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Information Exchange Between Cortical Areas: The Visual System as a Model

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Abstract

As nearly all brain functions, perception, motion, and higher-order cognitive functions require coordinated neural information processing within distributed cortical networks. Over the last decades, new theories and techniques emerged that advanced our understanding of how information is transferred between cortical areas. This review surveys critical aspects of interareal information exchange. We begin by examining the brain's structural connectivity, which provides the basic framework for interareal communication. We then illustrate information exchange between cortical areas using the visual system as an example. Next, well-studied and newly proposed theories that may underlie principles of neural communication are reviewed, highlighting recent work that offers new perspectives on interareal information exchange. We finally discuss open questions in the study of the neural mechanisms underlying interareal information exchange.

Keywords: corticocortical communication; interareal information exchange; visual cortex;

1. Introduction

Formed by hundreds of billions of neurons, the human brain is probably the most sophisticated information processing organ globally. What is remarkable is not only the enormous number of neurons but, above all, how these neurons and the brain regions they form communicate in a well-organized and highly efficient manner. Neuronal communication constitutes the indispensable basis for complex brain functions, as a single neuron performs no behaviorally relevant complex task. Thus, perception, motion, and higher-order cognitive functions rely on precisely coordinated neural activity and information exchange between cortical areas (Heekeren and others 2008; Pinto and others 2019; Steinmetz and others 2019).

The exchange of information in the brain can be described on different levels. The core process underlying information exchange on all levels is the communication between two single neurons. In particular, from a microscale perspective, information exchange between cortical areas can be considered as neurons in one cortical area communicating with neurons in other cortical areas. Therefore, in order to understand cortico-cortical interactions, it is vital to understand the principles of how two single neurons communicate. Researchers have learned much about the properties of single neurons and those of simple neuronal networks, and we know that neurons exchange information by generating action potentials transmitted along their axons to reach their target neurons through synaptic transmission (Felleman and Van Essen 1991; Scannell and Young 1993). Like a calculator, the (target) neurons continuously sum up excitatory and inhibitory synaptic inputs over time and space. Once this sum reaches or exceeds a critical threshold, action potentials are triggered by the target neuron. In this sense, cortico-cortical communication is a seemingly simple process.

However, what complicates matters is that a single neuron can receive input from up to ten thousand presynaptic neurons, and, in turn, any single neuron can impact up to ten thousand postsynaptic neurons (Pittman 2019). This vast number of potential connections results in considerably complex neuronal circuits and network topologies, challenging to investigate. This challenge is particularly true when we try to understand complex brain functions that rely on the interaction of many cortical areas, each containing millions of neurons.

Instead of understanding neuronal communication at a microscopic level, cortical information processing can be approached from a macroscopic point of view. This macroscopic viewpoint can be achieved using computational modeling in combination with modern electrophysiological methods, optical recording or functional imaging where the signals measured represent many neurons' activity rather than a single cell's activity (see Table 1 and Rossini and others 2019; Esposito and others 2020). These methods have successfully been used to understand cortico-cortical information exchange.

The current review focuses on the information exchange at the macroscopic, cortical level. We will first examine how cortical areas connect structurally since anatomical links provide the basic framework for interareal information exchange. Investigating brain functions requires a thorough understanding of the underlying anatomy (Friston 2010). Besides, it is vital to comprehend the principles that coordinate the human brain's network activity. A rich-club organization principle has been suggested to address how information exchange can be coordinated within cortical networks (van den Heuvel and Sporns 2011; Kim and Min 2020). Next, we will use the visual system as an exemplary model to illustrate how visual perception results from cortico-cortical information exchange. Specifically, we summarize how information flows *into*, *within*, and *beyond* the brain areas responsive to visual stimulation. In the following, we will review some of the well-studied and newly proposed mechanisms for cortico-cortical information exchange, focusing on neural oscillations and communication subspaces. We will conclude this review by highlighting and discussing open questions that need to be answered to understand cortico-cortical information exchange further.

Box 1: Brain connectivity

Brain connectivity can be investigated using different approaches. *Structural connectivity* (anatomical links) refers to the physical structure between neural elements (e.g., synaptic connections and fiber pathways). *Functional connectivity* is defined as a statistical relationship between the recorded measures of multiple brain areas. The underlying concept assumes that areas are coupled or part of the same network if their functional behavior is consistently related to each other. Based on various assumptions of the underlying neurobiology and the model construction and selection, *effective connectivity* is considered a more powerful tool to capture stimulus-dependent or task-dependent patterns of causal influences between neural nodes. It describes the effect that one neural node exerts on another (Friston and others 2003; Park and Friston 2013).

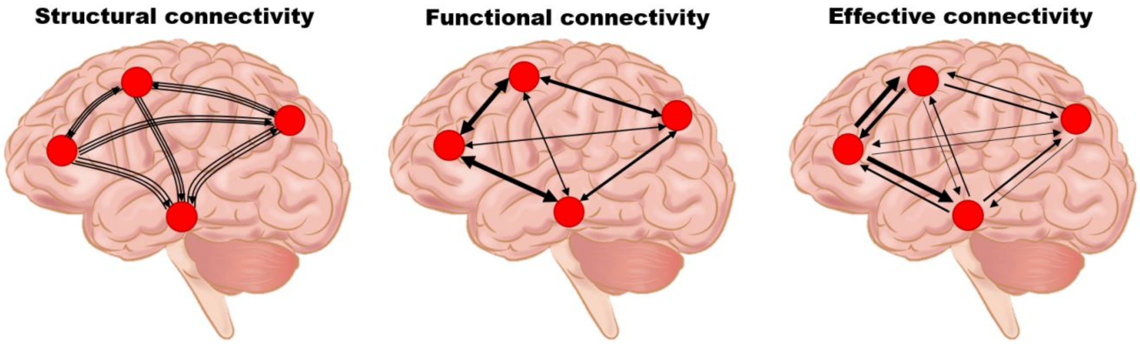

Fig. 1 Illustration of structural connectivity (e.g., fiber pathways), functional connectivity (statistical correlations), and effective connectivity (directional information flow) among four brain regions.

