Trends in Neurosciences

Feature Review

Long-Range Attention Networks: Circuit Motifs Underlying Endogenously Controlled Stimulus Selection

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Attention networks comprise brain areas whose coordinated activity implements stimulus selection. This selection is reflected in spatially referenced priority maps across frontal-parietal-collicular areas and is controlled through interactions with circuits representing behavioral goals, including prefrontal, cingulate, and striatal circuits, among others. We review how these goal-providing structures control stimulus selection through long-range dynamic projection motifs. These motifs (i) combine feature-tuned subnetworks to a distributed priority map, (ii) establish endogenously controlled, long-range coherent activity at 4–10 Hz theta and 12–30 Hz beta-band frequencies, and (iii) are composed of unique cell types implementing long-range networks through disynaptic disinhibition, dendritic gating, and feedforward inhibitory gain control. This evidence reveals common circuit motifs used to coordinate attentionally selected information across multi-node brain networks during goal-directed behavior.

Trends

Attentional selection is distributed across a fronto-parieto-collicular priority map.

Attentional control originates in multiple distributed prefrontal-subcortical goal systems.

Coordination of attention networks proceeds through large-scale phase synchronization.

Cell-specific circuit motifs route attention information at beta and theta bands.

Subprocesses Controlling and Implementing Stimulus Selection

Top-down or **endogenously controlled attention** (see Glossary) [1] does not exist as any entity, but instead describes the set of influences that biases sensory processing towards achieving a goal [2]. The main endogenous influences underlying what we attend entail (i) basic task rules that deterministically suggest which sensory events are relevant and which are distractors, (ii) value expectations that suggests probabilistically which stimuli are most relevant for achieving a goal state, and (iii) motivational states that describe which stimuli will serve best to satisfy a specific need or desire. Accordingly, neuronal representation of rules, expectations, and motivational states are the three main endogenous sources that control which external stimuli will be selected for prioritized processing.

For understanding endogenous attentional control of stimulus selection it is therefore necessary to understand how brain circuits encoding rules, values, and motivational states affect and coordinate selective processing in sensory circuits. We survey recently gathered evidence in rodents and primates about this question, following a heuristic framework with six separable attention processes that separate into subprocesses controlling attention versus others that implement attention as outlined in Box 1.

This heuristic suggests that attentional stimulus selection is implemented in a **priority map** that is widely distributed across many areas of a fronto-parietal-collicular network that activates whenever attention is deployed in the macaque (Figure 1A) and human brain (Figure 1B) [3–5]. We propose that endogenously controlled stimulus selection in this network is implemented

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http://dx.doi.org/10.1016/j.tins.2015.08.009

Box 1. Mapping Brain Regions onto Subcomponent Processes of Attention.

Endogenously controlled attention can be divided into processes that temporally precede (i.e., control or guide) and those that reflect (i.e., implement) stimulus selection at the neuronal level. Both processes are essential for the successful selection of relevant sensory information.

When mapping attentional subcomponent processes onto brain regions, it is important to acknowledge the limited knowledge we have about how long-range connectivity implements attentional stimulus selection. In this situation we propose a heuristic framework of endogenously controlled attention that encompasses six separable subcomponents and allows for causal influences between all brain structures implementing these attentional functions. In this framework the main determinant of what is attended is a goal representation [125] (Figure IA). Goals are translated into 'task rules' or 'attentional sets' through which they affect attention networks. A second determinant of attention are value expectations that guide attention even in the absence of an explicit goal or in novel contexts (Figure IB). The third factor curtailing and guiding attentional stimulus selection are motivational states – mapped most tightly onto activation in subcortical brain areas (Figure IC). In addition to these three causal factors for endogenous attention, successful stimulus selection is reflected in enhanced stimulus representation in a distributed priority map across a fronto-parieto-collicular network [3,8] (Figure ID). This spatially referenced priority map flexibly links to relevant sensory representations by combining (physical) saliency information with endogenous attention biases. Priority maps are likely instantiated through a flexible linkage with feature-tuned neurons with spatial receptive fields in sensory cortices (Figure IE; Figure 2, in main text). Feature-tuned neurons are considered to be 'adaptive processors' [6] because they adjust their tuning to external input according to expectations and task contexts [126]. Neural circuits in the pulvinar support the sixth attentional subcomponent process to integrate and relay widespread signaling of attention information (Figure IF). Please note that few studies have investigated the influence of value predictions and motivational states (Figure IB,C) in terms of the attentional control of sensory stimulus selection (e.g., [1,53,127]). Both aspects are more frequently studied with respect to their influence on decision making and reinforcement learning problems [128–131]. In both of these contexts, value predictions and motivational states (including the utility of stimuli) are appreciated as major drivers of stimulus selection.

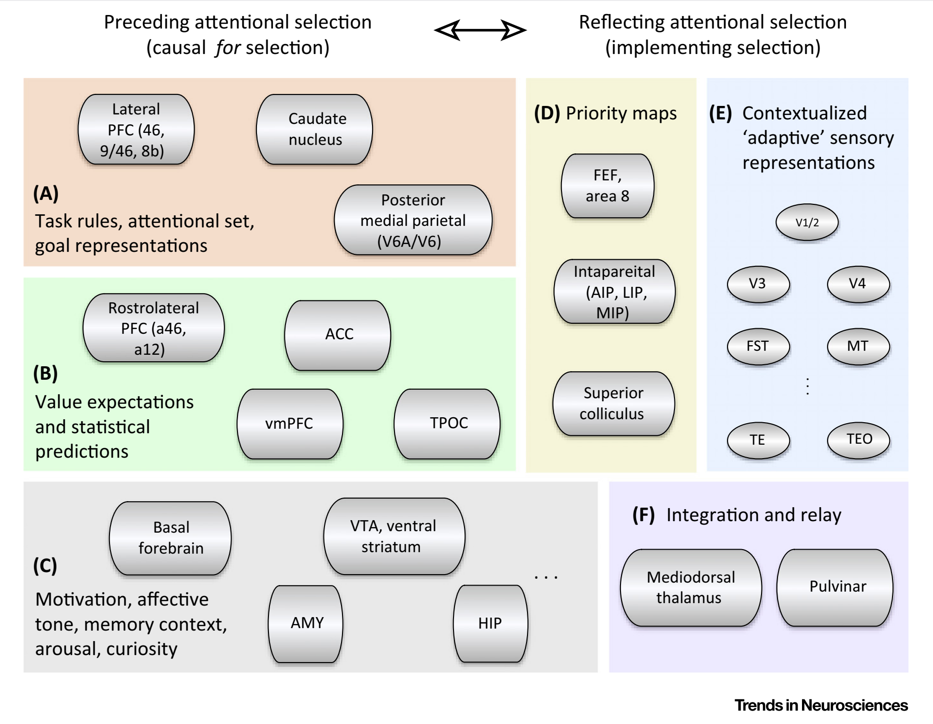

Figure I. Heuristic Framework of the Neuronal Control of Endogenous Attention. Six separate subcomponent processes of attention (colored boxes) map onto separable (but not independent) larger brain systems (gray outlines).

through the formation of feature-tuned subnetworks that flexibly coordinate frontal, parietal, and collicular neuronal responses with context-sensitive, feature-tuned neurons in multiple sensory cortices (Figure 2) [6]. Neurons in this distributed priority map encode stimulus information that combine bottom-up sensory information with endogenous goal information.

Glossary

Dynamic circuit motif: conceptual framework that understands neuronal activation signatures (e.g., enhanced firing rates, or a period of enhanced gamma-frequency synchronization) as a state-specific activation of a uniquely defined neural circuit (cells, their interconnectivity, and synaptic activation time constants) to implement a generic computational function, such as the gating of synaptic inputs to enhance relevant and suppress irrelevant inputs.

Endogenous control of attention: control of stimulus selection that originates from internally generated biases. Endogenous control substitutes for the often-used term 'top-down control' to highlight (i) that there are multiple internal processes biasing attention (instead of only one coming from an underspecified and simplified 'top'), (ii) that in recurrent brain networks no single discernible 'top' is evident or anatomically plausible, and (iii) to prevent important endogenous influences being ignored that are classically not considered to be 'top-down' influences, but which apparently influence and control stimulus selection, for example influences from the value expectations, the history of recently received rewards, the history of previously performed selections, the eye fixation history, and others.

