CellPress
OPEN ACCESS

Review

Common and distinct neural mechanisms of attention

Ruobing Xia,[1] Xiaomo Chen,[2] Tatiana A. Engel,[3] and Tirin Moore [ID] [1,*]

Despite a constant deluge of sensory stimulation, only a fraction of it is used to guide behavior. This selective processing is generally referred to as attention, and much research has focused on the neural mechanisms controlling it. Recently, research has broadened to include more ways by which different species selectively process sensory information, whether due to the sensory input itself or to different behavioral and brain states. This work has produced a complex and disjointed body of evidence across different species and forms of attention. However, it has also provided opportunities to better understand the breadth of attentional mechanisms. Here, we summarize the evidence that suggests that different forms of selective processing are supported by mechanisms both common and distinct.

Different forms of selective processing

The senses are constantly bombarded with stimulation. Although early stages of sensory processing extract a wealth of information from the environment, only a small fraction of that information is used to guide behavior at any given moment. Instead, the sensory input that is perceived, remembered, decided about, and acted upon is largely, and conveniently, confined to contextually relevant stimuli. This selective processing is generally referred to as attention, a basic cognitive function that interfaces with all other high-level functions of the nervous system, from memory to motor control.

In testing hypotheses about the neural circuitry of selective attention, as with hypotheses about the circuit basis of any class of behaviors, it is crucial to rigorously consider the precise form or forms of attention used. Sensory stimuli can be preferentially detected and/or discriminated in a variety of behavioral contexts in humans [1,2], and this is likely also the case in most model organisms. In this review, we highlight two widely studied types of attention, goal-driven and stimulus-driven, but there are other important types, such as cross-modal attention (selection of stimuli across sensory modalities) [3,4], and other dichotomies (e.g., spatial versus feature and object-based attention [2]). Each of these types appears likely to have different and dissociable neural circuit components, if only because the behavior differs qualitatively between each. Moreover, different species likely vary considerably in their engagement in these different types of attention.

To date, the types of task used to probe attention mechanisms have varied significantly across different laboratories (e.g., behavioral response or type of cues), even when the same model organism and type of attention are studied [5–8], and indeed even within human studies [9,10]. These differences appear likely to yield discrepancies in the conclusions drawn about underlying circuit mechanisms (Box 1). In this review, we briefly survey a broad swath of recent studies aimed at identifying mechanisms of attention across model species, including humans, and across different types of attention, with an eye toward identifying neural mechanisms both common and distinct. We highlight evidence from non-human primates as it provides the best mechanistic

Highlights

The quest to identify neural mechanisms of selective attention has broadened in recent years to include multiple forms of attention, multiple species, and multiple levels of analysis.

New data reveal distinct and causal roles of the superior colliculus and parietal cortex in stimulus-driven visual attention.

Convergent evidence across species has identified a role of motor-related signals in the control of goal-directed attention.

Fluctuations in cortical activity associated with global arousal interact with goal-driven attention and both predict perceptual performance.

Neural oscillations reflecting attentional control in human and non-human primates suggest an underlying rhythmic mechanism synchronized to theta.

[1]Department of Neurobiology and Howard Hughes Medical Institute, Stanford University, Stanford, CA, USA
[2]Department of Neurobiology, Physiology, and Behavior, University of California, Davis, CA, USA
[3]Princeton Neuroscience Institute, Princeton University, Princeton, NJ, USA

*Correspondence:
tirin@stanford.edu (T. Moore).

> **Box 1. Choosing valid behavioral paradigms**
>
> There are myriad technical challenges faced in identifying the neural mechanisms of particular behaviors. Unsurprisingly, among them is the challenge of designing valid behavioral paradigms, where valid refers to congruence with either natural behavioral phenotypes of a given organism or a particular human behavior. The choice of behavioral paradigms naturally has a pivotal role in the conclusions that can be drawn from any given experiment. Consider, as an example, the early conclusions that the superior colliculus (SC) and the frontal eye field (FEF) were solely involved in oculomotor control in primates, and not involved in covert spatial attention [133,134]. That conclusion followed reasonably from the observation that, whereas visually driven activity in both areas is enhanced in advance of eye movements directed to neuronal receptive fields (RFs), no enhancement is observed when monkeys covertly attended to RF stimuli. Crucially, however, the covert task used in those early studies required monkeys to divide attention between a peripheral RF stimulus and the central fixation point, as either could change luminance with equal probability. By stark contrast, during the same (divided attention) task, neurons in parietal cortex exhibited clear enhancement [134]. It is now well established that the activity of neurons in all three structures is strongly modulated when monkeys perform tasks in which they covertly attend to a single one of multiple visual stimuli [5,88,135]. Thus, it appears that the discrepant results between parietal cortex and SC and FEF might simply reflect differences in the spatial precision and competitive interactions within the visuotopic maps of the latter and former. Thus, the choice of the behavioral paradigm is clearly consequential in interpreting the role of putative underlying mechanisms.

bridge between evidence from human and other animal models. We begin by discussing new evidence on the mechanisms of goal-driven and stimulus-driven attention. Next, we summarize recent insights into the relationship between mechanisms of attention and arousal. Last, we consider evidence of the neural oscillations that reflect attentional control.

Goal-driven versus stimulus-driven attention

The tendency of organisms to selectively process only a subset of sensory input appears to come in a variety of forms. Among these, goal-driven and stimulus-driven attention represent two forms of attention that have been characterized extensively in human psychophysical studies [1,11]. Goal-driven attention describes selective sensory processing due to an endogenously generated signal (e.g., representation of a rule, strategy, or motivational state). By contrast, stimulus-driven attention describes selective processing based solely on the physical properties of stimuli. Stimulus-driven and goal-driven attention have been widely assumed to be dichotomous and indeed appear to involve distinct underlying neural mechanisms [12]. In humans, two separate frontoparietal networks are thought to contribute differently to goal-driven and stimulus-driven attention, specifically a dorsal network to the former and a ventral network to the latter [13,14]. Nevertheless, these two types of attention may not be sufficient to account for all instances of stimulus selection. For example, some human psychophysical studies suggest that selection history contributes independently of task goals and stimulus salience [15,16], adding a third potential factor in attentional selection. Others have suggested that these types can be broken down even further [17]. This added complexity places even greater importance on the careful design of behavioral paradigms used in future studies aimed at identifying underlying neural mechanisms of attentional selection, particularly in animal models. Nonetheless, these two forms of attention provide a good starting point in the effort to identify common and distinct neural mechanisms of attentional selection.

Mechanisms of goal-driven attention

Insights into the mechanisms of goal-driven attention have been noted for more than a century, or at least since early neurological descriptions of attentional disorders resulting from brain damage in humans [18] and in animals [19]. Furthermore, sensorimotor and premotor networks have been implicated in the control of goal-driven, spatial attention for nearly as long, gaze control networks being a prime example (reviewed in [20]). In humans, the preparation of gaze movements necessarily results in perceptual benefits at targeted locations [21,22], and those perceptual benefits signify the defining effect of attentional deployment. Additional human psychophysical evidence indicates that similar perceptual benefits accompany planned hand movements [23,24],

suggesting that multiple effector systems independently influence sensory processing as a means of adaptively selecting relevant stimuli during sensory-guided behavior. By now, it is clear that the preparation of eye movements is sufficient to alter activity in the visual systems of human [25] and non-human primates [26–28]. Moreover, the influence of eye movement preparation on visual activity is robust even when dissociated from covert attention [29], consistent with human psychophysical data [30]. Correspondingly, there is now considerable evidence of a causal role of gaze control networks in the control of goal-directed spatial attention, having first been shown in non-human primates [31,32], and subsequently in humans [33,34], birds [35], and mice [36]. Collectively, this evidence demonstrates that circuits involved in the preparation of eye and head movements also exert a direct influence on the visual system and visual performance, indicating that these circuits represent both 'intended' and 'attended' goals.