Table 1. Techniques and Methods for Analyzing Brain Connectivity

	Techniques	Measures/Analytical Methods
Structural Connectivity	Anterograde/Retrograde tract tracing Optogenetics and chemogenetics Diffusion of dyes Tissue classification Diffusion tensor imaging (DTI)	Linear Fascicle Evaluation (LiFE) Ensemble Tractography (ET)
Functional Connectivity	Electroencephalography (EEG) Magnetoencephalography (MEG) functional magnetic resonance imaging (fMRI) Positron-Emission-Tomography (PET)	Coherence Mutual information Phase-locking value Directed transfer function Graph theory

Effective Connectivity	functional magnetic resonance imaging (fMRI) Electroencephalography (EEG) Magnetoencephalography (MEG) Transcranial magnetic stimulation (TMS) Transcranial direct current stimulation (tDCS) / Transcranial alternating current stimulation (tACS)	Dynamic causal modeling (DCM) Granger causality

2. Interareal connections

Just as cars can go faster on paved roads, neurons can communicate more efficiently when provided with an adequate anatomical structure. In this sense, structural connectivity (see Box 1) lays the ground for interareal information exchange. Our knowledge of cortico-cortical connectivity has advanced substantially over the last few decades. Early studies suggested that every cortical area only connects to a few other areas (Van Essen 1979). Later, Felleman and Van Essen (1991) published a seminal study and reported 305 projections among 32 visual areas. This number continues to increase (e.g., inputs to V1 expanded from a half-dozen to 20) since improved tracers and more systemic methods became available (Rockland and others 1994; Rockland and Van Hoesen 1994; Falchier and others 2002; Clavagnier and others 2004; Gattass and others 2005). More recently, Markov and colleagues (2014) injected retrograde tracers into 29 of 91 cortical areas in the macaque, revealing 1615 interareal connections, 30% of which had not been detected before. At a more macroscopic level, the anatomy of the white matter (WM) fiber tracts as revealed by diffusion tensor imaging (DTI) also provides valuable insights into the intra- and inter-hemispheric structural connectivity (See Box 2 and Zalesky and Fornito 2009; Assaf and others 2020). Studies on structural connectivity reveal the complexity of anatomical connections in our brain, which raises the question of how information exchange can be coordinated within such a complex network and how divergent functions can be implemented within such a relatively fixed and highly complex structure.

Box 2 White matter fiber bundles

Briefly, white matter fiber bundles have been classified into three types. *Association fibers* connect cortical areas within a hemisphere. Short association fibers connect primary and secondary sensory association areas and further connect with multimodal sensory areas. Long association systems connect the modality-specific association cortex and multimodal areas in the occipital, temporal, and parietal lobes with the premotor and prefrontal cortex. *Commissural fibers* connect corresponding cortical areas in the two hemispheres. *Projection fibers* connect the cerebral cortex with the other parts of the central nervous system, such as the brain stem and spinal cord, in both directions (Table 2 and Fig. 2, for more details, see Jellison and others 2004; Rossini and others 2019).

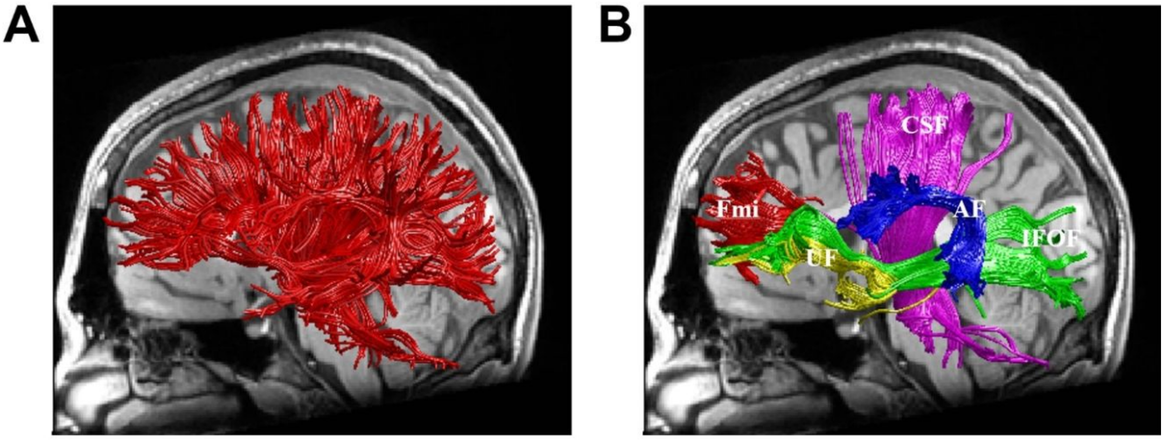

Fig. 2 (A) A side view of the human brain showing the pathways interconnecting brain areas revealed using DTI. (B) Five major white matter fiber tracts: Fmi, forceps minor, which connects the lateral and medial surfaces of the frontal lobes and crosses the midline via the genu of the corpus callosum; CST, corticospinal tract connects cerebral cortex with the spinal cord, responsible for voluntary motor control of the body and limbs; UF, uncinate fasciculus connects the temporal pole, anterior parahippocampus, and amygdala with inferior portions of the frontal lobe, e.g., the orbitofrontal cortex; AF, arcuate fasciculus connects the temporal cortex and inferior parietal cortex to locations in the frontal lobe (e.g., Broca's and Wernicke's areas involved in producing and understanding language); IFOF, inferior fronto-occipital fasciculus connects frontal, temporal, and occipital lobes.