Priority map: describes the distribution of activity across multiple neurons tuned to various stimulus locations, stimulus feature dimensions (color, motion directions, shape, etc.), and stimulus values. 'Priority', or 'attentional weight', is evident in the peaks of the activity distribution. Priority maps reflect by definition the integration of internal attentional relevance and external (physical) saliency.

Stimulus-specific subnetwork: a subnetwork describes a subset of neurons whose activity is temporally coordinated. Subnetworks are stimulus-specific if there is a unique composition of cells that coordinate their firing when a specific stimulus is processed or attended. A stimulus-specific subnetwork may entail all those neurons tuned to different sensory features, values, or locations that are among the neurons constituting the peaked regions of the attentional priority map. We argue that stimulus-specific subnetworks are rapidly established through the activation of dynamic circuit motifs that integrate diverse endogenous goal information with bottom-up sensory information.

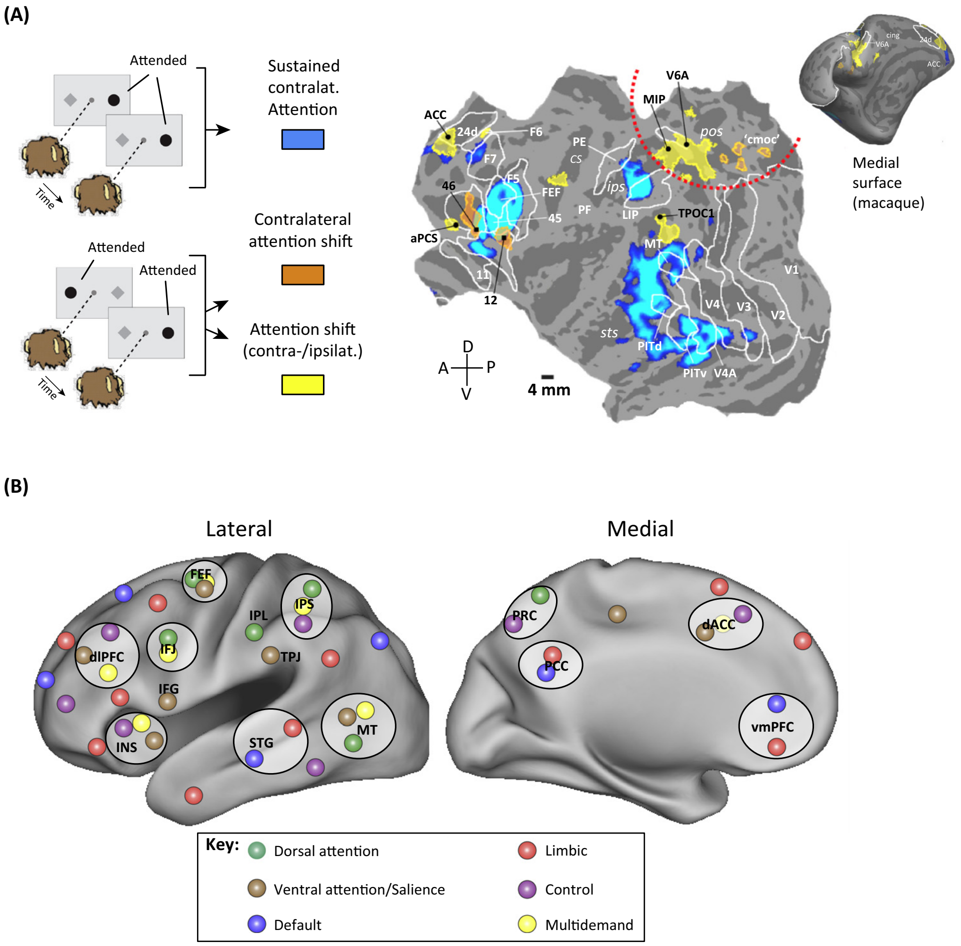

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Figure 1. Attention Networks in the Macaque and in the Human Brain. (A) Reliable, widespread fMRI activation indexes shifting and sustaining spatial attention across macaque cortical fields (here: left hemisphere). The attention task included a ‘stay condition’ with covert stimulus selection on the same spatial position between trials (upper left) and a ‘shift condition’ with different spatial target locations between trials (bottom left). The flat map contains blue regions that showed enhanced activation during sustained contralateral attention, signifying spatial prioritization. Yellow regions were activated for attention shifts stronger than for sustained attention. The shift activity was independent of the direction of attention (without spatial main effect). Orange regions show directionally-specific attention shift effects that are stronger than sustaining attention at a location. The red broken line outlines the border towards the medial parietal occipital cortex. Abbreviations: ACC, anterior cingulate cortex; aPCS, anterior principal sulcus; cmoc, caudomedial occipital cortex; MIP, medial intraparietal; TPOC, temporal parietal occipital cortex. Adapted from [5]. (B) Diversity of network nodes in the human brain underlying attention and cognitive control. The colored dots show hot-spot coordinates for individual networks according to [132]. During cognitively-demanding tasks the control network exhibits increased activation whereas the default-mode networks shows reduced activation [133]. The control network overlaps with the multi-demand network which has been proposed to organize relevant facts, rules, and requirements into a ‘task model’ that then drives activity in large parts of the brain to perform the required task [134]. Two networks have been implicated in different aspects of attentional control. The dorsal attention network, which overlaps with regions involved in saccadic eye movements, has been proposed to endogenously control the allocation of attention to contralateral space. The ventral attention or salience network, localized predominately in the right hemisphere, is thought to be necessary for target detection and reorienting to novel or behaviorally-relevant stimuli [135,136]. A limbic network is involved in affective or emotional processing [137]. Abbreviations: dlPFC, dorsolateral prefrontal cortex; FEF, frontal eye field; IFG, inferior frontal gyrus, IFJ, inferior frontal junction, INS, insular cortex, IPL, interior parietal lobe; IPS, intraparietal sulcus; MT, middle temporal area; TPJ, temporal parietal junction.

