Review article

Two what, two where, visual cortical streams in humans

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ABSTRACT

ROLLS, E. T. Two What, Two Where, Visual Cortical Streams in Humans. NEUROSCI BIOBEHAV REV 2024. Recent cortical connectivity investigations lead to new concepts about 'What' and 'Where' visual cortical streams in humans, and how they connect to other cortical systems. A ventrolateral 'What' visual stream leads to the inferior temporal visual cortex for object and face identity, and provides 'What' information to the hippocampal episodic memory system, the anterior temporal lobe semantic system, and the orbitofrontal cortex emotion system. A superior temporal sulcus (STS) 'What' visual stream utilising connectivity from the temporal and parietal visual cortex responds to moving objects and faces, and face expression, and connects to the orbitofrontal cortex for emotion and social behaviour. A ventromedial 'Where' visual stream builds feature combinations for scenes, and provides 'Where' inputs via the parahippocampal scene area to the hippocampal episodic memory system that are also useful for landmark-based navigation. The dorsal 'Where' visual pathway to the parietal cortex provides for actions in space, but also provides coordinate transforms to provide inputs to the parahippocampal scene area for self-motion update of locations in scenes in the dark or when the view is obscured.

1. Introduction

Until recently, much of our understanding of the connectivity of the visual cortical streams which is fundamental to understanding their functions has relied on anatomical investigations in macaques, complemented by functional connectivity studies in humans (Mishkin et al., 1983; Felleman and Van Essen, 1991; Kravitz et al., 2011, 2013; Glasser et al., 2016a; Grimaldi et al., 2016; Colclough et al., 2017; Stevens et al., 2017; Pitcher and Ungerleider, 2021; Yokoyama et al., 2021; Reznik et al., 2023).

However, recent investigations of the connectivity of the visual pathways in humans, and how they connect onwards to the hippocampal memory system, the orbitofrontal cortex emotion system, and the temporal lobe semantic systems, are revolutionizing our understanding. One example is that a ventromedial visual pathway has recently been followed in humans from early visual cortical regions via ventromedial visual cortical regions to the medial parahippocampal gyrus and thereby to the hippocampus (Rolls, 2023a; Rolls et al., 2023a; 2023f). This

revolutionizes our understanding by showing how representations of spatial scenes can be formed by ventral visual stream computations involving combinations of features analogous to the ventrolateral visual stream computations that combine features to lead to representations of objects and faces in the inferior temporal visual cortex (Rolls, 2021d).

This paper describes this recently developed understanding of visual cortical processing streams in humans, and builds on much new information about the human visual cortical streams from recent investigations of tractography, functional connectivity, and effective (directed) connectivity in humans, based on the excellent data collected by the Human Connectome Project. A feature of what is described here is the use of the Human Connectome Multimodal Parcellation (HCP-MMP) of the human cerebral cortex, which by using structural cortical measures (cortical myelin and thickness), functional connectivity, and task-related fMRI has been able to define 360 cortical regions each with potentially different connectivity and functions (Glasser et al., 2016a; Huang et al., 2022). The functions of many of the regions defined in this atlas are interpretable in that many correspond to regions defined

anatomically and physiologically in macaques and now in humans, and the great body of neuroscience research on these well-defined regions can be brought to bear to understand their functions (Glasser et al., 2016a; Kandel et al., 2021; Rolls, 2023d).

Given this context, this paper describes the connectivities of four major cortical visual streams in humans, and provides insight into their functions by referring to some of the recent discoveries on the functions of the regions in these different cortical streams. Innovative ways in which the treatment here goes beyond many discussions of the visual cortical pathways is that it provides insight into the functions of these visual streams by considering their onward effective (causal) connectivity to different cortical systems, including the hippocampal memory system (Rolls et al., 2022b; 2023f), the semantic systems in the anterior temporal lobe (Rolls et al., 2022a), and the reward and emotion system in the orbitofrontal cortex and amygdala (Rolls et al., 2023a, b; 2023e; 2023f); and also by considering what activates these same cortical HCP-MMP regions in fMRI investigations (Rolls et al., 2024b).

Two 'What' and two 'Where' visual cortical streams in humans are described. The 'What' pathways are involved in representing 'What' objects, faces, face expressions, head and face gestures and movements etc are being viewed. The 'Where' pathways are involved in representing spatial scenes, where we are looking in them, and in actions in space such as reaching and grasping. Although four key streams for visual cortical processing are presented, the possibility of additional ways that cortical visual processing can be organized are not excluded, particularly when top-down attention may dynamically organise cortical visual processing (Rolls, 2023d).

The methods used to trace these pathways include diffusion tractography (Huang et al., 2021), functional connectivity, and effective connectivity (Ma et al., 2022; Rolls et al., 2022a, 2022b, 2023a, 2023c, 2023i) performed on 7 T structural and functional MRI data from the same set of 171 Human Connectome Project participants (Glasser et al., 2016b) (and now supported by resting state fMRI analyses in 956 HCP participants at 3 T), and magnetoencephalography (Rolls et al., 2023f) performed on 88 participants in the Human Connectome project (Larson-Prior et al., 2013). Diffusion tractography measures the direct anatomical pathways between brain regions and not the direction, and is usefully complemented in the above research by functional and effective connectivity as diffusion tractography may sometimes make false positives where pathways cross, and may miss some, especially long, pathways. Functional connectivity is measured by the Pearson correlation between the fMRI BOLD (or other) signals between a pair of cortical regions, may reflect indirect interactions and common input, and does not provide evidence about the direction of any effect. A high functional connectivity does though reflect how much a pair of brain regions is interacting, and does reflect function in that it is different between the resting state and the performance of tasks in the same 956 HCP participants (Rolls et al., 2024b). Resting state connectivity was used in the investigations described here, as it may provide a basic connectivity matrix that can be investigated even if participants may not be able to perform a particular task, as in some mental disorders. Effective connectivity aims to measure how much two brain regions influence each other in each direction, and utilises time delays to estimate what are sometimes described as causal effects. Effective connectivity is especially important to measure between cortical regions, for at least in cortical hierarchies the anatomy is asymmetric, with typically cortical layers 2 and 3 projecting forwards up the hierarchy to layers 2 and 3 in the next cortical region, whereas the backprojections tend to originate in the deeper cortical layers, and project back to layer 1 of the preceding cortical region to terminate on the apical dendrites of cortical pyramidal cells, and may accordingly have weaker effects that can be shunted by bottom-up forward inputs (Markov et al., 2013, 2014; Markov and Kennedy, 2013; Rolls, 2016a; 2023d). The effective connectivity that we have measured is described as a whole brain generative effective connectivity, in that it is the effective connectivity matrix that can generate the functional connectivity and the delayed functional connectivity (2 s

for fMRI, 20 ms for MEG) between all 360 cortical regions, and uses a Hopf algorithm with a model of cortical connectivity based on interacting Stuart-Landau oscillators (Deco et al., 2019, 2023; Rolls et al., 2022b; 2023f).

The names of the regions in the HCP-MMP atlas (Glasser et al., 2016a) in the revised order used by Huang, Rolls et al. (2022) and their cortical divisions are shown in Table S1, with views of the brain with the HCP-MMP regions labelled, and coronal slices, provided in Fig. S1. All the analyses described here were performed with the data mapped to the surface version of the HCP-MMP1 atlas (Glasser et al., 2016a), as that can provide more accurate localization of cortical regions, though the extended version of the HCP-MMP1 atlas can also be useful, as it adds 66 subcortical regions, and can be used with volumetric data (Huang et al., 2022; Rolls et al., 2023g, 2024b; Zhang et al., 2024b).

In previous research two cortical visual streams were identified, a ventral 'What' and a dorsal 'Where' stream (Ungerleider and Mishkin, 1982; Mishkin et al., 1983; Baizer et al., 1991; Ungerleider and Haxby, 1994). On the basis of neuropsychological studies, it was proposed that in humans the dorsal visual stream might be considered an 'action' rather than a 'Where' stream (Goodale and Milner, 1992; Milner and Goodale, 1995; Milner, 2017; Gallivan and Goodale, 2018). This visuomotor or visuospatial concept for the dorsal stream was adopted by others (Kravitz et al., 2011), who identified connectivities to premotor and prefrontal cortices, that are now clearly identified in humans (Rolls et al., 2023d). For the 'ventral visual system', outputs were discussed (Kravitz et al., 2013) to the striatum (cf. Caan et al., 1984; Johnstone and Rolls, 1990; Williams et al., 1993), medial temporal cortex (cf. Rolls, 2023a), ventrolateral prefrontal cortex (cf. Rolls et al., 2023d), and orbitofrontal cortex (cf. Thorpe et al., 1983; Rolls and Baylis, 1994; Critchley and Rolls, 1996; Rolls et al., 1996; Rolls et al., 2006). Based on the response properties of neurons in the macaque in the cortex in the Superior Temporal Sulcus (STS) in which neurons respond to combinations of object including face and motion selectivity (Baylis et al., 1985; 1987; Perrett et al., 1985b; Hasselmo et al., 1989a; 1989b; Rolls et al., 2024b) that often have social significance, it was proposed (Hasselmo et al., 1989a) that the STS system is a separate system from the ventral visual stream for face and object selectivity, and the dorsal visual stream, but receives from both of those two streams. Consistent with this, it was shown (Boussaoud et al., 1990) that there are connections from motion-related regions FST and MST in the dorsal visual stream to the more anterior STS regions where we discovered cells responding to face expression and motion, as just described. This third visual stream to the cortex in the Superior Temporal Sulcus has recently been accepted (Pitcher and Ungerleider, 2021). A posterior part of this system has been implicated in actions on moving objects (Wurm and Caramazza, 2022). Consistent with the spatial clustering of groups of neurons with similar responses recorded in the inferior temporal visual cortex (Baylis et al., 1987; Hasselmo et al., 1989a), and consistent with self-organizing mapping of a high dimensional space to 2D cortex (Rolls, 2023d), multiple clusters of face vs body activated cortical regions have been identified in these regions (Weiner and Grill-Spector, 2013). In another study, multidimensional scaling of human resting state functional connectivity suggested that in addition to dorsal and ventral visual pathways, there may be a lateral pathway that could be related to visual processing for language (Haak and Beckmann, 2018).

The aims of the newer investigations focussed on here that go beyond previous research were as follows. First, an aim was to understand cortical connectivity using a well-grounded human cortical parcellation based on anatomical evidence, functional connectivity, and task-related fMRI to define 360 human cortical regions with potentially different structure, function, and connectivity that could be used by many investigators to promote comparison between different investigations, the HCP-MMP atlas (Glasser et al., 2016a). Second, an aim was to use three measures of cortical connectivity with HCP data from 171 HCP participants, with the measures being effective connectivity, functional connectivity, and diffusion tractography (Huang et al., 2021; Ma et al.,

2022; Rolls et al., 2022a; 2022b; 2023a; 2023c; 2023f). A third aim was to anchor the interpretation of the connectivity maps by using evidence from single neuron investigations in macaques (Rolls, 2021d, 2023d, a), and from task-related visual activations to faces, places, body parts, and tools performed with HCP data with 956 participants and that use the HCP-MMP parcellation (Rolls et al., 2024b). A fourth aim was to follow the visual pathways through the cerebral cortex to obtain evidence on how the visual pathways connect to other brain systems, including those for episodic memory in the hippocampal memory system (Rolls, 2023a), for emotion in the orbitofrontal cortex (Rolls, 2023c), and for semantic processing related to language (Milton et al., 2021; Rolls et al., 2022a). A fifth aim is to provide an overview for the vision research community and other neuroscientists of some of the recent advances being made

using the HCP-MMP atlas in understanding human visual cortical connectivity and function using that well-defined parcellation framework (Glasser et al., 2016a), and to underline the advantages of using that atlas to compare results from different investigations. Reference to Fig. 6, which illustrates the four visual cortical streams described here, may be useful in the following by providing an overview.

