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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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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.

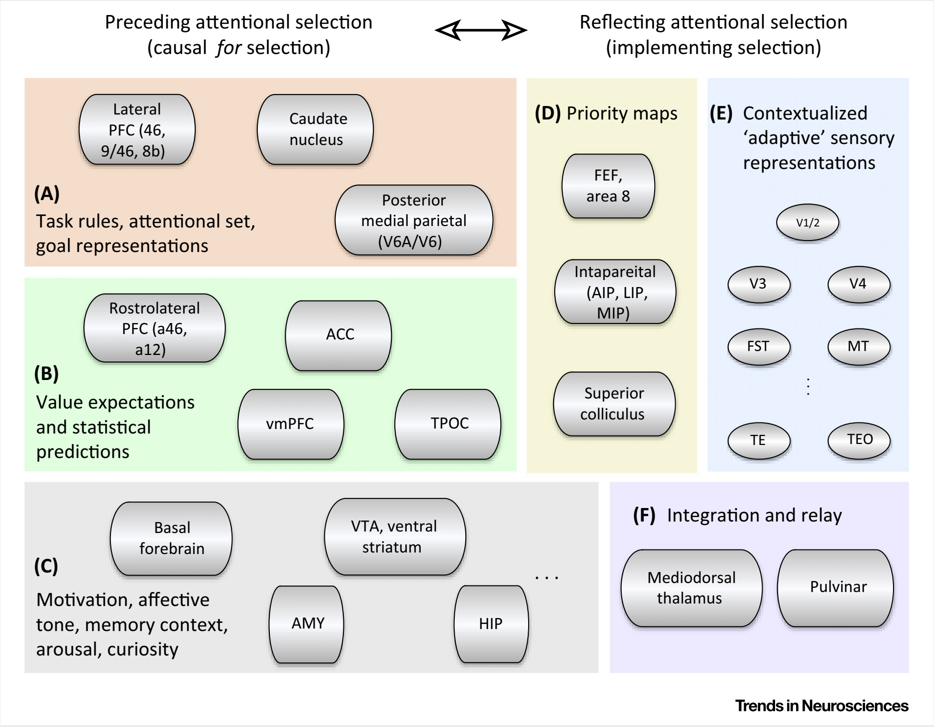

Figure I. Heuristic Framework of the Neuronal Control of Endogenous Attention. Six separate subcomponent processes of attention (colored boxes) map onto separable (but not independent) larger brain systems (gray outlines).

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