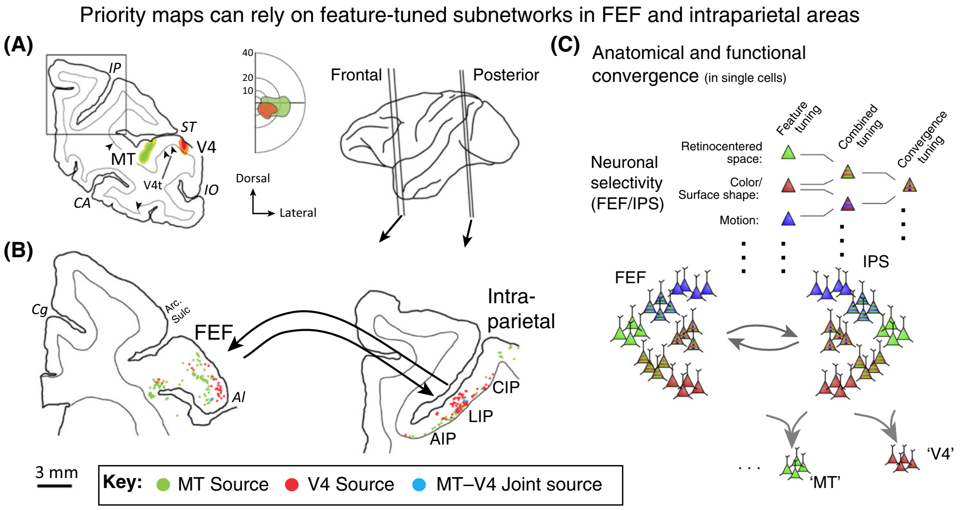

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Figure 2. Anatomical Segregation of Feature-Tuned Inputs from Areas MT and V4 to the Frontal Eye Field (FEF) and Intraparietal Cortex (IP) Suggests that Frontal-Parietal-Collicular Priority Maps Can Become Dynamically Tuned to Attended Stimulus Features by Integrating Input from Feature-Selective Visual Areas. (A) Injection sites for retrograde label in MT (green) and V4 (red) and the respective eccentricities of receptive fields. The right panel shows the macaque brain surface with vertical lines marking the section that is selected for the coronal frontal and parietal-occipital slices shown in B. (B) Coronal sections showing FEF (left) and intraparietal cortex (right) with dots showing neurons retrogradely labeled from MT (green), from V4 (red), or from both areas (blue). (C) Frontoparietal areas are convergence zones for space- and feature-selective long-range input such as the MT and V4 inputs shown in A. The long-range anatomical connectivity pattern suggests that unique sets of cells in FEF and IP are tuned to simple features (and connect flexibly to MT, V4, etc.), while other cells show tuning to combinations of simple features depending on attentional relevance, and yet another subset of cells ultimately becomes tuned towards behavioral relevant feature-location conjunctions (termed 'convergence tuning' in the figure). According to this schema, attentional priority maps are based on flexibly forming subnetworks of neurons tuned towards task-relevant feature across visual processing areas. Note that in the anatomical tracer studies, less than 3% of FEF projection cells sent axon branches to both V4 and MT, suggesting that subnetwork formation likely requires an active binding mechanism within the FEF–IP network. Panels (A,B) adapted from [138].

However, even during the basic shifting of spatial attention to one of two visual stimuli, feature-tuned subnetworks of frontal and parietal cortex intersect with additional cell populations in prefrontal and subcortical structures. These brain circuits are devoted to encoding rules (especially in lateral prefrontal cortex, caudate nucleus), value expectations (especially ventromedial frontal cortex, anterior cingulate cortex, ventral striatum), and motivational/affective states (especially amygdala, basal forebrain) (Box 1) [5,7]. Based on this evidence we will survey in the following recent insights about (i) how a distributed priority map is formed across a frontal-parietal-collicular network, (ii) how stimulus priority is controlled in prefrontal, anterior cingulate and subcortical areas, and (iii) how diverse circuit motifs implement the endogenously controlled gating of sensory information.

Implementing Stimulus Selection in Coordinated Fronto-Parietal-Collicular Priority Maps

Monkey physiology as well as human MEG (magnetencephalography) and fMRI have documented that frontal cortex (frontal eye field, FEF; supplementary eye field, SEF) and intraparietal cortex [LIP (lateral), AIP (anterior), CIP (caudal), MIP (medial)] enhance stimulus and object attributes when attention is deployed based on feature cues ('search for red'), spatial cues ('search there'), object cues ('search for Waldo'), and possibly category-specific cues [5,8–11]. Attention in these studies describes the covert selection of relevant over irrelevant stimuli defined by unique feature combination and located at unique spatial coordinates [12]. Because most visual stimulus selection proceeds with some spatial reference, and overlaps with oculomotor orienting, the attentional enhancement in the fronto-parietal-collicular network is considered a spatial reorienting network [3]. One cortical core area is the FEF, whose anatomical connectivity profile is to a large extent conserved between human and non-human primate brains [13,14] (Figure 3). A second cortical core is the intraparietal sulcus (Figure 2), containing neurons that become selective to combinations of stimulus features (e.g., specific color–motion combinations) when they are task-relevant, in other words when they are attentionally selected for prioritized processing [4,15]. This feature tuning in intraparietal cortex is highly flexible, with individual neurons shifting their preferred combination of visual features (e.g., upward motion and red color) towards those feature combinations that are task-relevant [4].

At the subcortical level, this network encompasses the superior colliculus (SC), an evolutionary old multilayered structure on the roof of the midbrain. The SC, or its homolog the optic tectum in non-mammalian vertebrates, plays a major role in orienting responses. In primates, the SC is best known for its role in saccadic eye movements [16], but it is also pivotally involved in endogenously controlled, covert stimulus selection [17–19]. In particular, the integrity of the SC to spatially prioritize visual stimuli is likely a necessary condition for attention to affect behaviors. This conclusion is suggested by a recent finding that intact spatial attention modulation of neural responses in cortical areas MT and MST (middle temporal and medial superior temporal) is not sufficient for successful spatial detection performance because spatial cueing benefits disappear when the intermediate and deep layers of the SC are inactivated even when visual cortex neurons remain attentionally modulated [20]. Notably, this study documented in separate experiments that selective attentional modulation of visual cortex neurons translates into behavioral benefits in spatial-cueing paradigms, but that this behavioral effect is camouflaged when the SC is inactivated [20]. These findings reveal that stimulus selection in cortical networks, here evident in selective attentional modulation of feature-tuned neurons in MT/MST, does not

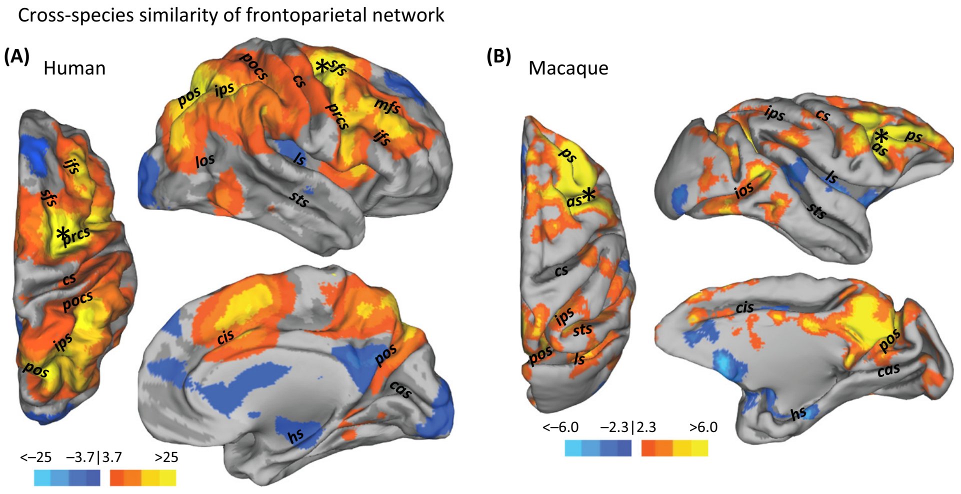

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Figure 3. Functional Connectivity of Frontal Eye Field (FEF) Seeds in the Right Hemisphere in Humans (A) and Macaque Monkeys (B). (A) dorsal (left), lateral (top), and medial (bottom) views of the right FEF functional connectivity in humans ($n = 12$). Thresholded z-score maps normalized to the space of the PALS-B12 template [139] are overlaid. Asterisks indicate the location of the FEF seeds. (B) The same as in (A) but for FEF in monkeys ($n = 6$) in the space of the F99 template [140]. Abbreviations: as, arcuate sulcus; cas, calcarine sulcus; cis, cingulate sulcus; cs, central sulcus; hs, hippocampal sulcus; ifs, inferior frontal sulcus; ios, inferior occipital sulcus; ls, lateral sulcus; lus, lunate sulcus; mfs, middle frontal sulcus; pocs, posterior central sulcus; pos, parieto-occipital sulcus; prcs, precentral sulcus; ps, principal sulcus; sfs, superior frontal sulcus; sts, superior temporal. Adapted from [13].

imply that the selective stimulus representations affect behavioral output areas, but that additional processing stages decide how priority map information is used for overt behavioral guidance (see [21]). In other words, cortical mechanisms underlying stimulus selection, including priority map formation in frontal and parietal cortex, may act as a conditional controller of stimulus selection that itself is under continuous influences from other behavioral circuits estimating so-called state-spaces in light of learned instructions and contextual cues [21,22].

Assuming that priority map formation reflects an indirect control about which stimulus is selected, it is important to understand whether prefrontal area 8 (including FEF), parietal cortex, and the SC establish priority independently from each other and in the absence of apparent cortico-cortical and corticotectal interactions [23], or whether a distributed priority map is

Box 2. Cell-Specific and Task-Selective Long-Range Subnetworks Underlying Goal-Directed Behavior and Attention

In 1981 Mesulam suggested that attention functions are genuine network functions [45]. He conceptualized attention functions as being realized by separable ensembles of neurons distributed across a unique set of brain areas, in other words by function specific subnetworks. Figure IA (adapted from [45]) highlights centrist or holistic perspectives that are implausible. Accordingly, only a rigorous network approach is capable of elucidating how functional subnetworks of cells across brain areas coordinate during attention (Figure IB). More than three decades later, these subnetworks of higher cognitive functions are being delineated in ‘functional tracing’ studies combined high-density recording, optogenetic manipulation, electrical stimulation, and advanced behavioral testing approaches.