The aims of this paper are thus to consider new evidence in humans especially about the cortical connectivity of key cortical visual streams, and also their computational functions and outputs to other brain systems. Further evidence on visual cortical processing in humans based on activation studies, neuropsychology etc, is available elsewhere (Ungerleider and Mishkin, 1982; Baizer et al., 1991; Goodale and Milner, 1992; Ungerleider and Haxby, 1994; Milner and Goodale, 1995; Kanwisher
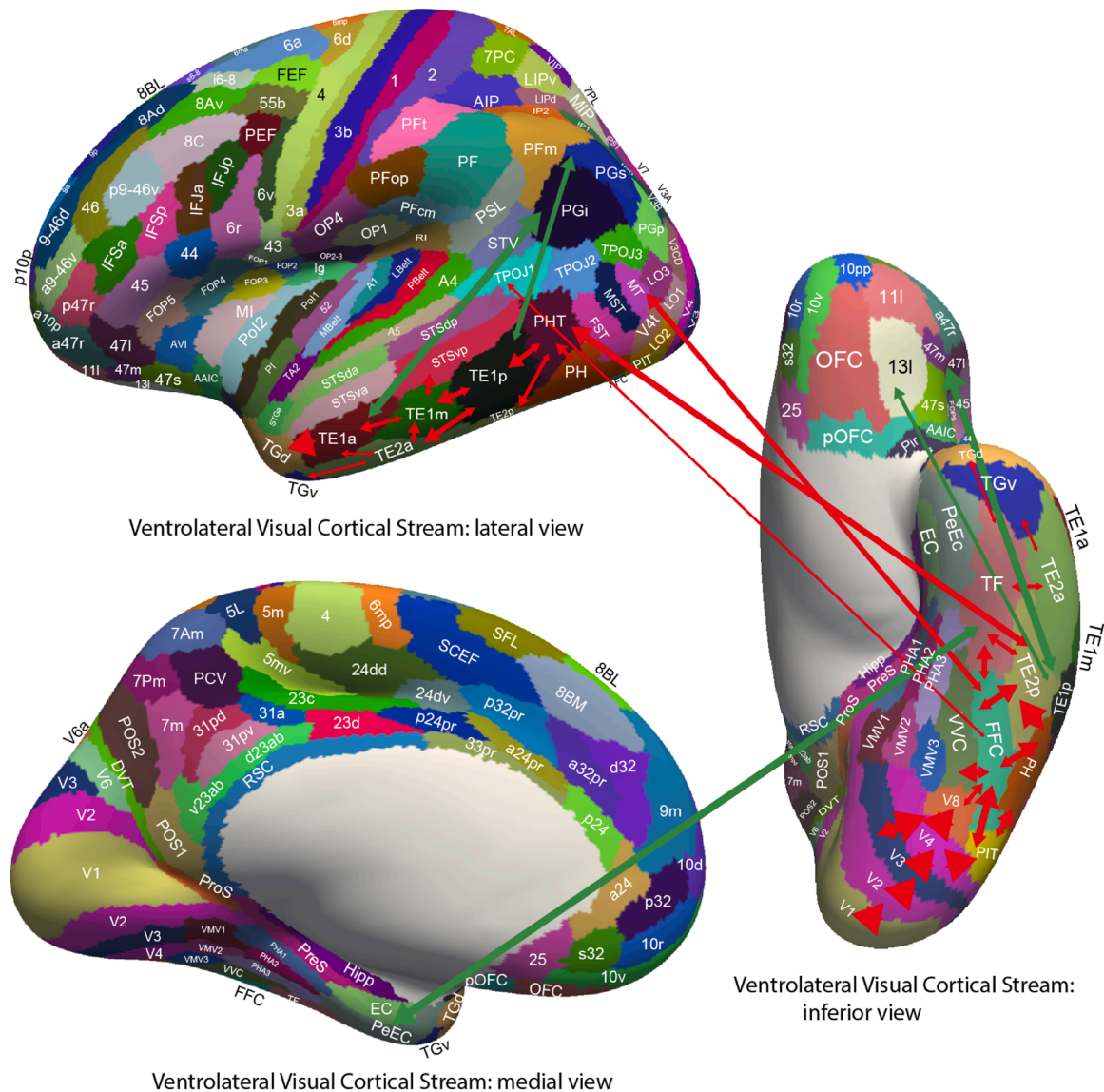
Fig. 1. Hierarchical organisation of the Ventrolateral Visual Cortical ' What' Stream measured with effective connectivity, functional connectivity, and diffusion tractography with Human Connectome project data for fMRI (Rolls et al., 2023a) and MEG (Rolls et al., 2023f). First V1 > V2 > V3 connect to V4. Second, V4 has connectivity to FFC (fusiform face cortex), V8 and PIT. Third, FFC, V8 and PIT have connectivity to TE1p and TE2p, which are the last mainly unimodal visual inferior temporal cortex regions where faces and objects are represented. Fourth, TE1p and TE2p have connectivity to TE1m, TE2a, TE1a and the temporal pole TGd and TGd. This fourth level anterior temporal lobe region is multimodal, in that it also receives auditory cortex input from auditory cortex regions such as the Belt regions; and from somatosensory regions in the frontal operculum (FOP) and opercular (OP) regions. A green arrow shows how the Ventrolateral Visual Stream provides 'What' input to the hippocampal memory system via lateral parahippocampal gyrus TF to perirhinal PeEc, hippocampus etc. Two green arrows show how posterior inferior temporal visual cortex regions TE1p and TE2p and more anterior temporal cortical regions have effective connectivity to the lateral orbitofrontal cortex (47 m, 47l , a47r) and medial orbitofrontal cortex (13 l). The Ventrolateral Visual Stream also has connectivity with the semantic regions, such as STSvp in the ventral bank of the superior temporal sulcus, and inferior parietal visual regions PFm, PGs and PGi as indicated by 2 green arrows. The widths of the lines and the size of the arrowheads indicate the magnitude and direction of the effective connectivity. (After Rolls et al., 2023a).

et al., 1997; Epstein and Kanwisher, 1998; O'Doherty et al., 2003; Crane and Milner, 2005; Dehaene et al., 2005; Epstein, 2005; Grill-Spector et al., 2006; Epstein, 2008; Said et al., 2010; Dehaene and Cohen, 2011; Kravitz et al., 2011; Said et al., 2011; Epstein and Julian, 2013; Kravitz et al., 2013; Weiner and Grill-Spector, 2013; Hahn and Perrett, 2014; Deen et al., 2015; Weiner and Grill-Spector, 2015; Kamps et al., 2016; Gerbella et al., 2017; Isik et al., 2017; Milner, 2017; Weiner et al., 2017; Gallivan and Goodale, 2018; Rizzolatti and Rozzi, 2018; Epstein and Baker, 2019; Pitcher et al., 2019; Silson et al., 2019; Deen et al., 2020; Gamberini et al., 2020; Sulpizio et al., 2020; Caffarra et al., 2021; Hori et al., 2021; Natu et al., 2021; Orban et al., 2021a; Orban et al., 2021b; Passarelli et al., 2021; Pitcher and Ungerleider, 2021; Urgen and Orban, 2021; Yeatman and White, 2021; Kosakowski et al., 2022).

2. A ventrolateral visual 'What' cortical stream for object and face representation

Measurement of effective connectivity and functional connectivity with fMRI (Rolls et al., 2023a) and magnetoencephalography (Rolls et al., 2023f), and of connections using tractography (Rolls et al., 2023a) has revealed the following ventrolateral 'What' cortical stream, illustrated in Fig. 1 (see also Fig. 6). First V1 > V2 > V3 connect to V4. (">" indicates connectivity mainly between adjacent regions in a hierarchy, and stronger in that direction than the reverse, at least on the short timescale of the first few hundred ms after a visual stimulus is shown (Rolls et al., 2023f).) Second, V4 has connectivity to FFC (fusiform face cortex), V8 and PIT (Posterior InferoTemporal). Third, FFC, V8 and PIT have connectivity to TE1p and TE2p, which are the last mainly unimodal visual posterior inferior temporal cortex regions where faces and objects are represented in humans (Rolls et al., 2023f). Fourth, TE1p and TE2p have connectivity to TE1m, TE2a, TE1a and the temporal pole TGd and TGd. This fourth level anterior temporal lobe region is multimodal, in that it also receives auditory cortex input from auditory cortex regions such as the auditory cortex Belt regions; and from somatosensory regions in the frontal operculum (FOP) and opercular (OP) regions (Rolls et al., 2023a; 2023d; 2023f; 2023h). The effective connectivity shown in Fig. 1 is supported by the temporal order of the activations of different ventral stream cortical regions illustrated in Fig. S2 (Rolls et al., 2023f).

This ventrolateral visual cortical stream corresponds to the macaque ventral pathway to the inferior temporal visual cortex (corresponding to TE1p and TE2p in humans), in which face and object cells were discovered with invariant representations and sparse distributed encoding (Perrett et al., 1979, 1982; Tovee et al., 1993, 1996; Rolls and Tovee, 1995; Tovee and Rolls, 1995; Abbott et al., 1996; Rolls et al., 1997b, 1997c; Rolls and Treves, 2011), and these discoveries have been followed up including the patches in which face cells are found (Tsao et al., 2006, 2008; Freiwald et al., 2009; Li and DiCarlo, 2010; Fisher and Freiwald, 2015; Aparicio et al., 2016; Sliwa and Freiwald, 2017; Shepherd and Freiwald, 2018; Freiwald, 2020; Hesse and Tsao, 2020). The invariant aspects of the representation in the inferior temporal visual cortex are ideal as an input to memory systems for episodic memory in the hippocampus, and for reward association memory in the orbitofrontal cortex, because once a memory has been formed to one instance of a particular face or object, generalisation occurs to other views, retinal positions, sizes etc of the face or object (Rolls, 2021d, 2023d). Inferior temporal visual cortex representations (in macaques) are invariant with respect to position on the retina (Tovee et al., 1994), size and contrast (Rolls and Baylis, 1986), spatial frequency (Rolls et al., 1985), and also for some neurons view (Hasselmo et al., 1989b; Booth and Rolls, 1998). The responses of inferior temporal visual cortex neurons can be invariant with respect to position on the retina when a blank background is used with receptive fields of for example 78 degrees, and they shrink in complex natural scenes and may encode the position of different objects, which is very useful when there are multiple objects in the scene (Trappenberg et al., 2002; Rolls et al., 2003; Aggelopoulos and Rolls, 2005). Although single neurons can thus be very translation

invariant, across a population of neurons some information is evident about location (Hong et al., 2016), especially in complex natural scenes (Aggelopoulos and Rolls, 2005). An important property of inferior temporal cortex representations is that they represent what object or face is being viewed, independently of its reward or punishment value, as showed by reward reversal tasks and by devaluation experiments (Rolls et al., 1977). This allows for objects and faces to be seen independently of whether they are rewarding or not, which of course is very useful for an input to episodic memory systems in the hippocampus in which learning about where objects have been seen can be useful in case later they become rewarding and a goal (Rolls, 2023d).

