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Attention as an effect not a cause

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Attention is commonly thought to be important for managing the limited resources available in sensory areas of the neocortex. Here we present an alternative view that attention arises as a byproduct of circuits centered on the basal ganglia involved in value-based decision making. The central idea is that decision making depends on properly estimating the current state of the animal and its environment and that the weighted inputs to the currently prevailing estimate give rise to the filter-like properties of attention. After outlining this new framework, we describe findings from physiological, anatomical, computational, and clinical work that support this point of view. We conclude that the brain mechanisms responsible for attention employ a conserved circuit motif that predates the emergence of the neocortex.

Frameworks for thinking about attention

Current thinking about attention is guided by several well-established metaphors: 'bottleneck', 'spotlight', 'zoom lens' [1–3]. These metaphors share the central idea that there is a fundamental resource limitation that constrains information processing by the brain [4]. This resource limitation enforces trade-offs – some objects are selected as the focus of perception and action but only at the expense of others, which are given lower priority. Such metaphors also imply that attention is responsible for determining how sensory data are represented in the brain: what is illuminated by the spotlight? In this opinion article, we present an alternate framework that does not treat attention as a cause but instead views it as an effect – in particular, that it arises from processes that determine how sensory (and other) data are interpreted by the brain. We start by outlining and comparing these two frameworks.

Attention as a regulator of sensory representations

Attention is most often described as a causal agent that exerts its effects on the sensory side of the complex cascade of sensory–motor processes in the brain (Figure 1A). This perspective was first described explicitly in the filter model of Broadbent (1958), which posited that only a limited subset of sensory signals reached later stages of processing. The original model placed the filter directly after the extraction of basic stimulus features, prompting a vigorous debate about the location of the filter [1]. There is now a general consensus that the filter-like property of attention limits but does not fully exclude basic features from further elaboration and that the curating of sensory data may occur either early or late in sensory processing [5,6].

The idea that sensory data are actively filtered has been strikingly corroborated by results from neurophysiology experiments. It is well documented that neurons in sensory areas of the cerebral cortex modulate their firing depending on how attention is allocated and that this effect occurs both early and late in processing. For example, in the visual system, modulation with attention is known to occur both at relatively early stages of visual processing, such as among edge-detecting neurons in the primary visual cortex, and also at later stages where more complex features are represented [7,8].

These physiology experiments have also identified a central principle for achieving the filtering of sensory data – competition for representation within the neocortex (Figure 1A). As demonstrated in several influential models [7,9–13], computations occurring in neocortical circuits can implement competition between sensory inputs that results in the enhanced representation of some signals at the expense of others, consistent with the filter-like properties of attention.

Moreover, this competition is believed to be regulated by feedback signals from later stages of processing – in particular, the frontal and parietal cortex [13–15], and also the superior colliculus (SC) in the midbrain [16]. These brain regions provide 'priority' signals that bias competition for representation in sensory cortex, establishing routes for both top-down and bottom-up control of attention. By actively filtering the representation of sensory signals, these cortical attention mechanisms control which data is then available to drive perception, action, and memory.

Attention as an effect of interpreting sensory (and other) data

Our alternative framework views attention as an effect rather than a causal agent. The central premise of this framework is that attention arises as a functional consequence of circuits centered on the basal ganglia involved in value-based motor and non-motor decision making (Figure 1B). Here we introduce the key features of this framework; in the next section, we present some lines of evidence in its favor.

Good decision making depends crucially on properly identifying the current state of the animal and its environment. If the state cannot be identified, the subject is left confused and indecisive. Defining the 'state' is complex, and involves interpreting many diverse sources of information – not only the sensed features of the external world, but also the internal status of the subject, their prior knowledge, and their ongoing needs. At each moment,

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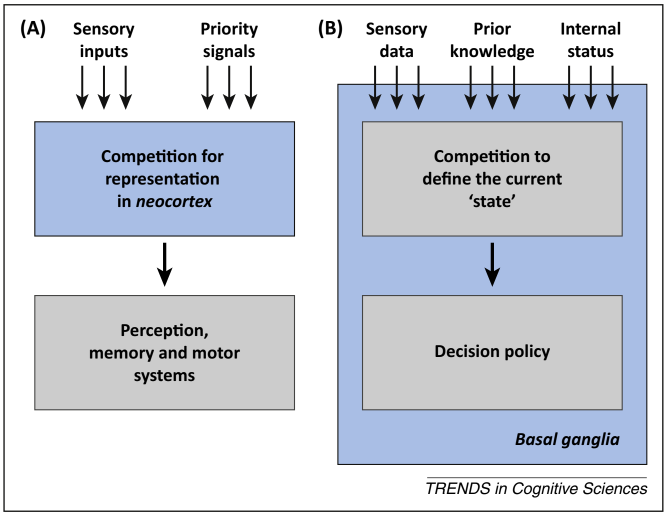

