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How the brain shifts between external and internal attention

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SUMMARY

Focusing on relevant contents to guide adaptive behavior is a core property of the brain. For decades, scientists have investigated mechanisms to anticipate, select, prioritize, and prepare sensory signals according to goals, memories, and salient events. More recently, researchers have considered how these attention functions operate within internal representations. However, neither external nor internal attention in isolation captures everyday behavior. The brain frequently and seamlessly shifts between contents from the sensory stream and those held in mind. In this perspective, we ask how the brain shifts between external and internal attention. We describe similarities and differences between selective external and internal attention, present competing hypotheses regarding the operating principles of between-domain shifts, and highlight putative brain areas and mechanisms. We discuss the scarce experimental forays comparing attention shifts between vs. within domains and contemplate how these constrain theoretical and computational models. We conclude by suggesting open questions to guide investigation.

SELECTING RELEVANT CONTENTS TO GUIDE BEHAVIOR

A basic requirement of successful behavior is picking out relevant contents from the many competing offerings. This primordial ecological task is the responsibility of selective attention (hereafter attention for short). Attention comprises the functions that anticipate, select, prioritize, and prepare contents to guide behavior.[1] These abilities confer a strong selection advantage and undoubtedly played an important role in the evolution of flexible and adaptive primate cognition.

Attention, therefore, is an essential infrastructural property of the brain. Investigation of its laws and workings has been central since the dawn of experimental psychology as a scientific discipline.[2–5] Today, attention remains a thriving experimental field, with researchers revealing principled mechanisms at various scales of organization—from behavior to large-scale networks, systems, and cells.

For most of its history, attention research has been concerned with unpicking how we apprehend relevant signals from the external sensory environment. Yet, from early theoretical descriptions, it was acknowledged that selective attention also operates within the internal environment of the mind to focus on useful memories and ideas to inform behavior.[4] As the scientific field matured, research began to address how the brain modulates activity related to mental representations to guide performance.[6–8] The investigation of internal attention still considerably lags its external counterpart, but it is gaining momentum in revealing the neural systems, dynamics, and mechanisms for up- and downregulating internal contents. Most investigations concern focusing attention within the domain of working memory, although in principle similar approaches can be applied to other types of internal domains, such as long-term memory.[9]

The time is ripe for the next major upgrade in attention research—to address a foundational matter that has received surprisingly little consideration: how the brain shifts between contents in the external and internal domains. Many tasks for investigating attention, directed either externally or internally, have relied on one-shot interactions with simple perceptual or working-memory arrays. In these situations, it is sufficient to consider external or internal attention in isolation. However, in natural, temporally extended, and dynamic contexts, the seamless crosstalk between external and internal attention becomes clear. Most everyday tasks involve shifting between sensory and memory contents iteratively to guide behavior. Cycling to work, for example, we focus on the road ahead, crossing pedestrians, and moving cars as we remember the turns to take, potholes along the way, and the child on a scooter we just passed.

We use “external” and “internal” contents as a shorthand for neural signals related to processing stimuli from the external, sensory stream vs. internal representations untethered to the sensory stream, respectively. We acknowledge that all neural signals are ultimately internal to the brain. Nevertheless, the distinction is vital. As we go about our routine activities, we select contents from the external environment as they are processed *de novo* in sensory, associative, and motor regions, or from contents available from previous experience accessible only through their neural engrams.

How the brain shifts attention between external and internal contents is a fundamental building block of flexible cognition and a core aspect of how the brain engages adaptively during its interactions with the world. The distinction between external

Box 1. External and internal modes of cognition

Most research into the neural basis of behavior and cognition has concentrated on understanding our interface with external sensory signals to drive behaviors such as action, decision-making, and learning. Starting by investigating this externally facing, perceptual mode of cognition made sense. It enabled rigorous systematic control over the input stimulation, which is fundamental to understanding the lawful relations between the sensory environment and the corresponding neural or behavioral responses.[3,10] These external modes of cognition may occur in the presence of actual sensory input (e.g., focusing on the car in front of us) or in its absence (e.g., anticipating the appearance of a car).[11]

As methods advanced, researchers have increasingly embraced the investigation of internal modes of cognition. Internal cognitive modes are many and varied. To our knowledge, there is no agreed-upon definitive taxonomy.[12,13] Internal cognitive modes are defined by mental processing decoupled from the external perceptual environment, regardless of the presence or absence of external stimuli.[14] They can bear different degrees of proximity to external sensory processing. Some can be dependent upon sensory processing, such as in the recollection of memories from different timescales,[9] while others build on past experience more loosely, such as imagination, creativity, prospection, planning, and mind wandering.[15–17] Internal modes also span from adaptive to potentially harmful—for instance, from peaceful meditation to self-denigrating rumination.

Proposals are beginning to emerge about the relationship between the external and internal cognitive modes. Some proposals emphasize antagonistic properties and argue for a competitive relationship.[18–20] Others suggest that external and internal modes can coexist without competition unless they draw on shared and limited high-level processing, such as intentionality.[14] Still others propose that the two modes are adaptively complementary.[21] They highlight the ubiquity of cycling between external and internal modes at multiple timescales, from tens of milliseconds to the circadian sleep-wake cycle, and stress the computational utility of fluctuating between modes for neural plasticity and learning. Not surprisingly, there are many more interesting open questions than reliable answers at this early stage of inquiry.

and internal attention is separate from the broader differentiation between externally and internally directed modes of cognition (Box 1).

EXTERNAL ATTENTION

Attention research comprises a longstanding, productive community combining rigorous psychophysics with sensitive neural measures across spatial scales—networks, regions, circuits, cells, and molecules.[22,23] Most research continues to examine the pickup and processing of signals coming from the sensory stream. The result is an advanced and growing understanding of the behavioral and neural mechanisms of external attention control and modulation.

Attention-related modulation of sensory signals results from bottom-up factors related to the intrinsic stimulus salience, top-down factors related to goals, and contextual factors related to memory traces of different types and time scales.[9]

These different sources of attention improve perception through distinctive psychophysical mechanisms, which are further influenced by the sensory and motor characteristics of task.[24] A large-scale network of multisensory dorsal parietal and frontal regions, together with integrative subcortical regions, controls the focus of spatial, object-based, and feature-based attention.[25] The dorsal frontoparietal network is closely related to regions involved in oculomotor control.[26,27] Signals from the frontoparietal network interact with ongoing processing in cortical and subcortical regions, modulating activity according to neuronal receptive-field properties. Many types of cellular and circuit-level modulatory mechanisms have been revealed, such as elevating tonic activity,[28] enhancing neuronal responses,[29] filtering out competing signals,[30,31] changing noise levels,[32,33] and synchronizing neuronal firing.[34] Attention-related modulation occurs across various sensory[35] and motor areas.[36]

Contributions of neural oscillations to regulating excitability and routing of various signals to promote the binding of perceptual objects are increasingly entertained.[37] Studies densely sampling behavior at various intervals after a transient event have revealed a rhythmic fluctuation in the quality of perception within the 3–8 Hz range.[38,39] The coupling of neural oscillations in attention-control and visual areas with these behavioral fluctuations suggests they play a causal role in attention functions.[40,41]

In addition, attention functions also operate on information not directly mapped onto receptive-field properties, such as the timing of events[8,42,43] or higher-order attributes of stimuli, such as semantic properties.[44,45] A full, integrated understanding of the psychological and neural principles and mechanisms of external attention is still on the horizon, but many pieces of the puzzle are in place.

