

Feature Review

The ventral visual pathway: an expanded neural framework for the processing of object quality

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Since the original characterization of the ventral visual pathway, our knowledge of its neuroanatomy, functional properties, and extrinsic targets has grown considerably. Here we synthesize this recent evidence and propose that the ventral pathway is best understood as a recurrent occipitotemporal network containing neural representations of object quality both utilized and constrained by at least six distinct cortical and subcortical systems. Each system serves its own specialized behavioral, cognitive, or affective function, collectively providing the *raison d'être* for the ventral visual pathway. This expanded framework contrasts with the depiction of the ventral visual pathway as a largely serial staged hierarchy culminating in singular object representations and more parsimoniously incorporates attentional, contextual, and feedback effects.

History and overview

Cortical visual processing is commonly thought to proceed along two distinct pathways: a dorsal pathway projecting into parietal cortex and a ventral pathway projecting into temporal cortex. These pathways were identified in monkeys as anatomically and functionally distinct systems of multisynaptic connections emerging from the striate cortex [1] (Figure 1a). The dorsal pathway was described as coursing through the occipitoparietal cortex to the posterior part of the inferior parietal lobule (area PG) [1,2], with a likely further extension to the dorsolateral prefrontal cortex (DLPFC/area FDΔ) (Figure 1a) [3]. The ventral pathway was described as coursing through the occipitotemporal cortex to the anterior part of the inferior temporal (IT) cortex (area TE) [1,2], with a likely extension into the ventrolateral prefrontal cortex (VLPFC/area FDv) [3]. In monkeys, lesions in the dorsal and ventral pathways yielded dissociable deficits in spatial and object vision, leading to their characterization as ‘Where’ and ‘What’ pathways, respectively [1–3]. Although the general functional characterization of the dorsal stream as a ‘Where’ pathway has been extensively debated (e.g., [4,5]), the characterization of the ventral stream as a ‘What’ pathway supporting the processing of object quality or identity

(Box 1) has remained largely unchallenged (but see [6]). The aim of this review is not to fundamentally alter this characterization, but rather to integrate the now better explored neuroanatomical and functional properties of the ventral pathway into an expanded and more fully specified framework.

In particular, we argue that the ventral visual pathway is a recurrent and highly interactive occipitotemporal network linking early visual areas and the anterior IT cortex (aIT) along multiple routes through which visual information is processed. Extrinsically, major projections to at least six subcortical and cortical regions arise from different parts of the pathway, supporting many different forms of object quality processing (Box 1). This framework synthesizes the neuroanatomical and functional findings in monkeys and humans and can more parsimoniously incorporate numerous effects clearly dependent on recurrent processing, such as attention, masking, and context. In explicitly associating neuroanatomy and function, this framework also provides traction on several difficult theoretical issues, including why different areas in the network show such diverse and clustered categorical selectivity, why there is consistency across individuals in the location of these clusters, and how regions from different putative levels of the hierarchy communicate to enable recurrent processing.

For the purpose of stepping through this complex and detailed framework, it is useful to contrast it with the conception of the ventral pathway as a serial staged hierarchy (Figure 1b). According to this view, visual information from the striate cortex (visual area V1) passes through a sequence of processing stages in the extrastriate cortex until complex object representations are formed in the anterior part of the IT cortex, area TE (Figure 1b,c). It is thought that each stage of this hierarchy creates successively more complex representations by aggregating the output of the simpler feature detectors in the previous stage (Figure 1d). This idea was based partly on the apparently hierarchical response properties of cells in V1 and V2, which gave rise to formal computational models of processing in the ventral pathway [7,8]. The hierarchical view also drew support from the gradually increasing receptive field (RF) size, onset latencies, and complexity of stimulus selectivity of neurons (e.g., [9–11]) as one

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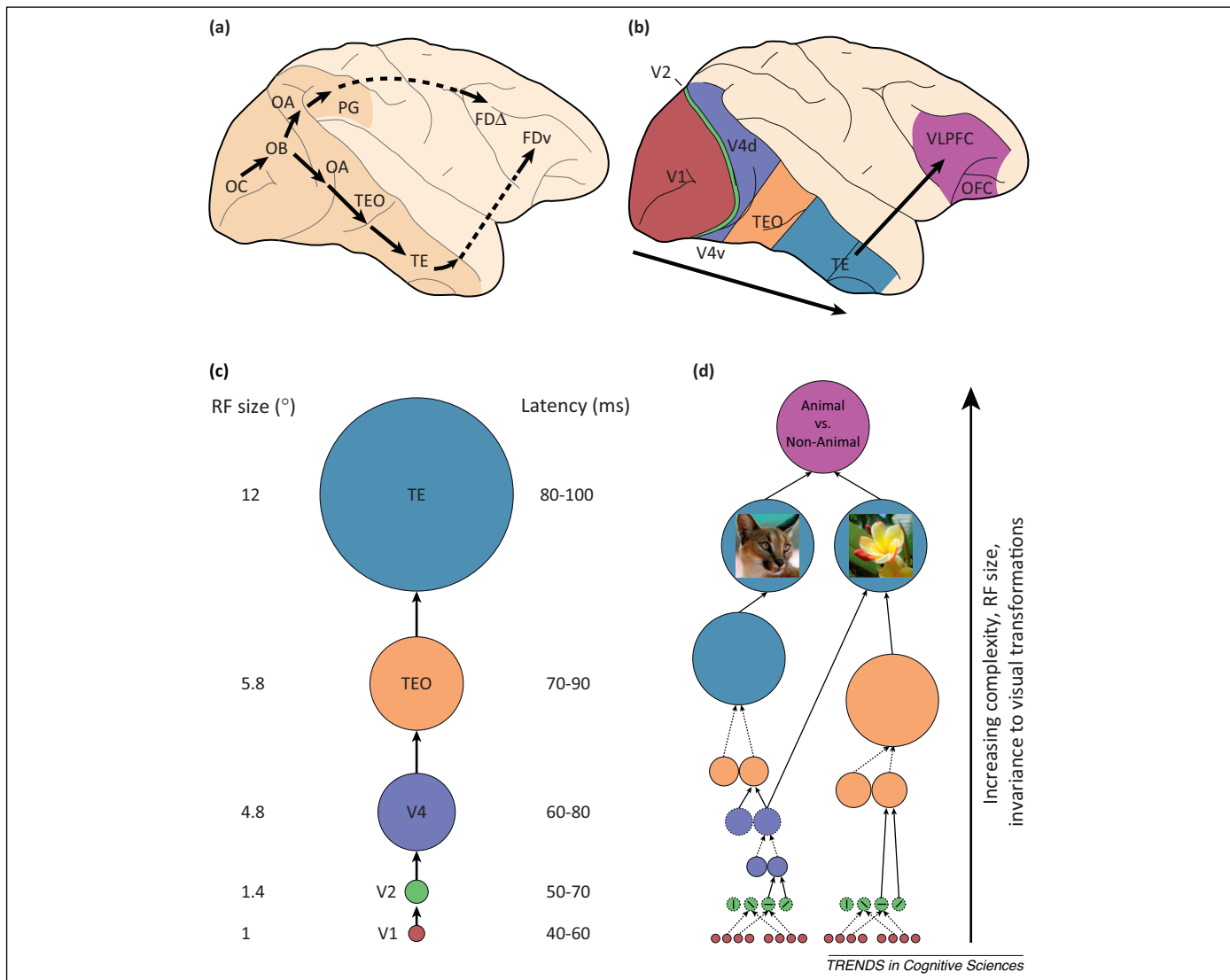


Figure 1. Frameworks of object quality processing. (a) Original formulation of the ventral and dorsal pathways in the macaque monkey. The ventral pathway was described as a multisynaptic pathway projecting from the striate cortex [cytoarchitectonic area (OC)] to area TE in the inferior temporal (IT) cortex, with a further projection from TE to the ventrolateral prefrontal region FDv. The dorsal pathway was described as a multisynaptic pathway projecting from the striate cortex to area PG in the inferior parietal lobule, with a further projection from PG to the dorsolateral prefrontal region FD_Δ. On the basis of the behavioral effects of lesions in monkeys, the ventral pathway was characterized as supporting object vision ('what'), whereas the dorsal pathway was characterized as supporting spatial vision ('where'). Based on [1], [2], and [3]. (b) Schematic of current understanding of the components of the ventral pathway that lie along the lateral surface of the macaque brain and their projection to the ventrolateral prefrontal cortex (VLPFC) and orbitofrontal cortex (OFC). Note the similarity between the original characterization and a more recent, but still incomplete view. Adapted from [12]. (c) Schematic of the commonly assumed model of serial information flow from visual area V1 through the anterior IT cortex (aIT) (central route). The size of each circle reflects the average receptive field (RF) size of neurons in that region from recent recordings (V1 [9], V2/V4 [40], area TEO [281], area TE [59,60,62]). The numbers to the right of each region give the approximate range of latencies of first response [9]. Color scheme as in (b). Adapted from [9] and [12]. (d) Schematic of a recent version of the HMAX model [7] of object recognition. The model comprises numerous units, each of which either sums (unbroken lines) or takes the maximum (broken lines) over its inputs. The earliest units (red/green) loosely correspond to V1 and V2, have very small RFs, and are selective for simple features (e.g., oriented lines). The next layers (purple/V4) aggregate the responses of these simple feature detectors to support units with larger RFs and selectivity for more complex stimuli. This process is applied at each subsequent layer of the model through pools of units analogous to area TEO (orange) and area TE (cyan) until units are reached with large RFs and selectivity for whole objects. These units then project to decision units thought to be analogous to neurons in the VLPFC and OFC. According to the model, the complexity of the representations, RF size, and, critically, invariance to visual transformations increase from early to late units through the iterative sum and max operations applied by each unit to their inputs. Note that in the model there are some bypass connections (units on the right) constituting an 'indirect' route for information transfer (Figure 3) that do not appear in the central route depicted in (c). Adapted from [7].

proceeds rostrally along the ventral pathway (Figure 1c). This view is rarely explicitly stated in its totality (but see [12,13]), although components of it were present in the original characterization of the pathway [1] and continue to underlie numerous theories in the field.

We highlight three aspects of our modified neuroanatomical and functional framework that distinguish it from this conception. First, anatomical evidence indicates that the ventral pathway is actually a complex network of feedforward and feedback projections, some of which are

unidirectional (i.e., non-reciprocal) feedback connections and others of which bypass intermediate areas, allowing direct communication between putative early and late stages of the hierarchy (Figure 2a; see also Figure 3 and related text for further details). Second, there appears to be a strong link between retinotopic position and the intrinsic neuroanatomy, such that even high-level object representations are constrained by retinotopic position. Finally, various regions within the occipitotemporal network project differentially to at least six distinct subcortical and

Box 1. General functions of the dorsal and ventral pathways

One of the key principles we highlight in both this review and our previous review of the dorsal pathway [5] is that the functional properties of a region are intimately related to its connectivity. This principle makes it difficult to describe the general function of an entire pathway given its complex and diverse connectivity. Nonetheless, here we will try to provide a high-level intuition about the general functions of the dorsal and ventral pathways.

The dorsal pathway is an occipitoparietal network that lies between the early visual cortex and specialized cortical structures involved in visually-guided action, somatosensation, spatial audition, navigation, and spatial working memory. The type of visual information required by these processes is very general. For example, an observer's hand and the target of a reaching movement can appear in any retinotopic positions and the occipitoparietal network must still create an accurate map of their relative positions to guide the action effectively. The need to represent these sorts of relationships naturally leads to the formation of coordinate systems and general reference frames. Thus, the dorsal pathway specializes in capturing arbitrary and dynamic spatiotemporal relationships between multiple items. Over time, however, the occipitoparietal cortex also contributes to the long-term representation of non-arbitrary spatiotemporal relationships as demonstrated by findings in apraxias [4] and tool-selective regions [282] localized within the posterior parietal cortex. This view has the advantage of parsimoniously incorporating numerous non-visual functions associated with the dorsal pathway (e.g., number [283], sequences [284], melody [285], prosody [286]).

In contrast to the dorsal pathway, the ventral pathway does not need to capture these sorts of arbitrary relationships to support the functions of its extensions nor does it have a strong connection with motor output. Rather, it is an occipitotemporal network that bridges the early visual cortex and specialized cortical and subcortical structures involved in various forms of memory and learning, specifically habit formation, emotion, long- and short-term memory, reward, and value. These structures are involved in forming specific representations or associations involving stable aspects of visual information, rather than capturing arbitrary dynamic relationships among multiple items. The term 'processing of object quality' (see also [1,2]) is an inclusive term meant to capture the wide variety of stable visual information that can be processed as the basis of these associations. Specifically, it refers to the processing of the features or perceptual dimensions (e.g., shape, color, size, brightness) that are available in the information passed to the striate cortex from the retina. These dimensions might be readily available in the input (e.g., retinotopic position, brightness) or they may be a conjunction of basic dimensions (e.g., shape, faceness). Any stimulus can be represented as a coordinate or configuration along all of the dimensions that the occipitotemporal network represents. The key aspect of ventral pathway representations is not that they are tied to particular physical objects, but that they capture a stable configuration of visual information (e.g., texture, scenes).

