

## Cognitive independence and interactions between cerebral hemispheres

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### A B S T R A C T

The two cerebral hemispheres can often operate independently. But interactions between them are critical for cognition and have been implicated in a number of neuropsychiatric disorders. Neurophysiological studies have long focused on a single hemisphere. Here, we review recent studies showing neurophysiological evidence showing both independence and interactions between the hemispheres during complex behavior.

### 1. Introduction

Our brains remarkably divide the processing of information from the world around us. This is particularly evident in how vision, touch, and motor control are split between the right and left hemispheres. This split offers advantages such as parallel processing for our bilateral bodies. The separation between left and right visual hemifields is well-known in lower-level visual cortex. For a while, this split was thought to be “remedied” by large bilateral receptive fields at higher cortical areas. But we now know that it persists to some degree even as information ascends the visual cortical hierarchy. A bias toward contralateral space remains evident at the highest levels of cortex and cognition. The left and right sides of vision appear to draw from separate cognitive resources and distinct attentional mechanisms. The division between hemispheres raises a compelling question: How does the brain track and retain visual information as it moves between the left and right side of space? As objects move across our visual field or we shift our gaze, does information simply disappear from one hemisphere and reappear in the other?

These two themes, independence and interactions between the cerebral hemispheres, form the basis of this review. A recent review focused on rodent genetic and cellular imaging studies addressing similar questions (Ocklenburg and Guo, 2024). Here, we focus on their implication and role in cognition in human and non-human primates (NHPs). John Duncan has been a key contributor to this body of work, pioneering new methods, introducing novel ideas, and conducting crucial studies in this field (Erez et al., 2022; Everling et al., 2002; Kadohisa et al., 2013, 2015; Powell et al., 2006; Rajimehr et al., 2022; Vandenberghe et al., 2000).

### 2. Independence between hemispheres

Sensory information coming in from one side of the body is processed by the opposite, contralateral cortical hemisphere. As information ascends the cortical hierarchy, it becomes progressively more shared across hemispheres. Some of this interhemispheric crosstalk is thought to be due to subcortical routes or smaller cortical fiber tracts (Amaral et al., 1984; Demeter et al., 1985; Di Virgilio et al., 1999; Szczupak et al., 2024). But decades of anatomical and neuropsychological studies suggest it is primarily mediated by the corpus callosum, a large bundle of nerve fibers directly connecting the two hemispheres (Gazzaniga, 2000; O’Reilly et al., 2013; Roland et al., 2017; Sperry, 1968). Callosal fibers mainly connect corresponding cortical regions in the two hemispheres (Innocenti, 1986; Jarbo et al., 2012). The few connections breaking this rule target areas closely linked to the corresponding region (Barbas et al., 2005). This wiring scheme has been substantiated by studies of resting-state functional connectivity in humans (Gee et al., 2011; Salvador et al., 2005; Stark et al., 2008).

The cumulative result of this interhemispheric signal mixing is a gradual increase in position invariance as you ascend the cortical hierarchy. Neuronal receptive fields become progressively larger and the coverage of the visual field by neural populations in each hemisphere extends further across the midline into the ipsilateral visual field. Initially, it was believed this culminated in a fully bilateral representation in cortical regions critical for cognition. However, much of the early work was conducted under anesthesia (Gross et al., 1972).

In the awake, attentive brain, receptive fields are often much smaller (DiCarlo and Maunsell, 2003), and a bias toward the contralateral visual hemifield remains even at the highest levels of cortex. In the lateral prefrontal cortex, neuronal receptive fields can extend across the