INTERNAL ATTENTION

The ability to direct attention selectively to one among multiple representations held in mind has long been recognized. It is part of the most rehearsed definition of attention, which emphasizes selective processing of objects or *trains of thought*.[4] Nevertheless, the empirical investigation of "internal attention" greatly lagged its external counterpart. The contemporary study of internal attention opened with working-memory studies that introduced retroactively informative cues (retrocues) during the delay interval.[6,46] Retrocues that predict which item of a multi-item working-memory array will be relevant at the end of the trial confer significant performance benefits. The large and reproducible behavioral benefits of retrocues overturned the standard view that attention was ineffective beyond very brief sensory memories.[47] Since the early retrocue studies, we have come to recognize that internal attention operates in many task situations and can be triggered by multiple factors, such as sensory-driven capture, internal states, or intended action plans.[8]

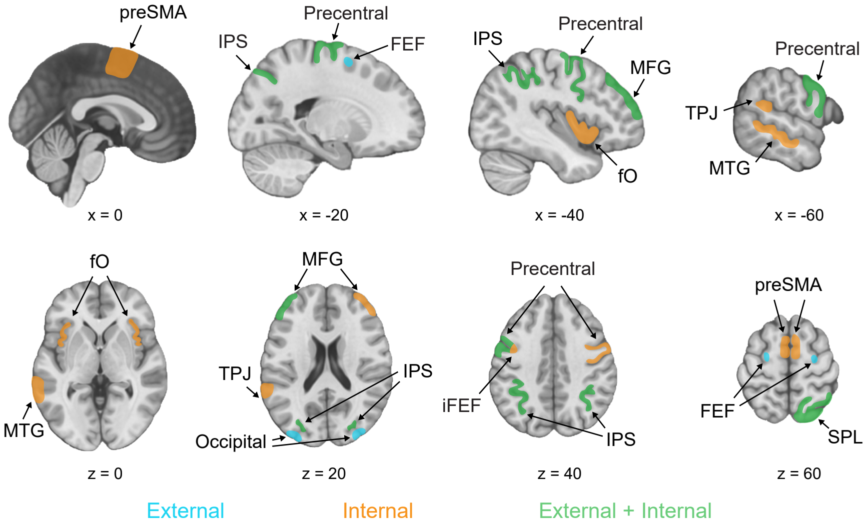

Figure 1. External and internal control areas

fMRI meta-analysis results based on Wallis et al.[60] Blue areas indicate activation during external attention, orange areas during internal attention, and green areas reflect regions activated during both. preSMA, pre-supplementary motor area; FEF, frontal eye field; MFG, middle frontal gyrus; IPS, intraparietal sulcus; fO, frontoinsular cortex; TPJ, temporoparietal junction; MTG, middle temporal gyrus; iFEF, inferior frontal eye field; SPL, superior parietal lobule.

Over its shorter time span, research on internal attention has made significant headway. Some behavioral findings are truly intriguing, such as evidence that focusing on specific content within working memory does more than merely prevent degradation of information through decay or interference. Instead, performance is improved after a retrocue and a further delay compared with when the content is probed earlier.[48,49] In some cases, internal attention can also improve the representational quality of the content that is reported.[50]

Similarities between external and internal attention

Many similarities between external and internal attention have been noted.[51,52] Like external attention, internal attention can be oriented based on spatial location,[6,46] objects,[53] features,[54] intended actions,[55,56] and temporal intervals.[57] Shifts of internal attention can also be voluntary or automatically driven by sensory events matching internal contents.[58]

Neurally, both external and internal shifts of attention engage the dorsal frontoparietal network[7,59,60] (Figure 1) and modulate various sensory areas based on receptive-field properties.[61–64] Both types of shifts are strongly related to oculomotor control and co-vary with microsaccades.[65–67] Similar to external attention, strong spatiotopic modulation of alpha-band activity marks changes in visual excitability resulting from internal attention.[60,68,69] Moreover, functional magnetic resonance imaging (fMRI) evidence reveals overlapping activation patterns in human parietal and visual cortices during external and internal attentional selection, suggesting some shared mechanisms.[70]

Intriguingly, dense behavioral sampling in working-memory tasks has also revealed rhythmic fluctuations in performance at similar frequencies as in perceptual studies.[71–73] Neural studies linking behavioral performance to rhythmic activity in attention-control areas are still wanting, but one human intracranial study has reported oscillatory processes in the hippocampus related to working-memory load and performance.[74]

Differences between external and internal attention

Important differences have also been highlighted between external and internal attention.[75] The different substrates on which external vs. internal attention operate provide different affordances. External attention operates on the crowded sensory canvas where stimuli compete for perceptual processing. At any given moment, focusing on one content means simultaneously degrading the processing of competing content. By contrast, internal attention in working memory operates on just a few encoded and processed contents previously extracted from the competitive perceptual process, likely enabling more effective integration and separation of these internal representations.[76,77] In addition to sensory attributes, motor affordances related to the encoded stimulus have also been extracted and are ready to be deployed or modulated.[78]

In contrast to external attention, behavioral studies show that internal attention can be flexibly deployed with minimal cost to concurrently unattended representations.[8] This is supported by tasks in which the probability of probing a memory item changes with the passage of time, revealing that attention can be dynamically and reversibly oriented within working memory.[57] In such tasks, participants are more likely to be probed about the object on one side of the screen after a short interval but about the object on the other side after a long interval. When probed early, performance—measured by accuracy and response time—is better for the item expected at that time and worse for the less likely item. However, when probed late, attention shifts to the initially unattended item. Performance for the previously degraded item recovers fully and exceeds performance for the previously attended item, which is now unexpected.

Neural studies also emphasize distinctive characteristics of internal attention. In addition to engaging the dorsal frontoparietal network, internal attention recruits medial and ventrolateral prefrontal regions (Figure 1).[7,59,60] These have been speculated to reflect selection and preparation of relevant internal contents for response output (i.e., output gating).[75] Neurophysiological observations suggest that additional frontal processes start early during internal shifts of attention.[6] External and internal attention produce distinct time courses of visual modulation: anticipatory spatial attention sustains spatiotopic alpha-band modulation until stimulus onset, whereas retrospective attention induces only a transient alpha change.[60] The findings bolstered the interpretation that internal attention can effectively select and reconfigure content to guide action without continued sustained attention.[75]

The future-facing nature of working-memory representations becomes clear in tasks that link working-memory items with prospective actions. When maintaining two items in working memory, each randomly located in different visual fields and linked to different response hands, a central probe triggers simultaneous selection of the item's position and the associated motor plan.[79] Additional evidence suggests that multiple and concurrent modulatory functions of attention are readily observed within the internal domain.[78] For example, microsaccade proxies of internal attention revealed concurrent modulation by voluntary and automatic attention.[58] This characteristic may derive from the better-separated representations of items in working memory.

Studies of internal attention in animal models are just beginning. A landmark study comparing external and internal attention in macaques[80] extends observations from human studies.[81] Monkeys benefited from spatial retrocues that directed attention to relevant items maintained in working memory, improving their accuracy in reporting the items' colors. The brain regions investigated (lateral prefrontal cortex, frontal eye fields, lateral intraparietal sulcus, and visual area V4) were sensitive to both external and internal spatial cues, with prefrontal areas showing a shared spatial attention code. As in the human work, interesting differences also emerged. Internal attention uniquely transformed the cued item into a different neural subspace that was invariant to the original position of the item, in line with proposals of output gating based on human studies.[75]

Contemplating the similarities and differences between mechanisms for control and modulation in external and internal attention provides a much richer perspective on the infrastructural attention functions than considering each domain in isolation. The composite view showcases the multiplicity of ways in which the brain can anticipate, select, prioritize, and prepare contents either from the sensory stream or from internal representations to guide behavior. Yet, this leaves untouched the next big question: how attention functions operate when crossing the boundary between the sensory stream and internal representations. Understanding shifts of attention between domains requires new experimental approaches, careful consideration of interrelations between representations in the different domains, and the formulation of tractable hypotheses.