In recent years, more has been learned about the specific mechanisms by which gaze control circuits contribute to goal-driven attention. In the primate brain, gaze control is achieved principally via the superior colliculus (SC), the lateral intraparietal area (LIP), and the frontal eye field (FEF), three sensorimotor structures that serve as interfaces between the visual and saccadic systems [37–39]. In the human brain, the FEF and parietal cortex comprise much of what is referred to as the dorsal frontoparietal attention network [40]. In the macaque, both the SC and FEF have been implicated in the control of visual spatial attention [32,41]. However, the attention-related modulation of visual cortical activity observed during goal-directed attention does not depend on the SC [6], in contrast to a clear role of the FEF [7,28,42,43]. The influence of FEF neurons on visual cortical activity appears to be achieved, at least in part, by direct retinotopic projections of FEF neurons to extrastriate visual cortex [44,45]. Similar to neurons within dorsolateral prefrontal cortex (dlPFC) and parietal cortex, many FEF neurons signal the location of remembered visual targets via spatially tuned persistent spiking activity, which is proposed to emerge from local and long-range recurrent connectivity [46,47]. To date, the function of FEF persistent activity either in motor preparation or spatial working memory, or both, remains uncertain (although see [48]). One study identified visual cortex-projecting FEF neurons by antidromic stimulation and found that, whereas only half exhibited visual properties and almost none exhibited motor properties, all of them exhibited persistent activity [49]. These neurons have also been shown to preferentially express dopamine D1 receptors compared with D2 receptors, and compared with locally projecting neurons [50], which is consistent with both the unique role of D1 receptors in memory-related persistent activity [51] and their involvement in the gating of visual cortical activity by the FEF [43]. The fact that persistently active FEF neurons preferentially project to visual cortex suggests that they have a distinct role in the selection of visual signals. Indeed, within the FEF, memory-related persistent activity is accompanied by an increased efficacy of visual cortical inputs to FEF neurons within the same local network [52]. Combined, this evidence points to a possible circuit within primate PFC by which gaze control networks select visual information during goal-directed, spatial attention (Figure 1A).

In addition to the evidence implicating gaze control networks in goal-directed spatial attention, newer evidence suggests an additional source of attentional control in the primate brain. Using fMRI, several investigators have independently identified a region in temporal cortex within the floor of the superior temporal sulcus (STS) of the macaque brain that is remarkably sensitive to attentional deployment [53–55]. This region of the STS sits near a confluence of motion-selective [middle temporal (MT) and medial superior temporal (MST)] and shape-selective (TEO) visual areas, yet itself appears to exhibit only modest stimulus selectivity [54,55]. However, the activity of neurons within this area is modulated approximately fourfold on average when attention is directed into the neuronal receptive field compared with outside [55]. Furthermore, electrical microstimulation of sites within this area significantly influences attentional deployment in a spatial-specific manner
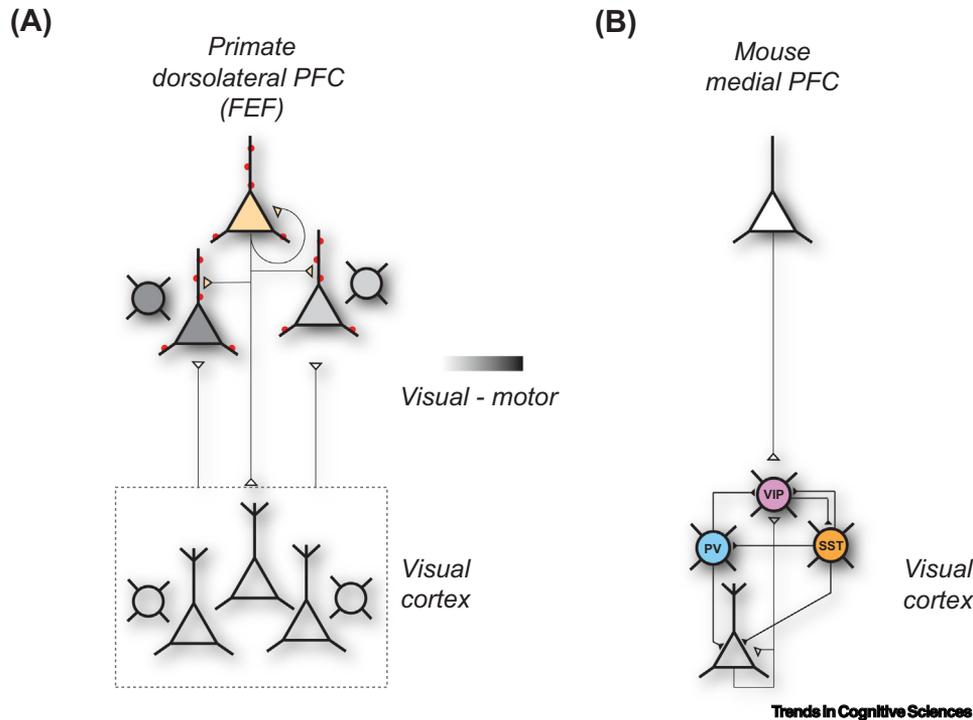
Figure 1. Neural circuitry of goal-driven attention. (A) Connectivity between visual and prefrontal cortex in the macaque. Diagram summarizes several lines of evidence. Connectivity between dorsolateral prefrontal cortex (PFC) and posterior visual areas exists largely between the frontal eye field (FEF) and retinotopic areas in extrastriate cortex [e.g., V3, V4, and middle temporal (MT)]. Projections to extrastriate cortex from the FEF originate largely from layer 2/3 [132]; projection neurons (peach) disproportionately exhibit delay-period activity during memory-guided saccade tasks [49]. Inputs to visual cortex from the FEF terminate predominantly and disproportionately onto the distal dendritic spines of pyramidal neurons across layers [44]. Visual cortex-projecting FEF neurons, along with other long-range projecting pyramidal neurons, express dopamine D1 receptors (red dots) at a much higher rate compared with inhibitory interneurons [50]. Input to the FEF from visual cortex targets neurons exhibiting both visual and motor properties, and those inputs are facilitated when monkeys remember locations matching the location of visual input [52]. (B) Summary of prefrontal–visual cortical circuitry in the mouse. Prefrontal projections principally target VIP+ inhibitory interneurons, which in turn inhibitory somatostatin+ inhibitory interneurons, thereby disinhibiting excitatory neurons. Abbreviations: PV, parvalbumin+ inhibitory interneurons; SST, somatostatin; VIP, vasoactive intestinal peptide. (B) Adapted from [8].

[55]. Both visual and attention-related activity in this area are dependent upon input from the SC [56] and FEF [57], and this area is directly connected with areas implicated in attentional control within parietal cortex and PFC [58]. This region of temporal cortex is also strongly activated during different types of visually guided eye movement, specifically vergence, smooth pursuit, and saccadic eye movements [59]. Nonetheless, its unique role in attention and visually guided behavior remains an open question. Notably, the location of this area within temporal cortex raises the possibility of homology with areas of the human ventral attention network [57,60,61].

Given the relative limitations of the tools available for dissecting neural circuits of attentional control in primates, attempts to do so in more genetically tractable animal models, particularly mice, have increased dramatically in recent years (reviewed in [8]). As would be expected given the obvious behavioral and cognitive limitations of the mouse model, the development of suitable tasks in mice to model selective attention in humans has posed a significant challenge for investigators [36,62]. Indeed, one might argue that focusing on mechanisms of more species-specific forms of goal-directed attention in the mouse, such as during locomotion, may be more fruitful (Box 2). Nonetheless, more recent attempts have used behavioral tasks that appear remarkably

---

Box 2. Locomotion and visual cortical enhancement in rodents

In primates, it may not be surprising that spatial attention arises, in part, from direct modulation of visual activity by gaze control neurons, given the importance of gaze control for visually guided behavior, largely due to the need to continuously reposition the fovea for high-acuity vision. However, this instance of a clear influence of motor control signals on sensory processing, one that extends even to non-foveate, nonvisually dominate species [35,36], suggests that other instances of motor-driven sensory modulation can be viewed in the context of visual attention. A prime example of this is the robust influence that locomotion exerts on visual cortical activity in mice. First described by Niell and Stryker [136], locomotor activity (running) in mice is associated with a dramatic increase in the visual responsiveness of area V1 neurons, without concurrent changes in spontaneous firing rate. In many ways, the effects of locomotion on neuronal activity resemble the effects of attention described previously in the primate visual system [137], including increased stimulus-driven spike rates [136,138], reduced spike count correlations [139], spiking variability [139,140], and changes in gamma local field potential power [136]. Notably, visual detection is enhanced during locomotion compared with when mice are stationary [140]. Moreover, both the behavioral and visual cortical effects depend on the type of visual task that mice are engaged in during locomotion [141]. Thus, it may be reasonable to consider the neural and behavioral effects of locomotion as a form of visual attention.