Thus, the standard dichotomy of spatial and object vision being supported by the dorsal and ventral pathway, respectively, is too restrictive. Any number of spatial dimensions (e.g., retinotopic position, stimulus motion), can contribute to ventral pathway representations and some aspects of object shape must be captured in the dorsal pathway to guide action effectively.

cortical structures (Figure 2b; see also Figures 7 and 8 and related sections for more detail). First, a unidirectional occipitotemporo-neostriatal pathway originates from nearly every area in the occipitotemporal network and projects to the neostriatum supporting the formation of stimulus-response associations. Second, different areas within IT give rise to the occipitotemporo-amygdaloid pathway, supporting the processing of emotionally salient stimuli. A third cortico-subcortical projection is the unidirectional occipitotemporo-ventral striatum pathway, which also originates in aIT and supports the assignment of stimulus

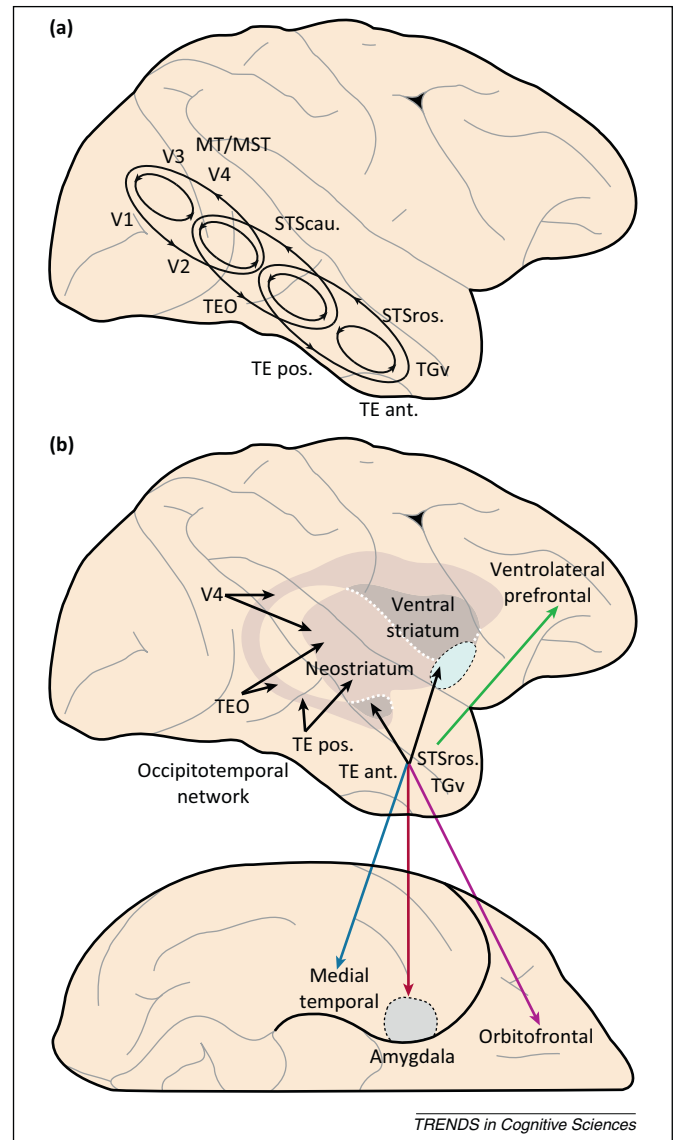


Figure 2. Schematic of proposed framework. (a) Schematic of the intrinsic connectivity of the ventral pathway on the lateral surface of the macaque brain. Note the inclusion of visual area V3, the middle temporal (MT)/medial superior temporal (MST) complex, and the superior temporal sulcus (STS), which are typically not included in reference to the ventral pathway. Rather than a simple sequence of projections leading to the anterior inferior temporal cortex, the pathway comprises a series of overlapping recurrent networks of various scales. At the most local level, there are approximately four subnetworks (small black ellipses), each with strong bidirectional connections among its components. Beyond their intrinsic components, these subnetworks are connected to each other via more extended, bidirectional, and non-reciprocal feedback connections that bypass intermediate regions (large black ellipses). (b) A summary of the extrinsic connectivity of the ventral pathway. At least six distinct pathways emanate from the occipitotemporal network. The occipitotemporo-neostriatal pathway (black lines) originates from every region in the network and supports visually-dependent habit formation and skill learning. All other projections originate in the network's rostral portion, although not all of these contribute equally to every pathway. One such projection targets the ventral striatum (or nucleus accumbens) and supports the assignment of stimulus valence. Another forms the occipitotemporo-amygdaloid pathway (red line) and supports the processing of emotional stimuli. The occipitotemporo-medial temporal pathway (blue line) targets the perirhinal and entorhinal cortices as well as the hippocampus and supports long-term object and object-context memory. Finally, the occipitotemporo-orbitofrontal pathway (purple line) and the occipitotemporo-ventrolateral prefrontal pathway (green line; Figure 1a,b) mediate reward processing and object working memory, respectively.

valence. Finally, there are three major cortico-cortical projections, all of which are reciprocal with their sources in aIT, including but not limited to area TE. These three projections are the occipitotemporo-medial temporal, occipitotemporo-orbitofrontal, and occipitotemporo-ventrolateral prefrontal pathways (Figure 2b), which support, stated briefly, long-term memory, object-reward association, and object working memory, respectively.

We begin with a review of anatomical and functional findings from within the occipitotemporal network, presenting the intrinsic reciprocal and nonreciprocal connections and their relationship to function. We then review the anatomical and functional organization of the six major output pathways (Figure 2b), highlighting implications for our understanding of the occipitotemporal network. Throughout the review, we also highlight findings that are accounted for by viewing the ventral visual pathway as a recurrent occipitotemporal network.

Occipitotemporal network: intrinsic connectivity

The intrinsic connectivity of this network in monkeys comprises a set of bidirectional projections along a caudal-rostral axis from the early visual areas in the occipital and preoccipital cortex (V1, V2, V3, V4) into IT (areas TEO and TE), and, most rostrally, the ventral temporal pole (TGv) and rostral portion of the ventral bank and fundus of the STS (STSV/f). The ventral visual pathway was originally viewed as a series of sequential projections (the single ‘central route’ in Figure 1c) between V1, V2, V4, TEO, and TE (also TGv; Figure 3a) [7,9,12,14–25]. The connections between the earliest visual areas (V1 and V2) established the rules for the lamina of origin and termination of feedforward and feedback connections [14,17,22,26]; namely, that feedforward projections originate mainly in layers 2 and 3 and terminate in layer 4, whereas feedback projections originate primarily in layers 5 and 6 and terminate in layer 1. Also, the functional properties of single cells within V2 were well predicted by a simple aggregation of responses across several V1 cells, with a slight increase in both RF size and selectivity for more complex stimuli (angles) than the orientation selectivity observed in V1. These basic functional observations gave rise to the idea that the ventral pathway was a serial hierarchy, with each sequential stage having progressively more complex selectivity and invariance to simple visual transformations such as retinotopic position.

However, there is now a wealth of anatomical evidence suggesting that the ventral visual pathway is actually a complex recurrent network. V1 projects directly not just to V2, but also to V3 [23], V4 [24,27], and the middle temporal area (MT) [28–31]. Thus, visual information from V1 can reach area TEO in two steps via V2, V4, or MT [15,18,24], violating a strict serial hierarchy at even the earliest stages of visual processing. There are also direct projections between the dorsal portion of V4 (V4d) and the dorsal subregions of posterior TE (TEpd) [24] and between the dorsal part of area TEO (TEOd) and the dorsal subregion of the anterior TE (TEad) [15,19,32] that bypass the intermediate regions (Figure 3a). In addition, there are unidirectional, non-reciprocal projections from putative late stages in the pathway to the early stages (Figure 3b).

Finally, although the laminar structure of projections has been used to determine levels in the hierarchy, projections beyond V1 to V2 do not strictly follow those rules, with feedforward connections terminating instead across a broad range of lamina in the target areas. For example, connections from area TEOd to TEpd/TEad and from TEad/ventral subregion of the anterior TE (TEav) to the STSV/f terminate throughout all six cortical layers [19,33].

The neuroanatomy of the occipitotemporal network and the putative central route (Figure 1c) is further complicated by the connectivity of the STSV/f (Figure 3a). V1 and the dorsal part of V3 (V3d) project directly to the MT, which in turn projects to the medial superior temporal area (MST), the floor of the superior temporal sulcus (FST), V4d, and TEOd [15,29,34]. Areas V4d, TEOd, and TEpd also project to the STSV/f [19,24], which then projects to aIT [33] (areas TEad, TEav, and the ventral temporal pole area TGv) (Figure 3a). Thus, the STS provides another major route through which visual information from ‘early’ stages of the central route can be transmitted to the most rostral temporal areas or ‘final’ visual processing stages without passing through the intermediate areas of the central route. These indirect channels may underlie the persistence of complex selectivity in aIT even after posterior regions have been extensively damaged (see section on intrinsic connectivity function below).

The details of intrinsic connectivity also highlight the importance of retinotopic position. First, V1, and indeed all subcortical inputs [35] to the occipitotemporal network, represent only the contralateral side of space and there is evidence that a contralateral bias persists even into aIT (see section on propagation of retinotopic biases below). Second, there is a neuroanatomical distinction between the input from the central and peripheral visual fields into the IT, resulting in a strong foveal bias throughout areas TEO and TE [12]. Conversely, the portions of the ventral part of V4 (V4v) that most strongly represent the periphery project to area TFO of the parahippocampal cortex, which in turn provides input to areas TF/TH of the parahippocampal cortex (Figure 3a) [24,36]. This medial pathway has only weak connections with the ventral portions of TEO or TE, making it a somewhat distinct channel for object quality information biased toward peripheral portions of the visual field (see [5] for a further review of the connectivity of these regions). Finally, there is bias in the input to the dorsal and ventral IT for the lower and upper visual fields, respectively, with relatively weak connections between these regions, particularly posterior to area TE (Figure 3a). Specifically, V4v, which represents the upper visual field, provides most of the direct cortical visual input to both TFO (in the posterior parahippocampal gyrus) and the ventral portion of the posterior IT (TEOv) [24], which, in turn, provide strong input to the posterior and anterior ventral TE (TEpv/TEav) [33]. By contrast, V4d, which represents the lower visual field, provides most of the direct cortical visual input to the dorsal posterior IT (TEOd) [24]. Area TEOd then projects anteriorly through the dorsal TE (TEpd/TEad) to area TGv [15,19,32,33] (Figure 3a). These biases for the upper and lower visual fields are reflected in the object representations of the IT in humans (see section on Retinotopy below).

