinar's role in sustained visual attention, stimulus awareness, and the filtering of irrelevant or distracting information [23,70–77]. Likewise, a recent study in humans showed that activity in the pulvinar and fronto-parietal cortices was modulated when a cue and a salient distractor were presented together [78]. However, this modulation did not occur when either of these stimuli was presented alone. Relatedly, an fMRI study in humans revealed increased activity in the dorsal pulvinar during directed spatial attention, mirroring fronto-parietal activation patterns [25]. Single-cell recordings in the lateral and inferior regions of the ventral pulvinar in primates [79,80] and in the LP-pulvinar complex of ferrets [81] align with the findings from humans. These animal studies revealed that pulvinar neurons are involved in sustained and directed spatial attention, although the specific neuronal activity (e.g., LFP rhythms such as alpha, theta, or gamma oscillations) associated with attention varies across these investigations.

Orchestrating cortical communication in neural networks

Another important function of the pulvinar, besides its role in visual attention, is its capacity to modulate information transmission within large-scale cortical networks. Two types of cortical processing, **feedforward and feedback processing**, underlie whole-brain activation. Extensive theoretical research proposes pulvinar-mediated feedforward cortical amplifications, backed by empirical evidence. Computational models, for instance, indicate that the pulvinar enhances external input responses throughout the cortical hierarchy, acting as a **firing rate coding** mechanism in visual processing [82–84]. Studies conducted in cats provide further support for this feedforward amplification, as, counterintuitively, inactivation of the lateral and medial subdivisions of the LP/pulvinar complex leads to increased spike counts tied to contrast changes in cortical areas at various hierarchical positions [53]. Similarly, mouse brain slice research indicates that the pulvinar's activity may exhibit driver-like characteristics, amplifying signals through transthalamic feedforward pathways. Notably, in these experiments, most of the pulvinar projections, originating from zones that receive inputs from the striate cortex and the SC, target layer 4 of extrastriate cortices [85]. These findings underscore the critical role of the pulvinar in visual

processing by highlighting its involvement in the contextual integration of cortical information, ultimately influencing higher cortical areas.

Expanding on these insights, the pulvinar's role in coordinating information transmission in cortical networks becomes clearer when considering **temporal coding**. In the context of feedforward propagation, transthalamic pathways are organized in such a way that they facilitate the emergence of nested oscillatory patterns within different cortical subnetworks [80,86]. Recent research supports this organization by revealing synchronized LFP coherence between cortical regions and the PLdm during both ongoing activity and attention-dependent tasks [80,87,88]. Notably, recent data suggest a direct link between pulvinar modulation and the amplification of **gamma rhythms** [86]. Conversely, neuronal populations in the prefrontal cortex generate oscillatory states characterized by low-frequency oscillations that align with pulvinar rhythms, including **theta rhythms**, **alpha rhythms**, and **beta rhythms**, primarily within the PM and PLdm [73,88]. Therefore, the pulvinar can be seen as a dynamic trigger facilitating communication between distinct cortical areas through the synchronization of oscillatory patterns, phase relationships, and rhythmic activity.

While the role of the pulvinar in feedback transmission is not yet fully understood, theoretical studies suggest that transthalamic pathways transmit alpha and beta rhythms back to the cortex [84]. Experimental data indicate that similar feedback-related low-frequency signatures observed in cortical areas of monkeys [60,62] also manifest in the human pulvinar [89]. These rhythms are predominantly generated within the cortex, particularly the prefrontal cortex [79,88,90]. However, eliciting thalamic responses requires significant effective connectivity, which can only occur if multiple cortical areas that project to the pulvinar are synchronously activated (given the modulatory nature of type 1 terminals). The precise number of top-down inputs (i.e., corticothalamic inputs) needed to trigger pulvinar responses remains unclear. An alternative hypothesis suggests that cortical inputs associated with the thalamic reticular nucleus generate a global inhibitory response within the pulvinar, leading to low-frequency oscillations [91]. Another mechanism suggests that slow oscillations may arise from asynchronous corticothalamic projections into discrete pulvinar clusters, leading to **winner-take-all** states of neuronal competition [47]. This hypothetical neuronal mechanism could facilitate the resetting of cortical feedback transmission by generating a bistable state (either **asynchronous or synchronous neuronal activity**) within the pulvinar, which is influenced by the distinct distribution of corticothalamic type 1 and 2 axons in the visual cortex. A similar bistable state has been experimentally observed in the primate dorsal and ventral pulvinar during object detection and passive viewing [92].