As shown in Figs. 1 and 6, the posterior inferior temporal visual cortex (regions TE1p and TE2p) and more anterior temporal cortical regions (e.g. TE1m, TE2a) project to the orbitofrontal cortex (Rolls et al., 2023e), to both the lateral orbitofrontal cortex (e.g. 47 m, 47 l, a47r) and to medial orbitofrontal cortex (13 l). These pathways provide visual inputs to the orbitofrontal cortex, which is the key brain region involved in emotion in humans as shown neurophysiologically, by activations to emotion-related stimuli, and by effects of damage to the human orbitofrontal cortex (Rolls, 2014, 2023c; Rolls et al., 2023b). For example, one-trial associations of visual objects and faces with reward are learned and reversed by neurons in the orbitofrontal cortex (Thorpe et al., 1983; Rolls et al., 1996; Rolls, 2023d), and devaluation influences these visual representations (Critchley and Rolls, 1996).

Another output of the ventrolateral visual cortical stream is especially via lateral parahippocampal gyrus region TF which provides 'What' inputs via perirhinal and entorhinal cortex to the human hippocampal episodic memory system (green arrow in Fig. 1) (Rolls et al., 2022b; Rolls, 2023a, d; Rolls et al., 2023a; Rolls et al., 2023f).

Another output of the ventrolateral visual cortical stream is to the semantic regions (Rolls et al., 2022a), such as STSvp in the ventral bank of the superior temporal sulcus (Rolls et al., 2022a), and inferior parietal visual regions PFm, PGs and PGi (Rolls et al., 2023c) as indicated by 2 green arrows in Fig. 1.
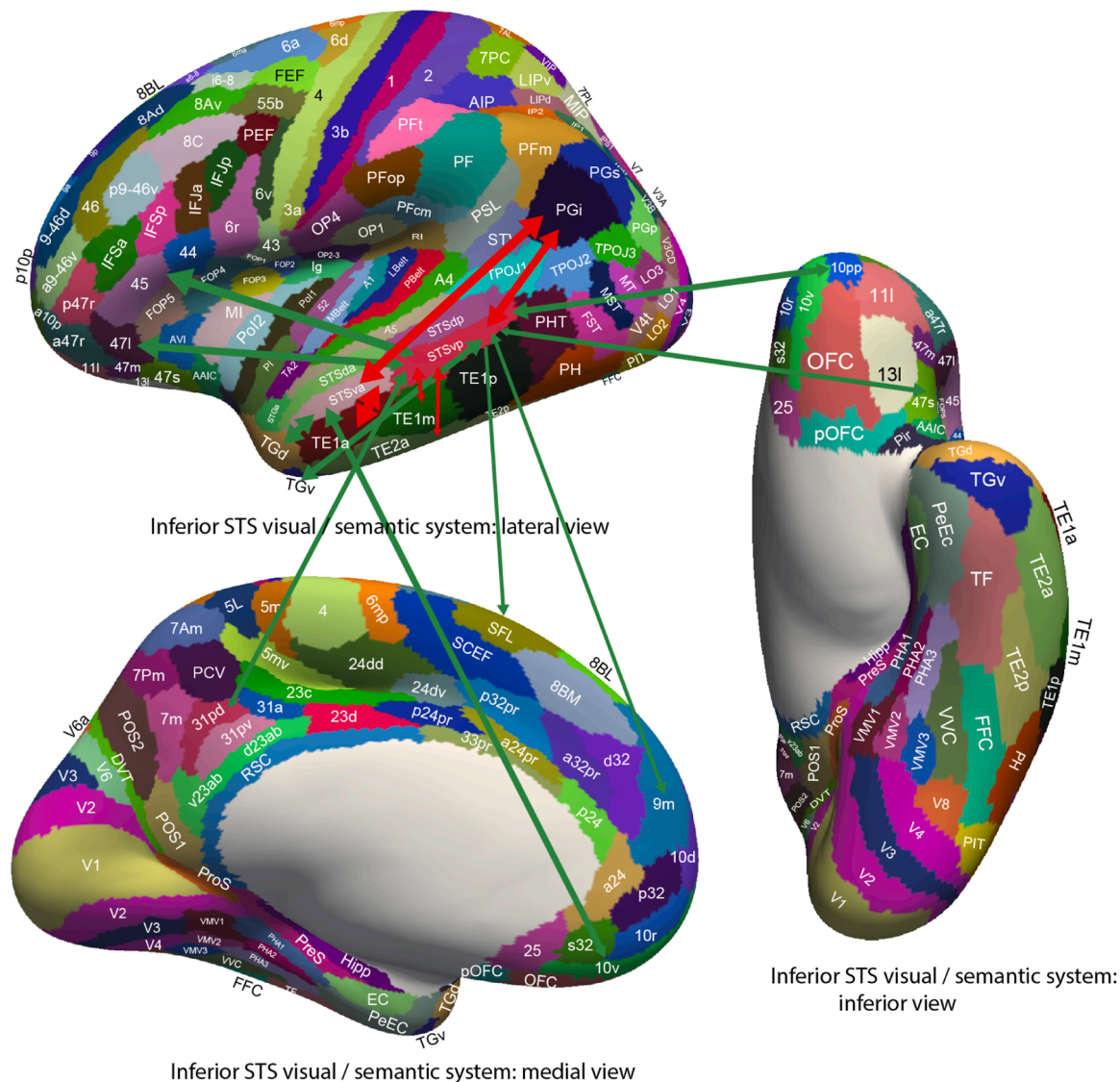
The connectivity maps produced in these investigations can now have function added for some of the visual cortical regions, using activations to faces, places (in fact scenes), body parts, and tools where the activations based on fMRI data from 956 HCP participants have been mapped to the same 360 HCP-MMP cortical regions used for the connectivity maps (Rolls et al., 2024b). This is part of the long-term plan to use the HCP-MMP for linking together investigations performed with different methods, including fMRI resting state functional connectivity and effective connectivity; fMRI task-related activations, functional connectivity, and effective connectivity; MEG task-related activations, functional connectivity, and effective connectivity, etc. The activations showed that faces and body parts strongly selectively activated HCP-MMP region FFC, linking this HCP-MMP region to ventral stream object and face processing; with also activation of lateral parahippocampal TF consistent with this being a route for object and face-related information in the 'What' system to reach the hippocampal memory system (Rolls, 2023a); with also activation of inferior parietal visual regions PGi, PGs and PFm together with TPOJ1 and TPOJ2 consistent with these being parts of the semantic system that represents different properties of objects, that extends from the inferior parietal cortex through temporo-parieto-occipital regions that would have been part of Wernicke's area, through to the anterior temporal lobe and pole regions (Rolls et al., 2022a). (There is of course much evidence that faces activate the fusiform cortex (Kanwisher et al., 1997; Weiner and Grill-Spector, 2013; Kosakowski et al., 2022), but the point here is to map what activates HCP-MMP regions such as FFC.) Body parts also activated TE1p and TE2p, consistent with the evidence that these are the last primarily unimodal regions in the ventrolateral visual cortical stream for building invariant representations of faces and objects (Rolls, 2021d; Rolls et al., 2023f), and with the characterisation of TE2p as a body-specific patch (Hori et al., 2021). Interestingly, the sight of tools activated regions VVC, VMV3 and PHA3, consistent with the gradient of

stimulus size increasing from the lateral FFC towards medial temporal cortex areas such as the parahippocampal gyrus (Malach et al., 2002; Kravitz et al., 2011; 2013; Hori et al., 2021), with the tools often being larger than the objects and faces in the HCP stimulus set (Rolls et al., 2024b). Scenes selectively activated more medially, in ventromedial regions, in the medial parahippocampal gyrus PHA1–3 and the regions immediately posterior to this VMV1–3 and VVC (Rolls et al., 2024b). Consistent with this gradient, very small visual stimuli, words, are represented in the visual word form area more laterally in the fusiform gyrus (Dehaene and Cohen, 2011). The representation of large stimuli such as scenes medially may be associated with more dependence on a wide field of view including some peripheral visual input from outside the fovea (Malach et al., 2002).

A key approach to understanding the operation of the ventrolateral visual cortical stream is that it builds representations of objects and faces by repeated convergence and competitive learning of visual feature combination representations over each of the stages V1, V2, V4, and inferior temporal visual cortex, with slow learning implemented by a

memory trace learning rule to allow the representations to be transform invariant by learning from the slowly changing statistics of the visual inputs provided by the environment, with a model of this VisNet (Wallis and Rolls, 1997; Rolls, 2021d; 2023d). For example, slow learning can allow different views and translations of objects to become associated together because for short periods of a few seconds the same object or face is likely to be being viewed, but with different transforms. There are a number of approaches of this type (Wiskott and Sejnowski, 2002; Wyss et al., 2006; Franzius et al., 2007; Schonfeld and Wiskott, 2015; Weghenkel and Wiskott, 2018). These computations utilise competitive learning, which is biologically plausible because it includes only local synaptic learning rules (Rolls, 2021d, 2023d). In contrast, deep learning approaches to visual object recognition in the brain (Yamins and DiCarlo, 2016; Rajalingham et al., 2018; Zhuang et al., 2021) are biologically implausible because backpropagation of error is required over many cortical regions, and because there is no target in the brain for each output neuron in supervised versions of deep learning (Plebe and Grasso, 2019; Rolls, 2021d, 2023d). Another approach is the proposal

Inferior STS visual / semantic system: lateral view

Inferior STS visual / semantic system: inferior view

Inferior STS visual / semantic system: medial view

Fig. 2. Superior temporal sulcus visual / semantic 'What' stream in especially STSva and STSvp. This stream receives visual input (red arrows) from the anterior inferior temporal cortex regions TE1a, TE1m, TE2a. Visual input (red arrows), probably related to moving objects, faces etc also comes from inferior parietal cortex visual regions PGi and to a lesser extent from PGs and PF. The other effective connectivities (green arrows) of these inferior STS cortex regions are with the temporal pole (TGd and TGv); with the memory-related parts of the posterior cingulate cortex (31pd and 31pv); and with reward-related ventromedial prefrontal cortex (vmPFC, 10 v and 10r) (Rolls et al., 2023a)). STSva and STSvp have connectivity directed towards Broca's area 44 and 45, and related regions (47 l), and to the Superior Frontal Language region (SFL), and with some prefrontal cortex regions including parts of areas 8 and 9 (Rolls et al., 2022a). (After Rolls et al., 2023a).

that important components (like principal components) that can be used to represent large amounts of variance across objects are used to encode objects and faces, and capture for example key measures of differences between faces that can capture face identity (Chang and Tsao, 2017; Hesse and Tsao, 2020; Chang et al., 2021). This approach is not unlike the VisNet approach, but needs a mechanism for learning the key (principal) components for sets of visual stimuli, and then for representing each object by a combination of these, whereas the VisNet approach is that competitive learning in neuronal networks is used to set up neurons that usefully capture the differences between different visual stimuli. The principal components approach also lacks a mechanism to learn invariances.