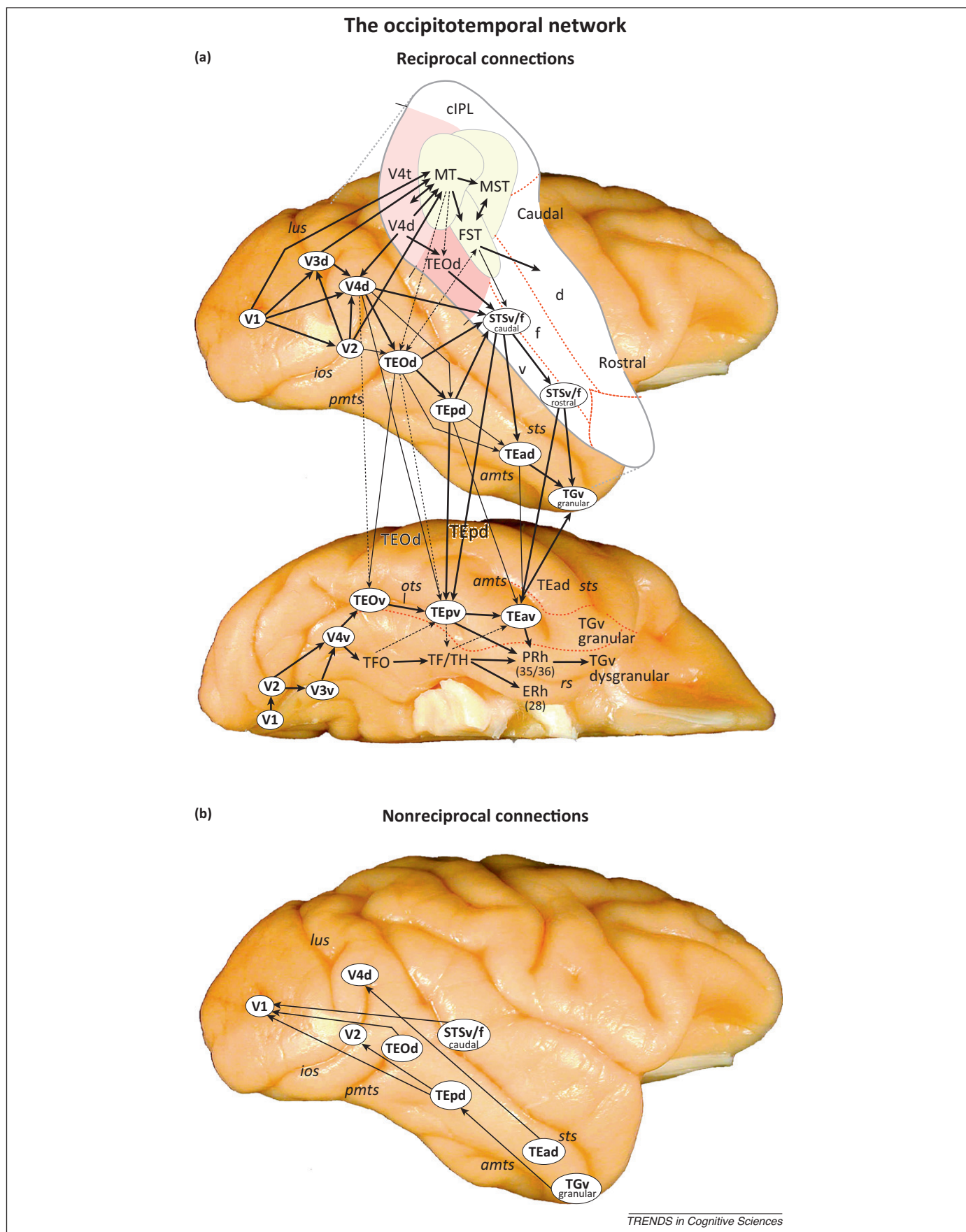


Figure 3. Intrinsic connectivity of the occipitotemporal network. (a) The connections that form the occipitotemporal network on lateral and ventral views of the rhesus monkey brain. This network comprises a set of direct and indirect reciprocal projections (shown by single arrow-head; double arrowhead, areas at the same hierarchical level) along a caudal-to-rostral axis from the primary visual cortex (V1) through different subregions of the preoccipital (V2; V3d/v), prelunate (V4d/v), posterior inferotemporal (TEOd/v) and posterior ventral bank and fundus of the superior temporal sulcus (STSv/f caudal), into the anterior inferotemporal cortex, including area TE (TEpd, TEpv, TEad, and TEav) and

Overall, the neuroanatomy thus not only argues against a strict serial hierarchy but also appears to propagate strong retinotopic biases along at least three dimensions of the visual field (contralateral vs ipsilateral, lower vs upper, and central vs peripheral). In combination with the unique input of the MT/MST complex into the STSv/f, this suggests that, rather than having just a single central route, the occipitotemporal network has at least four somewhat independent parallel routes, which, arranged dorsoventrally, pass through the STSv/f, TEOd, TEOv, or TFO (Figure 3a).

Occipitotemporal network: intrinsic function

Our review of the functional properties of the occipitotemporal pathway begins with functional findings related to the complex intrinsic connectivity and its relationship to and propagation of retinotopic biases. We then review two domains in which the proposed framework offers new traction: clustering of different types of selectivity and attentional/contextual effects. The purpose of the following sections is not to review fully the very large functional literature on the ventral visual pathway, but to provide a functional framework comprising key results, theories, and debates that complements the neuroanatomical framework specified in the previous section (Box 2 discusses the functions of aIT).

Functional implications of complex intrinsic connectivity

As discussed above, the gross neuroanatomy highlights numerous bypasses and other non-hierarchical patterns of connectivity (Figure 3) that complicate the central route. Critically, there is also strong evidence that these connections have functional consequences, because lesions of areas along the central route do not cause the profound effects in later regions that would be expected in a single serial system. For example, although extensive damage to V4d and area TEO in macaques (Figure 4a) reduces the ability of neurons in area TE to filter distracters, their basic firing rate and selectivity remain largely unaffected [37,38] (Figure 4b). This result implies either that information is flowing through an indirect and seldom-considered route (via MT/MST) or that some very small spared portion of V4/TEO is capable of driving neurons in TE. In either case, at a minimum, most of the central route (Figure 1c) is not necessary for the functions being assumed and formally modeled (Figure 1d) in TE. Nor are these findings unique; many bilateral lesion and disconnection studies have failed to silence neurons in aIT (see [39] for a review, including the lack of effects following

Box 2. Functions of the anterior IT cortex and the difficulties of establishing cross-species homologies

A major stumbling block to advancing our understanding of the ventral visual pathway is the paucity of knowledge about what visual functions, if any, are subserved by aIT in humans. One persistent problem is the lack of good fMRI signals from this region [289], although some fMRI studies and those using other methods [positron emission tomography (PET), lesions] have implicated the region in semantic processing [290]. Importantly, compared with the pronounced visual impairments that are produced by aIT lesions in monkeys, the reported visual effects of damage to this region in humans are less striking (perhaps due to many of the lesions being unilateral). This has led to the proposal that the human homolog of aIT in the monkey is the posterior IT cortex, where visual information and deficits are more typically localized. However, this proposal is difficult to reconcile with the primacy of aIT as the source of many output projections from the occipitotemporal network in monkeys (see Figures 7 and 8 and related text) and the likely conservation of those projections in humans.

PET studies have revealed responses in the anterior infero temporal cortex (e.g., [291]) during object vision and a recent fMRI study found that the ventral portions of the temporal pole (area TGV; see Figure 3a) are activated more by visual than by auditory stimuli [292], with different subdivisions showing differential activations for pictures of animals and tools [293]. Further, recent studies have reported a face-selective cluster in aIT [294], evidence that other areas in aIT contain information about facial expression, gaze direction, identity, and arbitrary facts associated with faces [295,296], and a face-specific deficit following damage restricted to aIT [89,297]. Finally, intracranial recording studies have demonstrated categorization for faces and animals in the anterior temporal lobe [108]. These studies clearly demonstrate that the human anterior temporal lobe does process visual stimuli and does contain stored visual information.

Beyond the domain of vision, the anterior temporal lobe has a number of characteristics consistent with its extensive connectivity with the cognitive memory system in the medial temporal lobe (MTL) (see Figure 8 and also the section on the occipitotemporo-medial temporal pathway in the main text). Beyond the deficits in object naming [298,299] observed after left hemisphere damage, visual representations in the anterior temporal lobe are stronger for familiar than for unfamiliar stimuli [298–300] and the region is strongly activated during the learning of associations between arbitrary facts about individuals (e.g., profession) and particular people [295]. However, much more work is needed to identify precisely where functional homologies in the visual functions of the human and monkey anterior temporal lobe begin and end.

pulvinar lesions). Consistent with the multiple parallel routes suggested by the neuroanatomical framework (Figure 3a), abolishing area TE-dependent behavior requires the bilateral removal of the entire prestriate cortex (V2, V3, V4, and portions of the MT/MST complex) on both the dorsal and ventral surfaces [39] (Figure 4c). Taken together, these results suggest that great care must be taken in proposing theoretical and computational

the temporal pole (area TGV) as well as the rostral STSv/f. Also shown is a connection between V4v through the medial temporal lobe [parahippocampal (TF/TH/TFO), perirhinal (PRh), and entorhinal (ERh) cortices]. The STS is opened to show the borders (red broken lines) and connections of different visuo-spatial cortical areas (different shades of pink and yellow, and white) in the ventral bank, fundus, and dorsal bank of the STS (see also [34]). Subdivisions within the inferotemporal cortex are based on the anatomical studies of Saleem and colleagues [33,138,199,287,288]. Note that the strength of the projection between different cortical areas is not uniform; some areas receive strong projections (thick lines), whereas others receive moderate to sparse projections (thin lines) or very sparse projections (broken lines). Based on this complex network of connections, there are at least four somewhat parallel routes (with cross-connections between them) through the occipitotemporal cortex: (i) within the STS; (ii) in the dorsal or lateral portion of IT; (iii) in the ventral or medial part of IT; and (iv) within the medial temporal lobe. Abbreviations: 28, ERh; 35/36, areas 35 and 36 of the PRh; amts, anterior middle temporal sulcus; cPL, caudal inferior parietal lobule; FST, floor of superior temporal sulcus; ios, inferior occipital sulcus; lus, lunate sulcus; ots, occipitotemporal sulcus; pmts, posterior middle temporal sulcus; rs, rhinal sulcus; sts, superior temporal sulcus; STSf, fundus of superior temporal sulcus; STSv, lower (ventral) bank of superior temporal sulcus; TEad, dorsal subregion of anterior TE; TEav, ventral subregion of anterior TE; TEOd, area TEO, dorsal part; TEOv, area TEO, ventral part; TEpd, dorsal subregion of posterior TE; TEpv, ventral subregion of posterior TE; TF/TH, areas TF and TH of parahippocampal cortex; TFO, area TFO of parahippocampal cortex; TGV, ventral temporal pole; V1, visual area 1 (primary visual cortex); V2, visual area 2; V3d, visual area 3, dorsal part; V3v, visual area 3, ventral part; V4d, visual area 4, dorsal part; V4t, V4 transitional area; V4v, visual area 4, ventral part. (b) Non-reciprocal connections on lateral view of the rhesus monkey brain. Note that unlike feedforward projections, TEOd, TEpd, and the caudal STSv/f send direct feedback projections to area V1 (Figure 3a).

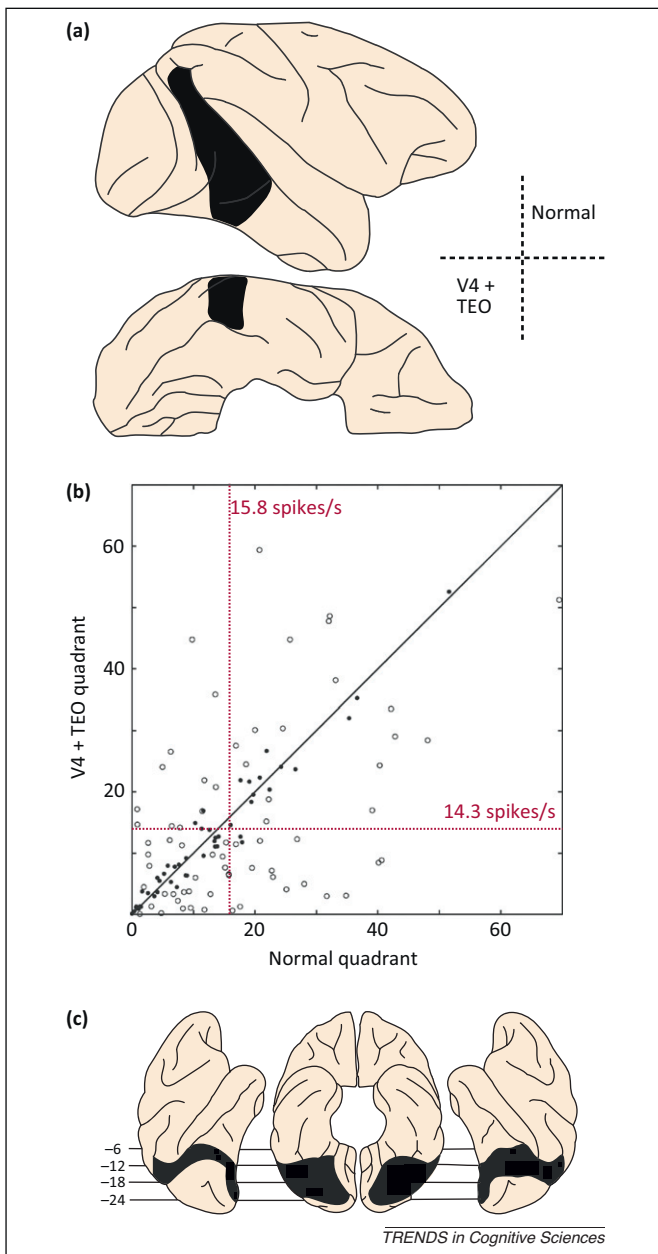


Figure 4. Test of the strict hierarchical model of object-quality processing. (a) Schematic of prefrontal lesions in macaque monkeys. In the left hemisphere (not shown) only the dorsal portion of visual area V4 (V4d) has been removed, whereas in the right hemisphere both V4d and all of area TEO have been removed (upper panel). Under the serial processing model in Figure 1, this should lead to profound reductions in the responsiveness and selectivity of area TE neurons to stimuli in the lower left quadrant. Adapted from [37,38]. (b) Recordings from neurons in area TE of the right hemisphere following the lesions depicted in (a). The x-axis gives the average spikes per second for 57 units for stimuli presented in the normal upper right quadrant. The y-axis gives the average response for the same stimuli in the affected lower left quadrant. Filled circles denote stimuli for which there is no difference in response between the two quadrants. Open circles denote stimuli where there was a difference in response. The black diagonal line is the identity line and any shift in response magnitude due to the lesions is reflected in most of the points being either above or below the line. Note that there is no such bias in the plotted points. The average response in both quadrants (red broken lines and numbers) do not differ significantly. Adapted from [37]. (c) Depiction of the lesions required to abolish area TE-dependent behavior. Note the extensive bilateral removal of the prefrontal cortex, corresponding to areas V2, V3, and V4, and portions of the middle temporal (MT)/medial superior temporal (MST) complex. Adapted from [39].

models of IT that presuppose a largely serial flow of information along a single central route through what is, in fact, an extremely complicated recurrent network.