The preceding paragraphs have highlighted the pivotal position of the pulvinar within the global neural network of the brain. Moving forward, we will examine prevailing brain theories and explore how the pulvinar integrates into these concepts, bridging the gap between current understanding and future research directions.

The global workspace theory (GWT) and GNW

The GWT is a prominent cognitive science theory that explains how distributed modules communicate to achieve higher-order cognitive states, including consciousness [93]. In this theory, a **fleeting memory** enables the system to access shared brain functions, and long-range connections between modules facilitate large-scale network operations [94]. The GWT posits that sensory brain structures provide network inputs, with modules filtering out irrelevant information to share relevant activity. Consequently, each module collaborates as a functional part of the system, unifying global meaning at each moment. An extension of the GWT, the GNW model, offers further insights into the neural architecture and workings of the brain in generating

conscious experiences [95,96]. An example of the GNW in action is the neuronal processing during the conscious detection of a **subliminal visual stimulus** [97]. This detection process unfolds in several steps within the cortex: crossing a cortical threshold, feedforward broadcasting, reverberating cortical activity, and feedback neuronal communication. The dynamics of this process, called ‘ignition’ in the GNW, can be summarized as follows [98]. When a signal from a visual stimulus reaches V1, it crosses a neural threshold, triggering activity propagation throughout the cortex. This activity cascades from lower to higher hierarchical levels, broadcasting feedforward information up to the prefrontal cortex. However, if the signal is not sufficiently strong, it decays exponentially throughout the hierarchy (Figure 2A₁). If the threshold is reached and the activity spreads across the entire cortex, the neuronal activity continues to reverberate through recurrent interactions within and between cortical areas [97]. The global neuronal response is then relayed back through the cortex toward lower-level regions. This process involves bidirectional communication, with feedforward and feedback connections both being essential to conscious experience. Cortico-cortical projections, especially long-range connections, contribute to nervous system integration and greatly impact a subject’s conscious states from the GNW perspective.

Integrating the pulvinar in the GNW

Based on findings discussed in earlier sections, the pulvinar may assume a critical role within the GNW by contributing to one or multiple stages of cortical ignition. These stages encompass the activation threshold, feedforward propagation, recurrent activation, and feedback integration processes (as depicted in Figure 2A₂).

As highlighted earlier, the pulvinar likely enhances cortico-cortical communication by amplifying signals through the feedforward pathway. This amplification is achieved through the pulvinar’s extensive projections to extrastriate cortical areas, particularly targeting layer 4. We propose that this transthalamic pathway serves to enhance the feedforward transfer of information between cortical modules by increasing the response gain along the cortical hierarchy, minimizing the dampening of signal propagation over distance [82,83,99]. Additionally, the pulvinar might be involved in cortical feedback processes, potentially facilitated by its hypothetical bistable activation or global inhibition associated with the thalamic reticular nucleus [91]. The cortico-pulvino-cortical feedback action may serve the purpose of resetting cortical feedback transmission, thereby promoting the initiation of subsequent cortical ignitions. In essence, the thalamus can be viewed as a ‘controller’ of information flow in the brain, regulating the exchange of information among cortical regions to facilitate the establishment of a global workspace.