An organizational principle that has been proposed is a rich-club organization (van den Heuvel and Sporns 2011; Kim and Min 2020). It assumes that the brain is segregated into different modules, each containing highly integrated areas through strong short-range connections on a local level. Some cortical areas function as rich-club hubs with dense connections to other modules, and some of their axons reach distant brain regions, acting as long-distance connections. These hubs facilitate information exchange between modules and allow global integration. Hence, different cognitive functions are achieved through global integration by recruiting different modules with different configurations (Park and Friston 2013). Consistent with this account, Bazinet (2020) found that less diverse unimodal areas, which participate in fewer integrative functions, e.g., the primary sensory areas, optimally exchange information at local scales. In contrast, more diverse multimodal areas, e.g., sensory association areas, optimally communicate at global scales (Passingham and others 2002; Mars and others 2018). This well-structured segregation and integration of the cortical areas help the brain process and exchange information more efficiently and flexibly.

Table 2. Major White Matter Fiber Tracts

Types	Fibers
Association fibers	Arcuate fasciculus Cingulum Superior longitudinal fasciculus Inferior longitudinal fasciculus Inferior fronto-occipital fasciculus Uncinate fasciculus
Commissural fibers	Corpus callosum Anterior commissure Posterior commissure
Projection fibers	Corticospinal fibers Corticopontine fibers Geniculocalcarine tracts Corticobulbar fibers

3. Visual information exchange

Based on the findings from structural connectivity, we will now examine how visual information flows *into*, *within*, and *beyond* the cortical areas responsive to visual stimulation to describe information exchange between cortical areas. Generally, the visual cortex receives visual information from subcortical projections, including the visual nuclei of the thalamus, which is then further processed and distributed across multiple visual areas. Furthermore, the visual system projects to and receives input from more distal brain regions, such as the frontal and parietal cortex. These patterns structure and constrain information exchange within the entire visual cortical network. We will elaborate on these processes in the following sections.

3.1 Visual information inputs into the cortex and thalamocortical interactions

Information processing in the brain starts with physical energy (e.g., visible light) entering our brain by stimulating a sensory organ which then translates and encodes this energy into a neural code. With its retinal ganglion cells and other cells, the retina performs the initial neural computations of incoming visual information, which is then transmitted along the optic nerves to higher visual processing areas (Boycott and Wässle 1999). The two optic nerves converge at the optic chiasm, and the axons then separate into two optic tracts that terminate in the thalamus's lateral geniculate nucleus (LGN). The coded visual signals are then projected to the primary visual cortex (V1) via the optic radiation (Goebel and others 2012).

According to the classical view of thalamocortical interaction, visual information processing is performed more or less exclusively within the cortex once the information has reached this level or processing. Thus, the thalamus was considered to function merely as a relay point transmitting visual signals to the cortical areas. However, recent evidence suggests that other thalamic nuclei not involved in the first-order transmission of visual signals to the cortex have crucial roles concerning other cortical functions. More specifically, aside from the first-order thalamic nuclei (e.g., LGN) transmitting the ascending sensory input to the cortex, the higher-order (or second-order) thalamic nuclei (e.g., pulvinar nucleus) receive signals from the cortex and are widely connected with other cortical regions, representing a part of a cortico-thalamo-cortical or transthalamic pathway (Sherman and Guillery 2013; Sherman 2016; Usrey and Sherman 2019, Fig. 3 and Box 3). For example, previous studies have identified cortico-pulvinar-cortical pathways in macaque that parallel the hierarchical feedforward and feedback visual processing. Specifically, the pulvinar receives signals from a lower (or higher) visual cortical area and transmits them to a higher (or lower) visual cortical area (Marion and others 2013; Markov and others 2014).

While the functions of the first-order nuclei are relatively clear, as they serve as a relay point conveying information from the sensory periphery to the cortex, the functions of the higher-order nuclei remain elusive. With regard to the cortico-pulvino-cortical pathway, two ideas have been proposed. One suggests that this pathway might provide the target cortical regions with an efference copy of the signals relayed from the cortical neurons in layer 5 to the subcortical structures (Sherman 2016). Efference copy refers to an internal estimate of the sensory consequences of upcoming self-generated behavior from the brain's motor areas to the sensory cortex, which can then be compared to the actual sensory feedback. It allows the organism to disambiguate self-generated movements from the outside world. This function is essential for visual perception since it allows perceiving a constant world even though the retinal image changes significantly with every eye movement we make. However, others argued that the dominant function of the pulvinar nucleus and other higher-order nuclei is unlikely to be relaying efference copy signals from one cortical region to another. According to a previous study, neurons in higher-order thalamic nuclei receive signals from various small cortical synapses (Rovo and others 2012), and convergence from multiple cortical synapses is required to activate the pulvinar. The information processed along that pathway is reorganized and transformed, making it unlikely to represent efference copies. Moreover, the projection of the pulvinar nucleus to the target cortical areas is diffuse, and most receptive field (RF) sizes of the pulvinar neurons are more extensive than their cortical inputs and outputs (Halassa and Kastner 2017). These experimental observations argue against the efference copy relay hypothesis.