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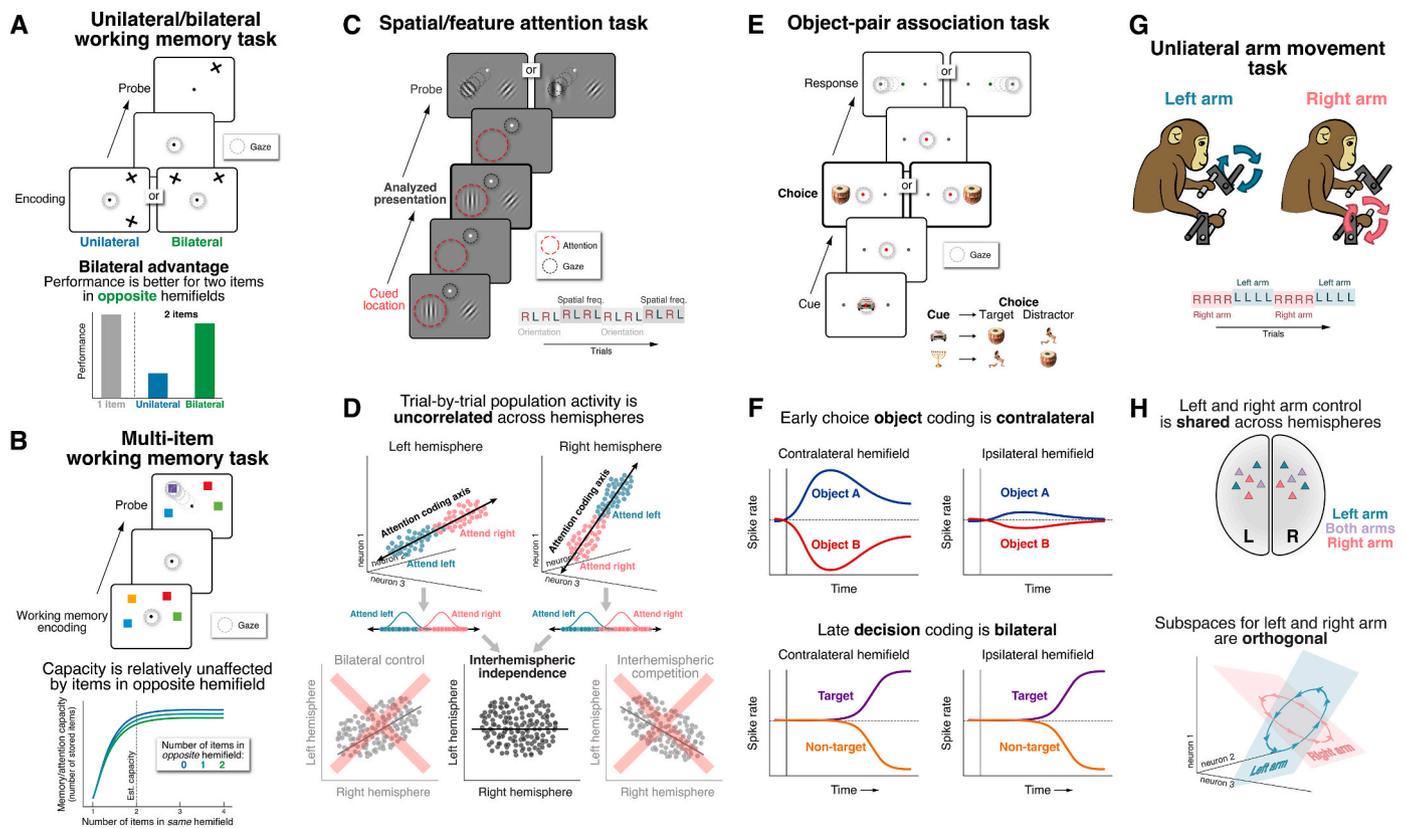
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midline and even sometimes be centered in the ipsilateral visual field. But the prefrontal population representation of space is clearly biased toward the contralateral hemifield, both for NHPs (Brincat et al., 2021; Bullock et al., 2017; Funahashi et al., 1990; Kornblith et al., 2015; Rainer et al., 1998; Viswanathan and Nieder, 2017; Wimmer et al., 2016) and humans (Hagler and Sereno, 2006; Kastner et al., 2007; Medendorp et al., 2007). In fact, impairments from damage to the prefrontal cortex in one hemisphere are largely restricted to contralateral space (Pasternak et al., 2015; Rossi et al., 2007; Voytek and Knight, 2010).

As a result, the two hemispheres appear to function surprisingly independently even for high-level cognitive functions like attention and working memory. Visual working memory seems to rely on severely limited resources. Only a handful of items can be held in memory at the same time before it reaches capacity (Luck and Vogel, 1997, 2013). This is thought to be due to interference or overlap between the neural activity patterns coding for distinct items held in memory (Duncan, 2006; Franconeri et al., 2013). When multiple items must be held in memory, performance is much better when the items are split between both visual

hemifields, rather than presented in the same hemifield (Fig. 1A) (Dimond and Beaumont, 1971; Umemoto et al., 2010; Zhang et al., 2017). This “bilateral advantage” suggests the limited resources used to hold information in working memory are at least somewhat independent for information coming from the two hemifields. This results in an increased overall working memory capacity when items are presented bilaterally (Fig. 1B). Even when storage reaches capacity in one hemifield, more items can be added to working memory if they appear on the opposite side (Buschman et al., 2011; Delvenne, 2005). Note that performance for bilaterally presented items typically remains slightly worse than that for a single item (Fig. 1A). This suggests relative, not complete, independence between processing in the two hemifields. Similar effects are observed in spatial selective attention. We can better divide attention to focus on multiple locations at the same time if they are in opposing hemifields rather than in one hemifield (Alvarez et al., 2012; Alvarez and Cavanagh, 2005). Space seems critical for observing a bilateral advantage. Attention or working memory for non-spatial features (e.g. color or form) do not seem to show a consistent bilateral advantage (Alvarez et al., 2012; Awh and Pashler, 2000; Delvenne,