Is the pulvinar a key player in triggering cortical ignition? There is physiological evidence supporting this notion, particularly in terms of threshold initiation, as electrical microstimulation of the thalamus has shown that the pulvinar can evoke synchronized activity across multiple cortical areas [63,100]. Furthermore, anatomical investigations have revealed the pulvinar’s extensive projections to various visual regions as well as multisensory, associative, and executive cortices, indicating its potential to synchronize and initiate cortical activity simultaneously [101,102]. Notably, the burst-like discharges observed in the pulvinar further suggest that such activity enhances the likelihood of activating cortical neurons, allowing them to detect changes in the environment [103].

While the exact ‘message’ conveyed by the pulvinar to the cortex remains debated, studies in cats and monkeys suggest the pulvinar acts as an information router, transmitting topographical signals to ensure coordinated processing of similar information across distant areas [65]. However, recent findings in mice propose that the information transmitted through the cortico-cortical and transthalamic pathways may exhibit differences [104], indicating that the pulvinar might also play a role in information processing. Nevertheless, it is likely that the transthalamic

pathway via the pulvinar contributes to the activation of cortico-cortical connections in the visual cortex, potentially encompassing attentional signals necessary for cortical ignition.

In this theoretical framework, the GNW of the brain is responsible for integrating and disseminating sensory information throughout the cortex. Here, the attentional system acts as a crucial filter that amplifies the most relevant information for conscious experience. Notably, signals from the prefrontal cortex, relayed by nuclei like the pulvinar, play a key role in this attentional filtering [88]. Recent findings underscore that pulvinar's ventral and dorsal regions in humans functionally complement the cortex, activating cortical zones responsible for object visual perception (processed in visual areas) and attention-guided vision (processed in frontal, parietal, and cingulate cortices), respectively [5,25,105]. Thus, given its direct communication with the prefrontal cortex and the SC, both pivotal in attention processes, the pulvinar significantly influences where subjects' attention is directed [11,16,79]. By selectively enhancing and amplifying sensory information, the thalamus may assume an essential role in shaping conscious perception and contributing to the overall global workspace. This role becomes particularly crucial when attention-directing signals from the pulvino-cortical coupling are weak or absent. In such cases, a subliminal stimulus quickly diminished across cortical stages [83], essentially 'turning off' the ignition [97]. In a nutshell, the pulvinar acts as a gatekeeper for thalamocortical coupling, allowing only the most relevant information to enter conscious experience.

The GWT suggests that conscious perception employs fleeting memory to handle limited capacity data, like working memory mechanisms. This involves sustained neural firing rates, even without external stimuli. This activity is observed in primates during figure-ground segregation tasks [106]. While pulvinar neurons' persistent activity remains unknown, two experimental studies found evoked sustained responses in the cat's pulvinar neurons by a visual flash, lasting up to 1 min post-stimulus presentation [107,108]. Recent theories predict sustained pulvinar responses [84], but it is unclear if their activity originates from reciprocal interactions with the cortex or recurrent pulvinar neuron processes. Regardless of the sources, persistent pulvinar responses may drive sustained activity in visual cortical neurons.

Expanding on prior research, we propose an enhanced ignition mechanism involving the pulvinar (Figure 2B). Initially, V1 forwards activity to the pulvinar and adjacent visual areas (Figure 2B₁,2B₂). Once the pulvinar exceeds its threshold (Figure 2B₃), it activates other cortices through transthalamic pathways. If pulvinar activation coincides with cortical feedforward input, cortical activity rapidly expands, enhancing neuronal activity (Figure 2B₄). When multiple higher-order areas target the pulvinar, its activity patterns undergo alterations, leading the pulvinar to disengage from contributing to the ignition (Figure 2B₅). This shift reduces the triggered ignition, allowing for the initiation of a new cycle of GNW (Figure 2B₆). This cyclic ignition and dampening process dynamically regulates higher-order processes.