Therefore, instead of relaying information, other researchers proposed a modulatory role for the pulvinar nucleus. Specifically, the pulvinar nucleus is likely to modulate direct cortico-cortical information flow by regulating synaptic efficacy in cortical areas (Olshausen and others 1993; Purushothaman and others 2012; Halassa and Kastner 2017). Consistent with this theory, several studies reported that inactivating the pulvinar had a considerable impact on neural activity in areas reciprocally connected to it (Purushothaman and others 2012; Zhou and others 2016; Guo and others 2017).

In summary, the functional role of the pulvinar nucleus is still under debate. Nevertheless, current evidence suggests a critical role of the pulvinar nucleus in interareal communication. It either relays efference copies to other cortical areas or modulates direct cortico-cortical signal transmission. These two functions are not necessarily mutually exclusive.

Box 3: Pulvinar nucleus and its function

The thalamus consists of first-order and higher-order nuclei. The LGN constitutes a first-order thalamic nucleus in the visual modality, whereas the pulvinar nucleus represents a higher-order nucleus. The pulvinar is one of the most prominent nuclei in the primate thalamus. Its main subdivisions are the inferior, lateral, and medial pulvinar. While the pulvinar mainly connects to the visual cortex, especially the inferior and lateral pulvinar, which are famous for their functional role in visual processing (Baldwin and others 2017), cumulative evidence suggests that the pulvinar is involved in further functions. Apart from the visual modality, the pulvinar contributes to auditory, somatosensory, pain, proprioceptive, and olfactory processing, suggesting a role in multisensory integration (Froesel and others 2021). The medial pulvinar, which widely connects with the non-sensory or association cortex (such as posterior parietal, inferior temporal, and prefrontal lobe), serves modulatory functions when simultaneously processing information from the different network modules (Homman-Ludiye and Bourne 2019). Apart from the sensory domains, the pulvinar is critically involved in motion and cognition. For example, a patient with a lesion of the dorsal pulvinar exhibited reach and grasp difficulties (Wilke and others 2018). Inactivating the pulvinar disrupted saccade initiation toward targets (Wilke and others 2013) and movement plan selection (Wilke and others 2010). Recent reviews also highlight the role of pulvinar in selective attention (Gattass and others 2018; Kastner and others 2020).

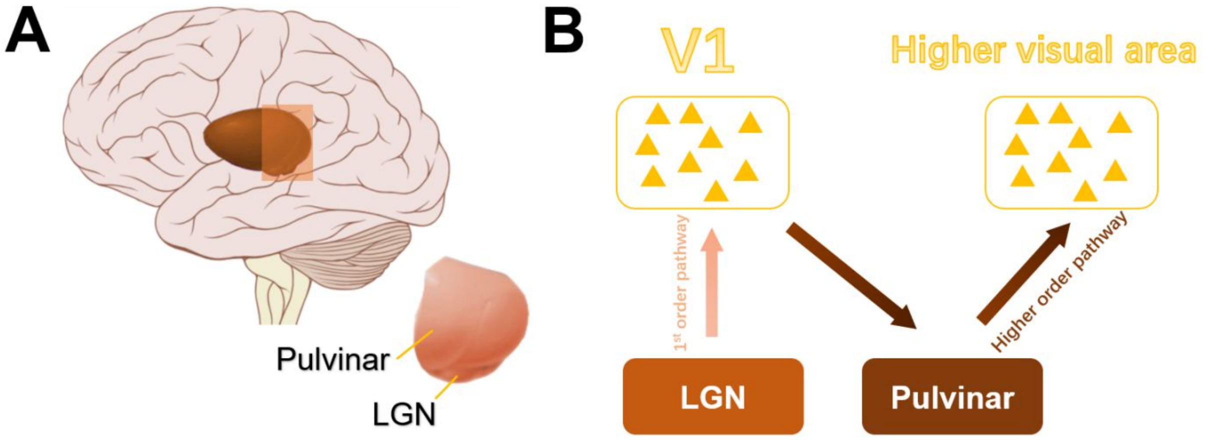

Fig. 3 (A) Illustration of the pulvinar nucleus and LGN. (B) Illustration of first-order pathways and higher-order pathways.

3.2 Visual information exchange within cortical areas responsive to visual stimulation

Our brain is a hierarchically organized system. The hierarchical direction of information exchange can be inferred from the cortical layers. Each cortical layer comprises more or less unique types of neurons. Felleman and Van Essen (1991) studied the termination patterns of cortical axonal projections in the visual cortex and categorized these pathways as feedforward, feedback, and lateral pathways. According to this classification, projections that mainly ended in the middle layer (layer 4) were classified as feedforward connections. Pathways that mainly terminated in the superficial and deep layers but avoided the middle layer were considered feedback connections. Besides, pathways terminating more evenly in all layers were described as lateral connections generally involved in intra-areal communication (Felleman and Van Essen, 1991).