3. A superior temporal sulcus visual / semantic 'What' stream in especially STSva and STSvp that represents moving objects and faces

Regions STSva and STSvp are ventral bank regions of cortex in the superior temporal sulcus. These regions receive visual input (red arrows in Fig. 2) from the anterior inferior temporal cortex regions TE1a, TE1m, TE2a, where objects and faces are represented. Visual inputs also come from inferior parietal cortex visual regions PGi and to a lesser extent from PGs, PGp and PFm (red arrows in Fig. 2). It is proposed below that these inferior parietal regions introduce inputs related to moving objects, faces etc. The other effective connectivities (green arrows) of these inferior STS cortex regions are with the temporal pole (TGd and TGv, regions involved in semantic representations (Rolls et al., 2022a)); with the memory-related parts of the posterior cingulate cortex (31pd and 31pv (Rolls et al., 2023i)); and with reward-related ventromedial prefrontal cortex (vmPFC, 10 v and 10r, which have strong connectivity with the orbitofrontal cortex (Rolls et al., 2023a). STSva and STSvp have connectivity directed towards Broca's area 44 and 45 and the related region 47 l (Rolls et al., 2022a) and to the Superior Frontal Language region (SFL); and with some prefrontal cortex regions including parts of areas 8 and 9 (Rolls et al., 2022a, 2023d) and the frontal pole (Rolls et al., 2024a).

When recording in the (macaque) inferior temporal visual cortex, visual neurons are often tuned to face identity and respond to stationary visual stimuli (Hasselmo et al., 1989a). In contrast, neurons in the cortex in the superior temporal sulcus may respond to face expression, and/or to moving visual images of the head. The movements encoded can include turning the head away, or closing the eyes, by the same single neuron, and as both break social contact, it has been proposed that these neurons represent information useful for social behaviour, and this of course includes the neurons that respond to face expression (Hasselmo et al., 1989a). The representation of visual object and face motion by these neurons can be quite remarkable, and in object-based coordinates, in that some neurons respond to for example the sight of ventral flexion of the head on the body regardless of whether the head is upright or inverted (Hasselmo et al., 1989b). Other neurons in the cortex in the superior temporal sulcus respond to the sight of body movements such as the sight of a person walking (Perrett et al., 1985b), or to gaze direction (Perrett et al., 1985a). Similarly, in humans face expression and movement can activate regions related to the STS regions (in the middle temporal gyrus) (Critchley et al., 2000), and are just anterior to regions such as TPOJ3 implicated in theory of mind (Schurz et al., 2017; Quesque and Brass, 2019; DiNicola et al., 2020). Theory of mind is a computation that clearly benefits from inputs about face expression and head motion that make or break social contact. In humans, representations of this type could provide part of the basis for the development of systems to interpret the social and emotional significance of such stimuli, including theory of mind (Rolls, 2023d). Consistent with this, PGi and PGs receive inputs from PCV (the precuneus visual area) and 7 m which are regions of medial parietal cortex related to the precuneus (Rolls et al., 2023i), which is implicated in visual and self-referential processing (Cavanna and Trimble, 2006; Freton et al., 2014).

Given that neurons in the cortex in the superior temporal sulcus can respond to visual stimuli that combine both object-based and movement information, we proposed that the cortex in the STS might provide another visual stream (additional to the so called ventral 'what' and dorsal 'where' visual streams (Ungerleider and Mishkin, 1982; Ungerleider and Haxby, 1994)) that combines information from inferior temporal 'what' processing and dorsal stream motion processing (Baylis et al., 1987; Hasselmo et al., 1989a). That concept, of a visual stream in the cortex in the STS for object/face motion processing that includes faces and is used for social perception (Baylis et al., 1987; Hasselmo et al., 1989a), now receives support (Pitcher and Ungerleider, 2021).

In an activation study with faces, places, body parts, and tools using the HCP-MMP atlas, faces did selectively activate some STS regions, but these were primarily in the right hemisphere, and this is consistent with the evidence presented here that the STS regions in the HCP-MMP atlas are involved in face processing, especially in the right hemisphere (Rolls et al., 2024b).

The connectivity in humans of the ventral STS regions is very revealing about where the motion aspects of what is represented in the cortex in the STS comes from. There is major connectivity of the ventral STS regions in humans with the visual parts of the inferior parietal cortex, especially PGi but also to some extent with PGs, PFm and PGp (Figs. 2 and 6) (Rolls et al., 2023a, 2023c). Some of these visual inferior parietal regions have some intraparietal visuo-motor inputs (IP1 and IP2) and connectivity with superior parietal 7Pm, and have connectivity with the spatial visuo-motor (dorsal / anterior) parts of the posterior cingulate cortex (23d, 31a) and not the memory related parts (Rolls et al., 2023c, 2023i). Based on this type of connectivity evidence, it is proposed that the visual inferior parietal cortex regions (PGi, PGs, PFm, PGp) are involved in the computation of representations of moving objects, with the motion information received from the intraparietal cortical regions and area 7, and the object information from the inferior temporal visual cortical areas consistent with the strong connectivity between TE regions and especially PGi shown in Figs. 2 and 6 (Rolls et al., 2023c). More generally, these visual inferior parietal regions are implicated in representing objects in space, as shown by spatial and object-based neglect, simultanagnosia, etc produced by damage to these regions (Vallar and Calzolari, 2018), but also more specifically in functions such as tool use (Kastner et al., 2017; Maravita and Romano, 2018) that may involve computations about the movements of multiple objects in space.

What is revealed by the connectivity studies described here is that there is a very large elongated region extending from the temporal pole (TGd and TGv) through anterior inferior temporal (TE) and ventral STS regions that is highly connected to the inferior parietal cortex visual regions, especially PGi (Fig. 2). This system is involved in the semantic representations of objects, faces etc (based on extensive evidence from fMRI investigations based on categorization of visual words and objects, and auditory words and stories, and on neuropsychological evidence (Milton et al., 2021; Rolls et al., 2022a; Rolls, 2023d)), with the inferior parietal parts contributing especially it is proposed here to the representations of moving objects and faces that is made available in the ventral STS 'What' system, and to the locations of objects in space. Interestingly, the connectivity of the ventral STS cortex visual stream is largely not directly with intraparietal or superior parietal visuo-motor regions, but with the inferior parietal visual regions (Rolls et al., 2023a), which are very greatly expanded in humans compared to macaques.

Apart from its close relation to semantic processing, this inferior bank of the superior temporal sulcus 'What' visual stream also has outputs to the ventromedial prefrontal cortex and lateral orbitofrontal cortex (Fig. 2, (Rolls et al., 2023a; Rolls et al., 2023e)) in which neurons are found that respond to face expression and head movement (Rolls et al., 2006), both important in the functions in emotion and social behavior of the orbitofrontal cortex (Rolls, 2019, 2021a, 2023d, c). This STS 'What' visual stream also has connectivity onwards to hippocampal

memory systems via the posterior cingulate cortex (Fig. 2 (Rolls et al., 2023a; Rolls et al., 2023i)).

4. A ventromedial visual cortical 'where' stream for scene representations

The traditional view has been that there is a ventral 'What' system and a dorsal 'Where' visual system; and that these connect to the hippocampal memory system where combinations of 'what' and 'where' can be formed to implement episodic memory (Ungerleider and Mishkin, 1982; Ungerleider and Haxby, 1994). However, as described in this section, a Ventromedial Visual Cortical 'Where' stream for scene representations has recently been followed with fMRI, MEG, and diffusion tractography (Rolls, 2023a; Rolls et al., 2023a, 2023f) that reaches medial parahippocampal cortex where the parahippocampal scene area is located (Sulpizio et al., 2020; Rolls et al., 2024b), which in turn provides scene inputs to spatial view cells in the hippocampus that indicate which part of a scene is being looked at (Rolls, 2023b, a; Rolls

et al., 2023a; Rolls et al., 2023f). This is thus a 'Where' visual cortical stream. The connectivity in this ventromedial visual cortical stream to be described is new, and follows on from the discovery of scene representations in the parahippocampal cortex and hippocampus in the form of spatial view cells (Rolls et al., 1989, 1997a, 1998; Feigenbaum and Rolls, 1991; Rolls and O'Mara, 1995; Robertson et al., 1998; Georges--François et al., 1999; Rolls and Xiang, 2005; Rolls et al., 2005; Rolls and Xiang, 2006; Rolls, 2023b, a), which was followed by scene-related activations in humans in what was termed the parahippocampal place area (Epstein and Kanwisher, 1998; Epstein and Baker, 2019).