As another similarity with attention, the cortical circuitry involved in the locomotor effects on visual cortical activity appears to involve a similar disinhibitory circuit, which has also been identified in the mouse in studies using standard attention tasks [64,142]. Last, although it remains unclear to what extent the influence of locomotion on V1 activity includes changes in global arousal and the associated effects of arousal [97,143], the observed effects nonetheless involve input from neurons specifically involved in locomotor control. Optogenetic stimulation of the mesencephalic locomotor (MLR) region in awake mice induces both locomotion and increases in the gain of V1 responses [144]. Notably, MLR stimulation below the threshold needed to evoke overt movements exerts similar changes in V1 activity. Thus, similar to the effects of FEF stimulation in primates [28], the effects of activating the MLR in mice are dissociable from motor output.

---

analogous to goal-directed attention in humans and non-human primates [63–65]. During such tasks, as in primates, improved psychophysical performance at attended locations is accompanied by spatially selective enhancements in visual cortical activity [64]. In addition, as in primates, PFC directly influences the activity and sensitivity of neurons in visual cortex [36,66].

More importantly, studies in the mouse revealed considerably more cellular and synaptic detail to circuits implicated in attention. For example, projections from PFC to visual cortex appear to influence visual activity via local disinhibitory circuits in which vasoactive intestinal peptide (VIP) local inhibitory interneurons are directly targeted by prefrontal cortical projections [64] (Figure 1B) VIP neurons in turn inhibit somatostatin (SST) inhibitory interneurons, resulting in disinhibition of excitatory neuronal activity. These two classes of interneuron may correspond approximately to calretinin+ and calbindin+ interneurons, respectively [67–69], although there is also evidence of a similar disinhibitory circuit motif in prefrontal–visual connections in the primate brain. Instead, thus far, pyramidal neurons appear to be disproportionately targeted by prefrontal projections [44]. In addition, in the mouse, a subset of frontal cortical neurons exerts modulatory effects on visual cortex indirectly via projections to the SC and pulvinar [70], thus raising the possibility of a similar circuit in primates.

Combined, the aforementioned evidence not only suggests the existence of similar mechanisms of attentional control across phylogenetically distant species, but also holds the promise that such mechanisms can be studied in more genetically tractable animal models. Nevertheless, regarding both points, the homology between neural circuit mechanisms of attentional control in rodents and primates remains very much in question. For example, the frontal cortical area in mice implicated in attentional control, specifically anterior cingulate cortex (ACC) [36,66], is likely not anatomically homologous with dlPFC in primates, and instead may be homologous with primate medial prefrontal (mPFC) areas [71]. Notably, however, mPFC in primates contains a supplementary eye field (SEF) that is heavily interconnected with the SC, FEF, and parietal cortex [72]. Primate SEF is also connected with areas within posterior visual cortex [73] and is activated during attention tasks [74]. Yet, the extent to which neurons in the SEF directly contribute to goal-directed attention in primates remains to be examined.

Mechanisms of stimulus-driven attention

Unlike the extensive evidence demonstrating the selective modulation of sensory representations throughout the brain during goal-driven attention [40,54,70,74], details of the effects of stimulus-driven attention are notably less clear [20]. By definition, a salient stimulus draws attention, and the salience of a stimulus can be conferred in several ways, including simply by virtue of greater physical energy (e.g., brighter, larger, or moving objects [1,75]) or by ethological relevance (e.g., face images or looming objects [76]). This form of salience can already be detected at very early stages of sensory processing in a winner-take-all fashion, such as in the midbrain [77,78]. Physical salience can also be conferred by the uniqueness of a stimulus relative to all others. In fact, models of stimulus-driven attention have been developed largely from human psychophysical studies investigating the influence of unique visual features on the allocation of attention [79–82]. Consistent with observations in human psychophysics [11,20,83], these models suggest that the neural mechanisms of stimulus-driven attention are separable at some level from those controlling goal-driven attention. A key aspect of these models is the proposition that the visual system analyzes different feature dimensions (e.g., color) more or less in parallel to compute local feature contrasts. The resulting feature contrasts can then be combined to form salience maps in which unique objects can be localized in space, regardless of the features that define them [80,84]. Neurophysiological studies in non-human primates have provided at least some evidence that this feature-independent global salience is computed, or at least amplified, within the posterior parietal cortex (PPC) [12,84–87], PFC [12,32,87,88], and SC [78,89,90]. However, the role of each candidate area has not been causally examined, and the relative contributions of these cortical and subcortical regions to salience computations remain largely unknown.

A recent study [91] provides the first causal evidence of a role of PPC in computing visual salience. In the study, the authors reversibly inactivated PPC in behaving monkeys and measured the effects of inactivation on salience representations downstream of PPC, in PFC, specifically the FEF (Figure 2). PPC inactivation selectively reduced the coding of visual salience by neurons in the FEF. Similar to neurons in visual cortex, FEF neurons exhibit relatively discrete classical receptive fields and, thus, can signal the location of isolated visual stimuli (Figure 2A, top). In addition, despite a general lack of stimulus selectivity [92], FEF neurons signal the location of stimuli with unique features (Figure 2B, top). However, inactivation of the PPC drastically reduces this effect. Specifically, whereas FEF neuronal responses to single, isolated visual stimuli were largely unchanged during PPC inactivation (Figure 2A, bottom), responses to unique stimuli (i.e., those with distinctive visual features) presented among competing stimuli, were diminished (Figure 2B, bottom).

In addition, to test for corresponding changes in salience-driven behavior, the authors measured the relationship between the salience contained within naturalistic images (Figure 2C) and the pattern of fixations of those images. Following PPC inactivation, monkeys exhibited a reduced influence of visual salience on the pattern of fixations within the contralateral visual space, when measured in head-centered or in eye-centered coordinates (Figure 2D). These results indicate that, in the monkey, neural activity within PPC contributes both to the emergence of salience signals in PFC and the influence of salience on behavior. However, it remains unclear how the results in the monkey map onto human dorsal and ventral attention networks, where the latter, but not the former, is proposed to underlie salience-driven attention. Nevertheless, some studies in humans have reported evidence that the dorsal network areas (e.g., intraparietal cortex) are also engaged during stimulus-driven attention [93–95]. An important goal of future studies in non-human primates and other animal models might be to examine the relative roles of other structures, including temporal cortical areas and SC, in the control of stimulus-driven salience and salience-driven behavior.
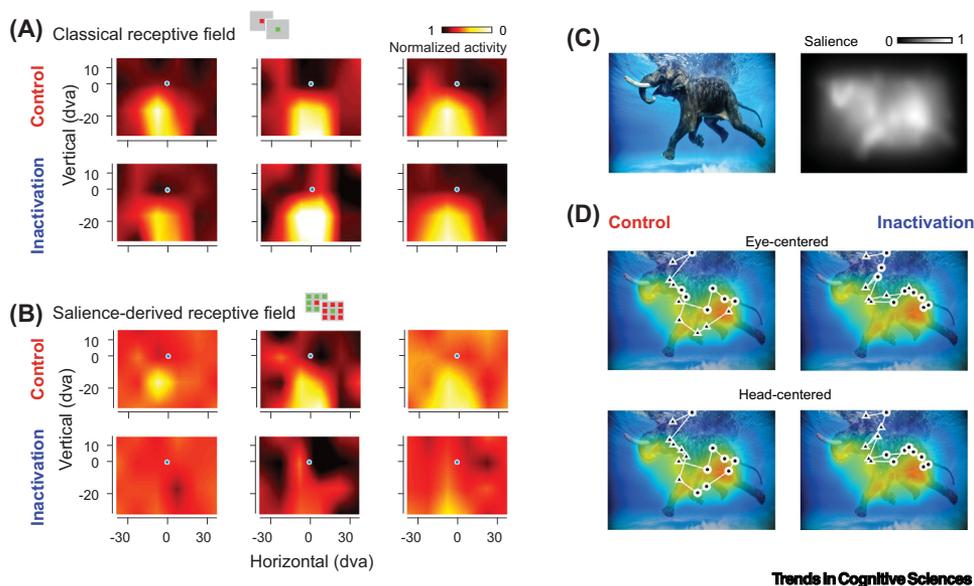
Figure 2. Contribution of parietal prefrontal cortex (PPC) to visual salience representations and salience-driven behavior. (A) Classical receptive fields (RFs), mapped with a single-colored stimulus presented in isolation, of three example frontal eye field (FEF) neurons during control (top) and PPC inactivation (bottom). Following PPC inactivation, the classical RFs remained largely unchanged. (B) Salience-derived receptive fields, mapped with a unique stimulus within an array of other stimuli that were differently colored, of the same example neurons during control (top) and PPC inactivation (bottom). Following PPC inactivation, in contrast to (A), the salience-derived RFs were dramatically diminished. (C) Example image from a free-viewing task (left) and the corresponding salience map within that image (right) [80]. (D) Correspondence between the computed salience and fixations made in the example image before (left) and after (right) PPC inactivation. Top-row fixations are labeled in eye-centered coordinates as contralaterally (triangles) or ipsilaterally (circles) directed saccadic eye movements. The bottom row shows the same fixations labeled in head-centered coordinates as landing in the contralateral or ipsilateral half of the image. Abbreviation: dva, degrees of visual angle. Adapted from [91].

