Review

Common and distinct neural mechanisms of attention

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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-directed 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.

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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 in-
deed 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 his-
tory contributes independently of task goals and stimulus salience [15,16], adding a third poten-
tial 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 neces-
sarily 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 [26] and non-human primates [27–28]. 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 (dIPFC) 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.
Both visual and attention-related activity in this area are dependent upon input from the SC and FEF, and this area is directly connected with areas implicated in attentional control within parietal cortex and PFC. This region of temporal cortex is also strongly activated during different types of visually guided eye movements, specifically vergence, smooth pursuit, and saccadic eye movements. 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.

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 [3]). 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 Nie and Stryker [139], 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 [138]. 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.

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.

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].
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.
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
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 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).

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).

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-episodes 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 arousional 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...
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].
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.

Acknowledgments
We thank E.B. Trepka and M.F. Panichello for comments on the manuscript. This work was supported by National Institutes of Health grants EY014924 (to T.M.), RF1DA055666 (to T.A.E.), EY029759 (to X.C.), and the Feil Family Foundation (to T.A.E.), the Alfred P. Sloan Foundation Research Fellowship (to T.A.E.), and a Ben Barres Professorship (to T.M.).

Declaration of interests
None declared by authors.

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