The Ventromedial Visual Cortical 'Where' stream defined by effective connectivity, functional connectivity, and diffusion tractography with fMRI and magnetoencephalography (Rolls et al., 2023a, 2023f) is illustrated in Fig. 3 (see also Fig. 6). In a first level, after V1, V2 has connectivity to ProS (the ProStriate cortex) (and some to DVT, the dorsal transitional visual area), which is where the retrosplenial scene area is located in humans (Sulpizio et al., 2020; Rolls et al., 2024b) (and not in region RSC). (In humans, the occipital place area OPA is located in
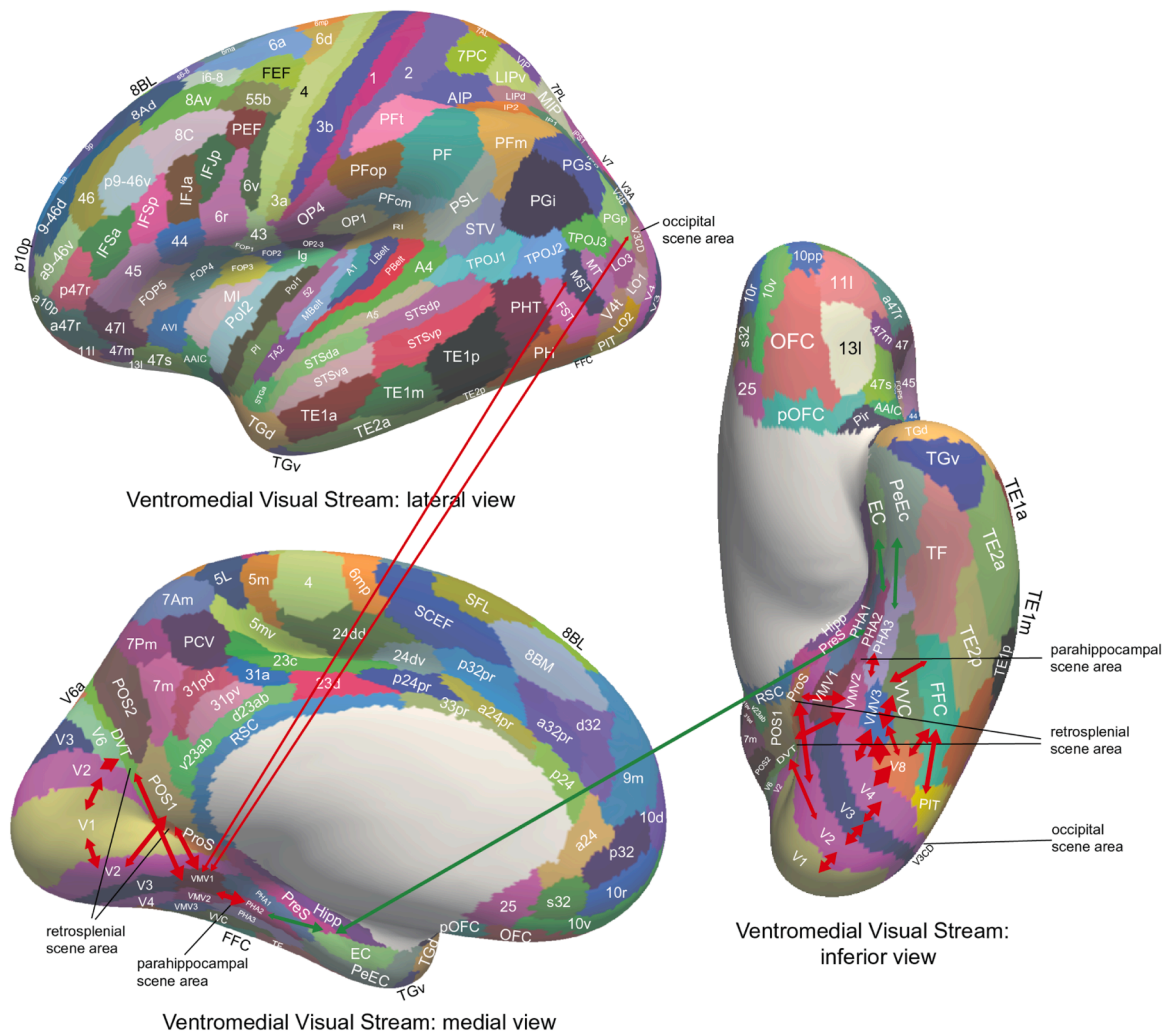
Fig. 3. Effective connectivity of the Ventromedial Visual Cortical 'Where' Stream for scene representations which reaches the parahippocampal gyrus PHA1 – PHA3 regions and the hippocampus. In a first level, after V1, V2 has connectivity to DVT (the dorsal transitional visual area) and ProS (the prostriate cortex) which are where the retrosplenial scene area is located in humans. In a second level, DVT and ProS have connectivity to ventromedial visual regions (VMV1-3 and VVC). These ventromedial visual regions also have effective connectivity from V3CD where the occipital scene area is located, from the nearby inferior parietal PGp region, and from MT, MST etc in the dorsal visual stream. In a third level, the ventromedial visual regions have effective connectivity to the medial parahippocampal regions PHA1-3. The connectivity from PGp to PHA regions is suggested in the text to be involved in idiothetic update of locations in scenes. The medial parahippocampal regions PHA1-3 also have effective connectivity from the ventrolateral stream region FFC (and also from some superior temporal sulcus STS and auditory regions). The parahippocampal scene area is located at the intersection of the ventromedial visual regions (VMV1-3 and VVC) and medial parahippocampal regions PHA1-3. In a fourth level the medial parahippocampal regions PHA1-3 have connectivity to the hippocampal memory system (green arrow). The widths of the lines and the size of the arrowheads indicate the magnitude and direction of the effective connectivity. (After Rolls et al., 2023f).

V3CD, V3B, and IP0 (Sulpizio et al., 2020).) In addition to ProS, region POS1 in the retrosplenial region is also selectively activated by scenes in a much larger sample of 956 HCP participants (Rolls et al., 2024b). In a second level, ProS has connectivity to ventromedial visual regions (VMV1–3 and VVC). These ventromedial visual regions also have effective connectivity from V3CD where the occipital scene area is located, from the nearby inferior parietal PGp region, and from MT, MST etc in the dorsal visual cortical stream (Fig. 3) (Rolls et al., 2023a, 2023f). ProS also has connectivity with POS1, which in turn has connectivity to PHA1–2 (see Fig. 6). In a third level in the hierarchy, the ventromedial visual regions have effective connectivity to the medial parahippocampal regions PHA1–3 (Fig. 3). The connectivity from PGp to PHA regions is suggested to be involved in idiothetic update of locations in scenes (Rolls, 2023b, a; Rolls et al., 2023a; Rolls et al., 2023f). The medial parahippocampal regions PHA1–3 also have some effective connectivity from the ventrolateral stream region FFC (and also from some superior temporal sulcus STS and auditory regions). The parahippocampal scene area is located at the intersection of the ventromedial visual regions (VMV1–3 and VVC) and medial parahippocampal regions PHA1–3 (Sulpizio et al., 2020), and clearly includes PHA1–3 (Rolls et al., 2024b). In a fourth level the medial parahippocampal regions PHA1–3 have connectivity to the hippocampal memory system (Fig. 3, green arrow). The parahippocampal scene area (also known as the parahippocampal place area PPA) extends from VMV regions anteriorly to include PHA regions (corresponding to TH in macaques), based on selective activations to viewing spatial scenes with a large sample size of 956 HCP participants (Rolls et al., 2024b). Spatial view cells are found in these anterior medial parahippocampal (TH) regions (as well as in the hippocampus) in macaques (Rolls et al., 1997a, 1998; Robertson et al., 1998; Georges-François et al., 1999; Rolls and Xiang, 2005; Rolls et al., 2005; Rolls and Xiang, 2006), and are proposed to underlie the spatial computations being performed in scene areas in humans (Rolls, 2023b, d, a). Identification of this as a separate visual pathway is confirmed by cluster and multidimensional scaling analyses based on resting state functional connectivity (Haak and Beckmann, 2018).

Consistent with this connectivity in humans, the retrosplenial scene area is found in ProS and nearby regions, and the parahippocampal scene area in the VMV and medial parahippocampal PHA regions (Sulpizio et al., 2020). ProS also has connectivity to POS1 (Fig. 6), and POS1 is a scene-activated HCP-MMP region (Hori et al., 2021; Rolls et al., 2024b), as are VMV1–3, VVC, and PHA1–3 (Rolls et al., 2024b), providing evidence that these HCP-MMP regions in the ventromedial visual cortical pathway are indeed involved in representing scenes. In humans, it has been suggested (Rolls, 2023b, a) that the Parahippocampal Place Area, PPA, should be thought of as the Parahippocampal Scene Area, PSA, as it responds to viewed scenes not the place where the individual is located (Epstein and Kanwisher, 1998; Epstein, 2005, 2008; Epstein and Julian, 2013; Kamps et al., 2016; Epstein and Baker, 2019; Sulpizio et al., 2020; Natu et al., 2021; Rolls et al., 2024b). Indeed, hippocampal spatial view cells respond to the part of the scene where a macaque is looking, and code for that in allocentric, world-based coordinates that are relatively independent of eye position, head direction, facing direction in the environment, and place where the individual is located (Rolls et al., 1989, 1997a, 1998; Rolls and O'Mara, 1995; Robertson et al., 1998; Georges-François et al., 1999; Rolls, 2023b, a). Neurons with many similar properties that respond to locations "out there" being viewed in space have been reported in macaques by others (Wirth et al., 2017; Mao et al., 2021; Zhu et al., 2023), in marmosets (Piza et al., 2023), and in humans (Tsitsiklis et al., 2020; Donoghue et al., 2023). In addition, some hippocampal neurons have been recorded in humans that respond during navigation towards the location of a particular goal in a virtual environment (Qasim et al., 2019, 2021). Further, in humans some medial temporal lobe neurons reflect the learning of paired associations between views of places, and people or objects (Ison et al., 2015) (just as discovered in macaques (Rolls et al., 2005)), and this implies that neurons coding for views of scenes are

important for human hippocampal function in episodic memory (Rolls and Treves, 2024). Macaque spatial view cells are found not only in the hippocampus, but also in the parahippocampal gyrus (Rolls et al., 1997a, 1998; Robertson et al., 1998; Georges-François et al., 1999; Rolls and Xiang, 2005; Rolls et al., 2005; Rolls and Xiang, 2006; Rolls, 2023b, a). Given this evidence, and the connectivity just summarized, it is proposed that the Parahippocampal Scene Area is a route via which hippocampal spatial view cells receive their information about and selectivity for locations in scenes. This direct route for 'where' information to the hippocampal memory system (Rolls et al., 2022b, 2023a) is complemented by connectivity via the posterior cingulate cortex (Rolls et al., 2023i).

There is evidence that in the hippocampus, spatial view information from this ventromedial visual cortical stream expressed in the firing of hippocampal spatial view neurons can be combined with information about objects received via the ventrolateral visual cortical stream to produce neurons that respond to combinations of objects and viewed spatial locations to implement object-spatial location episodic memory (Rolls et al., 2005; Rolls and Xiang, 2006). Other neurons in the hippocampus respond to combinations of viewed spatial locations and the rewards available at those viewed locations (Rolls and Xiang, 2005) to implement spatial location-reward episodic memory, using it is suggested reward information received via the pathways from the orbitofrontal cortex to the hippocampal system (Huang et al., 2021; Rolls, 2022; Rolls et al., 2022b, 2023e). The neural mechanism that underlies these associations is the highly developed recurrent collateral connection system between hippocampal CA3 cells, which act as an autoassociation or attractor network (Rolls, 1989, 2018; Rolls and Treves, 1994, 2024; Treves and Rolls, 1994; b, 2023d; Rolls et al., 2024c).

This Ventromedial Visual Cortical Stream for 'Where', scene, representations, to reach the hippocampal memory system may seem like a revolutionary proposal, given that previous thinking was that 'where' for hippocampal function was computed in the dorsal visual system leading to the parietal cortex (Ungerleider and Mishkin, 1982; Ungerleider and Haxby, 1994). In contrast, the evidence described here is that 'where' information, about locations in scenes that are encoded by hippocampal spatial view cells, reaches the hippocampus from the Parahippocampal Scene Area in PHA1–3 and VMV1–3, which has much connectivity with early (and medial) ventral visual stream cortical areas. Indeed faces are represented near to the Parahippocampal Scene Area in the fusiform gyrus FFC (Weiner et al., 2017; Pitcher et al., 2019; Natu et al., 2021; Rolls et al., 2024b); ideograms (or logograms) of words are represented just lateral to faces in the visual word form area in the fusiform gyrus (Dehaene et al., 2005; Dehaene and Cohen, 2011; Caffarra et al., 2021; Yeatman and White, 2021); and cortical regions that represent objects are nearby and project forward into the inferior temporal visual cortical areas involved in invariant visual object recognition (Grill-Spector et al., 2006; Rolls, 2021c, d). However, my proposal is that scenes are likely to be represented by combinations of spatially contiguous visual scene features that are computed using competitive learning in the ventromedial visual stream path, with neurons that respond to nearby parts of visual space having overlapping receptive fields so that they become associated together to provide a continuous attractor representation of a whole scene, with the correct topological arrangement because of the statistics of the inputs (Stringer et al., 2005; Rolls et al., 2008; Rolls, 2023d). It is in this way that I propose that visual scene representations represented by spatial view cells are likely to be formed from visual features of the type that are represented in ventral stream visual areas (Rolls, 2023d).