Arousal, cortical states, and attention

Neural circuits controlling selective attention have generally been considered independent from mechanisms regulating global arousal. Yet, attention and arousal have similar effects on neural population activity in sensory cortical areas [96]. Both processes involve similar modulations of tuning curves, spike–count correlations, and low-frequency oscillatory activity in local field potentials (LFPs) [97,98], and appear mediated by common neurotransmitter systems [99,100]. Moreover, optogenetic activation of basal forebrain (the primary source of arousal-promoting cholinergic input to the cortex) produces perceptual benefits and neural activity modulations typical of selective attention [101]. These similarities suggest that global arousal and selective attention tap into similar underlying circuitries, and recent work has provided more support for this idea.

The link between attention and arousal transpires within the synchronized neural activity fluctuations characteristic of cortical state. Slow synchronous transitions between periods of high activity and quiescence define cortical state at low arousal, such as during slow-wave sleep or anesthesia [96,102]. In the awake brain, slow fluctuations are less conspicuous and cortical state appears desynchronized in macroscopic measurements (e.g., electroencephalograms). However, even during active task engagement, local neural populations spontaneously transition between episodes of high and low activity, akin to synchronous transitions during sleep but on a much smaller spatial scale [103,104]. These local synchronized fluctuations are evident as spontaneous waves propagating laterally across nearby cortical columns, as observed within marmoset visual cortex (Figure 3A) [105,106]. The local waves have irregular timing and a varying degree
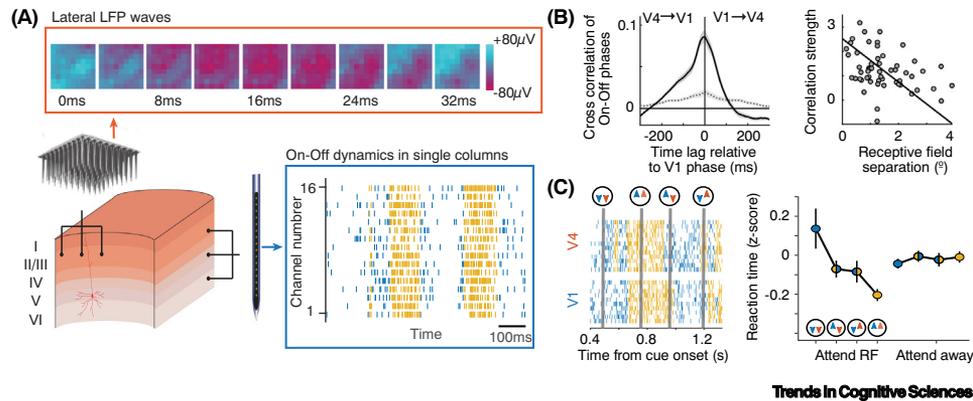
Figure 3. Coordination of local cortical states during selective attention. (A) Cortical activity fluctuations are organized along anatomical dimensions. Lateral recordings from nearby columns in marmoset visual cortex (e.g., using rectangular Utah arrays) reveal spontaneous waves in local field potentials (LFPs) that travel horizontally across the cortex (top, adapted from [105]). Laminar recordings from single columns (e.g., using linear multielectrode arrays) reveal spontaneous transitions between phases of vigorous (On) and faint (Off) spiking that occur synchronously across cortical layers (lower right, adapted from [107]). The population spiking activity is segmented into On (yellow) and Off (blue) phases with a Hidden Markov Model (HMM). (B) Left: cross-correlation between sequences of On and Off phases of activity in columns of macaque areas V1 and V4 comprising neurons with overlapping receptive fields (RFs) shows that On and Off phases in V1 and V4 tend to align (broken gray line; shuffled data). The cross-correlation asymmetry indicates that On–Off transitions in V4 tend to precede V1 transitions during attention. Right: the correlation strengths (area under the curve) decrease with the receptive field separation. Thus, the alignment of On–Off dynamics between visual areas is coupled to their retinotopic alignment. (C) Left: simultaneous spiking activity in V1 (bottom) and V4 (top) segmented with HMM (example trial of a spatial attention task) illustrates four possible configurations of On–Off phases in two areas (circles with arrows). Right: alignment of local On–Off phases between V1 and V4 predicts reaction times (RTs) on an attention task. RTs are fastest when both areas align in the On phase and slowest when both areas are in the Off phase at the time of stimulus change. No effect is observed when attention is directed to a location outside the receptive fields. Adapted from [108] (B,C).

of spatial organization, which together predict the magnitude of stimulus-evoked responses and the ability of the animal to detect a stimulus [105]. In single columns, synchronized fluctuations appear as transitions between phases of vigorous (On) and faint (Off) spiking across all cortical layers (Figure 3A) [98,107–109]. The On–Off phase of population activity also predicts the ability of an animal to detect stimulus changes in the attended location. The On–Off dynamics in single columns and lateral waves are likely related, with columns switching to the On phase when hit by a passing wave. However, a direct relationship between On–Off dynamics and lateral LFP waves has not yet been demonstrated.

Changes in the local On–Off dynamics highlight the entanglement between attention and arousal. The mean On-episode duration increases with arousal (indexed by a pupil dilation) [98,107]. Longer On-durations result in fewer transitions, marking a shift toward a desynchronized state as expected at higher arousal levels. During spatial attention, the On-episode durations also increase, but only in columns with receptive fields at the attended location [107,108]. Thus, during attention, cortical state shifts toward desynchronization locally within a retinotopic map. This parallel suggests that attention and arousal recruit the same circuit mechanisms but at different spatial scales. This notion is further supported by network models of On–Off dynamics in interacting cortical columns [110]. On–Off transitions in single columns can be captured as metastable dynamics, similar to models of synchronized activity during sleep or anesthesia [111,112]. In the network, On–Off activity propagates across columns as irregular waves. Attentional inputs modulate the spatial extent of On–Off dynamics, giving rise to distance-dependent changes in spike–count correlations as seen in the data [110]. Thus, local metastable dynamics may define the operating regime of cortical networks, where attention and arousal control the spatial extent of synchronized activity on local and global scales.