Feedforward pathways

The occipital cortex contains the primary cortical brain region that receives and processes visual information transmitted from the eyes via the central visual pathway. Visual information then travels along the feedforward pathways. Specifically, V1 is the first cortical area that receives information from the LGN and is presumably the best-understood region of the visual cortex. V1 has a very well-defined map (the retinotopic map) of spatial information in vision (Engel and others 1994; Sereno and others 1995). In V1, neighboring neurons represent neighboring areas in the visual field. Columns and maps for ocular dominance (Hubel and Wiesel 1962; Cheng and others 2001; Goodyear and Menon 2001) and orientation (Hubel and Wiesel 1962; Yacoub and others 2008) have also been reported. The summation of visual information from V1 provides an essential foundation for information processing in higher visual areas. Layers 2, 3, and 4β of V1 project to V2, transmitting feedforward information. The reciprocal link between V1 and V2 is one of the best-studied to date. The number of direct projections from V1 to V2 is approximately 20- to 25-fold greater than the number of LGN inputs to V1 (Van Essen 2005).

In addition to preserving the stimulus properties encoded in V1, neurons in V2 show complex spatial properties absent or rare in V1. For example, V2 neurons are capable of responding to more complex patterns of visual information, such as tuning for stereoscopic depth (von der Heydt and others 2000), relative binocular disparity (Thomas and others 2002), and subjective contour (Peterhans and von der Heydt 1989).

It is generally accepted that visual information is subsequently transferred to higher visual areas and gradually separated into two functionally specialized visual streams: the dorsal stream and ventral stream (Mishkin and others 1983; Ungerleider and others 1998). The ventral stream, originating in V1 and extending to the temporal lobe, has been referred to as the “what” stream. It exhibits relative specialization in object recognition. Object information is processed in the ventral stream, e.g., size, color, or shape, until an object is finally recognized. Extending to the parietal cortex, the dorsal stream, on the other hand, is involved in visually guided behavior and is often called the “where” (Ungerleider and Mishkin 1982) or “how” stream (Goodale and Milner 1992; Goodale and others 1994). This stream helps to locate the object’s space and allows for reaching movements. The dorsal stream has been further separated into two functional specific streams: a dorso-dorsal and a ventro-dorsal stream. The ventro-dorsal stream is considered to be involved in object awareness for action recognition or advanced sensorimotor information. The dorso-dorsal stream, on the other hand, is regarded to be responsible for the online control of actions, such as online processing during actual object interaction (Binkofski and Buccino 2018).

In addition to within-stream communication, dorsal and ventral streams also communicate (Felleman and Van Essen 1991; Distler and others 1993; Chen and others 2012; Vossel and others 2014). For example, multiple structural connections have been identified linking the two visual streams, especially between the inferior parietal cortex and inferior temporal cortex (Baizer and others 1991; Felleman and Van Essen 1991; Distler and others 1993; Webster and others 1994; Ungerleider and others 2008). Moreover, these connections are reciprocal, with dense feedforward connections across streams and corresponding feedback connections (Felleman and Van Essen 1991; Distler and others 1993; Nassi and Callaway 2009; Rosa and others 2009; Pollen 2011). In addition to direct reciprocal connections, the two visual streams project to the same regions, such as the prefrontal cortex (Baizer and others 1991; Distler and others 1993), which has also been shown to respond to visual stimuli. Tanila and others (1992) found that 29% of dorsolateral prefrontal neurons responded to visual stimuli in monkeys. Using fMRI, researchers even identified a visuospatial map in the prefrontal cortex of humans when conducting working memory tasks (Hagler and Sereno 2006; Kastner and others 2007; Funahashi 2013).

Feedback pathways

As mentioned above, information exchange includes both feedforward pathways and feedback pathways (Fig. 4). Feedback connections outnumber their feedforward counterparts in many instances. Three types of feedback pathways have been described: cortico-cortical, cortico-pulvino-cortical, and cholinergic (for details, see Review Pennartz and others 2019). Here, we focus mainly on cortico-cortical feedback connections in the visual domain. First, V1 receives reciprocal feedback projections from those visual areas it projects to, particularly V2, V3, and V4, considered as short-range feedback projections (Felleman and Van Essen 1991). The role of feedback connections (see also Box 4) in visual perception can be illustrated by size illusions such as the Ponzo illusion, where one of two identically sized stimuli is perceived as larger depending on the surrounding context. There are different explanations for the illusion effect (Yildiz and others 2021) and one of the most influential accounts is based on size-distance integration (see Sperandio and Chouinard 2015 for a review), with which the brain accounts for the fact that objects located at greater distances generate smaller retinal images than objects nearby. A possible underlying neural mechanism might involve a first sweep of feedforward visual processing of contextual information (e.g., the depth) and the initial size information in a higher visual area (e.g., the LOC). Once context information has been processed, feedback modulations from LOC could trigger perceptual size scaling, causing one object to be perceived as larger than the other. Using transcranial magnetic stimulation (TMS), Zeng and others (2020) showed that this process of size distance scaling could be altered at specific points in time. The most potent TMS effects, when applied over the early visual cortex (EVC), occurred later than those observed when stimulating LOC. This finding supports the idea of functionally relevant feedback modulation from LOC to EVC when forming a size percept.

Higher cortical areas such as temporal, parietal, and frontal cortex also send projections to V1 along the same hierarchical routes through long-range projections. Besides the primary visual cortex, other visual areas also receive feedback projections. For example, previous studies have shown that reciprocal connections exist between the frontal eye field (FEF) and V4 (Schall and others 1995; Stanton and others 1995; Ungerleider and others 2008), and that stimulating the FEF increases neuronal responses of V4 to a target stimulus in the RF (Moore and Armstrong 2003; Ekstrom and others 2008). Moreover, to investigate whether FEF modulates V4 during visual attention, Gregoriou and others (2009) recorded neural activity simultaneously in the FEF and area V4. They found that attending a stimulus in their joint RF induced stronger oscillatory coupling between the two areas, especially at gamma frequencies.

