

Distributed Visual–Vestibular Processing in the Cerebral Cortex of Man and Macaque

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Abstract

Recent advances in understanding the neurobiological underpinnings of visual–vestibular interactions underlying self-motion perception are reviewed with an emphasis on comparisons between the macaque and human brains. In both species, several distinct cortical regions have been identified that are active during both visual and vestibular stimulation and in some of these there is clear evidence for sensory integration. Several possible cross-species homologies between cortical regions are identified. A key feature of cortical organization is that the same information is apparently represented in multiple, anatomically diverse cortical regions, suggesting that information about self-motion is used for different purposes in different brain regions.

Keywords

Visual, vestibular, MST, VIP, PIVC, VPS, PIC, CSv

1. Introduction

In daily life, both humans and macaques are constantly on the move. Movement can only be effective if we continuously monitor our location in the external world and our trajectory through it. The principal sensory cues that

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enable us to perceive self-motion are visual and vestibular. In the case of vision, multiple cues are available but we make heavy use of what Gibson (1950) termed optic flow: the orderly, two-dimensional pattern of image motion cast on the retina by our surroundings as we move. Optic flow provides a rich source of information from which can be extracted our instantaneous direction of heading during locomotion (Warren and Hannon, 1988). If additional information about object distance is available for scaling, as it usually is, optic flow can in principle be used to establish the speed at which we are moving. However, the necessary computations are not trivial. During locomotion, we usually want to know about the heading of the whole body but optic flow specifies self-motion only in the coordinates of the eyes. The eyes move relative to the head and the head moves relative to the body. Only if these movements are known and factored in can whole-body heading be established (see for example Lappe *et al.*, 1999). Such information is available but the transformation is complex and may be error-prone. Another limit of visual cues to self-motion is that the retinal image contains not only flow generated by self-motion but also motion due to the movement of the objects around us. Only if these different sources of image motion can be parsed is accurate perception of self-motion possible (Royden and Hildreth, 1996; Warren and Rushton, 2009).

The vestibular system provides complimentary information. It offers several key advantages over vision. First, the vestibular organs, located as they are in the inner ear, provide information about movements of the head directly, eliminating the need to convert from eye-centred to head-centred coordinates and avoiding the errors that arise in so doing. Second, the vestibular signal is uncontaminated by the movement of external objects. On the downside, the mechanics of the vestibular organs are such that they provide information about head accelerations rather than velocities (see Angelaki and Cullen, 2008; Lopez and Blanke, 2011 for recent accounts of the vestibular system). The otoliths respond to the linear accelerations that occur during translational body motion and can specify direction of heading. However, the otolith organs also respond to head tilt relative to gravity, such that otolith signals require further processing to represent head translation (Angelaki *et al.*, 2004; Angelaki and Cullen, 2008). Information about speed of heading can be derived from the same linear acceleration signals but this is only possible when acceleration is non-zero; if we move with a constant direction and speed the vestibular system eventually goes quiet. As in the case of vision, the computations required to establish heading from vestibular signals are not trivial, even when good acceleration signals are available. Computing speed is particularly difficult (see for example Laurens *et al.*, 2017) and large systematic errors can occur.

Because the two systems have different limitations, there is scope for each to compensate for the other's deficiencies. Most fundamentally, (i) vision continues to work when accelerations are too small to provide reliable vestibular

information and (ii) vestibular signals persist when vision is obscured. Most of the time, however, both systems are operative and in these circumstances the two systems provide separate estimates of self-motion that can be combined to provide the best possible overall estimate. Given that both systems are error-prone, the potential for improving perceptual accuracy by cue combination is significant.

The vestibular system also assists vision more directly: at the level of sensory detection. When the head moves, vision is potentially disrupted. When head movements are detected by the vestibular organs, reflexive compensatory movements are initiated that tend to keep the eyes and head stable relative to the external world. An example is the vestibulo-ocular reflex (VOR, e.g., Dieterich & Brandt, 1995) in which head rotation produces a reflexive counter-rotation of the eyes, helping to maintain visual stability. Thus, vestibular cues generate reflexes to reduce unwanted optic flow. Neck proprioception and efference copies of motor signals (von Holst and Mittelstaedt, 1950) also assist.