GNW, predictive coding, and the pulvinar

Another potential explanation for the involvement of the pulvinar in cortical processing is provided by the predictive coding framework, as detailed in Box 2. In many of the initial formulations of predictive coding, similar to the GNW, only cortico-cortical connections were considered in the context of transmitting predictions and prediction errors through feedforward and feedback cortical pathways [109]. Interestingly, early on, a similar theory was suggested where the pulvinar, with its unique thalamic nucleus characteristics, adjusts cortical processes based on a global context of the external world [110]. These frameworks have since evolved to incorporate subcortical structures into their conceptualization of brain function, acknowledging the importance of neuromodulatory mechanisms and transthalamic pathways in neural processing (Figure 3).

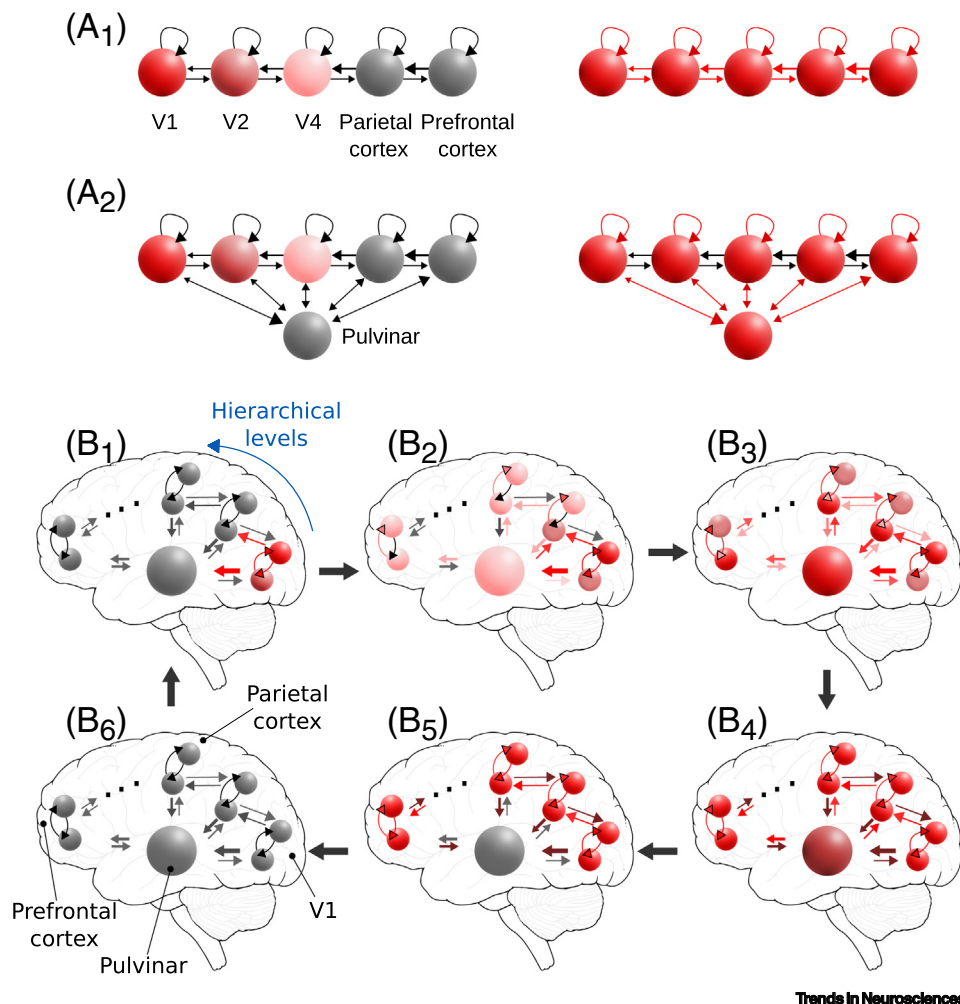


Figure 2. Processing in the global neuronal workspace. (A₁) Upon reaching the primary visual cortex (V1), a visual signal may surpass a neural threshold, enabling activity to propagate across the cortex in a feedforward manner. Without strong stimulation, this signal decays exponentially (left). As cortical areas reach the threshold, activity spreads across the cortex (right), reverberating through intra- and inter-area interactions and returning to lower-level regions. (A₂) Hypothetical contribution of the pulvinar in ignition evolution. As the signal arrives at the pulvinar via V1, activity rapidly expands through cortical areas, amplifying cortical activity if it coincides with feedforward input. (B) Hypothetical global neuronal workspace (GNW) cycle with the pulvinar: (B₁) V1 sends activity to the pulvinar and nearby visual areas. (B₂) The pulvinar activates other cortices via transthalamic cortical pathways, boosting activity (B₃). If targeted by multiple higher areas, pulvinar activity patterns change (B₄), causing the pulvinar to stop contributing to ignition (B₅), dampening the evoked ignition and allowing a new cycle to start (B₆).

This historical perspective aligns with newer theories that incorporate the pulvinar in predictive coding, emphasizing the pulvinar's distinctive role [111]. Beyond processing predictions and prediction errors, the pulvinar may compute the inverse variance (i.e., the precision of signals), thereby adjusting the balance between reliance on prior predictions and integration of new prediction errors [112]. This 'precision-weighting' mechanism may play a pivotal role in perception and cognition, offering a differentiated contribution to cortical processing distinct from prediction handling [113]. According to some conceptualizations, disrupting this mechanism may contribute to psychosis, such as seen in schizophrenia [112,114] (see also Box 3 for further details).

Box 2. Predictive coding and the pulvinar