The neuroanatomy also highlights that, even among early visual areas, the complex pattern of connectivity (Figure 3a,b) makes it difficult to assign a hierarchical level to any region within the pathway. This matches well with the relatively weak functional distinctions between adjacent stages of the putative central route that are observed anterior to V2 in monkeys, with even V2 and V4 showing largely overlapping functional properties (e.g., RF size and stimulus selectivity) [40]. Further, in both monkeys and humans, the predominant distinctions identified have been different visual selectivity among areas that occupy the same putative level of the hierarchy (e.g., face-selective regions; see section on clustering below). The best evidence for distinctions between levels of the putative hierarchy comes from a series of studies using the same artificial stimulus set, reporting a slowly (~50 ms) evolving representation of complex curvature in V4, and 3D shapes in IT [10,11,41]. These functional studies, along with many others, provide strong support for an increase in the complexity of representations from posterior to aIT, but cannot address either the necessity or the sufficiency of the central route for this increase.

Propagation of retinotopic biases

The intrinsic connectivity of the occipitotemporal network reveals a strong relationship between neuroanatomy and retinotopic position, with strong retinotopic biases in the primary inputs to the medial temporal lobe (MTL) (via area TFO), ventral surface (via TEOv), and dorsal surface (via TEOd). There is also some behavioral and functional evidence that even high-level visual object representations are at least somewhat position-dependent (e.g., [42–44]; see [45] for a full review). This contrasts with the general assumption that visual object representations become increasingly position invariant along the hierarchy, culminating in abstract representations of object identity in aIT. Below, we highlight the neural effects of retinotopic position along each of the three different divisions of the visual field: contra versus ipsi, upper versus lower, and central versus peripheral.

First, it is important to consider the contralateral bias present throughout the occipitotemporal network. Visual input from the left and right visual fields, even within the fovea, initially projects only to the contralateral V1 [46]. In both humans (e.g., [47]) and monkeys (e.g., [48,49]), each of the early visual areas (V1, V2, V3, and V4) contains a map of the contralateral visual field. These early visual areas seem to be largely comparable in the two species (Figure 5a,b) [50,51], with the possible exception of human V4d, the existence of which is a matter of current debate [52–54]. Human neuroimaging has revealed a strong contralateral retinotopic bias that extends far into the posterior IT (e.g., [55–57]). Although RF sizes increase [58–60], they retain a strong contralateral bias even in the monkey aIT, where they range in size between 2.8° and 26° with a reported mean of 12° [61,62] (Figure 5c). There is also growing evidence that the functional consequences of these biases extend to high-level object and pattern representa-

tions. In monkeys, unilateral lesions of area TE/TEO cause only contralesional impairments in a broad array of visual discriminations, including shape and color [63] (Figure 5d). In humans, the identity of individual objects in a given hemifield can be decoded much more accurately from the functional MRI (fMRI) response of the contralateral object-selective posterior fusiform sulcal cortex (pFs) (Figure 5b; pFs overlaps and extends VO1) than from its ipsilateral homolog, and more accurately within one position in the contralateral visual field than across positions (Figure 5e) [42] (see [64] for other demonstrations of stronger decoding within than across quadrants). Further, the identity of body parts can be more accurately decoded in the body-selective extrastriate body area (EBA) when they are presented in their typical field (e.g., right body in the left field) than in an atypical field (e.g., right body in the right field), indicating that long-term retinotopic experience shapes high-level representations [44] (Figure 5f).

Second, there are widespread functional eccentricity biases throughout the occipitotemporal network. Across early visual areas, there is a map of eccentricity with an expanded representation of the central visual field relative to the periphery (Figure 6a). In humans, as in monkeys, many of the IT regions within the occipitotemporal network lie immediately anterior to foveally biased early visual cortex (e.g., [54,65,66]) (Figure 6a), whereas the parahippocampal gyrus (TFO, TF/TH; Figure 6a) lies immediately anterior to the peripheral representations in early visual areas [67,68]. In monkeys, neurons within IT generally show a strong foveal bias (e.g., [62]), whereas neurons in TF/TH have larger RFs and a very weak foveal bias [69] and receive strong input from the parietal cortex and hippocampus [5]. In humans, the parahippocampal gyrus contains a scene-selective region (the parahippocampal place area [PPA]) that primarily represents the peripheral spatial boundary of scenes [70,71], whereas the portions of the IT area aligned with the foveally biased portions of early visual areas contain regions selective for faces [67,68] and words [72], suggesting that the availability of information about certain parts of space constrains the location of high-level selectivity (see also the section on clustering below). There is also recent evidence that object representations might be organized along a lateral-medial axis across the IT area according to real-world size regardless of retinal projection size in correspondence with the eccentricity gradient (i.e., small objects are represented laterally and large objects medially) [73], suggesting that eccentricity is a general organizing principle across the occipitotemporal network.

Finally, the upper and lower visual fields are represented in the ventral and dorsal portions of early visual areas, respectively (Figure 6b,c). The ventral visual areas project primarily to the ventral surface of IT and dorsal areas to the dorsal surface, with only weak projections between them caudal to area TE (Figure 3a). In humans, category-selective regions often come in pairs [74], with one region on each of the dorsal and ventral surfaces of IT (see also the section on clustering below). For example, the lateral occipital complex (LOC) [75], which shows stronger fMRI responses to intact than to scrambled objects, has ventral (pFs) and dorsal [lateral occipital (LO)] compo-

nents. The LO area has been reported to have a bias for the lower visual field [42,65,76], whereas the pFs was recently shown to have a bias for the upper visual field [42] (Figure 6d) (see also [76,77] for upper-field biases in other ventral regions). Further, many areas in the dorsal pathway, which receive most of their input from dorsal portions of the early visual areas, have a bias for the lower visual field (e.g., [78–80]) (Figure 6c). It therefore appears that the differential representation of the upper and lower visual fields may be an additional organizing principle across both the ventral and dorsal visual pathways.

The ubiquitous effects of retinotopic position are consistent with the retinotopic biases in input apparent in the intrinsic connectivity (Figure 3a) and it has been argued that retinotopic information could be useful in the representation of objects (see [81] for a model that incorporates retinotopy). Shared retinotopic information may also provide a common language in which regions with different selectivities can communicate. Further, the continuing discovery of retinotopic maps within object-selective cortex in the human IT suggests that retinotopy may be a general organizing principle in the ventral visual pathway.

Clustering

One of the most consistent findings regarding the intrinsic function of the occipitotemporal network to emerge in both humans and monkeys (e.g., [82,83]) is the presence of functional clustering in cortex with selectivity for particular object categories (e.g., body parts [84], faces [84], scenes [85], objects [75], tools [86], written words [72], color [87,88]). Beyond the prominence of clustering in physiological measurements, the observation of category-biased deficits/enhancements following lesions (e.g., [72,89,90]) and transcranial magnetic stimulation (TMS) of these clusters in human (e.g., [91]), as well as the effects of direct stimulation in monkeys [92], indicates that the clusters are behaviorally significant. The nature and origin of these clusters remain unclear (see [93,94] for recent proposals); they were not anticipated in the original formulation of the ventral pathway, which makes no predictions about differences within a putative level of the hierarchy. Yet, such clustering can be easily incorporated into the proposed framework, emerging naturally from an interaction between large-scale connectivity and experience.

Broadly, these clusters might emerge on either a phylogenetic or a developmental timescale. Phylogenetically, large numbers of interconnected neurons might have genetically specified selectivity for evolutionarily important categories. Clustering minimizes biologically expensive long-distance connections between these neurons (see [95] for a review), conveying an evolutionary advantage [96]. However, this explanation cannot account for the origin of the visual word form area, which is selective for orthography, a category too recent to have undergone evolutionary selection [97]. The strongest version of the alternative account is that the clusters emerge exclusively through experience, a proposal that is strongly challenged by the striking consistency in the location of these clusters across individuals.

The proposed framework offers an explanation for this apparent contradiction without positing distinct mecha-

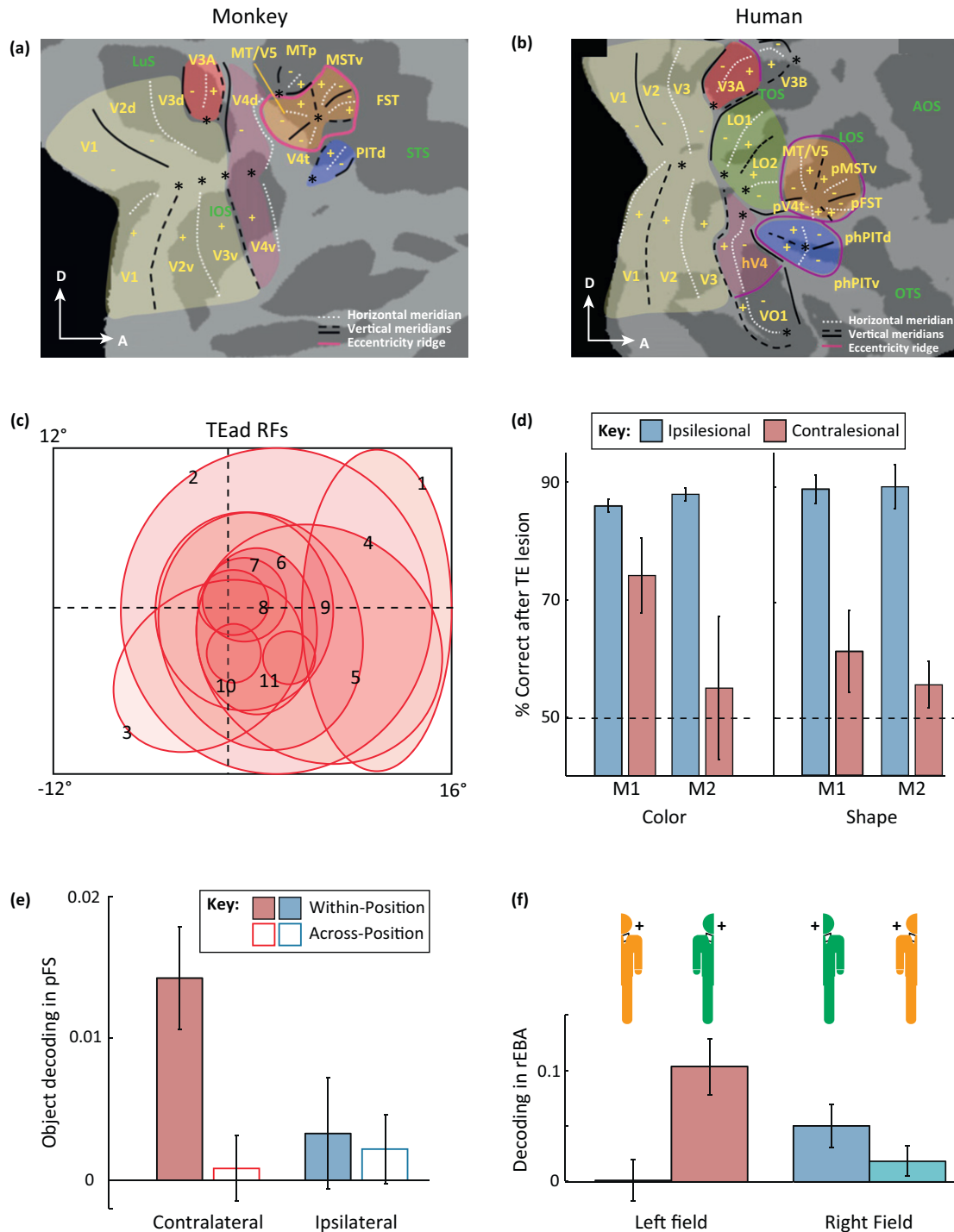


Figure 5. Retinotopy: contralateral versus ipsilateral. **(a)** Flat-map representation of the known retinotopic maps in the macaque. The map is created by inflating the cortical surface to bring the depths of sulci to the surface and cutting along the calcarine sulcus to flatten the map. Note the predominant lower field representations (-) in the dorsal early visual areas and the upper field representations in the ventral portions of the early visual areas (+). The various representations of the fovea are marked (*). Adapted from [51]. **(b)** As in (a) but for humans. Note the large degree of correspondence between monkey and human in the early visual areas (V1–V4). Note also the additional retinotopic areas anterior to V4 adjacent to both the dorsal and ventral portions of the early visual areas. Note that the VO2 region (Figure 6c) lies just anterior to the VO1 region (not shown). Adapted from [51]. **(c)** Schematic of receptive field (RF) size and location of 11 example neurons in the dorsal subregion of anterior area TE (TEad) in the macaque. Note the bias toward the contralateral field and the correlation between RF size and the eccentricity of the RF centers and that most RFs overlap the fovea. Adapted from [45] and [62]. **(d)** Results of color- and shape-matching tasks performed by two macaques (M1, M2) following unilateral lesions to either area TE (M1) or both TE and area TEO (M2). Note that performance is spared in the hemifield ipsilateral to the lesion but severely impaired in the contralateral field in both macaques for both tasks. Error bars denote standard errors across trials. Similar results were observed for a color-matching task. Adapted from [63]. **(e)** Plot of object identity decoding (individuation among 24 objects) from blood oxygenation level-dependent (BOLD) functional (fMRI) responses in human ventral object-selective cortex (the posterior fusiform sulcal cortex [pFS]; near to and overlapping area VO1 in panel (b)) as a function of: (i) stimulus presentations in the contralateral or ipsilateral field; and (ii) decoding within a single position or across positions in different quadrants of the visual field. Within-position decoding was quantified as the correlation in multivariate response patterns to two independent presentations of the same object in the same position minus the average correlation between that object and all of the other objects in that same quadrant. Across-position decoding was defined as the correlation in response patterns between an object and that same object in a different position minus the average correlation between that object and all of the other objects in the different quadrant. Note that significant decoding was observed only in the contralateral field