A full understanding of the sensory processes underlying perception of self-motion requires descriptions and explanations at different levels: behavioural, neurophysiological and computational. The capabilities and limitations of the visual and vestibular systems in perceiving self-motion have been reviewed previously (Andersen *et al.*, 1999; Angelaki and Cullen, 2008; Angelaki *et al.*, 2009; Bremmer, 2005; Cullen, 2012; Dieterich and Brandt, 2015; Fetsch *et al.*, 2013; Harris, 1994). The literature includes attempts to provide computational descriptions of the relevant sensory processes, which are too complex to be understood fully without considering quantitative aspects. In recent years, extensive new evidence has emerged concerning the vestibular response properties of neurons in various disparate regions of the macaque cerebral cortex, with a focus on visual–vestibular interactions. In parallel, data have emerged from the use of functional magnetic resonance imaging (fMRI) concerning the cortical regions involved in visual–vestibular interactions in humans. The present review focuses on the neuroanatomical substrates of those aspects of visual and vestibular processing that are relevant to perception of self-motion. A key aim is to identify commonalities and differences between the two species. This is relevant to the difficulties associated with linking primate physiology to human behaviour: not only are the two endeavours conducted at different levels of explanation but linking them ignores any species differences. Although the fundamentals of detection and subcortical processing of vestibular information may be similar in humans and macaques, this is less likely to be true at the cortical level. A helpful aid to linking physiology and behaviour may be to consider the roles of different cortical regions in the two species and their homologies.

2. Cortical Candidates for Visual–Vestibular Interaction

If visual and vestibular signals are to work together to provide a best estimate of self-motion, they must first be brought together in the same brain regions. Although extensive visual and vestibular processing occurs subcortically, the most likely locations for this to occur are cortical. The nature of the interaction between the two senses has received detailed consideration in recent years. A key concept in multisensory cue combination is that cues from different sensory systems may be combined in a way that is dynamic and depends on the reliability of the cues from moment to moment (Ernst and Banks, 2002; Knill and Pouget, 2004). In the case of visual–vestibular cue combination, Fetsch *et al.* (2009) demonstrated this dynamic quality behaviourally in both macaque and human subjects. Participants made heading judgements that were based on cues from both modalities. The participant was seated in a chair that was moved, by a motion platform, along a straight path with an acceleration–deceleration cycle designed to give good vestibular activity throughout. Participants could not see their environment but instead were presented with an artificial visual scene that simulated linear self-motion having the same acceleration profile. In some trials, the simulated optic flow matched the actual body translation but in others there was a mismatch between the heading directions indicated by the two modalities. It was found that participants made judgements of heading that were intermediate between the two stimulus directions. The reliability of the visual cues was then varied by adding a variable level of noise. In both humans and monkeys, systematically re-weighting towards the vestibular direction occurred as the visual cue became less reliable. Such dynamic cue weighting has also been modeled at the neuronal level. For example, Ohshiro *et al.* (2011) have provided a model of visual–vestibular integration employing divisive normalization. In each neuron, inputs from two or more senses are passed through a compressive input transformation and then summed with different weights. An expansive output non-linearity is applied to the combined signal and the output is divided by the summed activity of all neurons. The normalization model explains several established features of multisensory integration, including effects of cue reliability on neuronal responses (Morgan *et al.*, 2008). Another interesting feature of cue combination relates to the problem of distinguishing self-motion from object-motion. In a behavioural experiment, Dokka *et al.* (2015) trained monkeys to report heading direction from optic flow or inertial movement in the presence of a moving visual object. They found that object motion biases visual heading perception (motion is not accurately parsed) but when vestibular heading cues are present, the bias is substantially reduced.

Where in the brain do interactions such as these take place? In the realm of macaque neurophysiology, this question has been tackled primarily by testing

for vestibular responses in cortical regions already identified as important for the analysis of optic flow. Extensive and detailed data of this kind are now available. In the realm of human fMRI, numerous studies have described visual responses to optic flow but vestibular research is much less advanced. In monkeys, making single-unit recordings during natural vestibular stimulation (passive movement of the animal), although technically demanding, is possible. In humans, fMRI scanning during natural vestibular stimulation is not possible so progress has relied on artificial vestibular stimulation. Two methods are available. The first is galvanic vestibular stimulation, which typically induces a roll sensation, sometimes yaw and pitch rotations, but not linear translation (Fitzpatrick and Day, 2004). The second is caloric vestibular stimulation, which induces a sensation of left-right translational motion or yaw (Dichgans and Brandt, 1978) but cannot be configured to give forward motion, let alone to parametrically vary heading direction. Although several groups have successfully used these methods during fMRI to map the regions of the human brain that are active during vestibular stimulation (Fasold *et al.*, 2002; Frank *et al.*, 2014; Lobel *et al.*, 1998; Smith *et al.*, 2012; Suzuki *et al.*, 2001), measurement of sensitivity to heading direction is not currently possible. Ways forward in the future will perhaps not involve fMRI but will rely on technologies that can be used during natural vestibular stimulation. One possibility is the use of EEG (electroencephalograms), a technique beset with difficulties of interpretation but amenable to improved methods for reliable localization of sources. Otherwise we must await new technical developments in brain imaging, conceivably the refinement of near infrared spectroscopy (NIRS) to a level that permits imaging with a resolution of a few millimetres. Meanwhile, despite the relative paucity of human data, enough is known to begin to ask questions about possible cortical homologies between the macaque and human brains. Here we review the literature by considering each of the main candidate cortical areas in turn. The locations of the cortical regions discussed are shown in Fig. 1.