Predictive coding is a theory conceptualizing the brain as an organ of inference. According to this framework, the brain builds a model of its environment to craft plausible explanations of the sensory input impinging on it and makes constant predictions about possible future states of the world [128]. The internal model is continuously updated based on prediction errors, that is, mismatches between predictions and actual observed events. Neuroanatomically, this computational principle relies on feedback connectivity carrying (top-down) predictions about the environment, which are matched to feedforward sensory inputs to convey (bottom-up) prediction errors. To regulate the transfer of information between the feedback and feedforward pathways, the brain needs to select which of its representations (predictions), or its new sensory inputs (prediction errors) are best suited to steer behavior accurately. According to Bayesian inference, one of the many computations predictive coding can support [129], the brain weighs this information based on its precision. While prediction errors comfortably match the canonical connectivity of the cortex [128–130], the implementation of precision weighting is still up for debate. Functionally, precision weighting can be described as a gain control mechanism regulating the confidence in either prediction or prediction errors [111,131]. Gain control (modulator) connectivity is a prominent feature of higher-order cortico-thalamic synapses that have been thought to allow cortical areas to encode new salient and relevant features of the environment [132]. The pulvinar's engagement in attentional regulation and its output connectivity to superficial cortical layers is an ideal match for a role in precision modulation of the visual hierarchy, which also fits the long timescales of mesoscale integration associated with precision weighting (see Figure 3 in main text) [111,131]. As described in the main text, the properties of the pulvinar support its role as a modulator of prediction errors throughout the visual hierarchy, thereby ascribing precision to the cortical message passing.

Predictive coding relies on recurrent mechanisms, suggesting the brain's capacity for self-regulating activity within its neural network, as incorporated, for instance, in the GNW. In this context, higher-order thalamic nuclei can be seen as integral components of cortico-cortical loops, rapidly integrating information across different hierarchical levels to amplify bottom-up signals in the presence of low-variance input and vice versa. Notably, this process is not limited to the visual hierarchy alone. Both functional and anatomical evidence suggest that inputs from the prefrontal cortex can directly target V1 neurons through pulvinar axons, forming a macroscale recurrent circuit capable of accessing any cortical area [115]. The anterior cingulate cortex, for example, in mice: a prefrontal region linked to behavioral error and visual orientation actions [116,117]. Whether viewed from the perspective of the GNW or predictive coding framework, incorporating the pulvinar into cortico-cortical theories addresses crucial computational challenges, including hierarchical processing, recurrent propagation, and efficient communication within a distributed network of cortical areas.