One particularly comprehensive example is a recent identification of subnetwork specific long-range connections of cells in rodent ventral hippocampus (anterior hippocampus in primates) [141]. This study identified hippocampal projection cells by antidromically activating them either from prefrontal cortex (rodent infralimbic cortex), ventral striatum, or amygdala [141] (Figure IIA). Before delineating anatomical connectivity, the neurons were functionally characterized in a spatial navigation task, an arousal/anxiety-triggering maze environment, and a reward-guided rule selection task. This setting allowed the identification of distinct subnetworks of projection cells with unique functional fingerprints (Figure IIB). One subnetwork of overall task-responsive neurons was the most broadly projecting subnetwork, effectively connecting PFC, vStr, and amygdala in all tasks. Other subnetworks were task- and target-specific: one set of cells signaled reward-expectancy and connected hippocampus with mPFC and vStriatum, but not amygdala. Another set of cells activated during anxious states projected to the amygdala but not to the prefrontal cortex or striatum, while yet another subset of cells showed selective inhibition during reward expectancy and projected exclusively to the ventral striatum (Figure IIB).

These intriguing results provide a window into the selective routing of task-relevant information through segregated subnetworks. They provide direct evidence (i) that different functions activate neurons in the same brain area (‘local multiplexing of functions’), (ii) that each function is realized by unique sets of neurons in that brain area (‘forming segregated local subnetworks’), and (iii) that long-range connection patterns are function-specific and task-selective (signifying ‘unique typologies of long-range functional networks’).

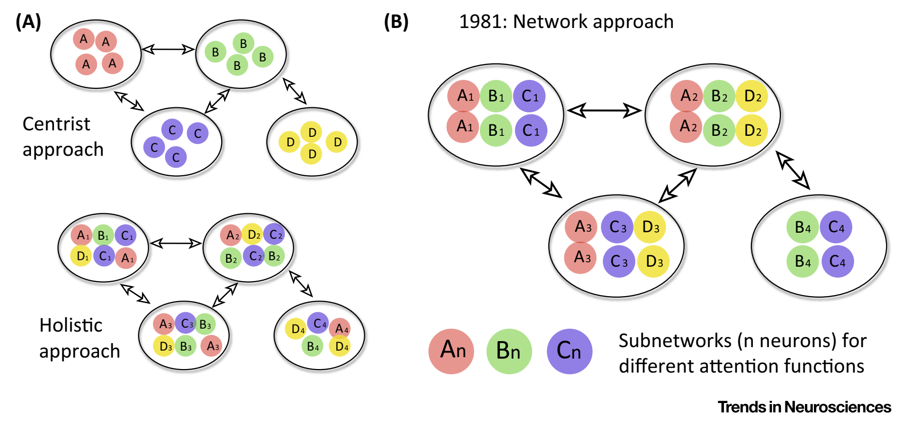
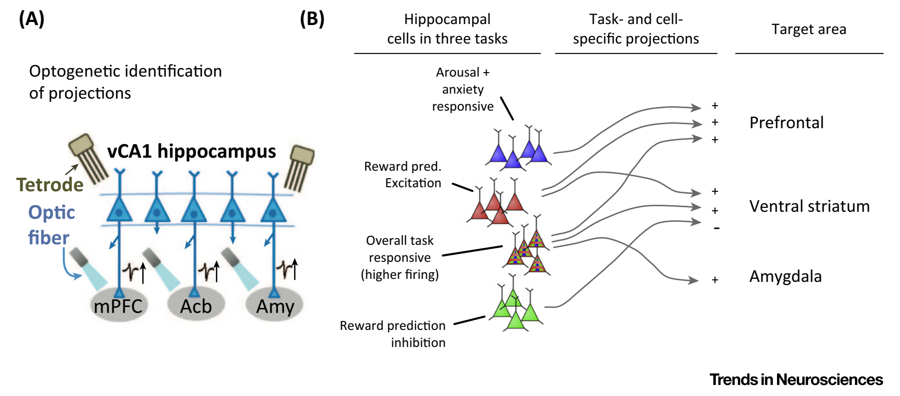


Figure I. Approaches with Different Assumptions About the Neuronal Organization of Attention Functions. (A) Visualization of two improbable organizational schemas. (B) Sketch of a highly probable neuronal schema organizing attention functions. A network approach acknowledges that neurons supporting the same function (illustrated by the same color) will be distributed in distant brain areas (illustrated as eliptic countours). Adapted from [45].



Trends in Neurosciences

Figure II. Task and Neuron-Specific Anatomical Projection Patterns by Hippocampal Neurons.

established across different areas by coordinated activity between areas (Box 2). Recent studies using anatomical tracing and inter-areal recording techniques suggest the latter, showing that endogenously controlled selection of stimulus features is dependent on the strength of fronto-parietal connectivity and proceeds by phase-synchronizing local activities at narrow-band frequencies [24–27].

The importance of direct frontoparietal connectivity for attention is readily documented in anatomical tracing studies revealing that the strength of frontoparietal white-matter fibers is related to the efficiency of attentional selection in visuospatial tasks [28,29].

The functional importance of these cortico-cortical connections for fast, ongoing goal-dependent stimulus selection is becoming apparent in direct beta-frequency specific coordination during attentive processing [30–34]. In one recent study, local field potential (LFP) activity in prefrontal and intraparietal cortex synchronized long-range at a narrow ~12–25 Hz beta-frequency band [31,35]. This 20 Hz synchronization was maintained during the short term delay of the match-to-sample task suggesting that long-range beta synchrony indexes continued stimulus selection [31]. In support of this conclusion, the long-range beta synchronization was not a mere reflection of the activation state, but for a significant fraction of frontoparietal connections it systematically varied when objects of different identities and at different locations were selected. This result showed that beta-band synchronization carried object and location specific information. In addition, the extended anatomical coverage of recording sites during the task allowed the identification of the anatomical specificity of information carrying beta-rhythm interactions between prefrontal and parietal subfields. Of a total of 24 possible area combinations between frontal and parietal cortex, only three area combinations carried information about the selected object or location in correlated beta-band activity. These area combinations included prominently area 8 including FEF in prefrontal cortex and area LIP in the lateral intraparietal cortex [31].

If endogenously controlled (attentional) stimulus selection is established through flexibly formed subnetworks, it is expected that fronto-parietal coordination extends to sensory cortical areas providing the actual feature maps (Figure 1). Consistent with this assumption, beta-rhythm coherence is not only evident for parietal cortex with frontal and prefrontal cortices, but it indexes selective stimulus processing across all major visual processing stages [33]. This far-reaching conclusion was revealed in a recent study using high-density micro-electro-mechanical recording technology spanning visual, parietal and frontal areas in non-human primates engaged in covert attention to peripherally presented stimuli (see also [36]). During attention, subdurally recorded LFPs in parietal area DP (dorsal prelunate) synchronized at a narrow 15–25 Hz beta-band with visual areas V4, V3, V2, and V1. Long-range beta activity carried information about whether attention was prioritizing the contra- or the ipsilaterally presented stimulus. Intriguingly, during beta coherent states the higher-order (parietal) areas statistically explained beta activity at lower visual areas, as inferred from Granger causality analysis about the putative direction of information flow during beta coherent coupling. This prominent Granger causal feedback direction from higher to lower areas was specific to the beta frequency-range, and associates beta coherence with endogenous attentional expectancy across frontoparietal and fronto-temporal-parietal networks [30,34,37]. This beta-band specific association with feedback processes contrasted with a prominent Granger causal feedforward direction of information flow from lower to higher brain areas at low 3–6 Hz theta frequencies and at higher 70–90 Hz gamma-band activities [33].