THE BACK AND FORTH OF EXTERNAL AND INTERNAL ATTENTION IN EXTENDED CONTEXTS

In laboratory studies, people perform perceptual or working-memory tasks, shifting attention externally or internally on a trial-by-trial basis. In natural behavior, however, we seamlessly draw on both external stimulation and internal contents as we engage with the world.

Reflecting this everyday demand, studies of visually guided behavior in virtual-reality contexts reveal a continuous back-and-forth between sampling information from the external environment vs. relying on available internal representations.[82–84] While standard experimental tasks have repeatedly demonstrated that working-memory capacity is limited to around four items,[85,86] participants in immersive environments often fall well short of utilizing their theorized working-memory capacity. In a classic immersive working-memory task, participants copy a model stimulus array by picking up the corresponding pieces from a resource pool and placing them in the same array configuration within a workspace.[87] How much participants rely on internal working-memory representations can be estimated by measuring when participants look at the model during copying. Strikingly, participants rely on just over one object attribute on average, rather than loading multiple items into memory. After picking up a matching object identity from the resource pool, they frequently re-inspect the model to confirm its location before placing it in the workspace. As a result, memory demands remain surprisingly low through iterative alternation between perceptual and memory sampling. A fascinating question is what happens at these points of sensorimnemonic choice when deciding whether to rely on internal representations or sample external input. We know next to nothing about the factors determining these decisions[82] and how, in turn, the brain shifts its focus between sensory and memory contents.

While studies on sensorimnemonic decisions during natural, free-flowing behavior remain relatively rare, an increasing number of studies now manipulate both external and internal attentional demands at the trial level to mirror everyday multitasking situations.[88] For example, a recent electroencephalography (EEG) study[89] investigated the neural dynamics of returning to internal contents after interruption by an externally focused task. The findings revealed prompt reselection of both sensory and motor internal contents upon completion of the external task. Such experimental designs naturally elicit the spontaneous back-and-forth between external and internal domains without requiring explicit cues.

BETWEEN-DOMAIN SHIFTS: NEURAL POSSIBILITIES

Comparing attention shifts between visual sensory signals and working-memory representations provides a fruitful entry point into the broader investigation of between-domain shifts. The choice offers the most comprehensive experimental background on the mechanisms of external and internal attention. The visual sense, so developed in primates, dominates attention research, and internal attention has been studied almost exclusively within working memory. Starting from this safer vantage point should help advance the inquiry toward a richer understanding of how we seamlessly shift attention between different aspects of the multisensory stream and various types of internal representations—including working memory, long-term memory, and imagination—to guide intelligent, flexible behavior.

Overlap in external vs. internal contents in the brain

Understanding the relative natures of sensory vs. working-memory contents is an important first step in approaching between-domain shifts of attention. To what extent do these different contents draw on common neural processing and computations?

Our understanding is incomplete, but ample evidence points to strong commonalities and mutual interactions. The prevalent sensory-recruitment view of working memory suggests highly overlapping sensory processing serves both perception and working memory.[90–92] In the biased-competition model of attention, working-memory contents constitute the main source for top-down sensory modulation.[28,93] Indeed, items in working memory drive attention to matching sensory attributes even when disadvantageous for the sensory task.[94] In turn, sensory stimuli also automatically draw internal attention to working-memory items sharing their features.[58] So, whereas processing of sensory and working-memory contents could coexist entirely independently in principle, in practice they interact heavily.

Nevertheless, perceptual and working-memory contents are not coextensive. They generate distinct subjective experiences, and the brain must distinguish between them. A review of single-unit findings in visual perception and working memory in macaques suggests that earlier visual areas across ventral (V1-V2-V4) and dorsal (V1-V3-MT) streams mainly encode perceptual signals, whereas downstream areas contain populations of neurons that encode both sensory and working-memory signals.[95] Furthermore, even when sensory and working-memory contents are processed within a common region, they may recruit different neuronal populations and network-level activity. For example, in V1, sensory coding may be more dependent on feedforward input from the thalamus, whereas working memory may depend on top-down or reentrant activity into more superficial layers. Differences have also been observed in higher-order areas. Recordings in macaque prefrontal cortex show different spatial distributions and frequency compositions of oscillatory activity when coding the same feature values of stimuli being perceived directly vs. being recalled from memory.[96] In the macaque prefrontal cortex, some neurons specifically code either perceptually attended or remembered locations, whereas others code both. However, while hybrid neurons simultaneously represent both attended and memorized locations, their preferred locations for each domain differ.[97,98]

Human fMRI studies also highlight differences in the spatial tuning of stimulus processing during perception vs. working memory.[99] Population receptive-field mapping in visual areas shows sharp and strong spatial tuning during perception, which decreases progressively in spatial precision along the visual hierarchy. Instead, for working-memory representations, spatial tuning is weaker, less precise, and less variable across visual areas.[99]

Overlap in external and internal attention control

As described earlier, the neural systems for controlling external and internal attention involve many common areas and relate closely to oculomotor control. The granularity of this overlap, however, has not been scrutinized. Studies using sensitive, multivariate, or population coding methods to assess the direct functional overlap of neuronal populations are still missing (but see Panichello and Buschman[80]).

External and internal attention-control systems are both capable of modulating activity across sensory and motor areas.[1] However, it is not understood whether there are systematic differences in how the two modes of attention target their modulatory sites. There may be differences in exactly what neuronal populations or brain regions are preferentially targeted and in the specific mechanisms for routing information between control and modulation sites. For example, different oscillatory frequencies may help coordinate communication in the different cases (e.g., Buschman and Miller[100]).

The extent of functional overlap in control and modulatory sites and mechanisms will determine the degree of competition between external and internal attention. Ultimately, it will be fascinating to reveal how the external and internal attention-control systems differentially target external vs. internal contents for modulation while avoiding interference between the two.

Parallel or serial focus between domains

Understanding the points of independence and intersection between sensory and working-memory representations, and their control, is crucial for informing computational considerations of whether external and internal focus can proceed in parallel or necessarily compete. An interesting question is whether sensory and working-memory contents can be co-activated and independently modulated in tandem.

Findings so far hint at crosstalk and trade-offs between sensory and working-memory processing within visual areas. Brain-imaging studies have reported different amounts of interference between decodable working-memory content and visual stimulation during the delay. In one case, visual distraction eliminated decoding of memory contents in visual areas[101]; in another, the orientation of an irrelevant visual grating systematically biased the grating orientation in memory[102]; and in yet another, decoding of both memory and distracting visual content coexisted, depending on parameters of the distracting stimulus.[103] To the extent that working-memory representations require active visual processing, these interactions pose challenges to complete independence between external and internal contents. However, imaging methods are correlational, and the obligatory reliance of working memory on activity within visual areas remains an open question.[104]

Some studies point to a privileged role of association areas in maintaining working-memory contents.[105,106] While previous studies found varying levels of interference between sensory and memory content in the visual cortex,[101–103] activity in the posterior parietal cortex remained unaffected. The representational format in the parietal cortex during memory maintenance also differs from those in sensory areas, implying a transformation of representations to a more compressed or orthogonalized format that can better serve behavior.[103,106]

As insights emerge into the overlap between sensory and working-memory content within neuronal populations, brain areas, and networks, it will become possible to posit more cogent hypotheses regarding how external and internal contents coexist and whether attention functions can, at least partly, operate on both simultaneously. Multiple modulatory functions have been observed to operate in tandem within working memory, based on goals vs. sensory capture,[58] modulating sensory vs. motor attributes,[79] or selecting current vs. successive targets.[107] The precedent suggests that concurrent modulation may also be possible between external and internal contents targeting neuronal populations or brain regions that differentiate between them. Studies directly comparing sites and mechanisms of attention modulation for equivalent sensory vs. memory content—under matched task demands—at the cellular, population, and circuit levels are likely to be particularly informative (e.g., Panichello and Buschman[80]).