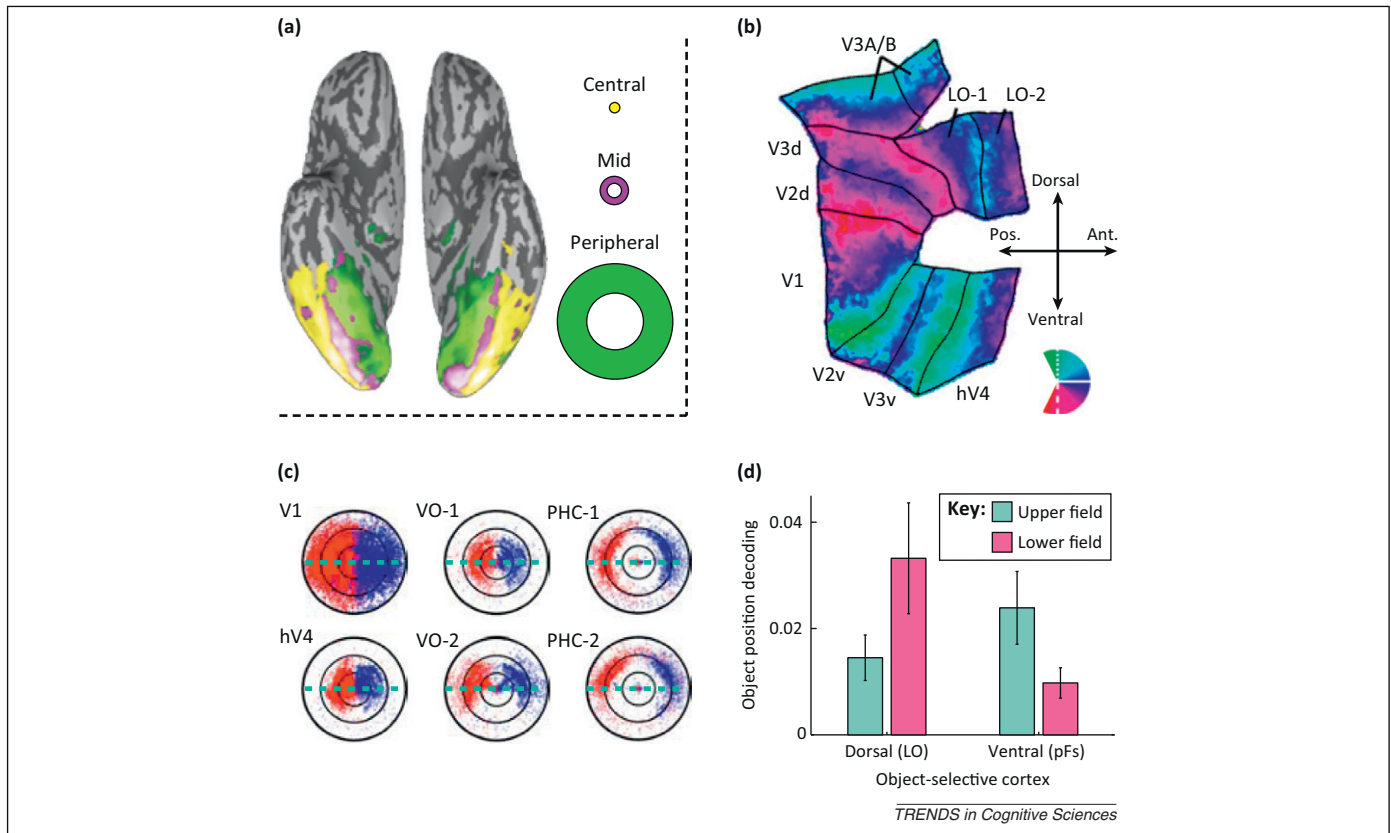


Figure 6. Retinotopy: fovea versus periphery and upper versus lower field. **(a)** Plot of the effect of eccentricity across the inflated ventral surface of the posterior temporal lobe. Participants were presented with concentric rings of various objects [68] at one of three eccentricities (right inset shows rings). The colors on the inflated surface represent which of the three eccentricities generated the strongest response in that cortical region. Note that the more medial regions of the temporal lobe exhibit a peripheral bias, whereas the more lateral regions show a foveal bias. Scene- and face-selective regions occur within these peripherally and foveally biased regions, respectively. Adapted from [68]. **(b)** Flattened plot of retinotopic maps from visual area V1 through human V4 (hV4) on the ventral surface and through area LO-2 on the lateral surface. The colors plotted represent the position of the rotating wedge that generated the strongest response (see partial pinwheel inset). Note the clear division between the upper and lower field representations for the dorsal and ventral portions of the early visual areas (V1–V4). Note also that the bias for the lower field on the dorsal surface extends into LO-1/2, as shown by the lack of a strong representation of the upper vertical meridian (green) in either region. Adapted from [66]. **(c)** Plot of the aggregated location in the visual field of the peak response across nine participants from voxels within different visual areas. The VO regions lie ventrally adjacent to hV4 (Figure 5b). The parahippocampal cortex (PHC) lies medial to the VO regions and closer to the peripheral representation. The horizontal broken lines in blue represent the horizontal meridian. Note that in V1 there is an even distribution of peak responses across the entire visual field, with equal representation of the upper and lower visual fields. In hV4, VO-1, and VO-2, all of which lie on the ventral surface, there is a clear bias toward the upper visual field (but see [52]). This bias is also seen in the PHC regions, which also show a bias for peripheral space consistent with their position in the peripherally biased extrastriate cortex (a). Adapted from [77]. **(d)** Plot of object-position decoding as a function of: (i) location of the object-selective region (dorsal or ventral surface); and (ii) presentation of objects in the upper or lower contralateral visual field. Object position decoding in object-selective cortex was stronger for the lower visual field in dorsal subregion (LO) and for the upper visual field in the ventral subregion (pFs). These biases are consistent with the position of the regions relative to the upper and lower field representations in early visual areas. Adapted from [42].

nisms for the origin of different clusters (e.g., [96]). Because connectivity among the areas of the occipitotemporal network is heterogeneous, information about particular stimuli or aspects of those stimuli is more strongly available in particular areas (e.g., see section on retinotopic biases above). Clusters then emerge from an interaction between this constraint and visual experience (see [98] for an example in monkeys). Categories that require a large population of neurons (e.g., those requiring extensive recurrent processing) will naturally exhibit clusters at those locations where the connectivity affords the necessary information (see [99–101] for related proposals). Thus, large-scale connectivity is an innate phylogenetic constraint on the availability of information to particular

areas of the cortex, creating a likely set of cluster locations that will be common across individuals given similar experience (e.g., exposure to faces). Importantly, although this set of locations may provide the most efficient wiring for representing a category, they are not the only possible set. In cases of cortical brain damage or unique experience, particularly early in development, entirely different clusters might arise, explaining the relatively spared abilities even of individuals who have undergone hemispherectomy (e.g., [102]). Recovery of function following damage to the large-scale connectivity may be much more difficult, even if the damage occurs early in life, as appears to be the case in individuals with congenital prosopagnosia, who demonstrate normal cortical activation in the IT to presented faces

and that this decoding was greater than that observed either across-positions or in the ipsilateral field. Complementary to the lesion results in (d), these results indicate that: (i) objects evoke reproducible patterns of activity only within the contralateral field; and (ii) the same object produces distinct patterns of response in different positions even in high-level object-selective cortex. Adapted from [42]. **(f)** Plot of body-part decoding (e.g., arm, torso) from BOLD fMRI responses in the human right extrastriate body area (EBA) as a function of: (i) stimulus presentations in the left or right visual field; and (ii) presentations of right or left body parts. Decoding was defined analogously to within-position decoding in (e). The combination of visual field and side of body is given by the body and fixation cross icons above each bar. Note that decoding is stronger for body parts presented in their typical combination of field and side of body (bars beneath green figures) than for those in atypical combinations (bars beneath orange figures). Note also the slightly stronger decoding of body part in the left (contralateral; red bars) than in the right (ipsilateral; blue bars) field. Adapted from [44].

but a weakened projection between posterior and anterior IT, as shown by diffusion tensor imaging (DTI) [103].

The simplest account of clustering in a high-level cortical area is that it reflects large-scale connectivity. Take, for example, the distinct clusters for face and scenes in the extrastriate cortex, which are reported to be more similar in monozygotic than dizygotic twins [104]. The human parahippocampal gyrus (corresponding to TFO/TF/TH in monkeys), which contains the scene-selective PPA and extends from the peripheral visual field (Figure 6b), is known to receive strong projections from V4v in monkeys (Figure 2a) and from the parietal cortex via the parieto-medial temporal pathway [5], which presumably conveys spatial information. On the basis of these connections, it is not surprising that the region predominantly represents the peripheral visual-field aspects of scenes [70,71]. By contrast, the portions of IT with a foveal bias contain regions selective for stimuli requiring fine discrimination, such as faces and words. Furthermore, it has been reported that the location of the ventral face-selective cluster in individual human participants can be predicted from large-scale connectivity as revealed by DTI [105].

The neuroanatomy also aligns to some degree with the specific within-category aspects of stimuli processed within particular regions. For example, in humans, major face-selective clusters have been identified in the banks of the STS and on the lateral [occipital face area (OFA)] and ventral [fusiform face area (FFA)] surfaces of the IT [100]. These three areas mirror three of the parallel routes we identified in the preceding sections (through the STSv/f, TEOd, and TEOv; Figure 3). There is also evidence that the type of face processing performed within each route is related to its primary input. Thus, the STS, which receives strong input from the MT/MST complex, shows strong sensitivity to expression and other dynamic aspects of faces in both humans and monkeys (e.g., [106]). By contrast, the other clusters (OFA and FFA) seem more sensitive to identity and other more stable aspects of faces [100]. Further, in monkeys, there is evidence from direct stimulation that the various face-selective clusters are strongly connected to one another [107], although more direct evidence from anatomical studies using tracers would help to determine what other systems might also be connected to these regions.

In summary, the prominence of functional clusters with different selectivities within the same putative level of the hierarchy represents a challenge to both the original formulation of the ventral visual pathway and the current conception. The proposed framework provides some traction on the genesis and stereotypical position of these clusters by considering large-scale connectivity (particularly the propagation of retinotopic biases) as a constraint on the regions within the occipitotemporal network where certain types of information are available to form stimulus-selective clusters.

Recurrent processing

The importance of recurrent processing (i.e., feedback and lateral interactions) is not sufficiently emphasized, on the assumption that the feedforward processing of visual information along the central route can be understood in

isolation. Although there may be an initial response to stimuli in aIT that occurs too quickly to incorporate stimulus-driven recurrent signals [108], those signals play a critical role in processing beyond the initial response [109] and top-down signals (e.g., attention, goals) contribute to the state of the entire network before stimulus onset. Enforcing a division between feedforward and recurrent processing makes it difficult to incorporate, for example, attentional, contextual, and masking effects. Indeed, rigid adherence to the concept of serial-order processing is a stumbling block to understanding the function and nature of representations in the occipitotemporal network.