On–Off dynamics are also coordinated with retinotopic precision across macaque visual cortical areas (Figure 3B) [108]. The On and Off phases tend to align between V1 and V4 columns with overlapping receptive fields. The On–Off phase alignment gradually decreases with the receptive field separation, suggesting a mirroring of spontaneous waves in V1 and V4. During attention, the interareal coordination of cortical state is enhanced and follows the reversed hierarchy (i.e., transitions in V4 tend to precede V1 transitions, and transitions in the FEF precede those in V4). Moreover, the alignment of On–Off phases across visual areas predicts faster reaction times in an attention task (Figure 3C) [108]. Thus, attentional modulation of cortical state appears to be local within each visual area and coordinated globally across areas. These links between attention and arousal open unique opportunities for studying how fundamental properties of neocortical circuitry that are likely common in mammalian species interact with mechanisms of sensory processing.
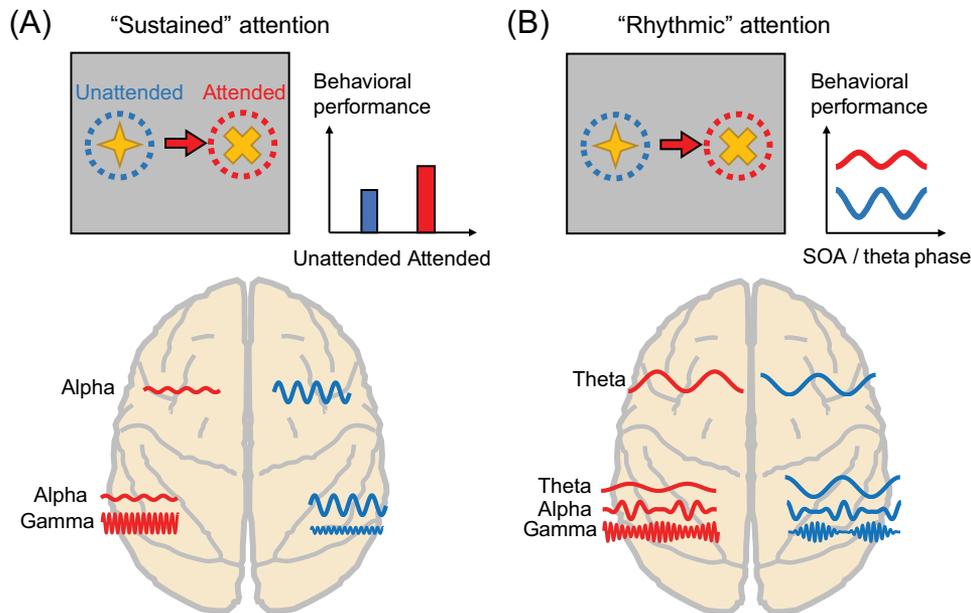
Neural oscillations reflecting attentional control

In addition to attentional modulation of neuronal activity and firing-rate states, a large body of research focusing on LFPs, electroencephalography (EEG), and magnetoencephalography (MEG), has established a strong correlation between neural oscillations and attentional deployment. Importantly, this insight has emerged from work that includes data obtained in humans, thus facilitating comparisons with similar measurements in animals.

One widely observed effect is the attenuation of alpha activity, specifically a power reduction of the intrinsic alpha-band oscillation (8–15 Hz), among regions in the dorsal attention network contralateral to the attended hemifield, as well as in visual areas that are tuned to the attended information [113] (Figure 4A). In addition, some studies also show that alpha activity can be evoked or enhanced where irrelevant stimuli are processed [114]. These effects suggest that an alpha rhythm is involved in selective disinhibition of attended representations through decreased alpha power and/or selective inhibition of task-irrelevant sensory processing through increased alpha power [115]. Such a role of alpha activity was recently tested using MEG neurofeedback [116]. By training subjects to manipulate their relative alpha power between two hemispheres of parietal cortex, this study provided evidence of a causal relationship between alpha asymmetry and behavioral measures of spatial attention. Interestingly, despite subjects showing similar behavioral benefits, the trained alpha asymmetry varied across subjects, some with only an ipsilateral increase and others with only a contralateral decrease, and some with both, consistent with the variability in the observed inhibition/disinhibition effects [115].

In contrast to lower frequency bands, stimulus-driven gamma-band activity (30–70 Hz) shows increased power and synchrony within representations of attended locations or features [117,118], similar to neuronal firing-rate modulation. In macaque visual cortex, gamma oscillations have been shown to propagate from granular to supra- and infragranular layers, whereas alpha oscillations propagate in the reverse direction [119]. Thus, they are thought to reflect feedforward and feedback processing, respectively. Indeed, attention modulates these rhythms in a similar laminar-specific manner [120], suggesting the recruitment of both feedforward and feedback pathways during attentional modulation. Moreover, MEG recordings in humans revealed that the trial-by-trial fluctuations in attentional alpha modulation during the prestimulus period predict the power of subsequent stimulus-driven gamma activity [121].

Together, this evidence suggests that alpha-band oscillations participate in attentional modulation through the gating of feedforward gamma activity. In addition to the potential gating modulation by alpha activity, studies in non-human primates also find attention-related gamma synchrony within higher-level areas (e.g., prefrontal areas and ACC), and between higher areas

Figure 4. Two frameworks for neural oscillations underlying attention. (A) Sustained attentional modulation of behavioral performance and neural oscillations. When endogenous attention is directed in a task (e.g., toward the right hemifield), the power of alpha oscillations in contralateral (left) frontal cortex decreases compared with ipsilateral cortex, associated with a mean difference in behavioral performance between attended (right) and unattended (left) conditions. In visual cortex, a similar alpha asymmetry can be observed, accompanied by an opposite modulation of stimulus-induced gamma activity (i.e., an increased gamma synchrony in the attended condition compared with the unattended condition). (B) Rhythmic attentional modulation of behavioral performance and neural oscillations. In a cued detection task, detection performance fluctuates as a function of the stimulus onset asymmetry (SOA), or the phase of theta-band neural oscillation found in frontal–parietal areas and visual cortex. The slow theta oscillation provides a phasic modulation of the amplitude of other neural oscillations (e.g., gamma). When attention is directed (e.g., toward the right hemifield), the theta phase-dependent fluctuations in behavioral performance at the attended target are attenuated compared with the unattended condition. This is accompanied by reduced theta power and phase–amplitude coupling in visual areas contralateral to the attended location.

(e.g., FEF) and visual cortex (e.g., V4), implying that gamma activity has a more direct role in the top-down modulation of attention [122,123].

Although attentional deployment is often thought of as a 'sustained' process, whereby behavioral and neural activity remain stably modulated for a period of time, recent studies have also revealed a 'rhythmic' nature of attention. During goal-driven covert attention, in addition to the measured behavioral benefit at the attended target (e.g., increased sensitivity), performance nonetheless fluctuates in a periodic pattern as though subjects are shifting their attention between the target and distractors [124] (Figure 4B). For example, these fluctuations have been observed for two stimuli at different locations [125] or two overlapping stimuli with different features [126]. In humans, these performance fluctuations are found to depend on the phase of theta-band activity (3–8 Hz) in the frontal-parietal network as well as in visual cortex [9]. In addition to behavioral effects, the phase of theta oscillations also modulates the amplitude of oscillations in other frequencies both locally and remotely, a phenomenon called 'phase-amplitude coupling' (PAC). Specifically, the 'good' theta phase (i.e., periods with enhanced behavioral performance) is associated with increased stimulus-driven gamma power, whereas the 'poor' phase features stronger alpha oscillation [127]. Such fluctuations of higher frequency neural oscillations and behavioral performance in theta cycles suggest a mechanism of rhythmic attentional scanning when multiple items are represented simultaneously [128].

Trends in Cognitive Sciences

The theta rhythm has been shown to propagate across brain areas in various directions. For example, in the monkey, studies show a greater theta-band influence from ACC to the FEF during sensorimotor mapping [129], and from the FEF to LIP during a goal-driven attention task [127], highlighting the role of the frontal cortex in leading the theta-rhythmic control of attention. By contrast, Granger Causality (GC) analysis reveals a feedforward direction of theta-band influence along the macaque ventral visual pathway, which is in fact suppressed during attention. This observation suggests that a different type of theta activity is driven by simultaneously presented stimuli and progresses from early to late visual areas [130]. These differences in the direction of theta modulation (feedforward and feedback) could correspond to two different forms of attention, such as stimulus-driven and goal-directed attention, respectively.

Future research is needed to clarify the cellular- and circuit-level bases of the aforementioned effects during attention. What are the sources and pathways of different neural oscillations and their attentional modulation? How does the oscillatory field activity reflect and/or interact with collective neuronal activity (e.g., how might the theta-rhythm oscillations relate to the modulation of On/Off states?). Studies using different animal models could shed light on these questions by combining behavioral metrics, genetic tools (e.g., gamma-band optogenetic stimulation within the frontal-cingulate network and its attentional effect in mice [131]), and different levels of recordings (e.g., combined recordings of lower frequency LFP and intracellular membrane potentials during attention-like improvement of mice behaviors [64]).

Concluding remarks

In recent years, a wealth of research has focused on the neural mechanisms and circuits involved in different forms of attentional control in both humans and non-human model species and at different levels of analysis. Nonetheless, more work is needed to isolate the mechanisms by which sensory information is selectively processed and to identify the mechanisms that are both common and distinct across species and different types of attention (see Outstanding questions). However, in some ways, the expanded breadth of attention studies has already yielded progress on both fronts. For example, it has revealed a common role of long-range cortico-cortical and subcortical input to sensory cortex from motor-related structures across species and types of attention. Furthermore, recent evidence has highlighted the importance of examining the interface between sensory coding and the dynamics of internal brain states, regardless of what those dynamics reflect, such as global arousal or behavioral goals. We suspect that future work will continue to benefit from a focus on that interface.