Controlled or competitive shifts between domains

At the extremes, two opposing scenarios could account for how the brain shifts between sensory and mnemonic contents. Shifting attention between the external and internal domains could invoke additional, superordinate control mechanisms or, alternatively, occur through a competitive process without additional controllers.

Invoking a master, superordinate controller is intuitive. As the brain evolved, simpler elements became controlled in increasingly sophisticated ways—such as going from a sensorimotor reflex (at the spinal cord level) to a habitual action (involving the motor cortex) to a contextualized action (engaging premotor regions) to a planned action (engaging prefrontal input).[108] In this vein, attention-control networks have been described for both visual sensory and working-memory processing. Perhaps, then, additional brain regions are invoked for the coordination and shifting of attention between these domains.

Within this scenario, an intuitive possibility is a superordinate control interposed between shifting external and internal attention, so that additional steps take place when shifting between domains (Figure 2A). Such a controller could determine whether the external or internal attention network has priority, with only the external or internal contents targeted by each network activated, respectively. Metaphors like a railroad switch at level crossings present themselves. Such a master control would likely leave behavioral traces. A clear prediction would be the slowing of attention shifts between domains compared with within domains.

However, other forms of superordinate control are also possible. Selective attention, in either domain, comprises several functions—anticipating, selecting, prioritizing, and preparing contents for behavior.[81] In principle, superordinate control functions could occur at any or multiple points (Figure 2B). For example, it may be possible to select and prioritize external and internal contents in parallel, but control functions may be necessary to mediate linking the relevant content to response output. The involvement of additional control functions may depend on the extent to which external and internal attention clash or compete for common neural processing at the various stages.[109,110] The specific points of additional control may become manifest depending on task parameters, like the degree of competition between stimulus material, sensorimotor rules, or response demands.

The alternative, no-master-control option, is harder to imagine but may be more parsimonious from a neural perspective (Figure 2C). Signals from external and internal contents may be modulated in tandem by their respective control networks. Dominance of one system over another may depend on the provenance of the relevant representational content at a given moment. Attractor network models provide an intuition for how distributed processing can lead to categorical representations through winner-take-all competition.[111] They can serve either decision-making or working memory[112] and, in principle, could be extended to incorporate competition between the sensory and working-memory domains.

Neural candidates for superordinate control

Should superordinate control exist, neighboring fields of inquiry offer hints regarding brain areas that might participate (Figure 3).

One suggestive candidate is the hippocampus. This old cortical structure is at the apex of the sensory hierarchy, at the interface with limbic structures.[113,114] It has been variously linked to learning and memory, novelty detection, exploration, navigation, imagination, and relational perception. The unifying computations that serve the breadth of its contributions are still avidly debated and may involve the ability to individuate, relate, and scaffold highly integrated signals within their spatial and temporal contexts (e.g., Ekstrom and Ranganath[115] and Murray et al.[116]). The hippocampus mediates both memory encoding and retrieval.[21] Given that encoding novel experiences (i.e., external signals) and retrieving relevant memories (i.e., internal signals) place opposing demands on the hippocampus, it has been suggested that the hippocampus alternates between external and internal sources of information by dynamically prioritizing different local circuitry.[117,118]

The hippocampus has been increasingly recognized to play a role in attention. Studies in macaques implicate the hippocampus in oculomotor control and suggest a role in memory-guided perception.[119] As previously noted, oculomotor control is closely related to covert spatial attention functions,[26,27,65–67] suggesting a putative contribution of the hippocampus in orchestrating attention-related perceptual vs. mnemonic sampling. Initial evidence is compatible with this possibility. Human neuropsychology and brain-imaging studies support the involvement of the hippocampus in guiding external attention based on long-term memory.[120–123] Moreover, hippocampal activity is also modulated by focusing attention on contextual attributes during encoding.[124] Poskanzer and Aly[122] observed increased functional connectivity of the hippocampus with the basal forebrain vs. the dorsal frontoparietal network when guiding attention by external vs. memory cues, respectively. The findings raise the possibility that the basal forebrain and dorsal frontoparietal regions prompt a transition between external and internal hippocampal modes.[122] Their findings echo rodent studies and computational modeling suggesting that cholinergic modulation by the basal forebrain plays a central role in dynamically shifting between external and internal states.[125,126] Specifically, elevated levels of acetylcholine have been proposed to promote an encoding mode—favoring the processing of external input—whereas reduced levels promote a retrieval mode, supporting internally guided recall. Similarly, intracranial recordings in humans during a cued-recall task have suggested a core function for the hippocampus to switch from perception to memory modes by triggering a recall cascade in brain regions associated with memory retrieval.[127]

Another plausible candidate is a higher-order network including additional lateral prefrontal regions beyond those typically involved in external or internal attention-control functions. Networks involving frontal cortices have been proposed to be organized in a hierarchical manner, with higher-order areas adding computational complexity to the control of behavior according to embedded contingencies, more abstract considerations, or longer temporal scales.[108,128,129] In particular, the network including the anterior mid-dorsolateral prefrontal cortex (BA