Consider that the function in area TE most directly affected by extensive damage to area TEO is not the basic response to stimuli (Figure 4) but the attentional filtering of distracters [38]. This result highlights the fact that many connections within the occipitotemporal network, perhaps especially those in the central route, might exist to enable functions more complex than simple selectivity. Visual attention, whether directed to spatial locations [110], objects [111], or features [112], is known to affect processing directly within areas of the occipitotemporal network responsible for perceptual processing (see [113] for reviews and models). Further, selection along any of these dimensions interacts with the other dimensions (e.g., [111,114]) to create a pattern of facilitation across the entire visual scene [115,116]. The dense bidirectional connections along the central route are likely to contribute to the complex interactions necessary to generate attentional effects that span both the entire visual field and multiple perceptual dimensions.

Recurrent processing probably underlies numerous psychological and neural phenomena that depend on processing beyond the initial visual response (see [109] for a review). For example, change blindness, in which a change in a visual scene goes undetected (e.g., [117]), often occurs when the change does not alter either the gist of the scene [118] or a currently relevant feature [119]. Interestingly, large, low-level changes in the input that are undetected evoke reduced activity throughout temporal and parietal vision-related cortex compared with the activity evoked by similar but detected changes [120]. Recurrent processing is also likely to underlie the well-studied effects of context and attention even in V1 (e.g., [114,121–124]).

Finally, backward masking, in which the presentation of a mask shortly after a stimulus impairs both behavioral performance [125] and activity in the occipitotemporal network in humans [126] and monkeys [127], also emphasizes the importance of recurrent processing. In a purely feedforward system, there should be no effect of a mask presented after a stimulus evokes the initial neural response, yet the mask profoundly impairs both performance and awareness. Whether backward masking depends on the interruption of ongoing processing within a region (e.g., [128–130]) or the disruption of feedback signals [131], it clearly demonstrates the importance of recurrent connections and of processing beyond the initial neural response for even basic visual object perception.

Output pathways: anatomy and function

We turn next to the six major subcortical and cortical output pathways from the occipitotemporal network. In

each section, we detail the neuroanatomical connection and any relationships that exist between the connection, the likely information it carries from the occipitotemporal network, and the functional properties of the target structure. All of the output structures are critical for various forms of learning and memory in the formation of associations with the visual stimuli (e.g., response, reward, affect, valence), in creating visual memories, or in the online utilization and manipulation of visual information (see [132] for a recent review). In combination, the functions subserved by these output structures provide the *raison d'être* for the occipitotemporal network (Box 1), which has little direct connectivity with motor output.

Cortico-subcortical output pathways

There are three major output pathways to subcortical structures, all of which are critical in forming associations between visual stimuli and non-visual information. First, the unidirectional occipitotemporo-neostriatal pathway arises from every subregion of the occipitotemporal network except V1 (Figure 7a) and supports the formation of links between stimuli and responses. Second, the occipitotemporo-ventral striatum pathway arises in aIT and supports the association with and processing of stimulus valence. Third, the projections from the occipitotemporal network to the amygdala arise primarily in aIT, but projections from the amygdala target almost every subregion of the network (occipitotemporo-amygdaloid pathway; Figure 7b) in contrast to the occipitotemporo-neostriatal pathway. This pathway is critical to a broad range of affective processing of stimuli.

Occipitotemporo-neostriatal pathway

Projections to the neostriatum from the occipitotemporal network, like those from the cerebral cortex generally, are largely organized topographically [16,35,133–139]. In particular, as illustrated in Figure 7a, the neostriatal projection zones of areas V2 and V4 lie within the most caudal part of the body of the caudate nucleus (i.e., the genu) and each of the more rostral cortical areas (TEO, subregions of TE, TGv granular, and the STSv/f) have overlapping but progressively more rostral projection zones in the tail of the caudate nucleus and the caudoventral parts of the putamen [135,138]. Neostriatal processing can affect motor output and cortical processing via projections to the globus pallidus and the substantia nigra pars reticulata (SNr). These structures project in turn to subregions of the thalamus (VA, VL, and MD) [140], which then project to different parts of the frontal cortex, forming several corticostriatocortical loops (see [140,141] for reviews). These loops have been implicated in numerous functions, including categorization [141,142] and working memory (e.g., [143]) as well as learning and selecting rewarded actions [144,145], and even directing information transfer among cortical regions [146].

However, the function most directly related to the inputs from the occipitotemporal network concerns visual discrimination learning based on the reinforcement versus extinction of stimulus-response associations; that is, habit formation or procedural learning [147]. In humans, these associations are typically implicit and not verbalizable (e.g.,

[148]) and although the importance of the pathway for visual habit formation is well documented [147,149–151], the precise role of the neostriatum in this implicit learning process remains unknown. Recent single-cell recording studies have reported neurons in the tail of the caudate nucleus that show strong selectivity for complex visual stimuli [152,153] and these neural representations are extremely stable over time (Kim and Hikosaka, Society for Neuroscience, 2011). These characteristics contrast with neurons in the head of the caudate nucleus, which demonstrate coding for explicit rules [154] and change their representations quickly [155], and whose stimulation can increase the rate of rule learning [156]. Determining whether these findings imply that the head and tail of the caudate nucleus serve fundamentally different functions, or whether this difference simply reflects the different sources of the cortical input into these areas of the caudate nucleus (e.g., [149,157]), awaits further study.

Occipitotemporo-ventral striatum pathway

Subregions within aIT (TEav, TGv granular, and the rostral STSv/f) give rise to unidirectional projections that target the ventral striatum (shell and core regions of the nucleus accumbens and olfactory tubercle) [16,138,139] (see also [133,134]) (Figure 7a). The ventral striatum receives dense projections from orbitofrontal cortex (OFC), medial frontal cortex, hippocampus, amygdala, and midline thalamic nuclei [158–162].

The functional properties of the ventral striatum have not been extensively studied in primates, although they have been so in rodents (see [163] for a review). The region is thought to participate in the assignment of value (positive and negative) to particular stimuli. In monkeys, single-cell recording studies have reported neurons in the region that respond to anticipated or received reward [164] and to the magnitude of that reward [165]. In contrast to the neural activity in the neostriatum [166], activity in the ventral striatum appears to be completely independent of the particular action that the monkey executes to receive the reward [166–168] (see also [169]). However, neurons in the ventral striatum of rats [170] and monkeys [171] do appear to encode the general effort or cost required to receive a reward. Lesions of the ventral striatum in rats impair the assignment [172] or reassignment [173] of value to particular stimuli and the vigor of responses to them [174], but not response accuracy [174] (see [175] for analogous results in monkeys). In human fMRI, the ventral striatum is generally activated by stimuli with an affective valence, whether positive or negative (see [176] for a review), in both social and non-social domains [177]. The area may also be generally activated by unexpected or novel stimuli [164,178] (but see [179]). These results, combined with its dense limbic and medial prefrontal cortex connectivity, suggest that the region may integrate the output of reward-based systems for the purpose of motivating or prioritizing actions. Differentiating the contribution of the occipitotemporal inputs to its function from those arising from the hippocampus, amygdala, and prefrontal cortices may prove challenging.

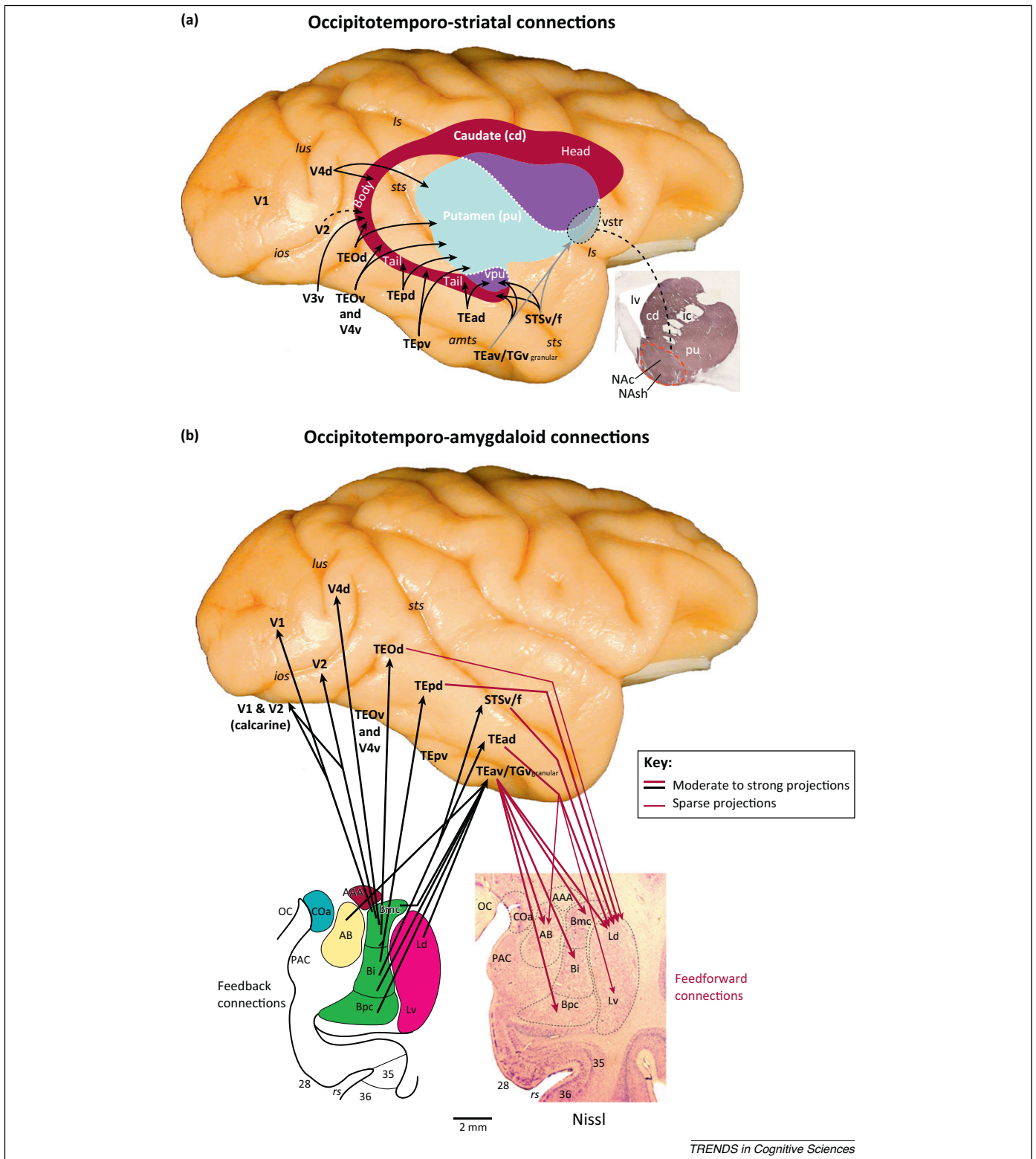


Figure 7. Subcortical pathway anatomy. **(a)** This illustration shows the topographic organization of projections from the occipitotemporal network to the neostriatum (caudate nucleus and putamen; red and blue/purple shaded areas) and the ventral striatum (vstr; gray shaded area). Inset: Photomicrographic section stained for tyrosine hydroxylase shows the ventral striatum region surrounded by a red dashed line, which includes the putamen (pu) and a ventral portion of the head of the caudate nucleus (cd), and the shell and core regions of the nucleus accumbens (Nash and NAc, respectively). Note that the caudal visual areas V2 and V4 project to the most caudal part of the body of the caudate nucleus (genu) and more rostral visual areas (subregions of TEO, TE, TGv granular, and the STSv/f) project to overlapping but progressively more rostral portions of the tail of the caudate nucleus and the caudoventral parts of the putamen. The subregions within aIT (TEav, area TGv granular, and the rostral STSv/f) also give rise to projections that target the ventral striatum (see main text for other details). Abbreviations: ic, internal capsule; ls, lateral sulcus; lv, lateral ventricle; vpu, ventral putamen; Vstr, ventral striatum. For other abbreviations see Figure 3. **(b)** This figure illustrates the organization of reciprocal (feedforward and feedback) connections between the occipitotemporal network and the amygdala. In contrast to the neostriatum, which receives input from nearly every cortical area along the occipitotemporal pathway but projects directly back to none, the amygdala receives the vast majority of feedforward projections (red arrows) from regions within aIT (TEad, TEav, area TGv granular, and the STSv/f) and sends feedback projections (black arrows) to almost every area in the network, including V1. Thick lines indicate moderate-to-strong projections and thin lines show sparse projections. Abbreviations: AAA, anterior amygdaloid area; AB, accessory basal nucleus of amygdala; Bi, basal nucleus of amygdala,

Occipitotemporo-amygdaloid pathway

In contrast to the neostriatum, which receives input from nearly every area in the occipitotemporal network but projects directly back to none, the amygdala receives most of its input from aIT but projects back to almost every area in the occipitotemporal network [16,136,138,180,181] (Figure 7b). The primary projections arise from TEav and TGv granular and target the dorsal subregion of the lateral nucleus (Ld) and the magnocellular, intermediate, and parvocellular regions of the basal nucleus (Bmc, Bi, and Bpc, respectively), as well as the accessory basal nucleus (AB). Secondary projections arise from TEad to the Ld, with weaker projections to the ventral subregion of the lateral nucleus (Lv) and the AB [32,138] and from the STSv/f to the Ld [182]. Finally, there are strong projections from TEpd [180,182] and weak projections from TEod to the Ld [32,180]. Efferents from the amygdala to the occipitotemporal network are exceptionally widespread [181,183], with connections arising from the Bi and Bmc nuclei to virtually every region in the network, including the primary visual cortex (V1). There are also strong reciprocal connections arising from the Bpc, Bi, and Ld nuclei to TEav (Figure 7b). Evidence from functional connectivity in humans likewise indicates a strong link between the basolateral nuclei and the occipitotemporal network [184].