The proposal here is thus that spatial scene, 'where', representations are built in a Ventromedial Visual Cortical 'Where' stream using combinations of visual features of the type present in different parts of scenes, and are used for the key 'Where' input to the hippocampal episodic memory system (Rolls, 2023b, a; Rolls and Treves, 2024).

5. A human dorsal visual cortical stream for 'Where', actions in space, self-motion update, and spatial coordinate transforms

The concept of a dorsal 'Where' stream (Ungerleider and Mishkin, 1982; Ungerleider and Haxby, 1994) was extended by Milner and Goodale to incorporate actions in space (Goodale and Milner, 1992; Milner and Goodale, 1995; Milner, 2017; Gallivan and Goodale, 2018). Consistent with this, neuronal activity and activations in fMRI studies reveal activity related to actions such as reaching and grasping in some intraparietal regions such as MIP, and in area 7 (Gnadt and Andersen, 1988; Andersen, 1995; Andersen et al., 2000; Bisley and Goldberg, 2010; Gerbella et al., 2017; Rizzolatti and Rozzi, 2018; Gamberini et al., 2020; Orban et al., 2021a, 2021b; Passarelli et al., 2021; Urgen and Orban, 2021). A property of the neuronal activity in these dorsal stream regions to the parietal cortex is that there are coordinate transforms from retinal coordinates in V1, to head-centred coordinates in VIP and LIP (Andersen and Mountcastle, 1983; Andersen et al., 1985; Andersen, 1989; Duhamel et al., 1997), and then to world-based (allocentric) coordinates such as a bearing in primate parietal area 7a (Snyder et al., 1998) and the posterior cingulate cortex (Dean and Platt, 2006). These coordinate transforms allow spatial representations such as retinal position to be updated by self-motion of the eyes to represent a direction in head-centred space (Salinas and Abbott, 2001; Salinas and Sejnowski, 2001; Rolls, 2020).

The connectivity of the human dorsal visual system analysed with effective and functional connectivity and tractography is illustrated in Fig. 4 (Rolls et al., 2023a) (see also Fig. 6). Visual information from V1 reaches (partly via V3, V3A and LO3) the MT+ complex regions (FST, LO1, LO2, LO3, MST, MT, PH, V3CD and V4t), and then the intraparietal regions (AIP, LIPd, LIPv, MIP, VIP IP0, IP1 and IP2), and then the area 7 regions (Fig. 4). Connectivity to the inferior parietal cortex region PGp, which in turn has effective connectivity to the parahippocampal scene area in PHA1–3 (Rolls et al., 2023c) is shown. Inputs to this dorsal visual 'Where' stream from ventral stream regions such as FFC and TE2p are shown with dashed lines. It is notable how greatly the inferior parietal cortex regions (PG… and PF…) have expanded in humans to separate the MT+ visual motion regions (e.g. MT, MST, FST) from the intra-parietal (e.g. LIP, VIP, MIP) and superior parietal area 7 regions (Fig. 4).
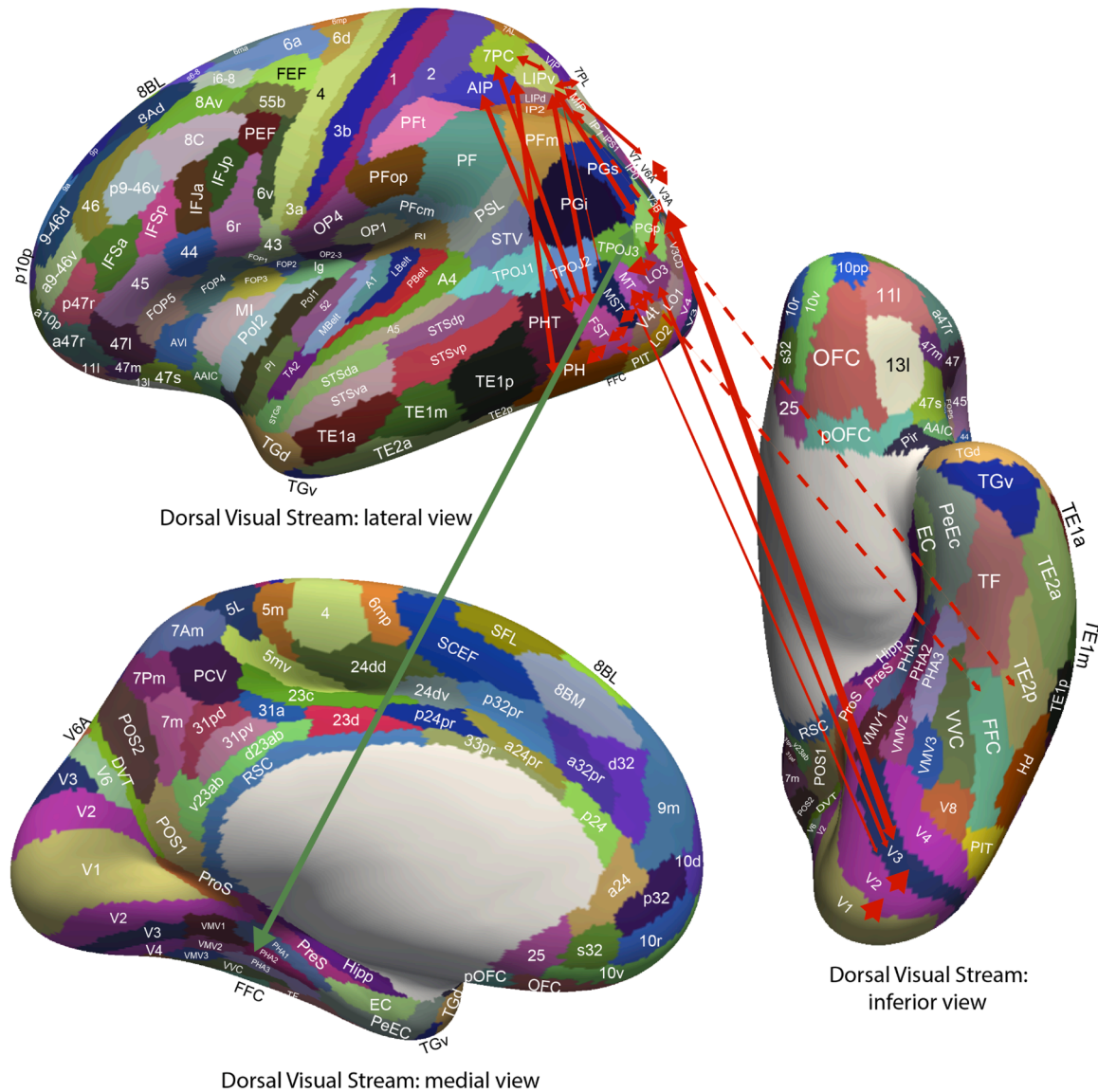
Fig. 4. Effective connectivity of the human Dorsal Visual Cortical 'Where' Stream which reaches (partly via V3, V3A and LO3) the MT+ complex regions (FST, LO1, LO2, LO3, MST, MT, PH, V3CD and V4t), and then the intraparietal regions (AIP, LIPd, LIPv, MIP, VIP IP0, IP1 and IP2) and then the area 7 regions: schematic overview. Connectivity to the inferior parietal cortex region PGp, which in turn has effective connectivity to the parahippocampal scene area in PHA1-3 (Rolls et al., 2023c) is shown. Inputs to this stream from ventral stream regions such as FFC and TE2p are shown with dashed lines. (After Rolls et al., 2023a).

The functions of the dorsal visual pathway in reaching and grasping, and in actions in space, have been described in the literature cited above. Of additional interest here is the 'where' connectivity from the dorsal visual system, especially via inferior parietal region PGp, to the medial parahippocampal regions PHA1–3 which in turn have connectivity with the hippocampal episodic memory system (green arrow in Fig. 4) (Rolls et al., 2023a; Rolls and Treves, 2024).

Interestingly, in an activation study with faces, places, body parts, and tools using the HCP-MMP atlas, even though the visual stimuli were stationary, the body parts and tools did selectively activate some motion-related dorsal stream regions such as FST, LO2 and LO1, consistent with the evidence presented here that the dorsal stream areas in the HCP-MMP atlas are involved in visual motion and visuomotor action processing (Rolls et al., 2024b).

Along the primate dorsal visual system, there is evidence for spatial coordinate transforms from retinal to head-based to world-based, as noted above and as illustrated in Fig. 5 (Rolls, 2020). These coordinate transforms allow spatial representations to be updated by self-motion. It has been shown that the responses of hippocampal and parahippocampal spatial view cells can be updated by self-motion, for example by eye movements (Robertson et al., 1998; Wirth et al., 2017). In line with this evidence, it is therefore proposed that the self-motion update of hippocampal system spatial representations is performed by the dorsal visual system, and communicated to the parahippocampal cortex by the connectivity from inferior parietal PGp shown in Fig. 4 (green arrow).

The representations provided by spatial view cells in the parahippocampal cortex and hippocampus are in allocentric, world-based coordinates (Rolls, 2023b, a), and therefore the idiothetic (self--motion) update provided by the dorsal visual 'where' stream needs to be in world-based coordinates. The process by which it is proposed the required coordinate transforms are performed is illustrated in Fig. 5 (Rolls, 2020). Part of the proposed mechanism is gain modulation (e.g. of retinal position by eye position to transform from retinal to head-based coordinates), which operates essentially by setting up neurons that respond to combinations of retinal position and eye position, and which is a well-described principle of computation in the dorsal visual system (Salinas and Abbott, 1995, 2001, 1996; Pouget and Sejnowski, 1997; Salinas and Sejnowski, 2001). It has been shown that the performance of a gain modulation system can be greatly improved by use of a 'slow' synaptic modification rule that essentially allows different combinations of inputs that correspond to the same spatial location to be associated together (Rolls, 2020), in a way that is analogous to

invariance learning of object representations in the ventral visual system (Rolls, 2021d). Using this combination of gain modulation and slow learning, the series of coordinate transforms shown in Fig. 5 can be successfully learned in a simulation of this aspect of the dorsal visual system (Rolls, 2020).

The summary of these processes for allocentric spatial view representations in the primate including human hippocampal system is that they are built using a feature combination process in a Ventromedial Visual Cortical 'Where' stream, and can be updated for a few minutes when necessary in for example the dark or when the view is obscured during for example navigation (Rolls, 2021b), using the self-motion update into the correct allocentric representation in the dorsal 'Where' visual stream communicated via PGp (Rolls, 2020, 2023b, d, a).

6. Cortical visual streams: synthesis

Fig. 6 provides a schematic overview of the four cortical visual streams described here, to help bring out their differences, and to enable some synthesizing points to be made. It must be remembered that in this figure every connection cannot be shown, and the full connectivity maps are provided elsewhere (Rolls et al., 2023a; 2023c; 2023f).