Declaration of interests

None declared by authors.

Outstanding questions

How similar or different across species are the circuit motifs (e.g., long-range disinhibitory motifs within neocortex) involved in the modulation of sensory responses during goal-driven attention? Likewise, are the circuit motifs similar or different across different forms of goal-driven attention, such as spatial versus feature or object based?

To what extent is the salience of a stimulus a function of the proportion of neural resources involved in processing it? For example, we might assume that olfactory cues will be more salient than visual cues in an olfactory-dominant brain (e.g., mouse) than in a visually dominant one (e.g., marmoset). If true, does that principle generalize to within sensory modalities of the same species, such as face versus non-face objects in the primate brain, where faces are disproportionately represented? Could this be a mechanism underlying ethological salience?

How do neuromodulators (e.g., acetylcholine or norepinephrine) influence the dynamics of cortical traveling waves and states? What are the unique contributions of different neuromodulators to arousal and attention?

Fluctuations in cortical states and traveling waves (e.g., within retinotopic areas) have been shown to influence sensory processing across space [105]. Given the modularity of sensory cortices (e.g., tonotopy in auditory cortex and feature and object-selective modules in visual cortex), might the same fluctuations also influence sensory processing across features and objects?

What is the functional role of oscillatory LFP activity during attentional control? What is its relationship with changes in spiking activity and information coding within neural circuits?

References

1. Egeth, H.E. and Yantis, S. (1997) Visual attention: control, representation, and time course. *Annu. Rev. Psychol.* 48, 269–297
2. Mangun, G.R. (2012) *The Neuroscience of Attention: Attentional Control and Selection*, Oxford University Press
3. Driver, J. and Spence, C. (1998) Crossmodal attention. *Curr. Opin. Neurobiol.* 8, 245–253
4. Wimmer, R.D. *et al.* (2015) Thalamic control of sensory selection in divided attention. *Nature* 526, 705–709
5. Bisley, J.W. and Goldberg, M.E. (2003) Neuronal activity in the lateral intraparietal area and spatial attention. *Science* 299, 81–86
6. Zénon, A. and Krauzlis, R.J. (2012) Attention deficits without cortical neuronal deficits. *Nature* 489, 434–437
7. Gregoriou, G.G. *et al.* (2014) Lesions of prefrontal cortex reduce attentional modulation of neuronal responses and synchrony in V4. *Nat. Neurosci.* 17, 1003–1011

8. Speed, A. and Haider, B. (2021) Probing mechanisms of visual spatial attention in mice. *Trends Neurosci.* 44, 822–836

9. Helfrich, R.F. *et al.* (2018) Neural mechanisms of sustained attention are rhythmic. *Neuron.* 99, 854–865

10. Corbetta, M. *et al.* (2000) Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nat. Neurosci.* 3, 292–297

11. Theeuwes, J. (2010) Top-down and bottom-up control of visual selection. *Acta Psychol.* 135, 77–99

12. Buschman, T.J. and Miller, E.K. (2007) Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science* 315, 1860–1863

13. Corbetta, M. *et al.* (2008) The reorienting system of the human brain: from environment to theory of mind. *Neuron* 58, 306–324

14. Bowling, J.T. *et al.* (2020) Top-down versus bottom-up attention differentially modulate frontal-parietal connectivity. *Hum. Brain Mapp.* 41, 928–942

15. Awh, E. *et al.* (2012) Top-down versus bottom-up attentional control: a failed theoretical dichotomy. *Trends Cogn. Sci.* 16, 437–443

16. Anderson, B.A. *et al.* (2021) The past, present, and future of selection history. *Neurosci. Biobehav. Rev.* 130, 326–350

17. Wolfe, J.M. (2021) Guided Search 6.0: an updated model of visual search. *Psychon. Bull. Rev.* 28, 1060–1092

18. Bálint, R. (2009) Seelenlähmung des 'Schauens', optische Ataxie, räumliche Störung der Aufmerksamkeit. *Monatsschr. Psychiatr. Neurol.* 25, 51–66

19. Ferrier, D. (1876) *The Functions of the Brain*, G.P. Putnam's Sons

20. Moore, T. and Zirnsak, M. (2017) Neural mechanisms of selective visual attention. *Annu. Rev. Psychol.* 68, 47–72

21. Deubel, H. and Schneider, W.X. (1996) Saccade target selection and object recognition: evidence for a common attentional mechanism. *Vis. Res.* 36, 1827–1837

22. Li, H.-H. *et al.* (2021) Different computations underlie overt presaccadic and covert spatial attention. *Nat. Hum. Behav.* 5, 1418–1431

23. Rolfs, M. *et al.* (2013) Reach preparation enhances visual performance and appearance. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 368, 20130027

24. Hanning, N.M. *et al.* (2018) Independent selection of eye and hand targets suggests effector-specific attentional mechanisms. *Sci. Rep.* 8, 9434

25. Saber, G.T. *et al.* (2015) Saccade planning evokes topographically specific activity in the dorsal and ventral streams. *J. Neurosci.* 35, 245–252

26. Fischer, B. and Boch, R. (1981) Selection of visual targets activates prelunate cortical cells in trained rhesus monkey. *Exp. Brain Res.* 41, 431–433

27. Moore, T. (1999) Shape representations and visual guidance of saccadic eye movements. *Science* 285, 1914–1917

28. Moore, T. and Armstrong, K.M. (2003) Selective gating of visual signals by microstimulation of frontal cortex. *Nature* 421, 370–373

29. Steinmetz, N.A. and Moore, T. (2014) Eye movement preparation modulates neuronal responses in area V4 when dissociated from attentional demands. *Neuron* 83, 496–506

30. Klapetek, A. *et al.* (2016) Attention allocation before antisaccades. *J. Vis.* 16, 11

31. Moore, T. and Fallah, M. (2001) Control of eye movements and spatial attention. *Proc. Natl. Acad. Sci. U. S. A.* 98, 1273–1276

32. Moore, T. *et al.* (2003) Visuomotor origins of covert spatial attention. *Neuron* 40, 671–683

33. Grosbras, M.-H. and Paus, T. (2002) Transcranial magnetic stimulation of the human frontal eye field: effects on visual perception and attention. *J. Cogn. Neurosci.* 14, 1109–1120

34. Ruff, C.C. *et al.* (2006) Concurrent TMS-fMRI and psychophysics reveal frontal influences on human retinotopic visual cortex. *Curr. Biol.* 16, 1479–1488

35. Winkowski, D.E. and Knudsen, E.I. (2006) Top-down gain control of the auditory space map by gaze control circuitry in the barn owl. *Nature* 439, 336–339

36. Zhang, S. *et al.* (2014) Selective attention. Long-range and local circuits for top-down modulation of visual cortex processing. *Science* 345, 660–665

37. Wurtz, R.H. and Goldberg, M.E. (1971) Superior colliculus cell responses related to eye movements in awake monkeys. *Science* 171, 82–84

38. Quian Quiroga, R. *et al.* (2006) Movement intention is better predicted than attention in the posterior parietal cortex. *J. Neurosci.* 26, 3615–3620

39. Bruce, C.J. and Goldberg, M.E. (1985) Primate frontal eye fields . I . Single neurons discharging before saccades. *J. Neurophysiol.* 53, 603–635

40. Fox, M.D. *et al.* (2006) Spontaneous neuronal activity distinguishes human dorsal and ventral attention systems. *Proc. Natl. Acad. Sci. U. S. A.* 103, 10046–10051

41. Bollimunta, A. *et al.* (2018) Comparing frontal eye field and superior colliculus contributions to covert spatial attention. *Nat. Commun.* 9, 3553

42. Monosov, I.E. *et al.* (2011) The effects of prefrontal cortex inactivation on object responses of single neurons in the inferotemporal cortex during visual search. *J. Neurosci.* 31, 15956–15961

43. Noudoost, B. and Moore, T. (2011) Control of visual cortical signals by prefrontal dopamine. *Nature* 474, 372–375

44. Anderson, J.C. *et al.* (2011) Pathways of attention: synaptic relationships of frontal eye field to V4, lateral intraparietal cortex, and area 46 in macaque monkey. *J. Neurosci.* 31, 10872–10881