Figure 1. Two frameworks for thinking about attention. **(A)** Attention as a regulator of sensory representations. In this commonly accepted framework, attention acts by regulating how sensory inputs are represented in sensory areas of the neocortex. Sensory inputs compete with one another for representation and this competition is biased by priority signals from other cortical areas. Perception, memory, and motor systems are then driven by the resulting filtered sensory signals. **(B)** Attention as an effect of interpreting sensory and other data. In this alternative framework, attention is a byproduct of circuits centered on the basal ganglia involved in value-based decision making. Here, competition does not affect how sensory inputs are represented but instead determines which estimate of the 'state' provides the best match to the current sensory data, prior knowledge, and internal status of the subject. The dominant estimate of the state then determines which decision policy is followed.

the subject must consider several possible estimates of the state; these different estimates could be generated by differentially weighting the possible inputs using something akin to Bayesian inference [17–19].

There are good reasons to presume that this process of state estimation involves the input nuclei of the basal ganglia, especially the striatum [19,20]. The striatum receives converging inputs from many sources, prominently from the cerebral cortex, but also from the thalamus, the amygdala, and elsewhere [21–24]. The striatum also receives dopamine signals that guide reinforcement learning; the learned associations between a particular state and the set of actions with the highest expected values establish a decision policy that guides the subject's behavior [25–29].

Thinking about context-dependent decision making in this way leads us to a very different model. Specifically, this alternative framework centers on competition between possible interpretations of the current state by the basal ganglia (Figure 1B) rather than competition to determine how sensory data is represented in the neocortex (Figure 1A). Because each possible state differs in the weights it assigns to the various inputs, each state can be viewed as a candidate template [30], with the best-matching template dominating the competition. As circumstances change, a candidate state that provides a poor match in one round of competition could emerge as predominant just moments later. This results in a linked chain of states, where the transition from one to the next is precipitated by some event, or change in an internal variable, that gives the new state more support than the preceding one and carries along with it a new decision policy (also see Box 1).

Attention can be explained by this competition between possible states. Because different sensory inputs and types of knowledge contribute unequally to different states, their influence on perception and action will be limited by the strength of their contribution to the state that currently dominates the competition. From this viewpoint, it is not necessary to change how sensory signals are represented to generate the phenomenology of attention. The filter-like properties associated with attention result from the particular weights applied to the sensory and non-sensory inputs that define the current state. The pattern of weighted inputs gives the appearance of limited sensory resources, because increasing the weight of one input necessarily involves reducing the proportional weight of all of the other inputs.

This framework also provides a definition for shifts of attention – they correspond to transitions from one dominant state to the next. If the transition is triggered by unexpected sensory data, this might be considered a stimulus-driven or bottom-up shift of attention; if it is prompted by a change based on internal state or knowledge, this might be an endogenous or top-down shift of attention. However, these categories are somewhat arbitrary [31]. In principle, shifts of attention could come in many different flavors, because transitions between states could be prompted by changes along any of the dimensions represented by the diverse inputs to the striatum.

Some arguments in favor of this new framework

We start with results from recent physiology studies of the midbrain that are difficult to explain with the conventional view of attention and then consider several other types of observations that implicate a centralized decision mechanism in the basal ganglia.

The SC regulates attention but not through the visual cortex

The SC is a highly conserved midbrain structure that contains a retinotopically organized map of the visual world. The primate SC is best known for its role in controlling orienting movements of the eyes and head [32], but recent experiments have confirmed that the SC is also necessary for the control of spatial attention [33]. For example, when activity in the SC is locally and reversibly suppressed (Figure 2A,B), animals have difficulty performing attention tasks for stimuli placed in the affected part of the visual field [34]. The deficit resembles clinical cases of extinction [35]: animals mostly ignore cued stimuli in the inactivated region when they compete with irrelevant stimuli placed elsewhere, but discrimination ability is largely intact when stimuli appear alone, even in the affected region.

Taken by themselves, these findings seem consistent with the established idea that attention works by controlling how sensory data are represented in the brain: the SC could be the source of 'priority' signals that bias competition for representation in sensory cortex. However, when directly tested, this interpretation was found to be incorrect. The test involved recording from neurons in cortical areas necessary for processing the sensory signals used in the task, at the same time that activity in the SC was suppressed (Figure 2C,D). The unexpected finding was that the enhanced responses of sensory neurons to attended stimuli (Figure 2E,F) were preserved during