The previous section suggests that, during endogenously controlled processing states, feedback processes across parieto-occipital cortex can be indexed by beta-rhythm coherence. This finding suggests that, among the many possible cells and circuits that that can give rise to beta-rhythm activity, there exists a neocortical **dynamic circuit motif** that activates when feedback-type connections are activated with attentional expectancy, possibly including deep-layer long-range projection cells that selectively integrate superficial-layer synaptic inputs ([38,39], see also [40] and Box 4).

Notably, the FEF sites that engaged in beta-rhythm interactions with parietal areas during short-term object and location memory [31], and during selective visual attention [30,33], also host LFPs and a neuronal population that shows selectively enhanced gamma-rhythm synchronization with V4 when their spatial receptive fields overlap attended stimuli [41]. This attention specific long-range connectivity was present in a subset of FEF cells that were visually responsive and it was absent in neurons with saccade-related tuning [41]. The prominent FEF–parietal beta-band synchronization suggests that during attentional states in which one stimulus is selected over other stimuli, the FEF hosts one subnetwork of neurons that engage long-range in gamma-phase synchronization with feature-specific area V4 (when selecting color + space combinations), and another subnetwork of cells that engage in selective beta-phase synchronization with parietal cortex (when selecting object shapes + space). An apparent prediction from these findings is that the beta network and the gamma networks emerge at the same time. We predict that this would become evident when all areas are recorded simultaneously in an attention-demanding task. This scenario would reveal the multiplexing of activities at different frequencies [27,33], realized by different dynamic circuit motifs [39], and probably based on partly segregated cells classes supporting activity at different rhythm frequencies [42,43].

The FEF and adjoining premotor cortex constitute the most anterior structures containing neurons with response selectivity to narrow spatial fields. This spatial tuning indicates that fronto-parietal subnetworks are engaged whenever the content of the attentional focus has spatial coordinates in eye-, head-, or body-centered reference frames necessary for continued visual exploration as well as for guiding gaze and body parts towards or away from relevant stimuli in space. In summary, feature-tuned priority maps in fronto-parietal-collicular networks reflect most conspicuously the selection of currently attended stimuli. This prioritization of stimuli can proceed without salient bottom-up changes of inputs that would come in the form of gaze changes (saccades) or abrupt stimulus onsets. As such the emergence of priority maps is endogenously controlled by representations of goals as discussed next.

Control of Long-Range Priority Networks from Lateral and Medial Prefrontal Cortex

The spatially tuned priority maps in FEF, parietal cortex, and SC are under a continuous influence of synaptic activity from brain regions encoding rules, value expectations, and motivational states. This synaptic influence likely exerts control over the spatial prioritization network by imposing selective gain onto the spatial priority map. Control can thereby take strong forms of gating, or it can take weaker forms of modulating and biasing neuronal processing towards relevant sensory features. It is likely that representations of rules, value predictions, and motivational states can exert both weak and strong forms of contextual gating of inputs on frontoparietal priority maps, depending on the precise endogenous goals and the necessary control demands [44].

Neurological and neurophysiological evidence suggested already in the early 1980s that higher-order goal-relevant representations are not exclusively encoded in spatially restricted cortical subfields, but are encoded in segregated subnetworks of neurons distributed across multiple brain circuits [45] (Box 2). An important hypothesis about such distributed encoding schemata is that higher-order and more complex goal-relevant representations are encoded in hierarchically nested subnetworks similar to the hierarchical coding schematas implicated in the control of action sequences [46–48].

Representations of Task Contexts Guide Stimulus Selection Networks

To influence behavior and attentional stimulus selection, goals, value predictions, or motivational states are translated into rules that map their contents onto specific stimulus features and possible responses. Therefore, rule representation, or conditional if–else mappings involving stimulus features of different complexities, appears to be a prerequisite for endogenously informed stimulus selection. In other words, during goal-directed behavior, the selection of one stimulus over other stimuli is often conditional on secondary information (for example on a goal, a cue color, or an object specific reward expectation) [49]. Such conditional allocation of processing resources, also known as flexible attention shifts, depends on lateral prefrontal cortices (PFC), as evident from lesion experiments [7,49–52]. Recent findings document that neurons across multiple subfields in lateral as well as in medial PFC encode attentional shift rules with fast response-onset latencies similar to latencies in the FEF–parietal network [53]. In this study, dorso- and caudolateral PFC (areas 46/9, and 8), rostrolateral PFC (area 46), superior PFC (area 9), medial PFC (area 32), as well as dorsal and ventral anterior cingulate cortex (area 24), hosted neurons with specific firing-rate information about the location and feature of target stimuli. Thus, specific information about attentional targets is represented in the firing of neurons across the entire medial to lateral extent of the PFC. Despite the overall widespread encoding of target information, encoding was more prominent in local clusters of cells, suggesting anatomical hot-spots for attention-relevant information consistent with ‘graded functional specialization’ as the overarching encoding scheme [15]. One of these hot-spots for rule encoding is in the caudolateral PFC areas 8 and 9/46 anterior to the FEF [54,55]. Neurons with rule-selective activity in this region project directly to the SC [56], and deactivation of this region by cooling alters task-selective activity in the SC [57], impairs rule maintenance for saccadic eye movement tasks [57,58], and reduces LFP beta-frequency power in the superior colliculus during task preparation [59].

For these lateral prefrontal circuits the rule-dependent attention signals emerge in response to various types of goal-defining cues including (i) spatial cues [60,61], (ii) feature-cues conveying a color-matching rule irrespective of location [53], or (iii) contextual cues to different features of otherwise identical stimuli [62,63]. These cues trigger control representations that can be decoded from different types of neuronal activity [32,64]. In particular, attentional relevant target information can be decoded from dynamic population patterns of neural firing [60,61,63,65,66] and they can be decoded from selective synchronization of neuronal firing to population-level beta-rhythm (~15–30 Hz) [62] and theta-rhythm (~5–10 Hz) LFP activity [67,68]. For example, in [62], non-human primates were contextually cued to covertly select the color or orientation feature of stimuli to make a two-way choice. LFPs and spike-phase relations to the LFP showed feature-selective beta-band synchronization with rapid onset times. This finding illustrates that synchronization of neuronal firing to population level LFP activity emerges for distinct subsets of cells for different feature rules. The composition of synchronized cells thereby defined the functional subnetwork and indexed the prioritized, goal-relevant information (here: the feature rule) that guided behavior.

This different strength of synchronization to beta-rhythmic LFPs across task contexts reflects task-specific tuning of attention networks. For one subset of neurons in prefrontal and frontal cortex such beta-band synchronization is evident only for one rule and not for alternative rules [62,69]. Another subset of neurons switches from synchronizing during attention to color features in the color-based context, to synchronizing during attention to stimulus orientation in the orientation-based context [62]. This switching of synchronization can be conceived of as a direct correlate of the flexible formation of distinct subnetworks of cells. Such subnetworks are defined by the beta phase at which participating neurons prefer to fire. The surveyed experiment suggests that the decisive factor determining which neurons participate in the rhythmically pulsed subnetwork is the actual task context that will guide attention towards the relevant stimulus features.

Long-Range Phase Synchronization Indexes Attention Networks and Stimulus Selection

The previous section suggests that neuronal synchronization of spike times to the LFP is a main carrier of goal-relevant stimulus information in prefrontal cortex and in the associated fronto-parietal-collicular priority map network. This conclusion is significant because beta-rhythmic LFP activity is a widespread phenomenon within the prefrontal cortex and within the nodes of the fronto-parietal-collicular network discussed above [33,34]. As such, beta activity directly indexes functionally coordinated network activity across multiple distant brain areas, coordinating local processes via long-range connections between lateral prefrontal and the anterior cingulate cortex [32], the caudate nucleus [70], and the hippocampal formation [71] during endogenously controlled attention tasks in the non-human primate.