45. Stanton, G.B. *et al.* (1995) Topography of projections to posterior cortical areas from the macaque frontal eye fields. *J. Comp. Neurol.* 353, 291–305

46. Wang, X.J. (2001) Synaptic reverberation underlying mnemonic persistent activity. *Trends Neurosci.* 24, 455–463

47. Hart, E. and Huk, A.C. (2020) Recurrent circuit dynamics underlie persistent activity in the macaque frontoparietal network. *Elife* 9, e52460

48. Jonikaitis, D. *et al.* (2023) Dissociating the contributions of frontal eye field activity to spatial working memory and motor preparation. *J. Neurosci.* 43, 8681–8689

49. Merrikhi, Y. *et al.* (2017) Spatial working memory alters the efficacy of input to visual cortex. *Nat. Commun.* 8, 1–10

50. Mueller, A. *et al.* (2020) Dopamine receptor expression among local and visual cortex-projecting frontal eye field neurons. *Cereb. Cortex* 30, 148–164

51. Ott, T. and Nieder, A. (2019) Dopamine and cognitive control in prefrontal cortex. *Trends Cogn. Sci.* 23, 213–234

52. Noudoost, B. *et al.* (2021) Working memory gates visual input to primate prefrontal neurons. *Elife* 10, e64814

53. Stemmann, H. and Freiwald, W.A. (2016) Attentive motion discrimination recruits an area in inferotemporal cortex. *J. Neurosci.* 36, 11918–11928

54. Bogadhi, A.R. *et al.* (2018) Brain regions modulated during covert visual attention in the macaque. *Sci. Rep.* 8, 15237

55. Stemmann, H. and Freiwald, W.A. (2019) Evidence for an attentional priority map in inferotemporal cortex. *Proc. Natl. Acad. Sci. U. S. A.* 116, 23797–23805

56. Bogadhi, A.R. *et al.* (2021) Midbrain activity shapes high-level visual properties in the primate temporal cortex. *Neuron* 109, 690–699

57. Bogadhi, A.R. *et al.* (2019) Spatial attention deficits are causally linked to an area in macaque temporal cortex. *Curr. Biol.* 29, 726–736

58. Sani, I. *et al.* (2019) Functionally defined white matter of the macaque monkey brain reveals a dorso-ventral attention network. *Elife* 8, e40520

59. Ward, M.K. *et al.* (2015) Mapping the macaque superior temporal sulcus: functional delineation of vergence and version eye-movement-related activity. *J. Neurosci.* 35, 7428–7442

60. Patel, G.H. *et al.* (2015) Functional evolution of new and expanded attention networks in humans. *Proc. Natl. Acad. Sci. U. S. A.* 112, 9454–9459

61. Sani, I. *et al.* (2021) The human endogenous attentional control network includes a ventro-temporal cortical node. *Nat. Commun.* 12, 360

62. Kim, H. *et al.* (2016) Prefrontal parvalbumin neurons in control of attention. *Cell* 164, 208–218

63. Wang, L. and Krauzlis, R.J. (2018) Visual selective attention in mice. *Curr. Biol.* 28, 676–685

64. Speed, A. *et al.* (2020) Spatial attention enhances network, cellular and subthreshold responses in mouse visual cortex. *Nat. Commun.* 11, 505

65. You, W.-K. and Mysore, S.P. (2020) Endogenous and exogenous control of visuospatial selective attention in freely behaving mice. *Nat. Commun.* 11, 1986

66. Huda, R. *et al.* (2020) Distinct prefrontal top-down circuits differentially modulate sensorimotor behavior. *Nat. Commun.* 11, 6007

67. Gabbott, P.L. and Bacon, S.J. (1997) Vasoactive intestinal poly-peptide containing neurones in monkey medial prefrontal cortex (mPFC): colocalisation with calretinin. *Brain Res.* 744, 179–184

68. Zaitsev, A.V. (2009) Interneuron diversity in layers 2-3 of monkey prefrontal cortex. *Cereb. Cortex* 19, 1597–1615

69. Froudist-Walsh, S. *et al.* (2021) A dopamine gradient controls access to distributed working memory in the large-scale monkey cortex. *Neuron* 109, 3500–3520

70. Hu, F. *et al.* (2019) Prefrontal corticotectal neurons enhance visual processing through the superior colliculus and pulvinar thalamus. *Neuron* 104, 1141–1152

71. Wise, S.P. (2008) Forward frontal fields: phylogeny and funda-mental function. *Trends Neurosci.* 31, 599–608

72. Schall, J.D. (1997) Visuomotor areas of the frontal lobe. In *Extrastriate Cortex in Primates* (Rockland, K.S. *et al.*, eds), pp. 527–638, Springer, US

73. Huerta, M.F. and Kaas, J.H. (1990) Supplementary eye field as defined by intracortical microstimulation: connections in macaques. *J. Comp. Neurol.* 293, 299–330

74. Kastner, S. *et al.* (1999) Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron* 22, 751–761

75. Knudsen, E.I. (2007) Fundamental components of attention. *Annu. Rev. Neurosci.* 30, 57–78

76. Cerf, M. *et al.* (2009) Faces and text attract gaze independent of the task: Experimental data and computer model. *J. Vis.* 9, 10.1–15

77. Mysore, S.P. *et al.* (2011) Signaling of the strongest stimulus in the owl optic tectum. *J. Neurosci.* 31, 5186–5196

78. White, B.J. *et al.* (2017) Superior colliculus neurons encode a visual saliency map during free viewing of natural dynamic video. *Nat. Commun.* 8, 14263

79. Egeth, H. *et al.* (1972) Parallel processing of multielement displays. *Cogn. Psychol.* 3, 674–698

80. Itti, L. *et al.* (1998) A model of saliency-based visual attention for rapid scene analysis. *IEEE Trans. Pattern Anal. Mach. Intell.* 20, 1254–1259

81. Koch, C. and Ullman, S. (1985) Shifts in selective visual atten-tion: towards the underlying neural circuitry. *Hum. Neurobiol.* 4, 219–227

82. Treisman, A.M. and Gelade, G. (1980) A feature-integration theory of attention. *Cogn. Psychol.* 12, 97–136

83. Salinas, E. *et al.* (2019) Voluntary and involuntary contributions to perceptually guided saccadic choices resolved with millisec-ond precision. *Elife* 8, e46359

84. Soltani, A. and Koch, C. (2010) Visual saliency computations: mechanisms, constraints, and the effect of feedback. *J. Neurosci.* 30, 12831–12843

85. Constantinidis, C. and Steinmetz, M.A. (2005) Posterior parietal cortex automatically encodes the location of salient stimuli. *J. Neurosci.* 25, 233–238

86. Gottlieb, J.P. *et al.* (1998) The representation of visual salience in monkey parietal cortex. *Nature* 391, 481–484

87. Katsuki, F. and Constantinidis, C. (2012) Early involvement of prefrontal cortex in visual bottom-up attention. *Nat. Neurosci.* 15, 1160–1166

88. Thompson, K.G. and Bichot, N.P. (2005) A visual salience map in the primate frontal eye field. *Prog. Brain Res.* 147, 251–262

89. White, B.J. *et al.* (2017) Superior colliculus encodes visual saliency before the primary visual cortex. *Proc. Natl. Acad. Sci. U. S. A.* 114, 9451–9456

90. White, B.J. *et al.* (2019) Superior colliculus encodes visual saliency during smooth pursuit eye movements. *Eur. J. Neurosci.* 54, 4258–4268

91. Chen, X. *et al.* (2020) Parietal cortex regulates visual salience and salience-driven behavior. *Neuron* 106, 177–187

92. Mohler, C.W. *et al.* (1973) Visual receptive fields of frontal eye field neurons. *Brain Res.* 61, 385–389

93. Kincade, J.M. *et al.* (2005) An event-related functional magnetic resonance imaging study of voluntary and stimulus-driven orienting of attention. *J. Neurosci.* 25, 4593–4604

94. Serences, J.T. and Yantis, S. (2007) Spatially selective repre-sentations of voluntary and stimulus-driven attentional priority in human occipital, parietal, and frontal cortex. *Cereb. Cortex* 17, 284–293