**Fig. 1. Examples of contralateral and bilateral organization in cortex.** (A) Unilateral vs bilateral working memory task. Performance is better when two items are held in memory from opposite visual hemifields (green), relative to two items from the same hemifield (blue). This “bilateral advantage” suggests at least partially independent resources for spatial working memory in the two hemifields. (B) Design of multi-item working memory task. Each trial, a variable number of items in each visual hemifield are encoded and held in working memory, then compared with a probe stimulus to identify which item changed. Note that this judgement involves remembering both the items’ colors and locations. Working memory capacity for items from one hemifield is relatively unaffected by the number of items from the opposite hemifield. This suggests capacity limits reflect partially independent resources in the left and right hemispheres. (C) Spatial/feature selective attention task. Attention is directed alternately to left vs right location, and to orientation vs spatial frequency feature. (D) The similarity of area V4 population spiking activity on each trial to ideal population patterns for attending to the left vs. right was quantified. Trial-by-trial fluctuations in this estimate of internal attentional state predict behavior (not shown), but are uncorrelated between the left and right hemispheres of V4. This suggests the effects of attention on visual cortex are independent between hemispheres. (E) Object-pair association task. Cue objects instruct a learned response to arbitrarily associated target objects, but to ignore non-target objects. Target or non-target choice objects can appear on the left or right. (F) Early prefrontal population spiking activity differentiates between choice objects mainly in the contralateral hemifield. Later activity differentiates targets vs non-targets in either hemifield. This indicates a dynamic shift from contralateral sensory representation to bilateral representation of decision/action in prefrontal cortex. (G) Unilateral arm movement task. Instructed movements are performed alternately with either the left or right arm. (H) Equal numbers of neurons reflect left and right arm movement in both hemispheres of primary motor cortex, but population activity subspaces for left and right arm movement are orthogonal. This suggests anatomical separation of left and right space by hemispheres may be replaced in motor cortex by computational separation into distinct bilateral population patterns. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2005). These results have been interpreted as evidence for independent control of spatially focused processing within each cortical hemisphere, which is deployed for both selective attention and working memory.

Neural correlates of the bilateral advantage can be seen in the neural activity of higher-order areas like prefrontal and posterior parietal cortex. The information conveyed in spiking activity about items held in working memory increases with the number of items (memory “load”) (Buschman et al., 2011). Critically, this effect only occurs for items coming from contralateral space. Neural information is not influenced by items from the hemifield *ipsilateral* to the recorded hemisphere. Similar effects occur for gamma-band (~30–100 Hz) power in local field potentials (LFPs) and EEG (Kornblith et al., 2015; Medendorp et al., 2007). In contrast, power in the alpha/beta band (~8–30 Hz) exhibits a stimulus-induced *suppression* that also increases with memory load, but for items in *either* visual hemifield (Kornblith et al., 2015; Medendorp et al., 2007). These results suggest that frontoparietal spiking and gamma reflect somewhat separate working memory stores in each hemisphere. Alpha/beta oscillations may reflect inhibitory control processes (Miller et al., 2018) shared across cortical hemispheres.

If frontoparietal systems for cognitive control are to some degree independent between hemispheres and feedback connections primarily target areas within the same hemisphere (Felleman and Van Essen, 1991; Innocenti, 1986; Jarbo et al., 2012), then their effects on the right and left visual cortex should also be independent. In a series of papers (Cohen and Maunsell, 2009, 2010, 2011), this prediction was confirmed using array neurophysiology and population analysis methods. They simultaneously sampled neural population activity in both hemispheres of visual area V4 of NHPs performing selective attention tasks (Fig. 1C). One task presented visual stimuli simultaneously in both hemifields, but cued spatial attention to only one of them at a time (Cohen and Maunsell, 2009, 2010). They computed the mean neural population activity patterns across trials when subjects attended to the left hemifield and across trials when they attended to the right (Fig. 1D, top). They then computed the similarity of the population activity pattern on each individual trial to these ideal states (Fig. 1D, middle). This produced a continuous estimate of subjects’ internal attentional state on each trial. The estimated attentional state reliably predicted subjects’ behavior (accuracy and reaction time) on a trial-by-trial basis. That is, performance was worse on trials where population activity collapsed toward the center point between “attend left” and “attend right” or when activity indicated that attention was directed to the incorrect hemifield.

Critically, the attentional states estimated from neural populations in the two hemispheres of V4 were uncorrelated across trials (Fig. 1D, bottom). That is, on trials where right V4 activity was closer than average to the ideal correct attentional state, left V4 activity showed no tendency to be closer or farther from its ideal attentional state. If attention operated in a unified bilateral fashion, both hemispheres would be modulated in the same direction, and they should have seen a positive correlation (Fig. 1D, bottom-left). Another possibility is that attention involves competitive interactions between hemispheres. A stronger attentional state in one hemisphere would induce a weaker state in the opposite hemisphere, resulting in negative correlations between them (Fig. 1D, bottom-right). Instead, the observation of uncorrelated attentional states between hemispheres (Fig. 1D, bottom-center) is consistent with independent attentional control in the right and left visual cortex. In a follow-up study (Cohen and Maunsell, 2011), they cued both the spatial location and stimulus feature (orientation or spatial frequency) to attend to (Fig. 1C). Analogous to the previous analysis, they computed the ideal population activity patterns for “attend orientation” and “attend spatial frequency” trials, then estimated the similarity of population activity on each trial to each of these. In contrast to spatial attention, they found that this estimate of feature attentional state *did* exhibit trial-by-trial correlations between hemispheres. For example, on trials where right V4 activity suggested stronger attention to orientation, left V4 activity also indicated the same. This suggests the mechanisms of feature attention are distributed across

both hemispheres, consistent with results from human behavioral studies discussed above. Taken together, these results suggest the top-down effects of spatial, but not feature-based, attention on visual cortex are independent between hemispheres. This is consistent with independent frontoparietal control systems for spatial attention.