Concluding remarks and future perspectives

This review synthesizes the pivotal role of the pulvinar in transthalamic cortico-cortical pathways, emphasizing its influence on visual and cognitive brain functions. It challenges traditional cortico-centric perspectives by highlighting the pulvinar's integration with cortical processes, such as inter-areal neural communication and attentional processing. The anatomical and functional findings of the pulvinar described here align with two key theories in neuroscience: the GNW theory and predictive coding. These findings suggest the pulvinar's vital role in cortical activation stages and fine-tuning neural networks.

The review also underscores unresolved questions. Firstly, the anatomical organization of pathways involving the pulvinar requires further characterization for a comprehensive understanding of physiological roles. Advances in optogenetics and connectomes offer promising avenues for exploring transthalamic connectivity. Future exploration involves understanding how the pulvinar nucleus aids in integrating and segregating cortical networks during complex cognitive functions. This avenue of research is not solely about mapping connections but also about decoding the orchestration of pulvinar and cortical networks in real time as subjects participate in ongoing cognitive tasks. Additionally, a critical area of research involves determining the contribution of the pulvinar to the overall efficiency of brain information processing. Examining the pulvinar's structural similarities with artificial neural networks presents a fascinating

Outstanding questions

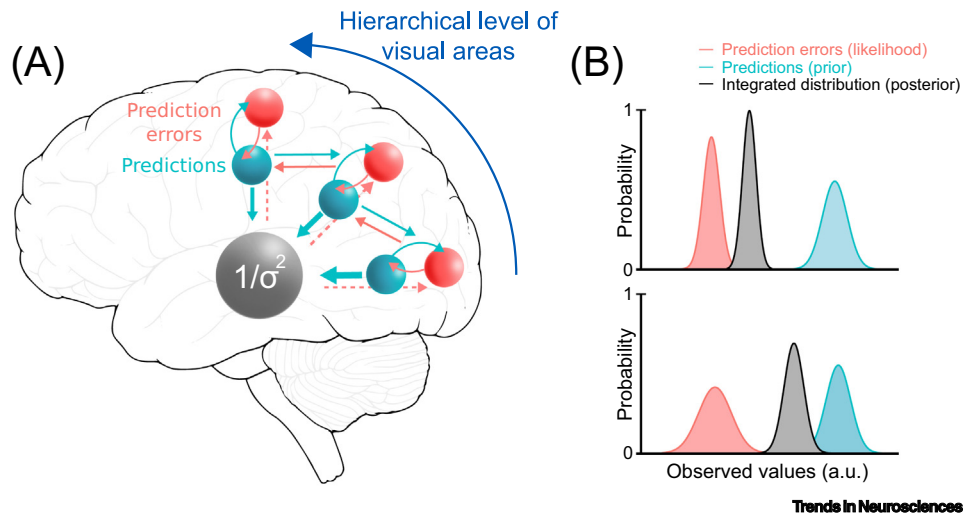
What role does the pulvinar nucleus play in the integration and segregation of cortical networks observed during the performance of increasingly complex cognitive perceptual tasks? How does the pulvinar's involvement contribute to the overall efficiency of information processing in the brain?

Are the well-described organizational principles of cortico-cortical neural architecture preserved and maintained in transthalamic pathways, specifically concerning the role of the pulvinar nucleus in integrating and segregating information between cortical regions during the execution of complex cognitive perceptual tasks?

Do individuals with schizophrenia exhibit fewer 'ignition events' (i.e., widespread brain activity triggers) than those without schizophrenia? Do ignition events in patients with pulvinar lesions differ from those of healthy individuals? If so, do patients with pulvinar lesions consistently display ignition events, or do these events show changes in frequency or characteristics?