The projections from the occipitotemporal network are likely to provide the input necessary for the visually-dependent emotional regulation for which the amygdala is critical (see [185,186] for reviews). Some have suggested that there is also a subcortical route through which the amygdala receives visual information to enable fast responses to emotional stimuli. However, the plethora of bypass connections (Figure 3a) in the occipitotemporal network and the details of the neuroanatomy of the likely subcortical route suggest that the cortical projections provide the vast majority of the visual input to the amygdala (see [187] for a review of these issues). The basolateral nuclei of the amygdala contain many neurons that are visually responsive [188] and broadly selective for the content of images [189], including facial identity and expression (e.g., [190]). Further, the lateral nucleus of the amygdala is activated when face-selective areas in the STS are electrically stimulated in monkeys [107].

The amygdala participates in, although is not necessarily critical for, numerous different forms of visual learning. For example, it signals the current reward value of a stimulus, rapidly changing its value representations during reversal learning [191]. However, lesions of the amygdala in adult [192] and infant [193] monkeys do not seem to impair reversal learning. Such lesions do cause mild impairments in paired associate learning [194], but the most striking deficit is a generally reduced fear response to aversive stimuli (e.g., [195]), leading to the suggestion that the amygdala might be more important for linking stimuli to instinctive (i.e., fear-induced) avoidance responses than for learning associations between stimuli and negative outcomes generally [196].

The functional role of the projections from the amygdala to the occipitotemporal network are poorly understood. These projections are very diffuse (Figure 7b), suggesting a role in orienting attention or awareness toward particular stimuli (see [186,197] for reviews) rather than in fundamentally altering specific representations. For example, lesions of the amygdala reduce the response of face-selective areas of the fusiform cortex to fearful faces, but do not change the fundamental selectivity of the region for faces generally [198]. The precise nature of the modulatory signals arising from the amygdala remains unknown, but such diffusely distributed signals are likely to direct attentional resources to the processing of visual stimuli signaling potential danger or other emotionally intense events.

Cortico-cortical output pathways

There are three major output pathways to cortical structures, all of which are critical in long- and short-term visual memory. In contrast to the subcortical pathways, the cortical outputs are bidirectional and originate in aIT, although from different subregions within it. First, the occipitotemporo-medial temporal pathway arises from every region in aIT as well as the TEpv (Figure 8; blue arrows) and supports the formation of long-term cognitive visual memories. Second, the occipitotemporo-orbitofrontal pathway arises primarily from the STSv/f, TEav, and area TGv granular and supports the association of visual stimuli with reward. Third, the occipitotemporo-ventrolateral prefrontal pathway arises primarily from the STSv/f with only a minor projection from TEad and supports object-based working memory.

Occipitotemporo-medial temporal pathway

This pathway comprises both direct and indirect projections arising from aIT (TEad, TEav, TGv granular, and STSv/f), and TEpv targeting various structures within the MTL (Figure 8; blue arrows), particularly the perirhinal cortex (PRh) (areas 35/36) [16,32,33,199–201], which projects in turn to both the entorhinal cortex (ERh) (area 28) [36,202,203] and the CA1/prosubiculum (proS) regions of the hippocampus [204] (Saleem and Hashikawa, SFN Abstract 24:898, 1998). In turn, the ERh projects directly to the dentate gyrus [205,206]. The projections from aIT into the rhinal cortices carry visual information used in the encoding of long-term memory of object quality, explaining the numerous findings indicating complex visual selectivity in these regions [207]. It has also been proposed that the rhinal cortices contribute to basic perception (e.g., [208]), but the empirical evidence for any non-memory-related role of the rhinal cortices in perception remains under debate (e.g., [209]). Importantly, areas TEav [210,211] and TEpv [210] also project directly to the CA1/proS (Saleem and Hashikawa, SFN Abstract 24:898, 1998) (see also [212] for the reverse projection). This projection is likely to contribute object information useful in generating selectivity for particular landmarks, places, and views of the environment found in the CA1/proS [5].

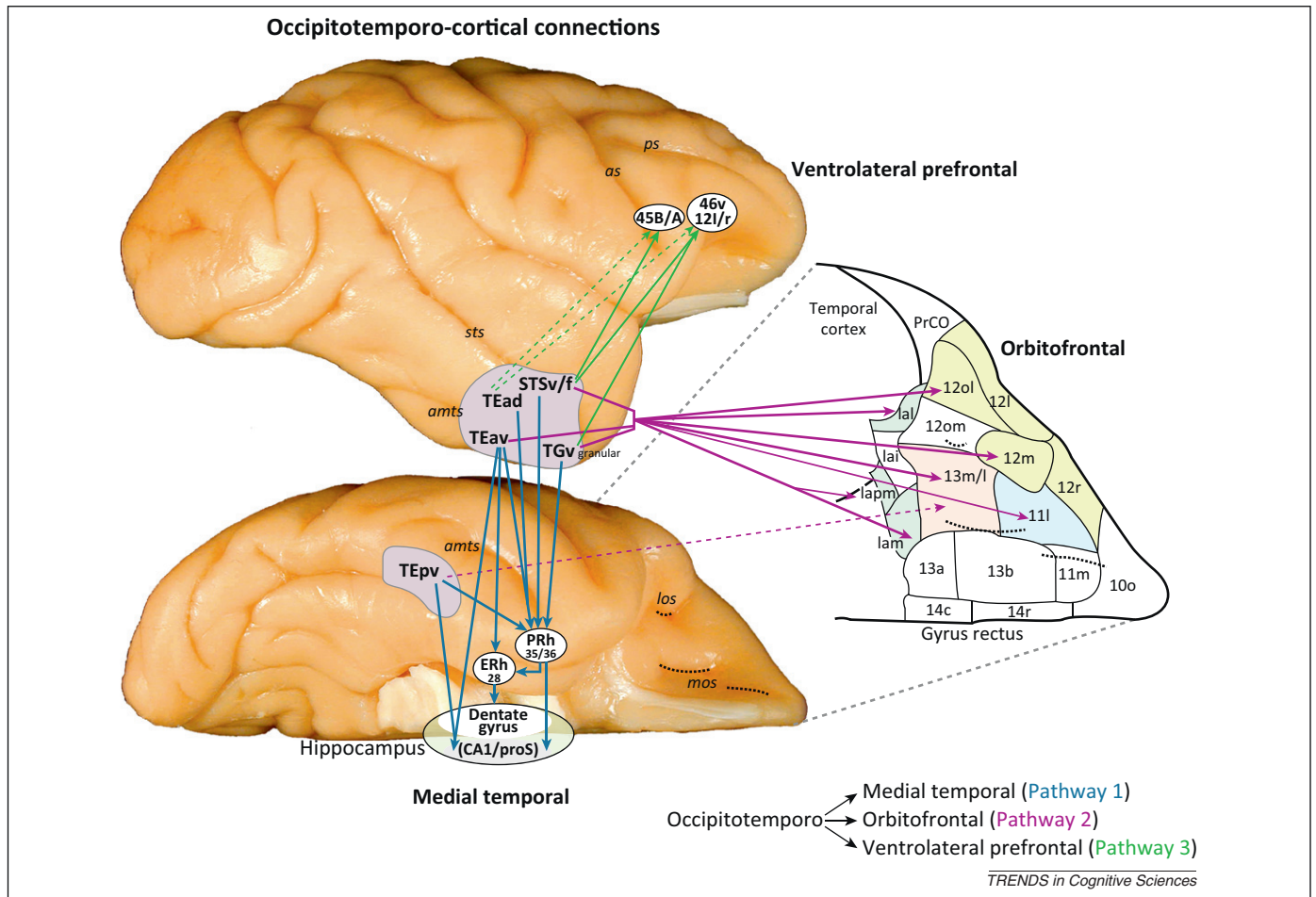


Figure 8. Corticocortical pathways on lateral and ventral views of the rhesus monkey brain. The orbitofrontal cortex and part of the temporal pole are redrawn from the original image (gray broken lines) to show the different cytoarchitectonic areas (subdivisions of areas 11, 12, 13, and 14 and caudal orbital insula areas lai, lal, lam, and lapm; [229,301]). The corresponding location of the medial and lateral orbital sulci (mos and los, respectively; black dashed lines) is also indicated in the drawing. Note that only the parts of the orbitofrontal areas that receive direct projections from the inferotemporal cortex are shaded in the drawing. For example, the lateral part of area 12o (12ol) receives a direct projection from the inferotemporal cortex, but the medial part of area 12o (12om) does not. Three major reciprocal corticocortical pathways (indicated by single arrowheads) originate from the rostral inferotemporal areas TEad, TEav, TEpv, and TGV granular, and the rostral STSv/f. These pathways target different areas in the medial temporal lobe (blue arrows), ventrolateral prefrontal cortex (green arrows), and orbitofrontal cortex (purple arrows). Note that central orbital areas (13m/l) also receive sparse projections from the rostral part of area TEad (not shown). Heavy solid lines indicate dense projections, thin solid lines moderate-to-dense projections, and dashed lines sparse-to-moderate projections. Abbreviations: 12l-12r-45A-45B-46v, ventrolateral prefrontal areas; as, arcuate sulcus; CA1, CA1 subfield of hippocampus; lai, intermediate agranular insular area; lal, lateral agranular insular area; lapm, posteromedial agranular insular area; lam, medial agranular insular area; los, lateral orbital sulcus; mos, medial orbital sulcus; PrCO, precentral opercular area, proS, prosubiculum; ps, principal sulcus. For other abbreviations see Figure 3.

There is clear functional dissociation between the types of long-term memory subserved by the MTL and the neostriatum (see above), exemplified by patient H.M., who after bilateral surgical removal of the MTL was unable to form new long-term memories of events or facts (i.e., episodic and semantic memory, respectively), yet was relatively unimpaired at learning new stimulus-response associations (i.e., habits and motor skills) [213]. Importantly, although H.M. could not form new memories, his memories formed before the surgery were less impacted (but see [214]), suggesting that the MTL is more critical for encoding and storing new information than for retrieving information that has already been encoded (e.g., [215–217]). However, the precise mnemonic functions subserved by subareas of the MTL are still being debated.

One prominent theory holds that the PRh supports familiarity-based recognition of a stimulus divorced from ‘where’ and ‘when’ the item was encountered, whereas the hippocampus supports the recollection of just such associated context (e.g., [218,219]). An alternative proposal is that

the apparent functional dissociation between PRh-dependent familiarity and hippocampus-dependent recollection is artifactual and, instead, both structures contribute to both familiarity and recollection (e.g., [220–223]). Resolving this debate by examining the effects of selective lesions has proved elusive for two reasons. First, the PRh is a critical source of visual input into the hippocampus, such that PRh lesions necessarily have an impact on the mnemonic functions of both structures regardless of any functional specialization they might have. Second, and even more problematic, no index of context recollection has yet been established in the monkey. Without this index, it is difficult to use lesions in the monkey as a model to test the necessity of the hippocampus for recollection.

Although a resolution of this debate is therefore not within sight, the sharp neuroanatomical distinctions between the PRh and the hippocampus argue strongly in favor of their having distinct mnemonic functions. For example, it has been proposed that the unique internal structure of the hippocampus is optimized to perform

pattern separation – a computational process whereby similar patterns are made more distinct from one another – enabling differential encoding of very similar events for selective recollection (e.g., [224–226]; see [227,228] for reviews). Further, the neuropathology in cases of developmental amnesia, in which damage appears to be limited to the hippocampus, seems to result in impairment only of recollection for specific events, leaving familiarity-based recognition largely intact. These findings suggest that although familiarity and recollection may lie along a continuum [220], and may not capture perfectly the functional distinction between the hippocampus and the PRh, the hippocampus does appear to perform a fundamentally distinct computation and thus is likely to mediate a different function from that served by the PRh.