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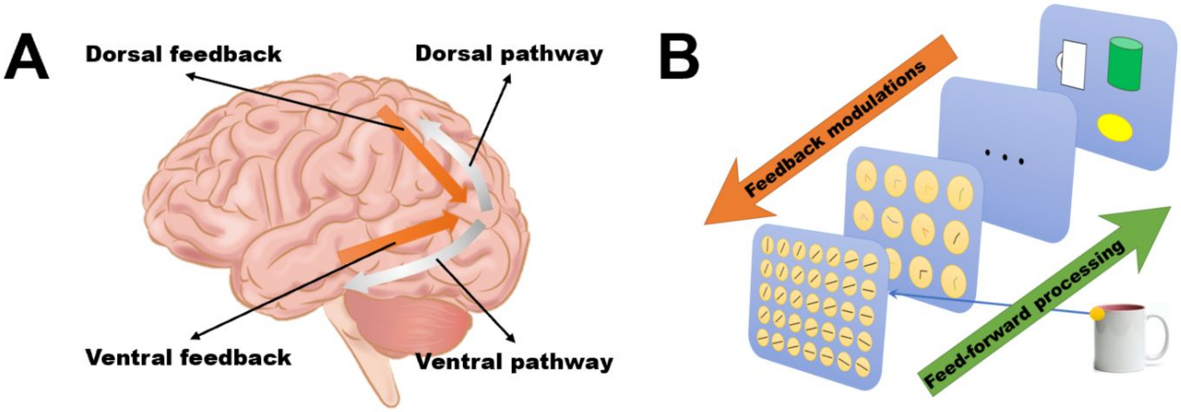

275 *Fig. 4 (A) The view of hierarchical feedforward and feedback processing separated in dorsal and*
276 *ventral pathways. (B) The two visual pathways. The hierarchy consists of a cascade of neurons*
277 *encoding more and more complex features through convergent object recognition.*

278 Box 4 Functional roles of feedback connections

Accumulating experimental and computational evidence indicates that feedback connections are essential for visual processing and other forms of cognitive processing. However, the exact functional role of feedback connections is still not fully understood, and different theories have been proposed. Possible theories range from i) sensory context modulation, ii) feedback of high-level information, and iii) prediction (for reviews, see Petro and others 2014; Pennartz and others 2019)). Sensory context modulation refers to feedback from higher cortical areas to the primary sensory areas, with contextual information only available in higher cortical areas. It results in filling in and integrating finer details of a visual image into what we perceive (e.g., Kanizsa illusion, Chen and others 2020; Chen and others 2021)). High-level information includes attention and value-related information (e.g., reward), which significantly affects the lower-level cortical areas (Shuler 2006; Herrero and others 2008; Goltstein and others 2013; Stanisor and others 2013). Prediction, as in the context of the predictive coding theory, proposes that feedback processing is actively involved in analyzing feedforward signaling. Specifically, feedback signals and iterative processing between higher and lower visual areas allow the brain to verify and match the predictions and perceptual interpretations formed at higher levels with current representations in lower areas. The system aims to minimize the discrepancy between the brain's prediction and incoming sensory inputs. The remaining discrepancy is called "prediction error" (Clark 2013; Barrett and Simmons 2015; Friston 2018; de Lange and others 2018). Recent research found that interareal interactions just after stimulus onset are feedforward but become feedback-dominated as the stimulus persists (Semedo and others 2021). The findings are well in line with the predictive coding theory as a new stimulus is unpredicted or unexpected, hence generating feedforward signals. While it persists, feedback processing tries to "explain away" the constant, predicted activity. Given the robustness of this effect, predictive coding has been suggested to be a general principle of cortical processing. Indeed, predictive coding provides a broad interpretive framework that can include stimulus-context modulation and high-level processing.

The processing of visual information involves both feedforward and feedback connections between visual cortical areas. An essential aspect of understanding the functional mechanisms of neural information processing is how specific these transmissions between different cortical areas are. In principle, both feedback and feedforward connections may carry unspecific signals representing the computational result of a specific cortical region. For example, in the case of feedforward processing, the primary visual cortex may have analyzed an incoming signal, and that particular result would then be transmitted to all higher visual areas for further processing via local computation. Alternatively, the primary visual cortex might transmit functionally specific inputs to higher target regions, implicating that each functional region generates multiple and different computational outputs in parallel. Concerning the functional specialization of higher visual regions, this view implies that functional specialization might not merely be a property of a single specialized region itself but may also reflect the communication structure with other areas in combination with their computational properties. Glickfeld and others. (2013) tested whether primary visual area neurons send functional target-specific synaptic inputs to the higher visual areas and identified a marked target specificity of these projections. That is, each higher visual area receives functionally specific sensory inputs from the superficial and the deep layers of the primary visual area. Therefore, instead of transmitting the same information to different cortical areas, each projection may transmit region-specific information. Similar results have also been reported for feedback connections (Briggs and Usrey 2009; Briggs and others 2016; Huh and others 2018; Federer and others 2021). For example, using virus-mediated labeling of feedback pathways of visual areas in macaque, Federer and others (2021) revealed that feedback pathways from V2 to V1 resemble the reciprocal feedforward pathways, forming parallel streams. Therefore, they suggested that the functionally specialized V2 feedback connections regulate the response of V1 to specific stimulus features. This organizational principle may be extended to feedback pathways of other sensory modalities.