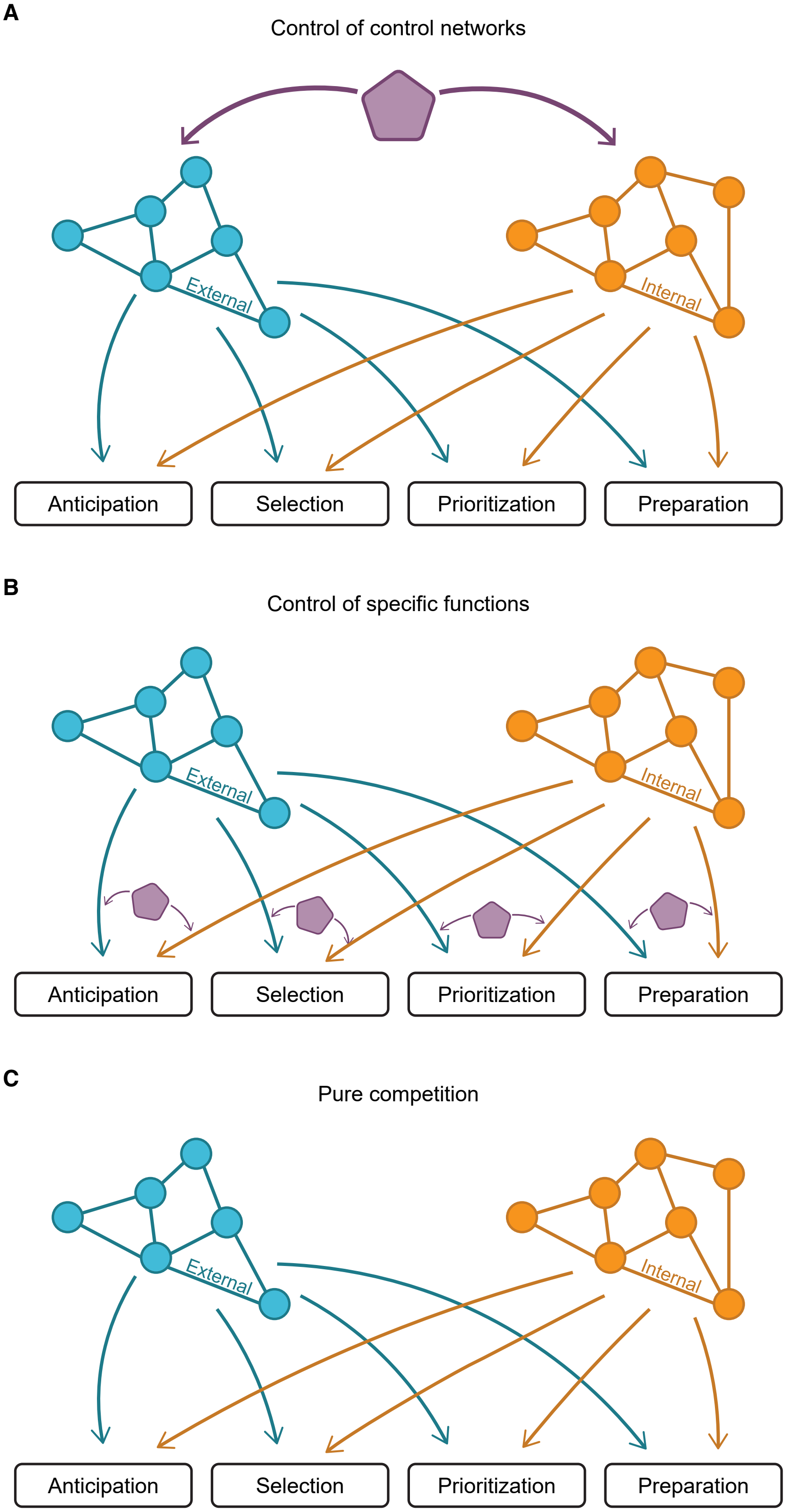

Figure 2. Scenarios for bottlenecks and modulation points during between-domain shifts of attention

(A) A superordinate control may govern shifts between external and internal attention. This controller may determine whether the external or internal attention network has priority, with only the external or internal contents targeted by each network activated, respectively.

(B) Such control functions could also influence any or all stages of attentional modulation.

(C) A superordinate control system for shifting attention between domains may not exist, and external and internal attention may directly compete for dominance.

Please note that showing the external and internal control networks as distinct in this figure does not imply their full anatomical separation or independence. Differences may also simply reflect functional modes of operation.

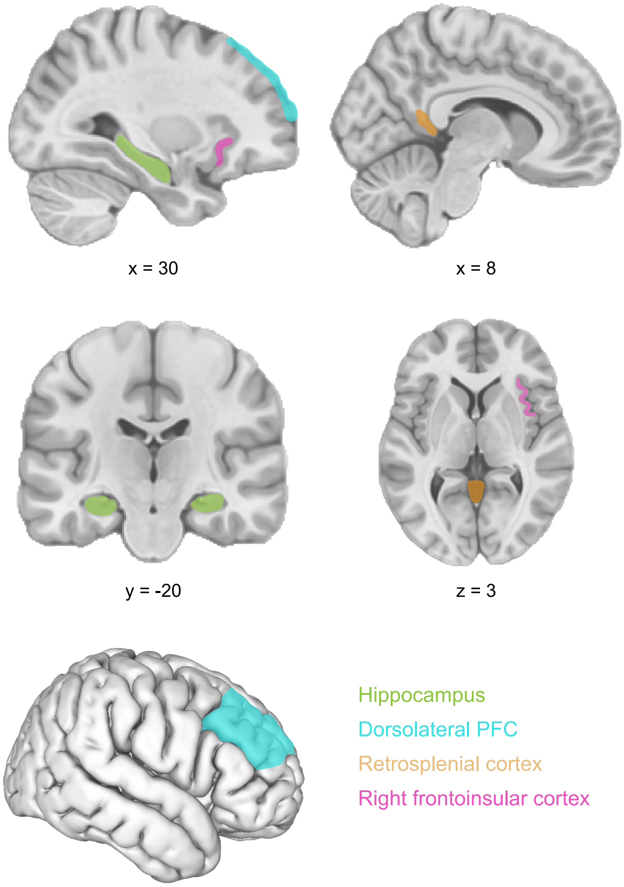

Figure 3. Putative superordinate control areas involved in shifting between external and internal modes
PFC, prefrontal cortex.

9/46) has been suggested to contribute the highest level of control.[128] This region is also of particular interest for being a convergence zone between brain areas and networks involved in external attention control and those involved in schema-related processing and internally oriented cognitive modes (Box 1).[130]

This anterior mid-dorsolateral prefrontal region is connected to caudal and anterior-posterior parietal regions[131] as well as multimodal associative cortices in the superior temporal sulcus, rostral superior temporal gyrus, posterior cingulate cortex, and paralimbic retrosplenial cortex.[132] The link to the retrosplenial cortex is interesting, as this area is coupled to limbic regions in the medial temporal lobe.[133] A recent fMRI study showed that the retrosplenial cortex shifted its coupling with other networks based on whether cognitive processing was externally or internally oriented and could therefore act as a hub for transitioning between the two domains.[134]

Other possible candidates include limbic prefrontal areas—ventromedial and orbitofrontal—implicated in representing abstract task-related information to guide planning and inference (see Badre[130]). Finally, the right frontoinsular cortex has been implicated in transitions between externally and internally directed modes of cognition and could help mediate shifts in connectivity (Box 1).[15,135–138]

Much work lies ahead in following these various leads to elucidate the brain network(s) and dynamics that mediate attention shifts between the external and internal domains. Doing this effectively will require well-controlled experimental designs that isolate the process of shifting attention between contents in the same vs. different domains.

Time scales for shifts between domains

To the extent that the external and internal focus of attention compete, studying the time courses of shifts will yield important insights.

Within both perceptual and working-memory processing, behavioral performance is suggested to ebb and flow in a rhythmic-like manner in a low-frequency mode (delta-theta ranges; see Pomper and Ansorge[73] and Dewey et al.[139]). Within external attention, the rhythmicity has been proposed to reflect competing sensory vs. motor processes—alternating moments of heightened perceptual sensitivity vs. oculomotor activity or preparation.[139] A variation on the interpretation, which we prefer, is that these moments reflect complementary phases of the symbiotic sensorimotor loops guiding our interactions with the environment.[140] An immediate curiosity is whether these rhythms coincide or alternate for external vs. internal attention.

Honey et al.[21] have proposed, on computational grounds, that the brain would benefit from cycling between external and internal modes to learn by iteratively sampling inputs and updating internal models at various timescales. Proposed time scales range from the tens of milliseconds of processing within the hippocampal microcircuitry to the many hours of the circadian sleep-wake cycle. Within the scheme proposed by Honey et al.,[21] the fast rhythms of perceptual and working-memory performance would most likely be expected to be in counter-phase.

Alternatively, sampling from the sensory and working-memory domains could be conceived as both contributing to an externally oriented mode of behavior. If rhythms primarily regulate excitability in sensory (or motor) regions, then reliance on contents that draw upon sensory (or motor) regions could ebb and flow in phase, whether serving external or internal attention. In other words, to the extent that working memory involves sensory (and motor) recruitment, performance rhythms would coincide. A recent EEG study using dense behavioral sampling to compare perception and working memory supported this scenario. Behavior in both domains fluctuated according to a common theta rhythm when humans performed dual tasks requiring external and internal contents to guide performance.[71]

Another interesting recent study tested the detection of a near-threshold visual stimulus during a working-memory task in which participants maintained 0, 2, or 4 memory items.[141] Visual-detection threshold increased with memory load, and, more interestingly, performance on the visual-detection task showed a rhythmic fluctuation that slowed from 7.5 to 5 Hz between low and high WM-load conditions. These results suggest intrinsic mechanisms of alternation between external and internal contents that may adapt flexibly to task demands.