Such long-range phase synchronization of neural circuits at beta frequencies could be realized by different long-range connectivity and circuit motifs [26,38,39,72] (Box 3). For example, inter-areal beta synchrony could depend on local beta frequency specific circuit motifs that are activated by otherwise asynchronous long-range inputs. Alternatively, inter-areal cortico-cortical synchronization could be an indirect consequence of inhibitory relays in thalamic nuclei, such as the pulvinar, that synchronize their outputs across their divergent cortical target regions. In another scenario, inter-areal synchronization is realized by cortico-cortical spike bursts entraining long-range cortical target areas to oscillatory activity (see below).

Disentangling the precise circuit motifs underlying long-range coordination at the beta- and theta-band frequencies will be central to understanding the actual mechanism by which **stimulus-specific subnetworks** are formed [73]. This formation of subnetworks establishes the distributed priority map that ultimately reflects which stimulus is attentionally selected across multiple cortical brain areas. Conceptually, the understanding of the rapid formation of the priority subnetwork requires appreciation of the relation of (i) the involved cell types and their synaptic interconnectivity, (ii) their dynamic activation signature at the time of stimulus selection, and (iii) their synaptic gating and integration processes that implement the selection and combination of goal-relevant stimulus information [39,73]. These three elements define what can be called a dynamic circuit motif [39], which describes synaptic, cellular, or small circuit structures, and whose activation implements a function (or computation) on synaptic inputs (Box 3). These functions are generic circuit transformations of synaptic inputs to new circuit output, including gain control, gating, and integration processes. Thus, this framework predicts that there is a finite set of dynamic circuit motifs used for endogenously controlled stimulus

Box 3. Circuit Motifs and Synaptic Fingerprints underlying Endogenous Control on Stimulus Selection

The functional impact of long-range connections implementing stimulus selection is realized by various circuit motifs [39,43,98,107]. Four major long-range motifs have been implicated to implement endogenously-controlled stimulus selection. First, a long-range feedforward excitation motif (Figure IAi) describes excitation that is balanced by inhibition only after initial activation. One prominent example includes dendritic gating through feedback-type excitatory inputs [80]. Second, feedforward inhibition (Figure IAii) is a particularly ubiquitous motif imposing temporal structure on activity [39]. Prominent examples are mediodorsal thalamus projections onto fast-spiking interneurons in anterior cingulate cortex [105] and frontal to sensory cortex feedback-type connections that impose a cortical gate on thalamic input [142]. Third, disynaptic disinhibition (Figure IAiii) is associated with specific interneuron types targeted by feedback projections [118,119]. It is directly linked to cingulate cortex modulation of visual cortical circuits where long-range disinhibition indexes improved sensory discrimination [143]. Fourth, long-range, GABAergic direct inhibition (Figure IAiv) is implicated to structure long-range neuronal communication, and could be a key source underlying robust long-range phase synchronization [144,145].

Circuit motifs entail specific synaptic connections in target areas. These synaptic projections form area-specific synaptic fingerprints. An example of a synaptic fingerprint are the projections of anterior cingulate output towards lateral prefrontal brain areas in the macaque that are believed to be important for monitoring and guiding attentional stimulus selection (Figure IB). One third of cingulate projections synapses onto inhibitory neurons in the lateral prefrontal cortex (Figure IB). Inhibitory connections are made onto (i) calbindin-expressing (CR^{+}) interneurons associated with dendritic inhibition, (ii) calretinin-expressing (CR^{+}) interneurons that likely disinhibit the target circuit, and (iii) parvalbumin-expressing (PV^{+}) interneurons linked to perisomatic inhibition of pyramidal cells. Depiction of the precise functional consequences of these synaptic fingerprints is a major challenge for future research. One guiding hypothesis for this endeavor is the ‘dynamic circuit motif’ hypothesis predicting that each long-range projection circuit establishes a unique function when activated (Figure IC) [39].

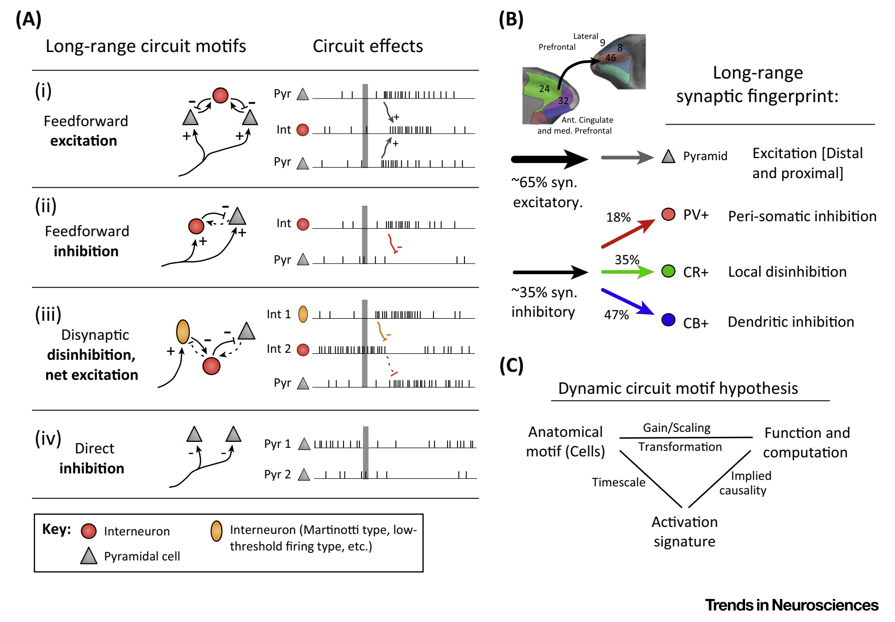


Figure I. Long-Range Connection Circuit Motifs and Synaptic Fingerprints. (A) Long-range circuit motifs and illustration of their activation over time. (B) Synaptic contacts of long-range projections from anterior cingulate cortex onto lateral prefrontal cortex are to ~35% on inhibitory neurons, and these inhibitory synaptic contacts are split into three major types of inhibition [146]. PV+, CR+, CB+ indicate different interneuron types expressing parvalbumin (PV+), calretinin (CR+), and calbindin (CR+), each associated with unique circuit effects (perisomatic inhibition, local disinhibition, and dendritic inhibition). (C) According to the dynamic circuit motif hypothesis, each long-range circuit motif and associated interneuron type likely implements a unique function/computation when activated [39].

selection, including motifs that implement context-dependent gating operations in sensory cortex where selection takes place, and context-dependent integration motifs that generate goals and integrate relevant information in higher-order association areas [39]. Importantly, however, the framework suggests that there are distinct circuit motifs implementing other subcomponent processes of attention such as the suppression of surround information, the active disengagement of focused stimulus selection, or temporally expanded inhibition-of-return [2]. Discussing their potential anatomical and functional implementations is, however, beyond the scope of this review.

Stimulus Selection Through Direct Cortico-Cortical Interactions

An important constraint on the candidate mechanisms that could control the formation of long-range networks is the required potential to activate multiple neuronal circuits at a similar time. This coactivation of brain regions indicates that the circuits participate in a common process or function. To realize such common functionality, spikes from a sending region need to impact on the receiving brain region in a reliable and predictable way [74]. For functional networks of endogenously controlled attention this postsynaptic effect is generated in the absence of any change in external bottom-up (e.g., feedforward thalamic) drive. These long-range traveling spikes thus have to be sufficiently impactful and reliable in affecting long-range networks through processes utilizing some yet unknown mechanisms.

Possible candidate mechanisms underlying the internal generation of impactful control signals will likely become visible in the amplification of neuronal responses in the presence of endogenous attention control when compared to the absence of endogenous control. Three prominent neuronal activation signatures fulfilling this criteria, that is, being evident in empirical studies on attentional states are (i) long-range activating effects through the firing of bursts as compared to non-burst events, (ii) long-range activation through resonance and pacemaking properties of circuits using periodic low-frequency (theta-band) activation, and (iii) long-range disinhibition effects through rapid neuromodulatory (e.g., cholinergic or noadrenergic) actions.