In a key series of papers, John Duncan and colleagues showed that prefrontal hemispheric independence is dynamic, changing over time and for different functions (Erez et al., 2022; Kadohisa et al., 2013, 2015). They studied prefrontal coding in a task requiring arbitrary associations between objects (Fig. 1E). Each trial, a central cue object was followed by a choice object on the left or right. If the choice object was part of a learned set that was paired with the cue (a target), a saccadic response was required after a brief delay. Otherwise, the NHP subjects were required to withhold response. Following presentation of the choice object, prefrontal spiking activity initially primarily carried information about the object’s identity within the hemisphere contralateral to where it appeared (Fig. 1F, top). However, after a few hundred milliseconds, prefrontal activity transitioned to represent whether a target object was present or not, regardless of which specific object it was (Fig. 1F, bottom). Given the task design, this activity might reflect the subject’s decision *per se* or preparation of the resulting motor response. Critically, this target-related activity was shared across both hemispheres—it had a similar magnitude whether the target appeared in the contralateral or ipsilateral hemifield. Unlike the earlier contralateral coding of object identity, this bilateral target representation was predictive of whether the subject would make the correct behavioral response on each trial (Kadohisa et al., 2015). These results suggest that prefrontal coding dynamically shifts from an early contralaterally-biased sensory representation to a later bilateral representation of information related to decision or action.

In contrast to the contralateral bias in sensory and frontoparietal regions, motor cortex has been shown to have a bilateral representation in which processing of left and right space is fully mixed between hemispheres. Left and right movements are, however, kept independent via distinct population spiking activity patterns distributed across both hemispheres (Ames and Churchland, 2019). The arm region of primary motor cortex was recorded bilaterally while NHPs made unilateral movements with their left or right arm (Fig. 1G). Signals for both arms were present at nearly equal strength in *both* hemispheres. They then compared the bilateral population activity patterns used to code for movements in each arm. They found the left-arm and right-arm patterns were completely independent. Even though they used overlapping sets of neurons distributed across both hemispheres (Fig. 1H, top), they formed orthogonal subspaces within the full state-space of all possible bilateral activity patterns (Fig. 1H, bottom). As a result, activity patterns used to control the left arm would have no effect on the right arm, and vice versa. Similar results have been found with a different motor task (Heming et al., 2019). Thus, although processing remains surprisingly lateralized in the frontoparietal regions most associated with cognition, these results suggest that the hierarchical trend of increased mixing across hemispheres culminates in a fully bilateral motor cortex. But they also suggest the possibility that *anatomical* separation of processing into the right vs left hemispheres may be gradually replaced with *computational* separation into orthogonal subspaces.

### 3. Interaction between hemispheres

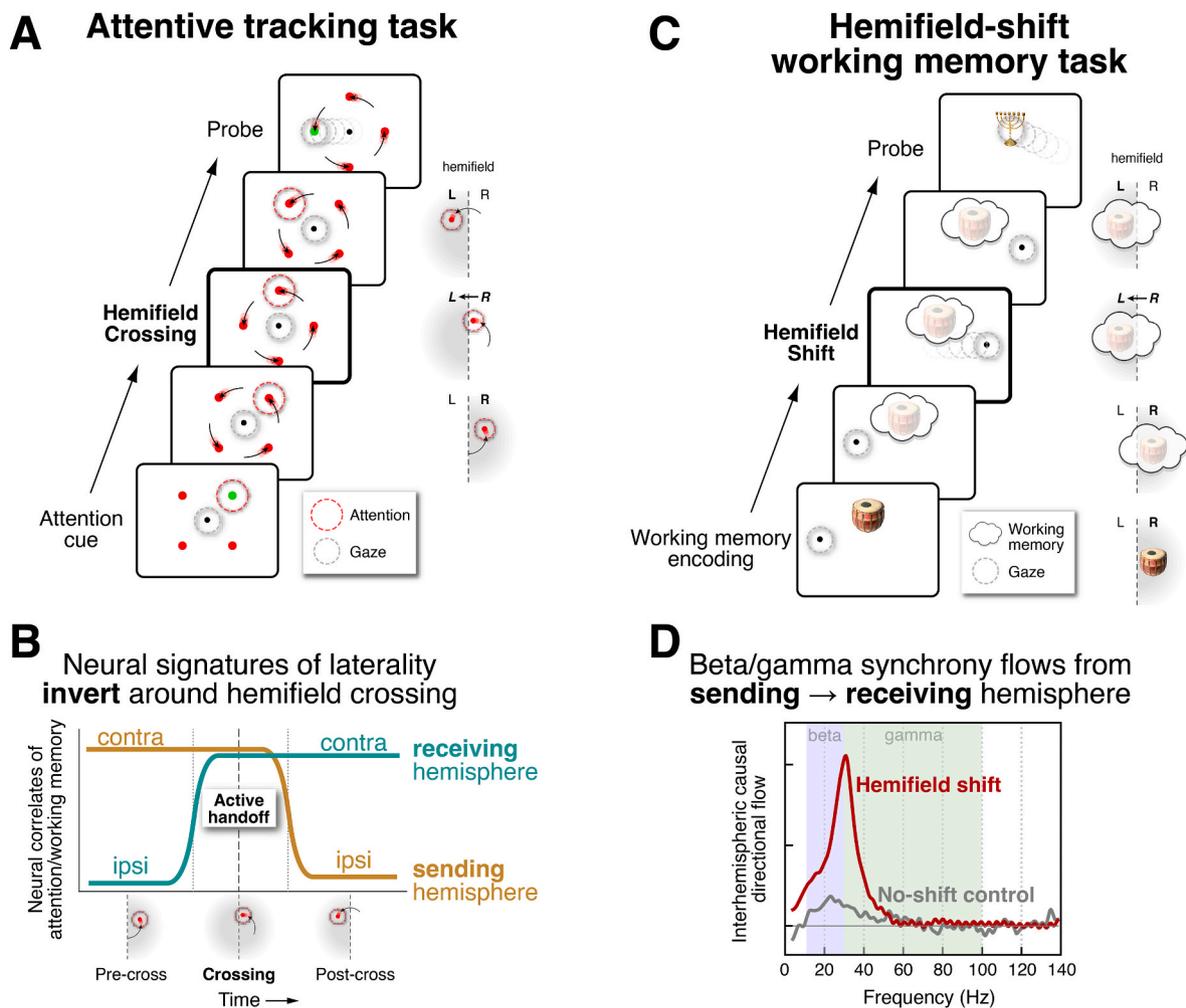
So far, we’ve reviewed evidence that cognitive processing of space can be quite independent between hemispheres. Though these studies were well-designed for this purpose, there is an important limitation to their generalizability. The studies did not demand any interaction between information in the left and right sides of space. Normal cognition, however, frequently requires interaction between the two halves of the visual world. We routinely make comparisons between information on our left and right. When a moving object crosses the visual midline, we are not surprised when it appears in the opposite hemifield. When a