3.3 Visual information exchange beyond the visual system

Visual information processing is not restricted to the visual cortex and is not independent of information processing in other modalities. An excellent illustration for interactions of visual information with auditory stimuli is the McGurk effect (McGurk and Macdonald 1976). In this illusion, participants' auditory perception of spoken syllables can be altered when seeing lip movements consistent with the pronunciation of another syllable. For instance, while hearing the sound of the spoken syllables “ba” and seeing lip movements of a person pronouncing “ga”, they are likely to hear a syllable sounding like “ga”. An interaction between the visual and the auditory domain can also be found on a neuroanatomical level. Anatomical projections between the visual and auditory cortices are well documented (Cappe and Barone 2005). ERPs and fMRI studies have shown that when tones are paired with visual stimuli of interest, the auditory cortex response is enhanced compared to visual stimuli that are not of interest. (Busse and others 2005). More recently, researchers revealed direct white matter connections between visual (occipital middle-temporal region) and auditory (planum temporale) motion-selective regions (Gurtubay-Antolin and others 2021). Furthermore, visual information also interacts with somatosensory information (see Manivannan and Suresh 2012 for a review). For example, haptic feedback affects visual slant perception (Ernst and others 2000). Moreover, proprioceptive cues have been shown to suppress autokinesis (i.e., motion perception without objective target displacement, Lackner and Zabkar 1977). On the neural level, fMRI studies showed that a tactile stimulus on either the left or right hand enhances the response to a visual stimulus delivered at a corresponding location (Macaluso and Driver 2001), promoting our interactions with the external world. More generally, haptic information can activate visually responsive regions in the occipital and parietal cortex (Stilla and Sathian 2008; Allen and Humphreys 2009), which is supported by anatomical data indicating that there are direct projections between the somatosensory and visual cortex (Cappe and others 2009; Cappe and others 2012). Besides interactions with other sensory modalities, the visual system closely interacts with the motor system. A particularly well-studied example is visual image processing during saccadic eye movements in primates (Wurtz and Sommer 2004). As mentioned above, neuronal copies of the extraocular motor commands that encode the saccade's spatio-temporal parameters are forwarded to central visual processing areas, where they are integrated with incoming visual inputs to generate a modified visual percept, thereby preventing the perception of illusionary object motion during a saccade.

4. Mechanisms of information exchange

4.1 Communication via neural oscillations

Spiking synchrony

As described above, target neurons function as a calculator, summing the synaptic inputs over short periods. Therefore, if the synaptic inputs are temporally coordinated (i.e., synchronized), they are more likely to generate a response in the target neuron (Salinas and Sejnowski 2001; Kumar and others 2010; Wang and others 2010). Indeed, several empirical studies suggest that synchronous thalamic spike activities are associated with more robust responses in their target cortical neurons (Alonso and others 1996; Roy and Alloway 2001), which might be critical for thalamocortical communication (Bruno and Sakmann 2006). Zandvakili and Kohn (2015) investigated how coordinated spiking activity enhanced cortico-cortical communication and showed that spiking in the input layer (i.e., middle layer) of V2 was preceded by a brief epoch of synchronous spiking in V1 but not in the superficial and deep layers. In other words, synchronous spiking in V1 increases the neuronal responses in V2 that receive direct synaptic input from V1, but such facilitation does not propagate through the local V2 circuit. On the one hand, spiking coordination in the source neuron improves the efficacy of cortico-cortical communication. On the other hand, the effects of spiking synchrony do not propagate through the downstream target networks. Moreover, spike synchrony between cortical neurons in a brain area is typically weak (approximately 1-5% of spikes in V1) (Bair and others 2001; Kohn 2005). Therefore, it remains to be elucidated whether spiking synchrony in the source area plays an essential role in regulating cortico-cortical information exchange.

Communication through coherence (CTC)

CTC is probably the most well-studied mechanism of interareal communication (Fries 2009). It suggests that synchronizing neural oscillations between two areas is a critical mechanism for interareal information exchange. Briefly, the basis of CTC is that continuous oscillations lead to increased excitability within a region. This increased excitability increases the likelihood that an incoming spike will generate additional spikes. Thus, information is transmitted most efficiently from one region to another when the oscillation frequency in one region is the same as in the other region, and the phase difference is commensurate with the peak propagation delay between the two regions. In other words, interareal communication is most effective (ineffective) when the phase of the oscillation frequencies (in particular the gamma bands, approximately 30–70 Hz) in the two areas are synchronous (asynchronous). Gamma oscillations involve rhythmic fluctuations in inhibition (Tiesinga and Sejnowski 2009; Buzsáki and Wang 2012). Thus, the efficacy of the input to the target region depends on whether it reaches the gamma phase at a time when the target neuron is more likely to be excited (the "good" gamma phase) or less likely to be excited (the "bad" phase) (for review, see Buzsáki 2009; Fries 2009; Wang 2010; Fries 2015). This view implies that coherence is a central and causal mechanism underlying interareal neuronal communication. An alternative interpretation is that coherence between brain areas might naturally emerge due to interareal communication, and hence representing a consequence rather than a cause for communication. This view has recently been put forward by Schneider and colleagues (Schneider and others 2021). They argued that synaptic potentials in a source area trigger synaptic potentials in a target region, hence generating highly correlated synaptic potentials at a delay resulting in coherence or Granger causality. Indeed, mathematical analysis and optogenetic perturbation indicate that it is afferent synaptic inputs that drive interareal coherence rather than spike phase locking in the target area. Hence, local field potentials coherence and Granger causality primarily reflect the dynamics of neuronal interactions in the source area but do not infer how much it drives the activities in the target area, which reflects the communication.