Long-Range Attention Networks, Burst Firing and Beta Synchronization

The firing of bursts instead of single isolated spikes is a well-understood cell-intrinsic mechanism that increases the impact of a neuron on postsynaptic target areas [75], but it has remained unclear whether burst-firing events or whether specific cell types with intrinsic burst mechanisms play a functional role in attentional selection at the network level beyond their local effects within areas [76]. In an attempt to discern the role of bursts for long-range attention networks, a recent study found that fast 200 Hz burst-firing events increased during selective attention states for neurons across the prefrontal and anterior cingulate cortex [32]. Among all neurons with burst firing, about one third of neurons synchronized their burst firing with the LFPs recorded in spatially-distant cortical fields (>15 mm away) at a narrow 15–25 Hz beta-frequency band. Long-range beta-band burst–LFP synchronization connected anterior cingulate and lateral prefrontal cortex, and thus synchronized those neural circuits that carry target information about which of two stimulus locations, features, and values are selected for prioritized processing [53].

The identification of burst firing events as a possible source for stimulus selection across attention networks is particularly important because (i) it suggests that only the small subset of putative interneurons and pyramidal cells that fire sufficient bursts over non-burst spikes are essential for inter-areal interactions [42], and (ii) it suggests that mechanisms underlying the generation of spike doublets and triplets are candidate means to control attention networks. In particular, previous rodent studies suggest that burst firing, but not the firing of single spikes, is controlled by dendrite-targeting interneurons that are of a non-fast spiking type [77,78], and crucially depends on dendritic calcium activation-triggered backpropagating spikes [79]. Burst firing may thus originate from mechanisms linked to internally generated activation states that are segregated from states dominated by feedforward driving synaptic propagation. Consistent with this suggestion, recent functional tracing studies directly demonstrated that dendritic activation through long-range feedback connections can trigger spike output to a local column in sensory

Box 4. Long-Range Dendritic Amplification of Feedback-Type Endogenous Control Information

Endogenously generated attention exerts control over large-scale brain networks through feedback-type connections. For cortico-cortical connections, these feedback influences arrive densely in superficial cortical layers synapsing on apical dendrites of deep layer 5 (L5) pyramidal cells. Based on this widespread connectivity schema, long-range feedback signals may thus act by dendritically gating the activity of a cortical column to different synaptic inputs [39,81]. An intriguing set of studies has documented that dendritic activation does indeed lead to supralinear output of L5 pyramidal cells to synaptic inputs that would otherwise cause no or low responses [79,147]. This observation from *in vitro* work has given rise to the hypothesis that L5 cells provide a generic cellular substrate to detect the coincidence of feedback- and feedforward-type inputs within a cortical column [81]. In particular, the hypothesis predicts that feedback information will amplify feedforward arriving information when both signals coincide within a ~30 ms time-window [148]. The main predictions of this framework were recently tested in a comprehensive study illustrating that long-range dendritic activation indeed improves stimulus selection [80]. The study first traced anatomically the feedback-type input from M2 to layers 1 and 6 of S1 in the mouse. Second, they quantified with two-photon calcium imaging actual Ca^{2+} responses specific to dendritic fields in superficial layers in the somatosensory cortex. Third, they showed that average dendritic activity in somatosensory cortex was dependent on intact feedback-type input from frontal (M2) cortex. Fourth, they revealed with electrophysiological laminar recordings that deep-layer somatosensory cortex underwent current sinks with feedforward (thalamic) stimulation, and anatomically segregated current sink activations in superficial layers following activation of feedback-type inputs. Notably, feedforward- and feedback-triggered activity temporally overlapped for a brief period, suggesting a transient integration window of ~30 ms for bottom-up feedforward inputs and feedback signals to result in amplified responses. Finally, the authors showed that preventing feedback inputs to somatosensory cortex through optogenetic inhibition of feedback axons reduces stimulus-discrimination performance. The task required mice to discriminate between tactile sensations in a maze to make a rightward/leftward choice towards a reward location. In summary, the study isolated the anatomical and dendritic substrate of feedback influences on stimulus selection in sensory cortex, and illustrated that axonal feedback connections are essential for actual perceptual performance [80].

cortex [80]. In this study, feedback stimulation triggered dendritic calcium spikes in superficial cortical layers, triggered action potentials in layer 5 neurons, and indexed improved perceptual performance when compared to a state that lacked dendritic feedback activation (Box 4). These findings suggest that burst firing during attention states could indicate enhanced coactivation of a cortical columns.

A possible consequence of this putative burst-firing state [81] could be the emission of bursts to those postsynaptic target regions that are nodes of the same multi-node functional network [32]. Thus, burst synchronization between those prefrontal circuits that endogenously control stimulus selection start to describe a circuit motif which implements attention networks through dendritic gating processes.

Long-Range Coordination of Goal-Relevant Information Through Theta Frequency Coherence

A second versatile means for controlling and coordinating goal-relevant information in the absence of external, bottom-up changes in sensory inputs is through periodic low-frequency activity. Prominent and sustained low-frequency oscillations at 4–12 Hz theta frequencies are evident in the rodent where theta-band coherence indexes activity correlations across all major structures implicated in goal-directed behavior [82–84]. Most importantly, theta-coherent network activation in the rodent provides an essential temporal reference for neuronal spiking activity to encode attention, choice, and memory information at selected phases during the oscillations (e.g. [85,86]).

In addition to the evidence that theta oscillations play essential functional roles for long-range coordination of endogenously generated information, there is compelling evidence that the underlying mechanisms generating and supporting theta-rhythmic firing of neurons provide an intrinsic gain control on theta-entrained neuronal populations [39,87–89]. For example, theta-rhythmic activity in the prefrontal cortex of rodents (infra-/perilimbic cortex) has recently been shown to recruit inhibitory neurons that intrinsically resonate specifically in the theta band. During optogenetically controlled theta, pyramidal cell firing is not only inhibited by these interneurons, as would be expected from interneuron activation, but also retains firing and even shows post-inhibitory gain of firing output [89]. This gain increase was specific to the theta frequency range. One widespread implication of this finding is that long-range theta-rhythmic entrainment of cortical circuits is expected to establish gain increases of neuronal firing that can persist even in the absence of further bottom-up induced depolarization.

In contrast to prominent sustained rodent theta oscillations, primate brains often show band-limited activation at 4–10 Hz frequencies for only few cycles [90–93]. Importantly, however, these few cycles of theta-rhythmic activation are consistently observed during endogenous controlled, attentional brain states within and between long-range brain systems encompassing macaque prefrontal and anterior cingulate cortex, parietal cortices, and sensory occipitotemporal cortex ([33,94], see also [68]). This evidence suggests that brief periods of 3–5 theta oscillation cycles indicate the large-scale coordination of brain circuits to a common excitability fluctuation. Recent evidence suggests that such a theta active state does curtail all periods of endogenously controlled processing during attentional tasks including the preparation [67], the shifting [95], and the sustaining [33,36,90,96] of stimulus selection. Theta activity in anterior cingulate cortex increases in power specifically when preparing for task rules [67]. When a color-rule cue triggers covert attention shifts, 4–10 Hz theta-band activation in lateral prefrontal cortex and anterior cingulate cortex phase aligns their activity and couples to theta-rhythm gamma-band activation at distant locations [95]. Importantly, this inter-areal theta–gamma coordination indexed successful covert stimulus selection. Its absence predicted errors of attentional performance that were behaviorally evident several hundreds of milliseconds later during the performance. Thus, the lack of theta phase coordinated gamma activity indexed the failure to establish an attention network [95]. In addition to the preparation and the shift of attention, theta activation in the lateral prefrontal cortex of macaques emerged during the sustained selection of stimuli in working memory, again indexing correct over failed working memory [96].

The theta-indexed attention state in the primate brain is particularly significant because observing theta-rhythmic LFP fluctuations allows one to directly infer that large populations of neurons fire preferentially during a brief window of the theta oscillation cycle [67,90,96]. Consequently, long-range theta-band coordination could be the source for efficiently coordinated versus uncoordinated and scattered information processing in the brain [97].

Subcortical Control of Cortical Attention Networks

According to the heuristic framework of attentional control (Box 1) major endogenous control and gating signals for cortico-cortical attention networks originate in subcortical structures, including, but not limited to, the mediodorsal thalamus, the pulvinar and the basal forebrain which we discuss below.