To probe the existence and variety of intrinsic rhythms for external vs. internal attention and their interrelation, much work lies ahead. Experiments will need to vary systematically sensory

Box 2. Experimental guidelines for studying between-domain shifts

Isolating shifts of attention to and from external and internal contents is tricky. It must be recognized that any external or internal attention condition necessarily involves some processing within the opposite domain. For example, internal shifts are often triggered by external cues, and focusing on external contents often requires internalization of cue instructions. Hence, rather than isolating pure conditions, it is necessary to acknowledge the influence of additional factors. Several important safeguards should be met that can help rule out common confounding variables that impede interpretation of the findings.

- Choosing experimental conditions that rely disproportionately on external vs. internal attention demands, acknowledging that there may be residual contributions from the other domain to be considered.
- Relying on types of internal representations that provide strong experimental control. Working memory is a particularly appropriate choice, also given its ecological role in guiding attention and other close links to attention.
- Measuring between-domain shifts in both directions—from external to internal and from internal to external—to separate general processes associated with between-domain shifts from specific processes related to a particular shift direction.
- Including robust baseline conditions involving within-domain attention shifts to test for the potential engagement of distinct brain regions or neural dynamics when shifting between domains. For drawing general conclusions, both external-to-external and internal-to-internal shifts are required.
- Equating the stimulus materials in the external and internal attention conditions to exclude differences in brain activity that merely reflect differential processing of sensory attributes.
- Equating the motor demands of the external and internal attention conditions to exclude differences in brain activity that merely reflect differential demands in response preparation, execution, conflict, or evaluation.
- Ensuring balanced behavioral performance across conditions to prevent confounding factors stemming from variations in task difficulty.
- Avoiding other discrepancies in nuisance variables such as levels of reward, motivation, and arousal associated with different domains or individual tasks.

parameters, task demands, and the time scales of integration required.

In addition to any default intrinsic rhythms, voluntary attention to contents in one domain or the other may additionally determine which state is prioritized. Furthermore, attention may also be involuntarily captured by salient stimuli in the external world[142] or working-memory contents.[58,143] Studies deliberately manipulating the focus of attention between domains can reveal the temporal dynamics for the various attention functions in each domain, from anticipating to preparing contents for action.

EXPERIMENTAL APPROACHES TO INVESTIGATE BETWEEN-DOMAIN SHIFTS

It is not trivial to investigate the psychological and neural mechanisms for shifting attention between the external and internal domains in a well-controlled way. The challenge may account for the scarcity of research (Box 2). Nonetheless, a few studies have ventured into this area, offering valuable preliminary insights.

Behavioral costs for shifting attention between sensory and working-memory domains

Early studies

A flurry of studies in the 1980s–90s investigated the behavioral consequences of shifting attention between the external and internal domains. These initial studies supported the operation of additional control mechanisms when shifting between domains. The first study we identified used successively presented arrays of verbalizable visual stimuli (letters) or placeholders (asterisks), which were maintained in working memory or visually present (Figure 4A).[144] In the perception condition, participants first saw placeholders (* * * * * *) and then letters (e.g., B H D R N F), which they simply had to read out as quickly as possible. In the memory condition, participants encoded letters (e.g., P F H L B N) and then viewed asterisks (* * * * * *). Upon the onset of the second display, participants named the memorized letters as quickly as possible. In the alternate condition, they encoded one array of letters (e.g., N T J) and then viewed a second letter display (e.g., F R D). Participants were required to name the visible and memorized letters in alternation (e.g., F N R T D J). Weber et al.[144] observed shorter list-completion times when participants relied only on one domain (perception or memory) compared with when they shifted between domains.

Follow-up studies highlighted difficulties in isolating the consequences of shifting between domains. Dark[149] proposed that behavioral costs could reflect the time to retrieve items from memory. Her task incorporated separate conditions for shifting from memory to perception and vice versa and included conditions where only a single shift between domains was necessary. The results indicated that shift costs were asymmetrical, with larger costs for shifting from perception to memory than from memory to perception. The cost differential was attenuated if the relevant memory content was precued, thereby short-circuiting the retrieval time. Later, Carlson et al.[150] used a task variant that required a manual response for each item reported and discovered response-time costs related to coordinating responses. When alternating reports across domains or within lists from the same domain, participants tended to report items in pairs, with brief pauses between pairs.

Research into the topic then cooled off, possibly discouraged by the many entangled cognitive processes that can muddy interpretation.

Recent studies

After a quiet period, the topic is once again capturing the scientific imagination. Researchers are returning to this neglected lynchpin of cognition with the benefit of improved

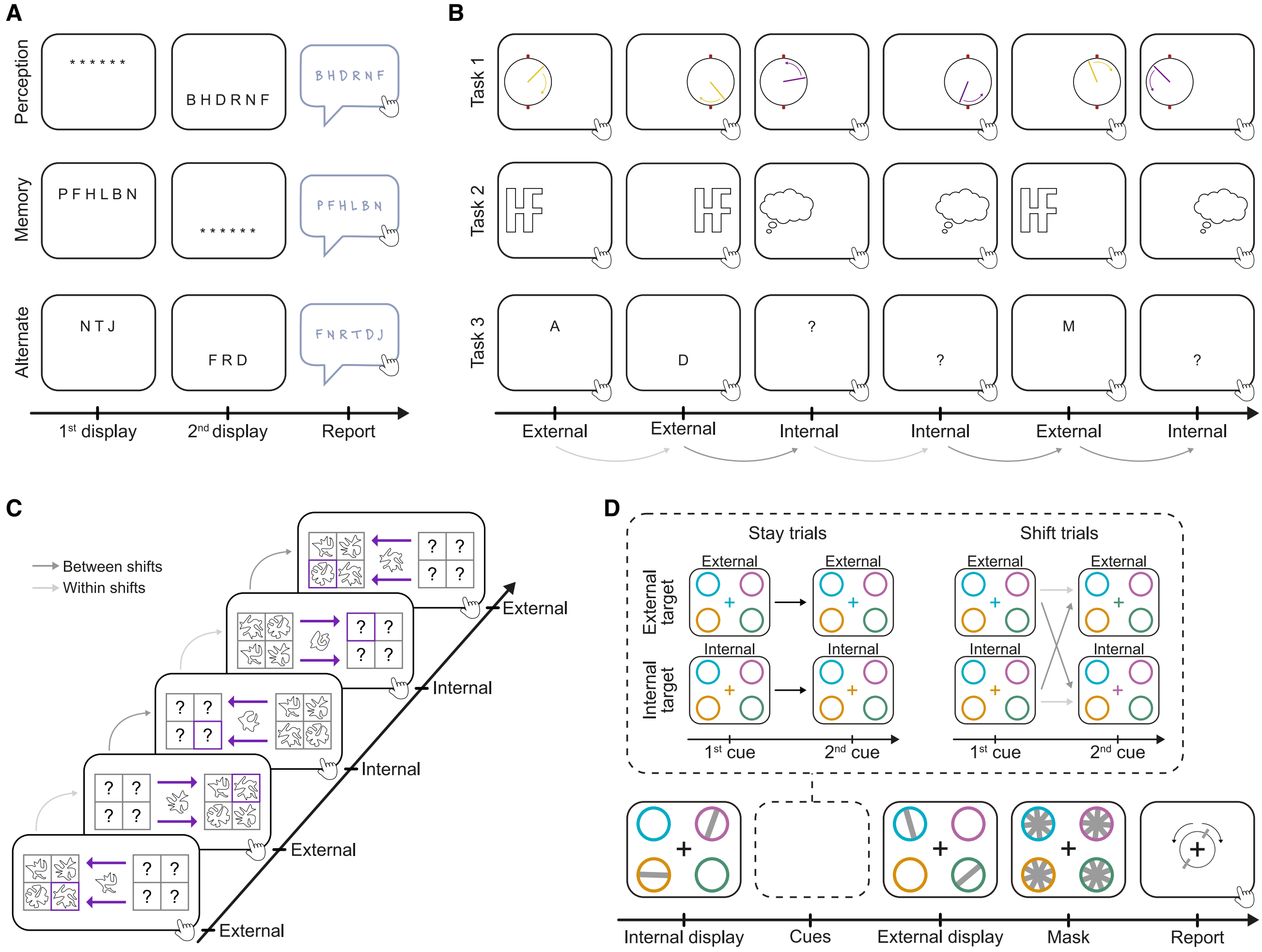

Figure 4. Four studies systematically comparing between- vs. within-domain shifts of attention