What mechanisms does the pulvinar employ to adjust cortico-cortical connections when there is a mismatch between the predicted visual stimuli and the actual visual experiences of an individual? How does this adjustment process influence perception, and what are the implications when these mechanisms malfunction, particularly in relation to visual disturbances observed in disorders like schizophrenia?

Do transthalamic connections in biological neural networks share similarities with 'skip connections' observed in deep artificial neural networks? Skip connections feed the output of a certain layer to other non-adjacent layers within a network, bypassing intermediate layers. Skip connections are used to reduce signal dampening in deep neural networks and improve efficiency when the complexity of a hierarchical network increases. By using skip connections to model the pulvinar, could researchers gain insights into how this region functions and how it interacts with other regions of the brain? Moreover, given the pulvinar's complex role, is it feasible for it to act both as a central hub with



multiple redundant cortico-thalamic-cortical loops and as a skip connection system?

Figure 3. Predictive coding along the visual hierarchy. (A) Schematic illustration of the visual hierarchy under the predictive coding principle, in which locally distributed feedback predictions (depicted in blue) are matched against visual input to produce prediction errors (depicted in red), updating the internal model of the brain. This model is a generative one, allowing the brain to perform inference on the causes of the sensory inputs, by mapping external causes in the environment to generate internal resultant sensory experiences. Putatively, predictions are sent from the cortex to the pulvinar, where the inverse squared variance (i.e., the precision) of cortical signals can serve to modulate the propagation of messages based on their reliability, allowing information irrelevant to the brain's models to be disregarded. (B) Integration of prediction error and prediction into a posterior distribution, for high and low precision input (top and bottom row, respectively), under the approximation of Gaussian distribution of signals. This integration rule, postulated by Bayes' theorem (Box 2), drives the integrated posterior distribution towards (or away) the lower levels of the visual hierarchy, depending on the inverse variance of sensory inputs.

research avenue. Such studies may inform the design of more advanced, sophisticated, and efficient artificial intelligence algorithms inspired by transthalamic anatomical and functional mechanisms. Finally, specific involvement in disorders like schizophrenia, especially concerning 'ignition events' (those critical episodes of neural activation or synchronization), promises to yield valuable insights about the role of the pulvinar in such disorders and possibly target therapeutic interventions (see [Outstanding questions](#)). Addressing these questions will help decipher the role of the pulvinar in the complexity of brain functions and may offer promising insights that will deepen current understanding of cognitive processes, neural networks' functioning, and brain information processing.

Box 3. Does pulvinar malfunction contribute to mental disorders like schizophrenia?

Among the various neuropsychiatric disorders suspected to involve pulvinar malfunction, schizophrenia stands out as one of the most extensively studied and well-documented conditions [8,133,134]. Schizophrenia is characterized by disturbances in perceptual processing (e.g., visual hallucinations) and cognitive functions (e.g., impaired working memory, reduced processing speed), some of which align closely with the key processes in which the pulvinar normally participates. In a study analyzing postmortem thalamus samples from schizophrenia patients using unbiased stereological methods, structural changes such as reduced volume and cell numbers were consistently reported, particularly in the pulvinar's medial subdivision [135]. Additionally, functional connectivity studies using neuroimaging techniques in people with schizophrenia have revealed reduced connectivity between the PM and the frontal cortex [114,134]. Similar findings have been observed in early psychosis subjects and persist in individuals with chronic schizophrenia. These structural changes have been associated with impaired emotional processing [136] deficits in selective attention [137,138], abnormal motion processing [139], and impaired face recognition [140], functions known to involve the pulvinar. While these observations strongly suggest a link between pulvinar dysfunction and schizophrenia, it is important to note that schizophrenia is a complex disorder with multifactorial origins. The precise mechanisms by which pulvinar dysfunction contributes to the development and progression of schizophrenia remain a subject of ongoing research. Further investigations are needed to unravel the intricate interplay between pulvinar abnormalities and the complex pathophysiology of schizophrenia.

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Declaration of interests

The authors declare no competing interests in relation to this work.

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