The Mediodorsal Thalamus and Flexible Switching of Goal Representation

The mediodorsal thalamus is a main relay of basal ganglia circuits with prefrontal and anterior cingulate structures, and is essential for flexible attentional prioritization [98,99]. In primates, mediodorsal thalamus neurons carry information about saccade targets in the form of corollary discharges (i.e., about ongoing gaze and attention directions) [100]. Recent studies in rodents have provided causal evidence that mediodorsal thalamus output to prefrontal cortex is essential for preventing perseverant responding in reversal learning task and for succeeding with non-match-to-sample tasks [101]. Silencing the mediodorsal thalamic nucleus (through transient inhibition or lesions) reduces mediodorsal thalamo-prefrontal coordination and impairs behavioral flexibility [101,102]. This coordination becomes evident in the synchronization of thalamic spike output to prefrontal LFP activity at ~13–30 Hz especially during choice periods in goal-directed tasks [101], that is realized by a unique interneuron circuit motif recruiting parvalbumin- but not somatostatin-expressing interneurons [103–105] (Box 3). This motif implements long-range feedforward inhibition within prefrontal cortex. Such feedforward circuits are well documented for thalamo-cortical interactions in sensory cortex [106,107], are implicated to impose temporal structure onto cortical activity [39], and likely underlie the flexible switching of prefrontal goal representation based on reward- and motivation-related arriving from striatum, amygdala, or hippocampal structures [108].

The Pulvinar and Rapid Coordination of Selected Sensory Information

The pulvinar is a structure that is essential for attentional control over sensory areas where it is believed to implement a widespread gain control on cortico-cortical networks and possibly route activity between local patches of cortex depending on the behavioral relevance of the routed information [109,110]. Local stimulation of the pulvinar activates pyramidal cells in superficial cortex with overlapping receptive fields, and de-activating these pulvinar projections reduces superficial neuron responses [111]. The functional consequence of this pulvinar activation has been demonstrated in a selective attention task: pulvinar spike output synchronizes at low alpha frequencies stronger with those visual cortical columns that process attended sensory information, and may coordinate the directed propagation of selected stimulus information across successive visual processing stages [109]. The pulvinar output not only synchronized with areas V4 and TEO at an alpha frequency, but it also indexed the Granger causal direction of cortico-cortical synchronization from area V4 to area TEO. The possible long-range motifs for such a differential gain modulation of cortico-cortical synchronization could entail presynaptic gain control in superficial cortical layers, or recurrent neural communication though coherence [110,112]. It awaits to be seen whether pulvinar circuits are interacting directly with prefrontal and other attentional control structures during actual stimulus selection, whether they amplify already selected information [110], or whether they act more passively in a manner similar to a blackboard [2].

Basal Forebrain Outputs Impose State-Dependent Long-Range Disinhibition

Attentional control depends on the right balance of synaptic neuromodulatory systems [113,114]. For example, long-range cholinergic innervation from basal forebrain nuclei onto cortical columns in sensory cortices enhances sensory representation and mimics the effects of selective attention towards receptive field location [115,116]. Recent results have documented that this long-range influence can act rapidly, relates to improved perceptual performance, and causally controls the gain of cortical responses through a disinhibition motif that acts via nicotinergic receptor subtypes (Box 3) [117,118]. Intriguingly, cholinergic long-range induced gain is likely realized by a segregated interneuron cell type [the vasoactive intestinal peptide (VIP)-positive neurons] that resides predominantly in the superficial cortical layers and facilitates local pyramidal cell output by removing suppression in the cortical column [119]. Accordingly, basal forebrain spike output likely serves as a powerful candidate to facilitate the selection of sensory representations that are tagged to be behaviorally relevant during endogenously controlled behavior. We believe that this rapid, long-range neuromodulation will act in concert with burst-firing mechanisms [32] (Box 4) and theta-frequency selective pulsing of cortical activity [67,95,96] to coordinate which sensory representation will be implemented in distributed fronto-parietal-collicular priority maps.

Concluding Remarks

We surveyed how nodes of large-scale attention networks implement the selection of relevant stimuli under endogenous ('top-down') control. Such internally initiated, in other words endogenously controlled, selection is different to any externally imposed selection of neuronal activity. External sources of attention are imposed by salient changes in sensory information that trigger strong changes in depolarization independently of prior selective attention, and span the whole neocortex including circuits in the FEF and in ventrolateral prefrontal cortex [5] (Figure 1A; see

Outstanding Questions

Which (and how many) processes are the origins of the endogenously generated control signals that bias stimulus selection? One prominent candidate origin are ongoing estimation of the state value predictions [53] or value functions [21,123] that are generated for specific tasks, contexts, or behavioral states, rendering attentional priority maps the result (rather than the cause) of neuronal control processes across frontostriatal circuits [21].

Which neurons switch their participation between endogenously controlled subnetworks that encode different stimuli? Neurons that show such subnetwork switching may serve as a hub in a network. Hub-like neurons may implement attention-specific gates/switches for the formation of large-scale subnetworks, rendering them functionally of particular importance. Hub-like neurons may localize to those brain regions that consistently activate during attention shifts (see Figure 1A in main text).

Should attention be conceived of as 'selecting specific stimuli' for prioritized processing, or rather as 'selecting contextual features' for prioritized processing? In the former formulation attentional feedback signals would carry specific information about precise stimulus features (e.g., the color red). By contrast, if attentional control signals are 'context signals', the endogenous signal would set a contextual approximation of relevant features (e.g., 'redness expected in the current context') that could apply to categories, objects, and features. This contextual approximation is then translated into the modulation of specific feature-tuned neurons by mechanisms that are intrinsic to sensory cortices, and independently of further feedback activations from, for example, prefrontal cortices [124].

What makes local circuit motifs efficient in not only selecting a stimulus (gating synaptic inputs) but also in participating in a distributed priority map? One hypothesis suggests that it is the mere number of cells available in a cortical column for establishing long-range amplification that determines whether relevant stimuli will be efficiently integrated in goal-directed processing or whether the cortical column will fail to have an impact on the network [107].

Outstanding Questions). Accordingly, peripheral saliency mechanisms may be prominent sources of attentional selection in many circumstances. However, the situation is different for internally generated goal information. For this endogenously guided stimulus selection, the start and end of stimulus selection must be intrinsically defined, and the control signals implementing changes of stimulus selection in distributed priority maps must be sufficiently strong to override ongoing sensory events irrespective of changes in saliency.

For this endogenously controlled situation, evidence suggests at least three means to induce and sustain selective attention networks in the form of burst synchronization, theta-rhythm spike timing, and rapid, long-distance neuromodulatory facilitation. We believe that additional long-range circuit motifs will become evident in attention studies that combine newest neurotechnological tools to measure the cell–circuit–systems levels at the same time in behaving animals spanning rodents and primate brains [120,121]. This endeavor promises to discover unique cell-specific and task-selective subnetworks of neurons whose composition changes rapidly and flexibly depending on the precise behavioral goals (Box 2) [27,39,122].

In conclusion, this review has delineated recent progress in understanding attentional stimulus selection from a network perspective. This approach was preconceived and initiated in seminal neurological studies in human subjects more than 30 years ago [45] (Box 2). Adopting this approach and integrating it with insights about the cellular mechanisms that could underlie selective network formation is promising essential progress in understanding how stimulus selection is controlled and implemented in large-scale brain networks in primate brains.

How precise are the timescales of dynamic circuit motifs that implement synaptic gates for attentional stimulus selection [39]? For example, the thalamocortical feedforward inhibition (FFI) motif may impose a strong temporal clock on cortical information processing that is set by the delay of feedforward inhibition to the initial excitation. These windows of opportunity could set the reference of excitability peaks in the cortex and impose large-scale phase resets. However, it is also well known that these FFI circuits undergo so-called paired-pulse depression, which blurs temporal precision and lengthens the 'time window of opportunity'.

Acknowledgments

This research was supported by grants from the Canadian Institutes of Health Research (CIHR) (T.W., S.E.), the Natural Sciences and Engineering Research Council of Canada (NSERC) (T.W., S.E.), and the Ontario Ministry of Economic Development and Innovation (MEDI) (T.W.)

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