(A) Task design based on Weber et al.[144]

(B) Task design based on Gilbert et al.[145]

(C) Task design based on Verschooren et al.[146]

(D) Task design based on Gresch et al.[147,148] Dark gray arrow bars indicate between-domain shifts, light gray arrays indicate within-domain shifts. In (A) and (D), participants shift between external and internal contents. In (B) and (C), participants shift between external and internal tasks/trials.

psychophysical methods and the ability to decode and track attention to perceptual and working-memory contents using brain imaging, neurophysiology, and even eye movements.

One main approach relies on adapting task-switching designs to compare performance when participants successively perform perceptual or memory tasks. For example, in a well-controlled study, participants compared a target to four visible items presented in a 2 × 2 grid (external) or to four previously memorized items encoded as a 2 × 2 grid at the beginning of a block (internal) (Figure 4C).[146] On each trial, cues indicated whether participants should use the visual or memory stimuli as well as the location of the stimulus to use for comparison. Trials were equally likely to follow those from the same or other domain so that four types of task-switch conditions could be compared. Within-domain switches comprised external-to-external and internal-to-internal trials. Between-domain switches comprised external-to-internal and internal-to-external trials. The results revealed higher and asymmetrical costs for task switching between domains. Costs were higher when switching from the external to the internal domain, mirroring results by Dark.[149] The pattern of higher and asymmetric between-domain shifts was further replicated in other similar cued task-switching designs.[151–154] The researchers suggested the asymmetrical effects reflect the default and dominant role of internal attention and of internally directed cognition more broadly.[155]

The task-switching approach has yielded interesting findings and insights. However, it does not fully isolate the processes specifically associated with shifting attention between contents in the external and internal domains. When switching between an internal task relying on one consistent array encoded into memory and an external task relying on a new array in each trial (e.g., Verschooren et al.[146]), the degree of proactive interference differs between domains. Furthermore, task-switching designs introduce additional confounding factors. Participants respond after each interaction with an external or internal array. Residual sensorimotor mappings and motor responses activated in the previous trial leave traces that can interact with processing and responding to the current stimulus content. Competition from lingering sensorimotor and motor traces plays a significant role in switching costs.[156] Evaluative functions related to responding in each trial, such as error monitoring and processing internal feedback,[157,158] may also influence the results.

An alternative to the task-switching approach is to manipulate shifts of attention in the service of a single task, without requiring intervening responses. To this aim, our studies borrowed from the designs using informative precues to orient attention to upcoming visual stimulation[142] and retrocues to orient attention to internal contents maintained in working memory.[6,46] The tasks used successive spatial cues to orient attention to locations of an array encoded into working memory or an upcoming visual array (Figure 4D). Critically, at the end of each trial, participants made a single response regarding either a remembered or a perceived item.[147] Participants first saw two oriented bars appearing in two of four colored placeholders located peripherally in the four quadrants (i.e., internal display). One bar stimulus always occupied a location in the left visual field and the other in the right visual field. Participants encoded the orientation of these stimuli in working memory. Toward the end of the trial, participants briefly viewed two additional oriented bars, which appeared at the two previously unoccupied locations (i.e., external display). Finally, they were prompted to reproduce the orientation of one of the four stimuli, accessed either from working memory (internal domain) or from perception (external domain). During the delay intervening between the working-memory and perceptual items, two successive attention-directing cues appeared. By matching the color of one of the placeholders, each cue oriented attention to an encoded or upcoming item. At the end of the trial, participants reported the item indicated by the second cue. Across trials, all four shift types occurred in unpredictable order in a factorial design that manipulated the type of shift (between- and within-domain) and the final item to be probed (internal or external).

Results revealed significant costs in shifting attention between domains compared with shifting within domains. Responses were slower after between-domain attention shifts regardless of shift direction. Orientation-reproduction errors were also higher after between-domain shifts, especially for shifts from the external to the internal domain. The results were consistent across experimental variations and remained even when long intervals followed the final cue, ensuring ample time to complete the second shift of attention.[147]

Taken together, although still inconclusive, the behavioral evidence points to additional processes being involved when attention shifts between sensory and working-memory domains as compared with shifts within either domain. Behavioral data alone, however, do not adjudicate between the costs reflecting the engagement of superordinate control functions or merely stronger competition that must be resolved when contents are in different domains.

First clues of the neural mechanisms for shifting attention between domains

A set of stand-alone brain-imaging studies compared brain activations when participants completed tasks based on visible stimuli or their related internal representations (Figure 4B).[145] In one task, participants either responded each time a clock hand passed the 12 or 6 marks (external task) or responded at the same pace based on an internalized representation of the clock hand movement (internal task). In another task, participants decided whether navigating around the edges of a visual stimulus required a clockwise or counterclockwise turn (external) or made similar decisions based on the memorized shape (internal). In a final task, participants decided whether visible letters contained all straight lines, curves, or a combination of both (external) or made similar decisions on imagined letters (internal). Behavioral performance varied markedly between tasks but also revealed additional costs when participants switched between domains.

Comparing brain activity from successive trials in different vs. the same domains revealed transient activation of the right anterior mid-dorsolateral prefrontal cortex (BA 9/46), right rostrolateral prefrontal cortex (BA 10), and bilateral superior parietal cortex (BA 7) when participants switched between vs. within domains (Figure 5A). The pattern of activation was similar regardless of the direction of domain switches (external-to-internal or internal-to-external switches). Similar findings were obtained in related studies by the same group examining external and internal attention in the context of prospective memory.[11,159]

Activation of the anterior mid-dorsolateral prefrontal and superior parietal cortex suggests the recruitment of a higher-order superordinate frontal-parietal control network. The researchers focused instead on the rostrolateral prefrontal cortex, proposing it functions as a supervisory attentional gateway, orchestrating the coordination of external and internal information in service of goal-directed behaviors. The findings underpinned the gateway hypothesis,[160] in which a metaphorical railway switch point directs the flow of external and internal information to central representations. Within this framework, routing of external vs. internal information often proceeds automatically based on competition between external and internal contents. However, the supervisory attention gateway intervenes in certain circumstances, such as when navigating unfamiliar situations.