First, the approach here shows how these cortical visual streams provide inputs to further brain systems, and this goes beyond most previous research. One example is that the human hippocampus can receive for its episodic memory functions, that typically involve associations between 'what' and 'where' events on a particular occasion (Treves and Rolls, 1994; Rolls and Treves, 2024), 'What' inputs about objects and faces from the inferior temporal visual cortex (Rolls, 2021d; 2023d) via lateral parahippocampal gyrus TF, perirhinal cortex, and entorhinal cortex; 'Where' inputs about the location being viewed in a scene as provided by spatial view cells (Rolls, 2023a) from the Ventromedial Cortical Visual Stream via VMV and PHA regions; and information from the dorsal visual stream intraparietal and area 7 regions via inferior parietal PGp. This latter input is proposed to be involved in idiothetic (self-motion) update of spatial view representations when the view is obscured (Rolls, 2023d, a), and it is appropriate for the dorsal visual stream to be involved in this computation, because it performs the coordinate transforms necessary in humans and other primates to compensate for eye position changes to provide a head-based representation, as well as further coordinate transforms (Fig. 5) (Rolls, 2020). A second example is that the inferior temporal visual cortex TE1p and TE2p together provide object and face information to the reward-related medial orbitofrontal cortex (e.g. 13 l), and punishment /
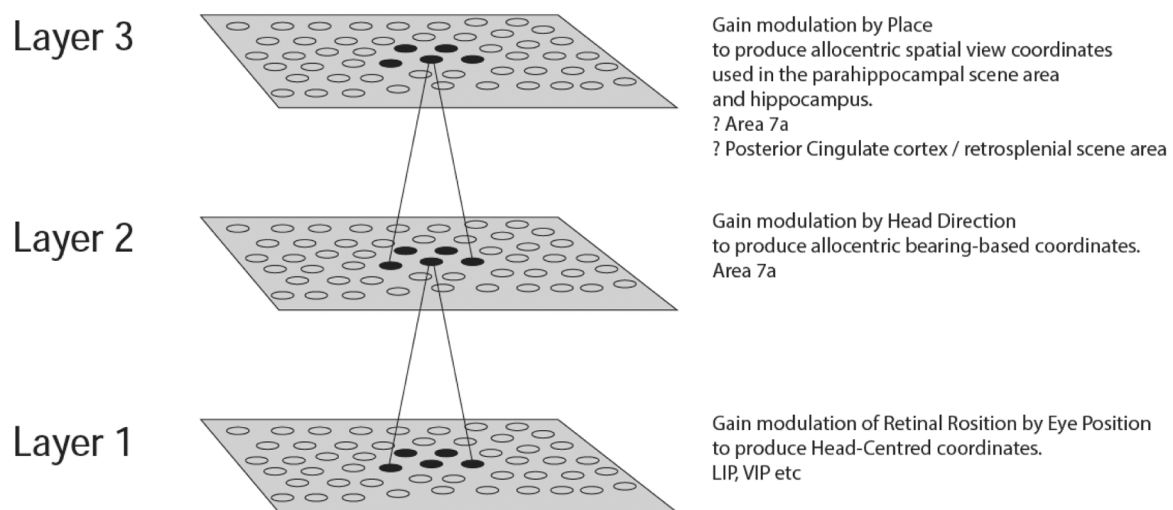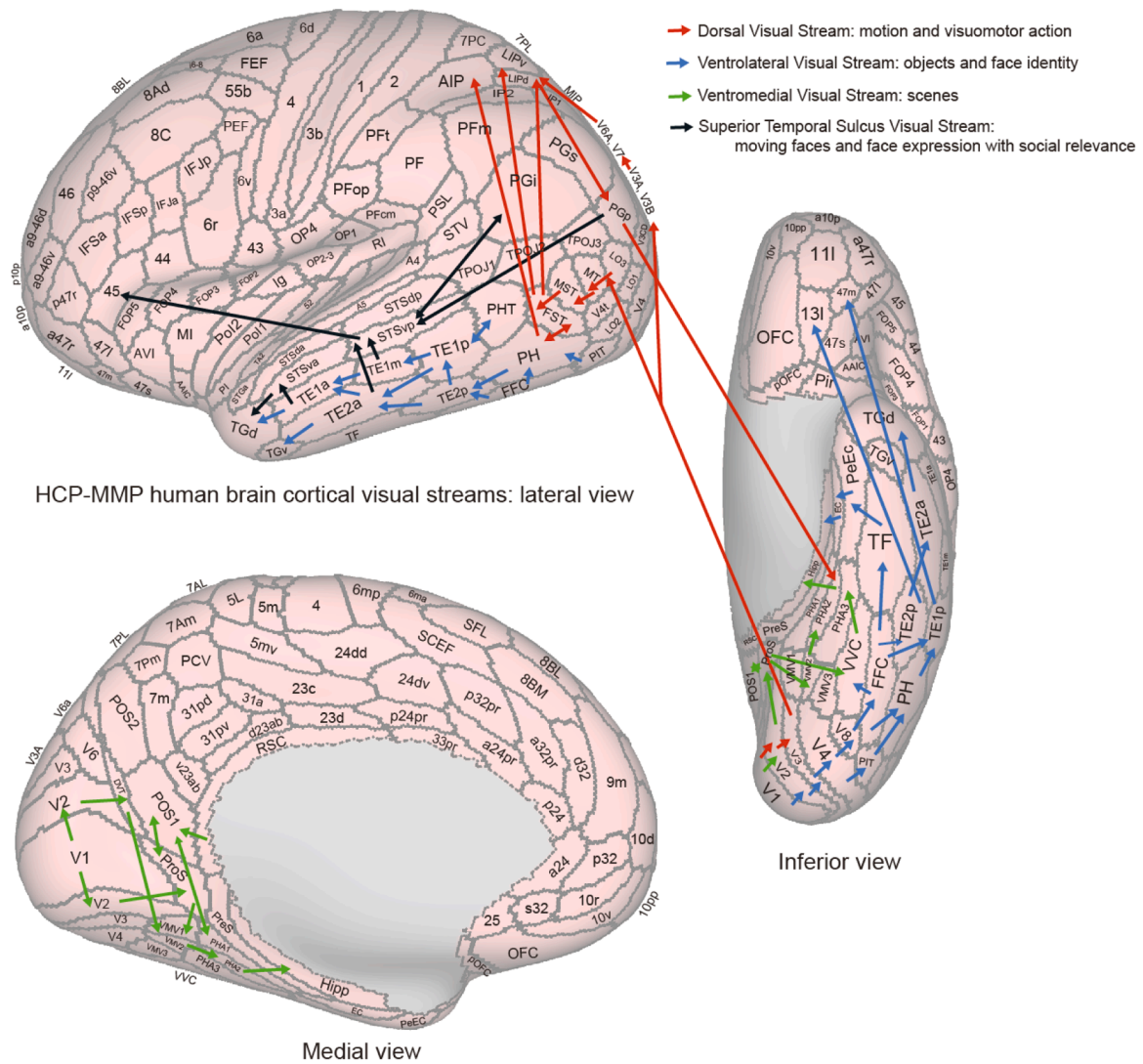

Fig. 5. Coordinate transforms in the dorsal visual system analysed with the VisNetCT model which uses gain modulation supported by a short-term memory trace-based synaptic learning rule (Rolls, 2020). Each neuron in a layer (or cortical area in the hierarchy) receives from neurons in a small region of the preceding layer. (After Rolls, 2020).

Fig. 6. Schematic diagram showing two 'What' and two 'Where' cortical visual streams. The cortical parcellation is the Human Connectome project MultiModal Parcellation (Glasser et al., 2016a), with the HCP figure with the most opened sulci. The VentrolateralCortical Visual Stream (blue), a 'What' stream, connects V1 > V2 > V3 V4 > V8 > FFC > TE1p and TE2p, with the latter the two last mainly visual cortical regions for invariant face and object representation. Beyond that there is connectivity via lateral parahippocampal gyrus TF, perirhinal cortex PeEc and entorhinal cortex EC to provide 'What' inputs to the hippocampus (Hipp). Beyond TE1p and TE2p there is connectivity to semantic regions in the anterior lateral temporal lobe regions TE1m, TE2a, TE1a and then to the temporal pole TGd and TGd. The Superior Temporal Sulcus Visual Cortical Stream (black), a 'What' Stream, in STSvp and STSva receives face and object inputs from ventrolateral visual stream regions in the anterior temporal lobe (TE1a, TE1a, TE2a), and visual motion inputs from inferior parietal PGp which in turn receives inputs from intraparietal regions (e.g. LIPd) and area 7 regions; and also has connectivity with visual inferior parietal PGi. Neurons in this system respond to socially relevant stimuli such as turning the head and eyes to make or break social contact, and face expression. The Dorsal Cortical Visual Stream (red), a 'Where' stream for motion and visuomotor action in space, connects V1> V2 > V3 > LO3 + MT > MST > FST which then connects to intraparietal regions (e.g. LIPd, LIPv, VIP, MIP) and parietal area 7 regions (e.g. 7PC). There is also connectivity V3 > V3A, V3B, V7 > V6A > intraparietal regions. The dorsal visual stream regions have connectivity via inferior parietal PGp to the medial parahippocampal PHA1-3 regions, and may be involved in self-motion update of spatial view representations. The Ventromedial Cortical Visual Stream (green), a 'Where' stream, connects V1 > V2 > the Prostriate region ProS and the Dorsal Visual Transitional region DVT where the Retrosplenial Scene Area is located (Sulpizio et al., 2020) > VMV1-3 and VVC > medial parahippocampal cortex PHA1-3 where the ParaHippocampal Scene or Place Area is located (Sulpizio et al., 2020; Rolls et al., 2024b) > the hippocampus Hipp. This stream provides evidence in primates including humans about where is being viewed in scenes, using spatial view cells (Rolls, 2023a). The full connectivity maps are provided elsewhere (Rolls et al., 2023a, 2023c, 2023f).

non-reward-related lateral orbitofrontal cortex (e.g. 47 m) (Rolls et al., 1996; 2006; 2023e; Rolls, 2023c). A third example is how the STS visual cortical stream has connectivity with multimodal semantic systems in the anterior inferior temporal cortex (TE1a, TE1m, TE2a), temporal pole (TGd and TGv), with area 45 which is part of Broca's area, and with PGi which is an inferior parietal semantic region (Rolls et al., 2022, 2023a, 2023; c; f).

Second, the approach here helps to make it clear how connectivity between the cortical visual streams is involved in what they compute. For example, the STS visual cortical stream contains neurons in

macaques that respond to certain types of objects, face, or body parts that are performing particular movements (such as a head turning away to break social contact, or for the same neuron closing the eyes) (Hasselmo et al., 1989b) or to face expression and gesture also important for social behavior (Hasselmo et al., 1989a), and the connectivity shown in Fig. 6 shows the pathways likely to be involved in humans. The pathways provide object and face-selective information from the Ventrolateral Visual Cortical Stream (TE1a, TE1m and TE2a), and motion information from inferior parietal PGp and PGi. The combination of ventral and dorsal visual stream information has been hypothesized to

be necessary for this computation in the STS visual cortical regions (Baylis et al., 1987), but the pathways described here show which pathways are likely to be involved in humans. Part of the importance of discoveries such as these is that they help to advance understanding of mental disorders, and indeed it has been shown that these STS regions have reduced connectivity with the emotion-related orbitofrontal cortex in people with autism spectrum disorder (Cheng et al., 2015). Many further examples of cross-connections are found in those that are present between the Ventrolateral Cortical Visual 'What' Stream and the Dorsal Visual 'Where' sSream, some of which are evident in Figs. 1–4 but which are shown in detail in the connectivity maps (Ma et al., 2022; Rolls et al., 2022b, 2023a, 2023c). These cross-connections enable some object information to reach the Dorsal Cortical Visual 'Where' Stream, and some information about motion to enter the Ventrolateral Cortical Visual 'What' Stream.