saccade shifts the visual scene across our field of view, our understanding of the world persists, even when information shifts from one visual hemifield to the other. We seem able to track and predict visual information regardless of where it appears and how it moves across our visual field.

Studies that require objects to be tracked across hemifields have indeed revealed interactions between hemispheres. In multi-object attentive tracking (Cavanagh and Alvarez, 2005; Pylyshyn and Storm, 1988) targets must be tracked as they cross hemifields. Subjects are presented with an array of objects, one or more of which are cued as targets (Fig. 2A). The targets must then be tracked with covert attention, and the non-targets ignored, as they move through space. Occasionally, their trajectories cross the midline into the opposite visual hemifield. Finally, a judgement must be made about whether a probed object is a target or not, or whether the probe's attributes match those remembered from the initial cue. Performance is good even when objects cross between hemifields, confirming information can be successfully tracked between them. The EEG signal in each hemisphere has a higher (more negative) amplitude when attention is focused within the contralateral hemifield than when focused in the ipsilateral hemifield (Luria et al., 2016). This is further evidence of the independence of attentional

control between hemispheres, as discussed above. When a target is tracked from one hemifield to the other, these amplitudes invert, consistent with a shift of attentional control from one hemisphere to the other (Fig. 2B) (Bland et al., 2020; Drew et al., 2014). The inversion occurs even when the total number of objects remains balanced across hemifields. This indicates that the inversion is not a sensory response. It is related to the focus of attention on the target. These results indicate that robust interhemispheric information transfer can be observed when interaction between visual hemifields is required.

The time course of interhemispheric transfer suggests it is an active process involving anticipation of incoming signals in the receiving hemisphere. The transfer involves two separable processes—target information is lost from the sending hemisphere (Fig. 2B, orange) and picked up by the receiving hemisphere (Fig. 2B, teal). One possibility is that these simply happen at the same time as the target crosses the midline. This passive mode of transfer would be analogous to how early cellphone towers transferred signals from a moving device. One tower dropped the call simultaneously with the next tower picking it up. This proved to be prone to catastrophic signal loss when the sending tower dropped the signal before it was fully secured in the receiving tower. In contrast, like modern cellphone towers, the brain appears to employ an



**Fig. 2. Examples of interaction between cortical hemispheres.** (A) Multi-object attentive tracking task. Each trial, one or more objects in each visual hemifield are cued as targets. The targets must then be tracked with covert attention as they move around the visual field, including sometimes crossing between the left and right hemifield. (B) As an attended target crosses between hemifields, its neural signatures invert, consistent with signal transfer between cortical hemispheres. The receiving hemisphere predicts the incoming target before the crossing. This “active handoff” means that signals briefly overlap in both hemispheres, which might help prevent signal loss during the transfer. (C) Hemifield-shift working memory task. An object is encoded into working memory from one hemifield, then a saccade shifts its remembered location to the opposite hemifield. (D) The transfer of remembered information between hemifields is accompanied by beta/gamma-band synchrony directed from the sending to the receiving hemisphere. This suggests rhythmic beta/gamma synchrony may facilitate interhemispheric communication.

“active handoff” process (Drew et al., 2014). As a tracked target approaches the visual midline, the hemisphere about to receive the target shows a ramp-up of activity well before the crossing time, as if it is anticipating the target. Further, activity in the sending hemisphere remains high well after the crossing. Thus, for up to a second or more, neural signals reflecting the target are shared across both hemispheres (Fig. 2B). It is as if both hemispheres are holding the baton. This was not simply due to an overlapping representation of the midline between hemispheres. When comparing identical trajectories in which the hemifield crossing was predictable vs. unpredictable, only the predictable trajectories showed evidence of active anticipation (Drew et al., 2014). These results indicate interhemispheric transfer involves some prediction. This seems to suggest an active handoff that could prevent signal loss during the transfer. It would ensure the signal is encoded in the receiving hemisphere before it is dropped from the sending hemisphere.