95. Geng, J.J. and Mangun, G.R. (2009) Anterior intraparietal sulcus is sensitive to bottom-up attention driven by stimulus salience. *J. Cogn. Neurosci.* 21, 1584–1601

96. Harris, K.D. and Thiele, A. (2011) Cortical state and attention. *Nat. Rev. Neurosci.* 12, 509–523

97. Vinck, M. *et al.* (2015) Arousal and locomotion make distinct contributions to cortical activity patterns and visual encoding. *Neuron* 86, 740–754

98. Beaman, C.B. *et al.* (2017) Sensory coding accuracy and per-ceptual performance are improved during the desynchronized cortical state. *Nat. Commun.* 8, 1308

99. Herrero, J.L. *et al.* (2008) Acetylcholine contributes through muscarinic receptors to attentional modulation in V1. *Nature* 454, 1110–1114

100. Lee, S.-H. and Dan, Y. (2012) Neuromodulation of brain states. *Neuron* 76, 209–222

101. Pinto, L. *et al.* (2013) Fast modulation of visual perception by basal forebrain cholinergic neurons. *Nat. Neurosci.* 16, 1857–1863

102. Steriade, M. *et al.* (1993) Thalamocortical oscillations in the sleeping and aroused brain. *Science* 262, 679–685

103. Vyazovskiy, V.V. *et al.* (2011) Local sleep in awake rats. *Nature* 472, 443–447

104. McGinley, M.J. *et al.* (2015) Waking state: rapid variations mod-ulate neural and behavioral responses. *Neuron* 87, 1143–1161

105. Davis, Z.W. *et al.* (2020) Spontaneous travelling cortical waves gate perception in behaving primates. *Nature* 587, 432–436

106. Petersen, C.C.H. *et al.* (2003) Interaction of sensory responses with spontaneous depolarization in layer 2/3 barrel cortex. *Proc. Natl. Acad. Sci. U. S. A.* 100, 13638–13643

107. Engel, T.A. *et al.* (2016) Selective modulation of cortical state during spatial attention. *Science* 354, 1140 LP – 1144

108. van Kempen, J. *et al.* (2021) Top-down coordination of local cortical state during selective attention. *Neuron* 109, 894–904

109. Tan, A.Y.Y. *et al.* (2014) Sensory stimulation shifts visual cortex from synchronous to asynchronous states. *Nature* 509, 226–229

110. Shi, Y.-L. *et al.* (2022) Cortical state dynamics and selective at-tention define the spatial pattern of correlated variability in neo-cortex. *Nat. Commun.* 13, 44

111. Jercog, D. *et al.* (2017) UP-DOWN cortical dynamics reflect state transitions in a bistable network. *Elife* 6, e22425

112. Levenstein, D. *et al.* (2019) NREM sleep in the rodent neocortex and hippocampus reflects excitable dynamics. *Nat. Commun.* 10, 2478

113. Worden, M.S. *et al.* (2000) Anticipatory biasing of visuospatial attention indexed by retinotopically specific α-band electroen-cephalography increases over occipital cortex. *J. Neurosci.* 20, RC63

114. Foxe, J.J. and Snyder, A.C. (2011) The role of alpha-band brain oscillations as a sensory suppression mechanism during selec-tive attention. *Front. Psychol.* 2, 154

115. Foster, J.J. and Awh, E. (2019) The role of alpha oscillations in spatial attention: limited evidence for a suppression account. *Curr. Opin. Psychol.* 29, 34–40

116. Bagherzadeh, Y. *et al.* (2020) Alpha synchrony and the neurofeedback control of spatial attention. *Neuron* 105, 577–587

117. Fries, P. *et al.* (2008) The effects of visual stimulation and selective visual attention on rhythmic neuronal synchronization in macaque area V4. *J. Neurosci.* 28, 4823–4835

118. Magazzini, L. and Singh, K.D. (2018) Spatial attention modulates visual gamma oscillations across the human ventral stream. *Neuroimage* 166, 219–229

119. van Kerkoerle, T. *et al.* (2014) Alpha and gamma oscillations characterize feedback and feedforward processing in monkey visual cortex. *Proc. Natl. Acad. Sci. U. S. A.* 111, 14332–14341

120. Buffalo, E. *et al.* (2011) Laminar differences in gamma and alpha coherence in the ventral stream. *Proc. Natl. Acad. Sci. U. S. A.* 108, 11262–11267

121. Popov, X.T. *et al.* (2017) FEF-controlled alpha delay activity precedes stimulus-induced gamma-band activity in visual cortex. *J. Neurosci.* 37, 4117–4127

122. Gregoriou, G.G. *et al.* (2009) High-frequency, long-range coupling between prefrontal and visual cortex during attention. *Science* 324, 1207–1210

123. Voloh, B. *et al.* (2015) Theta-gamma coordination between anterior cingulate and prefrontal cortex indexes correct attention shifts. *Proc. Natl. Acad. Sci. U. S. A.* 112, 8457–8462

124. Fiebelkorn, I.C. *et al.* (2013) Rhythmic sampling within and between objects despite sustained attention at a cued location. *Curr. Biol.* 23, 2553–2558

125. Landau, A.N. and Fries, P. (2012) Attention samples stimuli rhythmically. *Curr. Biol.* 22, 1000–1004

126. Re, D. *et al.* (2019) Feature-based attention samples stimuli rhythmically. *Curr. Biol.* 29, 693–699

127. Fiebelkorn, I.C. and Pinsk, M.A. (2018) A dynamic interplay within the frontoparietal network underlies rhythmic spatial attention. *Neuron* 99, 842–853

128. Fries, P. (2023) Rhythmic attentional scanning. *Neuron* 111, 954–970

129. Babapoor-Farrokhran, S. *et al.* (2017) Theta and beta synchrony coordinate frontal eye fields and anterior cingulate cortex during sensorimotor mapping. *Nat. Commun.* 8, 13967

130. Spyropoulos, G. *et al.* (2018) A theta rhythm in macaque visual cortex and its attentional modulation. *Proc. Natl. Acad. Sci. U. S. A.* 115, E5614–E5623

131. Norman, K.J. *et al.* (2021) Post-error recruitment of frontal sensory cortical projections promotes attention in mice. *Neuron* 109, 1202–1213

132. Pouget, P. *et al.* (2009) Visual and motor connectivity and the distribution of calcium-binding proteins in macaque frontal eye field: implications for saccade target selection. *Front. Neuroanat.* 3, 2

133. Wurtz, R.H. and Mohler, C.W. (1976) Organization of monkey superior colliculus: enhanced visual response of superficial layer cells. *J. Neurophysiol.* 39, 745–765

134. Goldberg, M.E. and Bushnell, M.C. (1981) Behavioral enhancement of visual responses in monkey cerebral cortex. II. Modulation in frontal eye fields specifically related to saccades. *J. Neurophysiol.* 46, 773–787

135. Ignashchenkova, A. *et al.* (2004) Neuron-specific contribution of the superior colliculus to overt and covert shifts of attention. *Nat. Neurosci.* 7, 56–64

136. Niell, C.M. and Stryker, M.P. (2010) Modulation of visual responses by behavioral state in mouse visual cortex. *Neuron* 65, 472–479

137. Noudoost, B. *et al.* (2010) Top-down control of visual attention. *Curr. Opin. Neurobiol.* 20, 183–190

138. Saleem, A.B. *et al.* (2013) Integration of visual motion and locomotion in mouse visual cortex. *Nat. Neurosci.* 16, 1864–1869

139. Erisken, S. *et al.* (2014) Effects of locomotion extend throughout the mouse early visual system. *Curr. Biol.* 24, 2899–2907

140. Bennett, C. *et al.* (2013) Subthreshold mechanisms underlying state-dependent modulation of visual responses. *Neuron* 80, 350–357

141. McBride, E.G. *et al.* (2019) Local and global influences of visual spatial selection and locomotion in mouse primary visual cortex. *Curr. Biol.* 29, 1592–1605

142. Fu, Y. *et al.* (2014) A cortical circuit for gain control by behavioral state. *Cell* 156, 1139–1152

143. Ferguson, K.A. and Cardin, J.A. (2020) Mechanisms underlying gain modulation in the cortex. *Nat. Rev. Neurosci.* 21, 80–92

144. Lee, A.M. *et al.* (2014) Identification of a brainstem circuit regulating visual cortical state in parallel with locomotion. *Neuron* 83, 455–466