Nested oscillations

Although plenty of evidence supports gamma oscillations as a modulator of cortico-cortical communication, some researchers argued that gamma oscillations could not be the primary mechanism for modulating interareal communication due to specific properties (for review, see Ray and Maunsell 2015). For example, the strength of gamma oscillations is established slowly and is relatively unstable (Burns and others 2011; Jia and others 2011), which suggests that they may not be able to quickly or reliably regulate interareal communication. Therefore, researchers proposed a nested oscillations framework based on the coupling of slow and fast oscillations (Florin and Baillet 2015; Hyafil and others 2015; Bonnefond and others 2017). Unlike CTC, the nested oscillations framework suggests that interareal connection is built by phase synchronization of oscillations at lower frequencies (< 25 Hz) instead of the gamma band. The power of the coherently oscillated frequency (e.g., alpha or theta) decreases simultaneously to produce a more extended excitatory period allowing for more information to be exchanged between the source and the target areas (Jensen and Mazaheri 2010). Correspondingly, asynchronous oscillations between the source and the non-target areas and the increased alpha power lead to a shorter excitatory period resulting in the blockade of communication. Moreover, gamma oscillations are nested within alpha oscillations. A more extended excitatory period allows for a longer time window for gamma activity in the source area to affect the target area. Since synaptic summation is performed within the time window of the gamma cycle, this rapid neuronal synchronization will have a substantial effect on the target area (Salinas and Sejnowski 2001). Consequently, gamma oscillations in the source and target areas will be correlated or even coherent. A macaque study investigating interareal communication between V1 and V2 showed that the gamma synchronization between two areas was shaped by 3 - 4 Hz theta rhythm supporting the view that cross-frequency coupling or nested oscillations facilitate the information exchange between cortical areas (Lowet and others 2016).

4.2 Communication Subspace

A new theory suggests that cortico-cortical communication is regulated by changing the extent to which neural activity in source areas matches the communication subspace that transmits the neural information to the target areas (Kaufman and others 2014; Elsayed and others 2016; Semedo and others 2019). The idea was initially developed by Kaufman and others (2014) to interpret the strong neural activities during a motor preparation period in the motor areas while not generating muscle contractions (for more details, see Kohn and others 2020). Specifically, this theory conceptualizes interareal communication as matrix multiplication. Non-target information (e.g., preparatory neural activity) of downstream areas can be attenuated by an alignment with the nullspace of the communication subspace matrix. The communication subspace acts as a bottleneck that constrains information flow, letting pass some types of information while others are blocked. For example, Semedo and others (2019) simultaneously recorded neuronal population responses in areas V1 and V2. They observed that the neural activity in V2 only correlated with a small subset of V1 activity, suggesting that only a small number of neural activity patterns were selectively transmitted from V1 to V2, while the majority were not. They proposed that “communication subspace” may nicely explain how different types of information (e.g., color or orientation) encoded by one brain region are selectively transmitted to different target brain regions. It might be an evolutionary and computational advantage to transmit only specific information the target regions require rather than the complete information. However, this method is based on correlations between activations in two brain areas and hence does not allow causal interpretations on how information flows between regions since the correlation of neural activities in these two areas might be caused by a third area that affects both (Ebitz and Hayden 2021).

5. Conclusions

This review compiled a broad range of data on how information might be exchanged between cortical areas, with a particular focus on the visual system. Most cortical areas connect to neighboring areas via strong short-range connections in a local module (e.g., the visual system). Different modules also connect to each other via rich-club hubs with dense connections to distant brain regions (e.g., the auditory system or motor system). Additionally, the observed patterns indicate that while the information moves along hierarchically ordered feedforward pathways, feedback or even transthalamic pathways allow flexible and efficient information exchange.

Furthermore, we reviewed well-studied and newly proposed mechanisms on how information is exchanged between different cortical areas. Some of these proposed mechanisms tackle the question of information exchange concerning different aspects, considering different features of the information exchange. Therefore, these mechanisms might not be mutually exclusive and exist in parallel or even depend on each other. Moreover, recent research has shown that the patterns of the information exchange between cortical areas were modulated by attention and varied over time (Mock and others 2018; Ferro and others 2021). Consequently, although our understanding of interareal communication has improved, many of the processes require further investigation.

For example, most proposed mechanisms address interareal communication where one source area only connects to one target area. However, as demonstrated in the current review, one cortical area is connected to multiple areas. Can the proposed mechanisms address this issue? Also, it becomes more and more evident that transthalamic pathways play an essential role in interareal communication. Nevertheless, the role of the transthalamic pathways in interareal communication remains elusive, compared to direct cortical-cortical pathways. Although several accounts have been put forward regarding the role of the pulvinar in the transthalamic pathway, more empirical data are needed to test these hypotheses and further elucidate the role of other parts of the transthalamic pathway. Ultimately, information exchange between cortical areas must be understood at the level of a single neuron. New techniques with sufficient spatial resolution to capture the rapid spatiotemporal evolution of spiking activity or action potential transmission of cortico-cortical dynamics are needed. Recent developments in this area might be able to shed some light on this problem. For example, neuropixels is a recently developed probe that distributes more than 1000 recording sites over a narrow, one-centimeter shank. It can record hundreds of individual neurons distributed across brain regions for weeks or even months (Steinmetz and others 2019; Steinmetz and others 2021). Although primarily used in rats and mice currently, a probe designed for non-human primates is on its way, which will help inform the information exchange in the human brain further.

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Declaration of Conflicting Interests

The authors have no competing interests to declare.