Third, the Ventromedial Visual Cortical Stream has been termed a 'Where' stream here because it leads to parahippocampal and hippocampal spatial view cells that encode where a primate is looking in a scene (Rolls, 2023a). The coordinates are allocentric (Feigenbaum and Rolls, 1991; Georges-François et al., 1999; Rolls, 2023b, a). The Dorsal Cortical Visual Stream leading to the intraparietal and area 7 parietal cortical regions is termed for consistency a 'Where' stream, but it is of course involved in visuomotor actions in space (Milner and Goodale, 1995; Andersen and Cui, 2009; Bisley and Goldberg, 2010; Orban et al., 2021b; Passarelli et al., 2021), with the representation in some parts of the system in egocentric coordinates which are needed for actions in nearby space, and in other parts of the system involving transforms beyond egocentric to allocentric (Snyder et al., 1998), as shown in Fig. 5 (Rolls, 2020).

7. Implications

The Ventromedial Cortical Visual 'Where' Stream providing spatial scene input to the hippocampal episodic memory system is somewhat revolutionary (Rolls, 2023b, a). A concept based on research in rodents is that there are place cells in the hippocampus, that the 'where' spatial representations come from the parietal cortex, and that navigation from place to place is performed by path integration using head direction and self-motion information (Hartley et al., 2014; Bicanski and Burgess, 2018; Edvardsen et al., 2020). However, that may not apply to primates including humans because with the well-developed foveal visual system, many neurons in the hippocampus respond to locations being viewed in scenes (spatial view cells), and correspondingly the human parahippocampal scene area responds to viewed scenes, not the place where the individual is located (Rolls, 2023b, a). In that context, the Ventromedial Cortical 'Where' Visual Stream (Rolls, 2023d, a; Rolls et al., 2023a; Rolls et al., 2023f) is of great interest, because it is likely to build 'where' representations of scenes by using neurons that respond to combinations of features, and then associating the overlapping scene fragments in a continuous attractor network to form a continuous scene representation (Stringer et al., 2005; Rolls et al., 2008; Rolls, 2023a).

The traditional view of the Ventral visual cortical stream is that it is involved in invariant object representation: a 'What' stream (Ungerleider and Mishkin, 1982; Mishkin et al., 1983; Baizer et al., 1991; Ungerleider and Haxby, 1994; Kravitz et al., 2011). One of the fundamental and new points made here is that in addition to a ventrolateral 'What' Visual Cortical Stream leading to the inferior temporal visual cortex (Rolls, 2021d; 2023d), there is a ventromedial 'Where' Visual Cortical Stream. This is a major conceptual revision of the classical view of a Ventral 'What' Visual Cortical stream and a Dorsal 'Where' Visual Cortical stream (Ungerleider and Mishkin, 1982; Mishkin et al., 1983; Baizer et al., 1991; Ungerleider and Haxby, 1994; Kravitz et al., 2011; 2013). Moreover, this is a fundamental advance relevant to understanding hippocampal function, for which the major theory is that the hippocampus combines single event 'What' and 'Where' information (Treves and Rolls, 1994; Rolls and Treves, 2024). The present paper

shows the relevant 'What' and 'Where' pathways for understanding hippocampal function in humans (see Figs. 1 and 3), and that is a fundamental and important conceptual advance. Moreover, many of the new findings are in humans (Ma et al., 2022; Rolls, 2022; Rolls et al., 2022b; Rolls, 2023d; Rolls et al., 2023a; Rolls et al., 2023c, e; Rolls et al., 2023f; Rolls et al., 2023i; Rolls et al., 2024b; Rolls et al., 2024c), and this is important for understanding human brain function and dysfunction, a key issue in neuroscience research.

Another contrast is that in rodents path integration when moving from place to place has been supposed to be implemented in hippocampal and closely related circuitry such as the entorhinal cortex grid cell system (Moser et al., 2017). However, given that in primates including humans the path integration must take into account eye movements, it appears that the path integration is performed using processes such as gain modulation in the dorsal visual stream leading to the parietal cortex, as described above. In this context, the connectivity from the parietal cortex to the parahippocampal cortex in humans is likely to be involved in the self-motion update of locations in a visual scene when in the dark or when the view is obscured (Robertson et al., 1998; Rolls et al., 2023a; 2023c).

Another major implication is that whereas navigation in rodents may be largely from place to place supported by idiothetic update and maintaining the 'cognitive map' (O'Keefe and Nadel, 1978) correctly oriented using visual cues from the environment (Hartley et al., 2014; Bicanski and Burgess, 2018; Edvardsen et al., 2020), in primates including humans navigation may often be closely based on viewed landmarks in scenes, with navigation often performed from viewed landmark to viewed landmark (Rolls, 2021b). This point is emphasised by the fact that humans find it very difficult to navigate accurately in the dark for more than a very few minutes; and that navigation does not normally take place in humans with the eyes closed, but depends on being able to view a scene, which is what is represented by hippocampal spatial view cells (Rolls, 2021b; 2023d, b, a).

The cortical connectivity in humans thus provides a useful framework for appreciating these two aspects of cortical organisation, that a 'Where' stream is ventromedial and feature-based, but can be idiothetically updated by connectivity from a dorsal 'Where / (Rolls et al., 2023f)action' stream in the parietal cortex (Rolls et al., 2023a).

The cortical connectivity also shows that the ventral bank of the superior temporal sulcus (STS) cortex visual stream that represents moving faces and objects has fascinating connectivity with the visual parts of the inferior parietal cortex in a great cortical system that has strong connectivity with language regions in TPOJ1–3, PSL (the Perisylvian Language region) and STV (Rolls et al., 2023a). I propose that the inferior parietal visual regions are important for linking the temporal lobe STS regions into visual motion regions in the intraparietal and superior parietal (area 7) regions. An implication is that the inferior parietal visual regions, PGi, PGs and PFm, contain representations of moving objects, which are important for actions in space, such as tool use, and for representing the spatial relations between several objects that are important in tool use. Interestingly, it is thought that there may be no comparable tool use region in macaques (Kastner et al., 2017). The STS cortical system is indeed of great interest in terms of semantic representations, for the ventral STS cortical components (STSva and STSvp) have strong connectivity with anterior temporal lobe regions (TE1a, TE2a, TE1m) and the temporal pole (TGv and TGd) which are multimodal regions, with somatosensory as well as visual inputs (Rolls et al., 2022; 2023; 2023a, f). There is a corresponding semantic system in the dorsal bank of the STS cortex regions (STSda and STSdp), which have major connectivity with auditory cortical regions, as well as with the TPO and related regions in an area that might correspond to Wernicke's area (Rolls et al., 2022a, 2023a). Both the ventral, visual, STS regions described here, and the dorsal STS regions, are not only semantic, but both have strong connectivity with regions 44, 45 and 47 l, which are Broca's area which is implicated in word production and syntax (Rolls et al., 2022a; Rolls, 2023d). It is of considerable interest

that the last mainly unimodal visual regions in the human ventrolateral visual stream are TE1p and TE2p, so that the whole anterior half of the human temporal lobe, including TE1a, TE2a and TE1m are multimodal semantic regions (Rolls et al., 2022a; 2023f; Rolls, 2023d).

Apart from the outputs of visual processing streams to the hippocampal episodic memory system and to semantic systems, the new research on visual processing streams described here also shows how the two 'What' visual streams have outputs to the orbitofrontal cortex and amygdala (Rolls et al., 2023b, a; Rolls et al., 2023e), brain systems involved in emotion and reward value processing (Rolls, 2014, 2023d, c; Zhang et al., 2024a). The visual inputs about faces and objects can be associated in the primate orbitofrontal cortex with primary reinforcers such as taste and somatosensory inputs to form representations of expected value (Thorpe et al., 1983; Critchley and Rolls, 1996; Rolls et al., 1996; Rolls, 2023d). Other orbitofrontal cortex neurons respond to face expression and head movements important in social behaviour, and are implicated in emotional and social behaviours to these stimuli as shown by the effects of damage to the human orbitofrontal cortex (Hornak et al., 1996, 2003; Rolls, 2021a). Some orbitofrontal cortex neurons respond when an expected reward is not obtained (Thorpe et al., 1983), and are termed "non-reward" or "negative reward prediction error" neurons (Rolls, 2019, 2023c). Consistent with this, the human lateral orbitofrontal cortex is activated in the reversal of a visual discrimination task when reward is no longer received (Kringelbach and Rolls, 2003; Rolls et al., 2020b), and damage to the human orbitofrontal cortex impairs this type of reward reversal learning and accounts for many of the changes in emotion and social behaviour that result (Rolls et al., 1994; Hornak et al., 2004; Fellows, 2011; Rolls, 2021a, 2023c; Zhang et al., 2024a). The responses of different orbitofrontal cortex neurons to expected value, outcome value, and negative reward prediction error are likely to provide key inputs to the dopamine neurons that respond to reward prediction error (Schultz, 2013, 2016a, b, 2017), via pathways through the ventral striatum and/or habenula (Rolls, 2017). The non-reward system in the lateral orbitofrontal cortex that responds to a mismatch between the expected value of a visual stimulus and the outcome value (Thorpe et al., 1983; Rolls, 2019, 2023c) is implicated in emotional behavioural responses to non-reward and thereby in depression (Rolls, 2016b, 2018a, 2019; Rolls et al., 2020a; Zhang et al., 2024a), with activations of the lateral orbitofrontal cortex to not winning related to the severity of depressive symptoms (Xie et al., 2021).

Another implication is the utility of the HCP-MMP atlas in enabling effects found in different studies, for example in connectivity (Rolls et al., 2023a, 2023f) vs activation (Rolls et al., 2024b) studies, to be mapped into the same space. Further, because we analyzed the activations present in every HCP-MMP cortical region, we were able to go beyond describing the activation to a class of stimulus by one or several peaks identified by MNI coordinates (Rolls et al., 2024b). Instead, we demonstrated the extent to which the cortical activations can in a graded way be found in a number of cortical regions, which moreover can extend beyond classical visual cortical regions to semantically related cortical regions such as somatosensory and auditory and orbitofrontal cortex regions depending on the type of the visual stimulus (Rolls et al., 2024b).

I finish by remarking that there are many new concepts described here, and that there is no intention to limit the concepts to just two 'what' and two 'where' visual cortical streams: there are likely to be many further specialised divisions.

Ethical permissions

This is a review paper, and no data were collected for this review paper.

Conflict of interest

The author has no competing interests to declare.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neubiorev.2024.105650.

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