This active handoff, while potentially more robust than a passive transfer, is not totally error-free. Performance often drops somewhat after tracked objects cross the midline, compared to similar trajectories that remain within a single hemifield (Bland et al., 2020; Minami et al., 2019; Strong and Alvarez, 2020). This “hemifield crossover cost”, like the bilateral advantage discussed above, only seems to occur for spatial judgements. It is not reliably observed when subjects must ultimately judge color or form attributes of the tracked objects independent from their location or trajectory (Strong and Alvarez, 2020). This is consistent with a communication bottleneck between partially independent attentional control systems in the right and left hemispheres (Strong and Alvarez, 2020). Indeed, frontoparietal callosal fibers tend to be thinner, and thus slower, than those connecting sensorimotor cortex (Caminiti et al., 2009). The crossover cost may also be due to the active handoff described above. Though it may help prevent complete signal loss, coding the target in both hemispheres may require more resources, especially when multiple objects are being tracked. This might reduce the fidelity of the representation, and thus, paradoxically, could partially explain the hemifield crossover cost in performance (Strong and Alvarez, 2020).

Similar mechanisms seem to be involved when information shifts between visual hemifields due to our own movement. As we shift our gaze around the visual world, objects correspondingly shift their retinotopic locations (in the opposite direction), sometimes from one hemifield to the other. Objects held in spatial working memory likely also show a corresponding shift, so that our memories remain aligned with perception (Zaksas et al., 2001). We have recently used large-scale bilateral array recording in NHP prefrontal cortex to study this (Brincat et al., 2021). We designed a variation of a standard working memory task in which remembered information was shifted between hemifields (Fig. 2C). On some trials, while information was being held in memory, we instructed the subject to shift gaze such that the remembered location of the object shifted from one visual hemifield to the other. Analogous to effects in attentive tracking, we found that shifts in gaze also transferred the working memories from one hemisphere to the other. When the gaze shift changed the remembered location of the object between hemifields, neural signatures of its laterality (spike rates, LFP power across multiple bands, and neural information about the item held in memory) inverted (Fig. 2B). We also found a behavioral cost when memories were transferred between hemispheres, similar to that seen for attention shifts. This was paralleled by a drop in neural information about the item held in working memory. These results show that working memories are transferred between hemispheres to compensate for changes in our gaze direction.

Importantly, there was evidence for an active handoff of the working memories between hemispheres. First, signals persisted in the sending hemisphere until well after they were present in the receiving hemisphere (Fig. 2B). This is similar to effects seen in human MEG for gaze shifts across visible visual stimuli (Fabius et al., 2020). In our study, the lack of anticipatory effects in the hemisphere receiving the working

memories was likely due to unpredictability of the cue instructing the gaze shift. Second, around the time of transfer, we observed a burst of synchrony between LFPs in the two hemispheres of prefrontal cortex with a direction of influence from the sending to the receiving hemisphere. This rhythmic synchrony occurred most prominently in the theta band and in a band straddling traditional beta and gamma bands (Fig. 2D). Interestingly, the latter band lies roughly in between those associated with cortical feedforward (gamma) and feedback (alpha/beta) processing (Bastos et al., 2015; Buschman and Miller, 2007; van Kerkoerle et al., 2014). Interhemispheric synchrony in broadly similar bands of human EEG was also observed when tracking moving objects between visual hemifields (Bland et al., 2020). These results suggest interhemispheric transfer due to gaze shifts also appears to involve an active handoff, with rhythmic synchrony facilitating interhemispheric communication.