Occipitotemporo-orbitofrontal pathway

Like the occipitotemporo-medial temporal pathway, the occipitotemporo-orbitofrontal pathway arises from TEav, area TGv granular, and the STSv/f, which project to the central (areas 11l and 13m/l), lateral (areas 12m and 12ol), and caudal (areas 1am, 1apm, and 1al) orbitofrontal cortex (OFC; Figure 8, purple arrows), with a weaker projection arising from the rostral portion of TEad and TEpv targeting the central OFC [229] (see also [230,231]). The OFC has been implicated in the processing of both primary and secondary reward, and this pathway may enable both by providing the visual input to: (i) the medial frontal affective processing system resulting in object-primary reward association; and (ii) olfactory and gustatory processing areas resulting in object-secondary reward association [232–235]. There is an extensive literature regarding OFC function in monkeys, humans, and rats (see [236–240] for recent reviews). Here we highlight and contrast findings in the lateral and medial OFC (lOFC and mOFC, respectively) that relate to the dense projections from the ventral pathway to the lOFC (Figure 8; colored regions in the orbitofrontal cortex).

Object reversal learning, in which animals must learn and then reverse the association between reward and one of a pair of objects, is impaired (slower learning of the reversal) with lesions of the OFC (both lateral and medial) in both monkeys (e.g., [241,242]) and humans [243,244]. Further, a recent single-cell recording study reported that orbitofrontal neurons encode the distribution of the expected relative to actual rewards [245], a useful representation for updating stimulus-reward associations. However, deficits in object reversal learning do not differentiate between the subareas of the OFC, because lesions of neither the lOFC [246,247] nor the mOFC [247] are sufficient to impair this function. This pattern of results might arise from either region being sufficient to support reversal learning, from damage to nearby structures caused by extensive OFC lesions [236] or, alternatively, from a critical mid-region within the OFC being completely removed when both partial lesions are combined but not when each partial lesion is performed separately.

There are some functional dissociations between the lOFC and mOFC that are well predicted by their differential visual connectivity with the occipitotemporal network. The lOFC, consistent with its strong input from the occipitotemporal network, appears more closely involved

in updating particular stimulus-reward associations [236,237,239]. For example, in monkeys, lesions of the lOFC impair the ability to assign a causal relationship between the choice of a particular stimulus and reward [237,248,249]. Lesions [247] or inactivation [250] of the lOFC but not the mOFC [247] impair reinforcer devaluation (i.e., decreased stimulus preference after satiation for the associated food). In humans, the lOFC shows strong activation whenever the expected value of a stimulus choice is updated [251].

By contrast, the mOFC seems more strongly involved in fine-grained comparisons between reward values [236,237]. Lesions of the mOFC but not the lOFC impair extinction [247] (i.e., cessation of responding to a stimulus that is no longer positive) and also impair decisions among a set of stimuli with only slightly differing reward values [249]. In humans, the mOFC also consistently signals the current level of reward regardless of whether expected values have changed [251].

Occipitotemporo-ventrolateral prefrontal pathway

Unlike the other corticocortical projections, the occipitotemporo-ventrolateral prefrontal pathway (Figure 8; green arrows) originates primarily in the anterior portions of the STSv/f and projects to areas 45A/B, 46v, and 12l/r in the VLPFC; a weaker projection also exists from TEad to these cortical areas [229,252,253] (Saleem *et al.*, SFN abstract 465.12, 2008) (see also [230,231]). The precise distribution of the dorsal and ventral visual pathways' terminals in the lateral prefrontal cortex as a whole may help resolve the conflict between two competing theories of its functional organization: complete convergence versus domain specificity.

Broadly, but strictly within the domain of vision, the entire lateral prefrontal cortex is thought to be involved in the maintenance and manipulation (e.g., attention [254], working memory [255–257], switching task set [258]) of task-relevant information represented in the posterior cortices (see [259–261] for reviews). However, the lateral prefrontal cortex is not thought to contribute to basic processing of that information, because even complete removal of this area does not impair basic perception or categorization [262].

On one account, the lateral prefrontal cortex is the ultimate site of integration between all forms of information, representing the final stage of the putative processing hierarchy [263]. Under this view, the necessity of integration implies that there should be no strict division between different forms of information (e.g., between spatial and object vision [264]) (Box 3 discusses areas where the dorsal and ventral visual pathways converge). However, there is strong anatomical and functional evidence for some domain-specificity (see also [259,265–267] for related proposals). The division between visuospatial and stimulus-quality information [268,269] (see [259,270] for others) has the strongest anatomical evidence, with clearly distinct projections from the dorsal and ventral pathways to the VLPFC (Figure 8) and DLPFC, respectively [5]. There is also direct evidence for functional specialization. In monkeys, there is strong spatial selectivity in dorsolateral [271,272] and a bias for object selectivity in ventrolateral

Box 3. Connections between the dorsal and ventral visual pathways

In this review of the ventral visual pathway and the previous review of the dorsal visual pathway [5], we have focused on the processing and connectivity unique to each one. However, there are many connections and points of convergence between them (in addition to the neostriatum and lateral prefrontal cortex) that might contribute to many different forms of visual processing.

Beyond the early visual areas (V1, V2, and V3), the pathways are directly connected via a direct projection between areas LIP and TEO/TE [230], as well as by their common inclusion of the MT/MST complex. This complex has connections with every region within the occipitoparietal network [5] as well as with V4d, TEOd, and the caudal portion of the STSv/f in the occipitotemporal network (see Figure 3a in main text). The MT/MST/FST complex is sensitive to many aspects of motion (see [302] for a review) and depth [303] and contains many neurons selective for shapes defined by motion (e.g., [304]). It is likely that this complex, in concert with areas in the intraparietal sulcal cortex, provide the depth and motion information needed to generate the selectivity for 3D (e.g., [305]) and motion-defined (e.g., [306]) shapes observed in IT.

The bidirectional connection between areas LIP and TEO/TE might also be important for the generation of the object selectivity sometimes observed in the occipitoparietal network even for 2D shapes not currently being acted upon (e.g., [307]). These results have been interpreted as evidence of independent shape analysis in the dorsal visual pathway, but damage to the ventral pathway reduces object-related activity in the parietal cortex [308], indicating that at least some of the object processing in the occipitoparietal network is dependent on the ventral pathway. Whether this connection is important for the generation of the 3D-shape selectivity observed in the occipitoparietal network (e.g., [309]) remains to be tested.

The MTL (the hippocampus together with the rhinal and parahippocampal cortices), which receives input from the dorsal pathway via the parieto-medial temporal pathway [5] and from the ventral pathway via V4v and aIT, is clearly a critical region of convergence. Damage to regions along the parieto-medial temporal pathway lead to various deficits in navigation and the coordination of egocentric and allocentric reference frames [5,310]. The parahippocampal cortex, which receives direct projections from the inferior parietal lobule and V4v in monkey evidences sensitivity to both object and spatial information in human [311]. Damage to the posterior portions of the parahippocampal cortex (TFO; see Figure 3a), which receives direct input from V4v can lead to agnosia for familiar landmarks [310]. Damage to the mid-anterior portion (posterior to the rhinal cortices), which has strong connectivity with the hippocampus and posterior parietal cortex, leads to a deficit in learning routes through new environments (e.g., [312]).

Finally, it should be noted that information from the two pathways can also be integrated in early visual areas by virtue of extensive feedback connections [313]. Recurrent signals from each pathway could affect processing in the other pathway by modulating processing in these early visual areas. Both pathways are also connected with the frontal eye field (albeit with far denser connection to the dorsal than to the ventral pathway), so eye movements initiated by one stream might also impact the other.

[272] neurons, and this evidence is complemented by a dissociation of deficits in spatial and object working memory after dorsolateral and ventrolateral lesions, respectively (e.g., [273]). Likewise, in humans, lesions of the dorsolateral portion are associated with selective deficits in spatial working memory [256,257], whereas ventrolateral lesions lead to deficits in working memory for faces [257] (but see [255]).

There is also evidence in monkeys for stimulus-specific domains within the VLPFC in the form of three discrete

‘patches’ of cortex that are selective for faces (PL, PA, and PO) (e.g., [274]). Face selectivity has also been observed with single-cell recording [266,275] and with fMRI in an analogous region in humans [276]. Two of these patches, PL and PA, overlap, respectively, 46v/12r/l and 45B, the two regions receiving direct input from the STSv/f (Figure 8). The third patch, PO, is within the OFC, suggesting that the location of face selectivity in the prefrontal cortex aligns with anatomical connectivity.

Regardless of the need for integration between different forms of information, communication between regions and the limited channels available necessitate some level of functional specialization (see also [259]). The resolution between the homogeneous and heterogeneous viewpoints of lateral prefrontal function is to propose a gradient of functional specialization [259,272] based on the relative strength of the inputs from the dorsal and ventral pathways. Such a gradient could also explain the occasionally conflicting reports of distinct and intermixed selectivity within the region [255,257,264,272] based on the precise location of recording or damage (see [260] for a contrasting proposal of dorsal-ventral organization).

Concluding remarks

Here we have proposed an expanded neural framework for the processing of object quality, in which the intrinsic connectivity of the ventral visual pathway is characterized as a recurrent network that provides visual information to at least six distinct cortical and subcortical areas, each mediating different forms of learning and memory. Characterizing the occipitotemporal pathway as a recurrent network parsimoniously accounts for several of its functional properties, and specification of its output targets provides insight into the function not only of those targets but also of the pathway itself (Box 1). In this final section, we highlight new empirical and theoretical considerations that arise from this expanded framework (Box 4).

One question concerns the functional consequences of the complex intrinsic connectivity beyond providing multiple routes for the flow of visual information, although this redundancy almost certainly underlies the striking recovery of function observed following lesions of the network but not of its output targets (e.g., [195,277]). In particular, the connectivity enables distinct areas to perform specialized processing of distinct aspects of stimuli (e.g., motion, shape) that are eventually synthesized into unified representations within neuronal populations in aIT and/or MTL [207]. This leads to a developmental theory of the functions of the alternate and central routes. Early in development, the central route might be important for creating representations of complex stimuli in aIT via the iterative aggregation prominent in some extant models of the central route (e.g., [13]). However, later in development, as a result of learned associations with representations in the alternative routes, these routes alone might be sufficient to drive complex representations in aIT even in the absence of the central route (e.g., [37]).

We have highlighted the likely contribution of visual information from the occipitotemporal network to the function of the target structures, but the proposed framework also raises questions about how signals from the

Box 4. Outstanding questions

- What is the homology or lack thereof in the visual properties of aIT in humans and monkeys?
- What are the visual properties of the major occipitotemporal output targets in humans?
- How do the major occipitotemporal output targets constrain functional organization and processing within the ventral visual pathway?
- How do the necessity and sufficiency of the components of the ventral visual pathway for its function change over the course of development?
- Do homologous splits between dorsal and ventral processing occur in sensory modalities other than vision?

target structures constrain and modify stimulus representations within the occipitotemporal network. First, the framework helps to explain why learning and task effects within the occipitotemporal network are generally small (see [278] for a review). In contrast to the occipitoparietal network [5], much of the occipitotemporal network does not receive direct feedback from the output targets. Although many regions receive efferents from the amygdala, only a subset of the more rostral regions receive any efferents from the other output targets. There are projections from all visual areas to the frontal eye-field, but the projections from the occipitotemporal network are generally much sparser than those from the occipitoparietal network [279]. Thus, the early and intermediate regions of the network receive largely indirect feedback about the utility of their representations for processing by the target regions, let alone for guiding adaptive action. This lack of direct feedback might allow these areas to more faithfully reflect the statistics of visual experience, creating stimulus representations that are more general and capable of contributing to adaptive action in many different contexts. However, it also implies that feedback-dependent changes (e.g., learning) within these areas will be smaller and take longer to develop than in areas with more direct feedback [278].

The extrinsic connectivity also raises interesting questions about how feedback contributes to its early ontogeny. The major projection targets with feedback connections (amygdala, medial temporal lobe, orbitofrontal, and ventrolateral prefrontal) receive most of their visual input from the most rostral regions of the occipitotemporal network. Given that visual responses in these rostral regions are likely to be undeveloped early in life (e.g., [280]), the informativeness of any visual feedback from the output targets is questionable. However, the orbitofrontal and anterior insular cortex are strongly tied to gustation, olfaction, and visceral sensation (see [158,233] for reviews), senses that are likely to be well formed early in life. These cortices might provide multimodal information that constrains the early development of the occipitotemporal pathway, reinforcing visual representations associated with strongly positive or negative stimuli in these modalities.

Finally, although this review and our previous review of the dorsal visual pathway [5] have focused exclusively on vision, the split we have described between dorsal and ventral processing (Box 1) may also apply to other sensory modalities. There is strong evidence that many areas within the parietal cortex may play critical roles in both

auditory and somatosensory processing in addition to vision. A comparison of the analogous dorsal/ventral divisions in other senses with those in vision may lead to new insights into the functions served by ventral and dorsal pathways within and across modalities.

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