Recent research using proactive and retroactive attention cues suggests that the interpretation of a superordinate controller brokering the flow of external vs. internal information may be premature. In cued attention tasks, although between-domain shifts incurred consistent behavioral costs, they were not accompanied by delays in shifting spatial attention between domains. In our recent studies, we recorded fixational gaze behavior[147] and magnetoencephalography (MEG)[148] to track the timing of shifting spatial attention between vs. within the external and internal domains. In contrast to the behavioral results, which showed slower response times when crossing domains, the eye-gaze and neural-oscillation proxies of spatial shifts followed equivalent time courses (Figure 5B). Both the initial and the subsequent spatial cues biased small eye movements toward the cued item location in the working-memory array or anticipated perceptual array. The results replicated oculomotor effects reported for external[65,161]

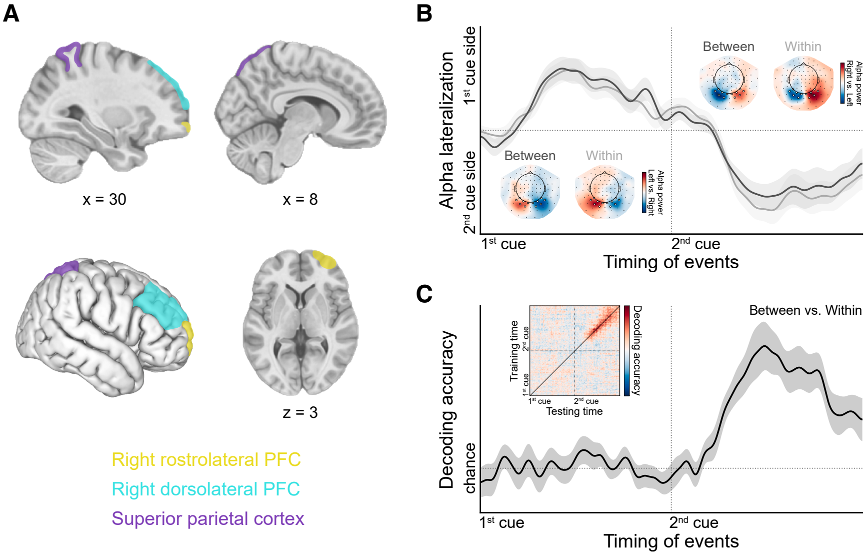

Figure 5. Neural differences (and similarities) in between- vs. within-domain shifts of attention

(A) Functional neuroimaging data based on Gilbert et al.[145] Highlighted regions show greater activation during between-domain compared with within-domain shifts. PFC, prefrontal cortex.

(B) MEG data based on Gresch et al.[148] Time course of alpha-band activity in visual channels, contralateral vs. ipsilateral to the attended hemifield following the second cue, did not significantly differ for between- vs. within-domain shifts. Topographical maps show alpha-power differences following first cues directing attention left vs. right and second cues directing attention right vs. left (i.e., first and second cues always directed attention to the opposite hemifields). Light gray time course indicates within-domain shifts; dark gray, between-domain shifts. Shadings indicate M ± SEM.

(C) MEG data based on Gresch et al.[148] Whole-brain multivariate pattern analysis successfully predicted the shift type (between vs. within) following the second cue, but not before. The inlay shows a temporal generalization matrix depicting classifier performance over time, and the diagonal reflects the dynamic nature of the decoding time course. Shading indicates M ± SEM.

and internal shifts of spatial attention.[67] At the time of the second cue, shifts in gaze started together and followed the same time course, regardless of whether spatial attention shifted between or within domains. In other words, spatial shifts were not impeded or slowed when crossing domains.

In the MEG study, the lateralization of alpha-band activity over the posterior scalp and in visual areas also followed the location of the cued encoded internal or anticipated external item. As in previous studies, alpha lateralization was more short-lived when spatial attention was oriented in internal, working-memory arrays than anticipated perceptual arrays after the first cue (see Wallis et al.[60] and Myers et al.[68]). Nevertheless, the onset and progression of alpha lateralization after the second cue were unaffected by whether spatial shifts occurred in the same or different domains (Figure 5B). These results extended the gaze-bias findings. Together, they make a compelling case that no additional, time-consuming step occurs before attention shifts are initiated, suggesting that the initial orienting functions are not the main bottleneck accounting for the behavioral costs in performance.

Other aspects of the MEG data provided initial clues into the neural processes involved in shifting attention between domains. Decoding of neural activity after the second cue showed clear differentiation of neural processing following between- vs. within-domain shifts (Figure 5C). The effects started early, evolved dynamically over time, and were broadly distributed over the scalp, hinting at differences at multiple processing stages in distributed networks. Interestingly, it was possible to decode the attentional domain indicated by the first cue at the time of the second cue. The findings align with observations that internal attention alters the neural states of items in working memory.[162,163] In turn, the different neural states can interact with neural processes of the attention shift triggered by the second cue.

When considered together, the nascent neural data pose an intriguing puzzle. The consistently observed behavioral costs for between-domain shifts are unlikely to reflect the operation of an early gateway between domains. Many possibilities remain open. The competition for attention priority may unfold without additional control mechanisms and may depend on the previous setting of attention allocation. This competition may take longer to resolve for between- than within-domain shifts. The initial observations that additional prefrontal and parietal areas are engaged by between-domain shifts[11,145,159] argue against this possibility. Alternatively, shifting focus between domains may invoke additional control mechanisms after initial spatial orienting, such as selecting contents, linking them to task rules, or preparing them for motor output. Making headway will require further investigation with various methods and systematic variations in task parameters and demands. Brain-imaging studies that capitalize on modern decoding and network analyses will be instrumental in revealing the contribution of additional brain areas or networks, if any, when shifting attention between domains. These future explorations will also help elucidate whether and how brain areas related to controlling external and internal attention differentially modulate sensory areas to prioritize contents for adaptive behavior. Animal models (e.g., Panichello and Buschman[80]) will be essential for deriving neuronal mechanisms at the circuit and cellular levels.

CONCLUDING REMARKS AND FUTURE PERSPECTIVES

In this perspective, we laid the groundwork for addressing one of the cornerstones of human cognition, which has received surprisingly little investigation. Refinements in behavioral, neural, and analytic methods make this the perfect time to ask how the brain shifts seamlessly and flexibly between stimuli in the sensory stream and in our minds to guide adaptive behavior. The few precious strands of research to date, from varied experimental approaches, converge on the presence of a cost when shifting focus between items in the external and internal domains. Yet, interestingly, proxies of spatial attention engagement show no delaying of the spatial shift itself.

Multiple big and exciting questions present themselves. What, if any, are the systematic neural bottlenecks for shifting between sensory contents vs. internal representations? How is the processing of external vs. internal signals organized within the brain in the first place? How are they kept apart, and how can the various attention-control functions (anticipating, selecting, prioritizing, and preparing) target each of them specifically? To what extent can processing and modulation within each of these two domains run concurrently? Which superordinate control networks intervene and when? It will be enlightening to unveil how additional regions interact with the networks for external and internal attention control to deliver the relevant contents to guide behavior or, instead, how external and internal contents battle for primacy simply through changes in activity levels, functional connectivity, or dynamics of external and internal attention-control networks.

In this perspective, we concentrated on working memory as a tractable internal domain for initial investigation. Compared with other internal domains, working memory offers a good degree of experimental control and draws from a substantial experimental literature. Traction gained by comparing shifts of attention between perception and working memory will pave the way for further enthralling questions about how the brain orchestrates the myriad external and internal signals to weave a cohesive subjective experience and direct adaptive action. How does the brain organize different types of internal domains—e.g., working memories, long-term memories, creative ideas, plans, mind wandering—and selectively focus within their contents?

Finally, focusing on content to select and prioritize it for behavior is only one of many operations that can be performed with signals from the external and internal domains. In addition to picking one content among its competitors, the brain also often compares, accrues, integrates, or relates contents in various other ways. Understanding how selective attention navigates between the external and internal domains will provide a level footing for these absorbing, fundamental, yet challenging lines of investigation.

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AUTHOR CONTRIBUTIONS

Conceptualization, A.C.N. and D.G.; writing – original draft, A.C.N. and D.G.; writing – review & editing, A.C.N. and D.G.; visualization, A.C.N. and D.G.

DECLARATION OF INTERESTS

A.C.N. is on the advisory board of *Neuron*.

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