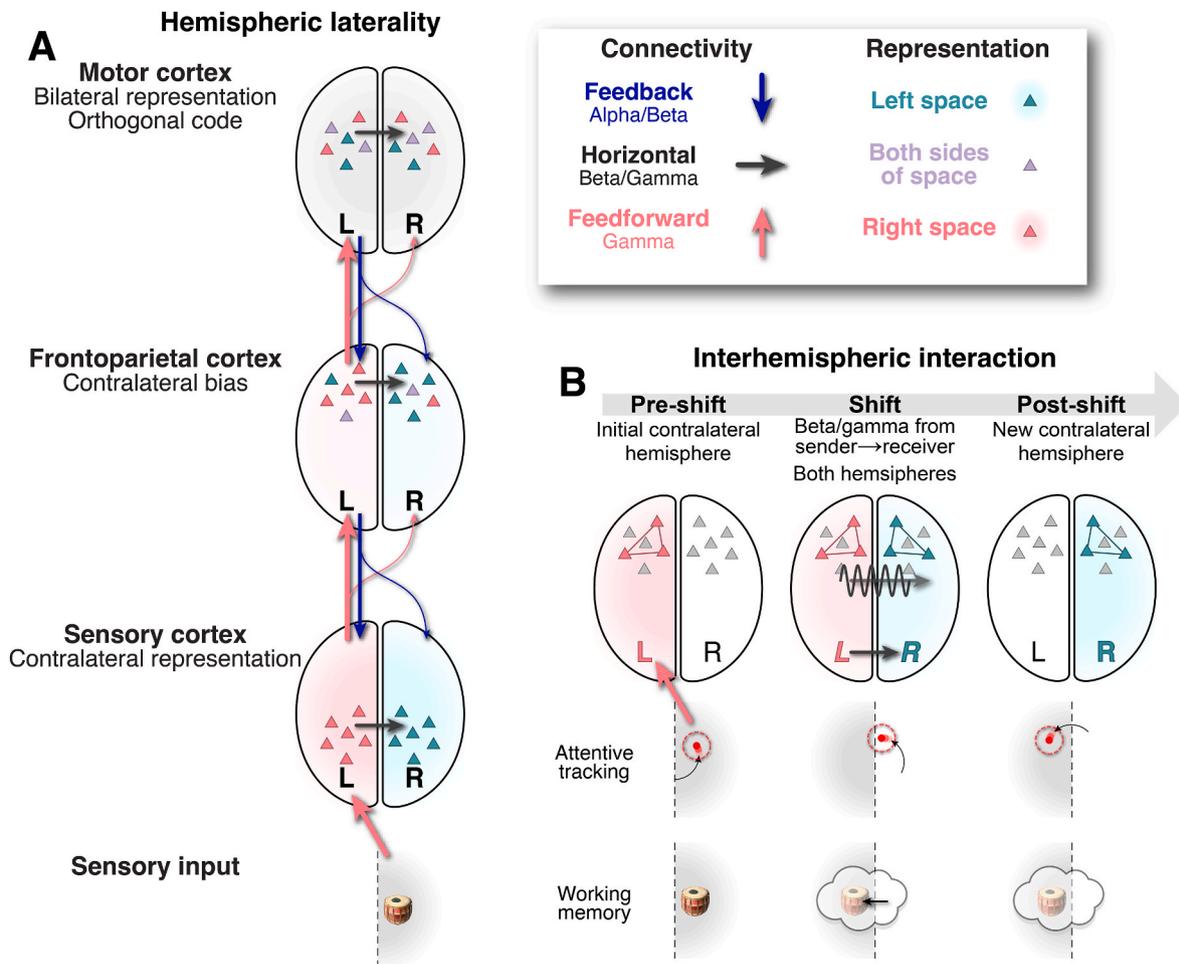
#### 4. Summary and future directions

The studies reviewed here show a surprising degree of neurocognitive independence between cortical hemispheres even at the highest levels of cortex. They also suggest some basic principles and mechanisms for how hemispheres communicate and transfer information between them when that is needed.

It is well known that processing is almost entirely contralateral in low-level sensory areas and becomes more mixed between hemispheres as you ascend the cortical hierarchy (Fig. 3A). However, the results reviewed here suggest the frontoparietal areas thought to contribute most to cognition remain biased towards representing contralateral space. This might reflect a system optimized for rapid, precise control of highly-lateralized sensory cortex. It allows control signals to be conveyed primarily through within-hemisphere feedback connections, avoiding slower paths through the corpus callosum. In fact, spatial attention and working memory act mostly independently in the two hemispheres of visual cortex and in the two visual hemifields behaviorally. Thus, this organization also allows for focused spatial processing to be deployed largely in parallel between the left and right sides of space.

This signal mixing between hemispheres may culminate in a fully bilateral motor cortex. This organization may be optimized for rapid bimanual coordination, necessary for functions like using tools and playing musical instruments. Because left and right arm signals are present in both hemispheres, bimanual interactions may utilize local connectivity within each hemisphere. Nevertheless, signals related to left and right arm movement are kept separate via segregation into orthogonal subspaces. This likely preserves the ability to produce movements in both arms independently and in parallel. Unlike most other signals in frontoparietal cortex, prefrontal beta oscillations and late decision-related spiking activity are largely bilateral. Perhaps these derive from feedback from premotor or motor areas with more strongly bilateral representations. This would be consistent with the idea that beta oscillations are most prevalent in motor regions (Chikermane et al., 2024) and are associated with feedback connections and top-down processing (Bastos et al., 2015; Buschman and Miller, 2007; Miller et al., 2018; van Kerkoerle et al., 2014). Studies of split-brain patients also find a broad distinction between interhemispheric independence for perceptual tasks (Luck et al., 1989) vs interhemispheric interaction for tasks relying on response selection or action planning (Pashler et al., 1994). The fact that motor processing exhibits some interhemispheric interaction even in the absence of a corpus callosum also suggests that subcortical pathways may also be involved.

We also reviewed behavioral and electrophysiological studies showing that, in situations where interaction between information in the two hemifields is required, there is active communication and information transfer between cortical hemispheres (Fig. 3B). This may have evolved to avoid catastrophic information loss during the transfer. Signals are anticipated in the receiving hemisphere and linger in the



**Fig. 3. Schematic summary of hemispheric laterality and interactions.** (A) Laterality of processing through the cortical hierarchy. Each hemisphere of sensory cortex largely represents contralateral space (for clarity, inputs and connections are only shown for right-hand space). As signals ascend the cortical hierarchy via feedforward connections (pink arrows), they become more mixed across both hemispheres, largely due to callosal connections between hemispheres (gray arrows). In frontoparietal cortex, signals remain biased toward contralateral space. In motor cortex, signals are fully mixed between hemispheres, but left and right movements are coded by distinct patterns of population spiking activity. Feedback connections (blue) from more bilateral regions likely also contribute to cross-hemisphere mixing in lower areas. (B) Interhemispheric processing when information is shifted between hemifields (right→left hemifield shift shown). Signals are initially biased toward the contralateral hemisphere. As information shifts between hemifields, signals briefly overlap between hemispheres in an “active handoff”, accompanied by interhemispheric beta/gamma synchrony directed from the sending to the receiving hemisphere. Finally, information is represented in the opposite, now-contralateral, hemisphere. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

sending hemisphere, maintaining redundant signals across both hemispheres for up to a second or more. Ironically, this process may also create a behavioral cost to interhemispheric transfer. Performance drops after transfer, possibly due to increased taxing of resources due to the redundant bilateral representation. Intriguingly, this is largely confined to spatial information. Neither the crossover cost nor the partially lateralized processing described above occur for feature-based attention and working memory. The similar domain over which both of these phenomena apply suggests they may reflect a common underlying mechanism. We propose the mechanism is that spatially-focused processing is partially lateralized to the contralateral cerebral hemisphere, with a communication bottleneck between hemispheres.

This pattern of results also suggests that focused processing of *non-spatial* object features utilizes a distinct, largely bilateral processing scheme. The neural circuitry underlying this dissociation remains a fruitful question for future research. One broad possibility is that cognitive control for feature-based processing is shared across hemispheres. This might suggest feature representations have preferential access to interhemispheric connectivity in frontoparietal cortex. Alternatively, feature-based top-down control may be largely within-hemisphere, but exhibit preferential interhemispheric spread in its

targets within sensory cortex. This would be consistent with evidence that anatomical (Rocheffort et al., 2009) functional (Nowak et al., 1995) connectivity between the two halves of visual cortex depends on feature selectivity.

Interhemispheric synchrony during information transfer seems to consistently occur at a “middle-frequency” band that straddles traditional beta and gamma bands. This may function as a sort of bridge between bottom-up signals associated with gamma and top-down signals associated with alpha/beta oscillations (Bastos et al., 2015; Buschman and Miller, 2007; van Kerkoerle et al., 2014). Alternatively, it might reflect slowing of higher-frequency cortical communication—typically in the gamma band—by transmission through thinner, and thus slower, callosal axons (Caminiti et al., 2009). Though we have focused on interhemispheric information transfer and coordination, it should be noted there is also evidence that some interhemispheric interactions are inhibitory in nature (reviewed in Bloom and Hynd, 2005; van der Knaap and van der Ham, 2011).

We are still in the early stages of understanding interhemispheric processing. It will be critical to compare multiple stages of the sensory-cognitive-motor hierarchy with the same paradigms and analyses. Would this confirm a gradual progression from segregation of left and

right space across hemispheres to their separation into orthogonal subspaces spanning both hemispheres? And where do frontoparietal areas fit into this scheme—do they have an intermediate level of subspace separation in addition to their partial anatomical separation across hemispheres? Would behavioral paradigms designed to probe cognitive control of action (Munoz and Everling, 2004; Verbruggen and Logan, 2008), rather than of perception, result in more bilateral coding in frontoparietal areas? Another key unanswered question is how to reconcile bilateral coding in motor cortex with the well-known contralateral effects of lesions there (Passingham et al., 1983). Since most of its connections to the spinal cord are contralateral, perhaps lesion-induced deficits are due specifically to loss of these descending connections. Additionally, the generality of “middle frequency” synchrony for interhemispheric communication must be evaluated and compared to feed-forward gamma and feedback alpha/beta across individuals and paradigms. Does interhemispheric beta/gamma consistently fall between these bands, supporting the idea that it mediates between them? Finally, in the human cortex many cognitive functions, such as language and attention, are largely lateralized to a single cortical hemisphere (Hellige, 1990). A complete understanding of interhemispheric processing will require elucidating the mechanisms underlying such asymmetric lateralization.

These questions are critical for understanding cortical function, but also for understanding and potentially treating its disorders. Impairments in interhemispheric oscillatory synchrony have been found in animal models of neurodegenerative diseases (Adaikkan et al., 2022). Reduced resting-state interhemispheric functional connectivity has been observed in humans suffering from a broad spectrum of neuropsychiatric disorders. These include anxiety (Wang et al., 2019), depression (Guo et al., 2013), schizophrenia (Hoptman et al., 2012), obsessive-compulsive disorder (Deng et al., 2019), and autism spectrum disorder (Anderson et al., 2011). It has even been suggested that decreases in interhemispheric connectivity might serve as a general biomarker for psychopathology (Yao and Kendrick, 2022). A foundational understanding of interhemispheric processing, combined with interventions translatable to human patients (Hayashi et al., 2022; Helfrich et al., 2014), offers hope for developing novel network-level treatments.

### CRedit authorship contribution statement

**Scott L. Brincat:** Writing – review & editing, Writing – original draft, Conceptualization. **Earl K. Miller:** Writing – review & editing, Writing – original draft, Supervision, Conceptualization.

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### Data availability

No data was used for the research described in the article.

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