3. MSTd

In macaques, the earliest and most studied cortical region containing neurons that respond selectively to specific types of optic flow is the area known as MSTd (dorsal portion of the medial superior temporal visual area). This region, occupying part of the upper bank of the superior temporal sulcus, is adjacent to the even more highly studied ‘motion area’ MT (middle temporal area) where motion sensitivity is very strong but thought to be restricted to laminar motion across the receptive field and not to extend to complex flow patterns. Using random-dot patterns that could be configured to simulate natural optic

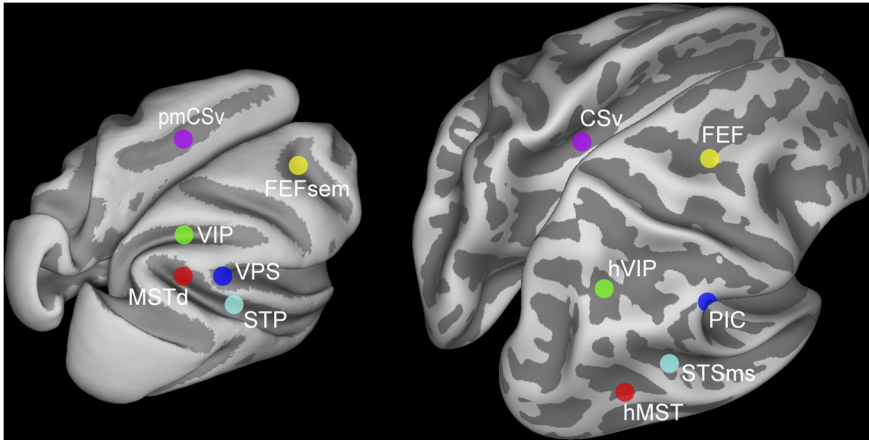


Figure 1. Posterior/lateral view of the cerebral cortex of the macaque (left) and human (right) brains (not to scale). The images are based on structural MRI templates available in CARET (Van Essen *et al.*, 2001) that have been 3D-rendered and partially inflated to expose the sulcal grey matter. In each species, the locations of candidate regions for visual–vestibular interactions are marked. The macaque image is modified from Cottureau *et al.* (2017). The human image shows approximate locations based on fMRI studies cited in the text. In most of the regions marked, both visual and vestibular responses are known to be present but note that vestibular responses have not so far been documented in macaque STP or pmCSv. Possible homologies between species are indicated by common colours. For clarity, cortical regions are marked in one hemisphere only but all exist bilaterally.

flow patterns, particularly rotation (such as occurs during head roll) and expansion (forward translation), early studies of MSTd (Saito *et al.*, 1986; Tanaka and Saito, 1989; Tanaka *et al.*, 1989) identified neurons with very large receptive fields that are sensitive to the directional structure of the local dot motion array within it. Although tuning was typically broad, different neurons showed clear preferences for different flow structures, suggesting that their function is to analyse optic flow and extract a visual estimate of self-motion. It was posited that MSTd receptive fields are constructed by assembling direction-sensitive components manifest as afferents from MT, where receptive fields are smaller. This notion remains valid today (e.g., Mineault *et al.*, 2012), although exactly how such assembly can best be characterized remains a matter of debate. Later studies showed that optic flow preferences form a continuum (Duffy and Wurtz, 1991) that includes spiral motion (Graziano *et al.*, 1994). A property central to the present review is that neurons with a preference for flow patterns that simulate linear translation of the head (e.g., forward, backward, or lateral motion) show a significant degree of tuning for the direction of simulated heading (Duffy and Wurtz, 1995; Page and Duffy, 1999). This makes it likely that MSTd is involved in determining direction of heading during self-motion, a contention supported by the fact that micro-stimulation of

MSTd can bias behavioural judgements of perceived visual heading in awake monkeys (Britten and Van Wezel, 1998) and that reversible inactivation of MSTd impairs visual heading judgements (Gu *et al.*, 2012).

More recently it has been shown that many visually responsive MSTd neurons also respond to vestibular stimulation resulting from whole-body movement in darkness (Duffy, 1998; Gu *et al.*, 2006; Page and Duffy, 2003). Cells are clustered according to vestibular heading preference (Chen *et al.*, 2008), as they are for visual direction (Britten, 1998). The origin of vestibular afferents to MSTd is uncertain but (as is also the case for visual afferents) it is unlikely to be the thalamus or the brainstem. It has been suggested, based on response latency, that vestibular information may reach MSTd by a somewhat circuitous cortical route (Chen *et al.*, 2011a). MSTd may therefore carry highly processed or specialized information. In particular, responses are dominated by velocity rather than acceleration (Fetsch *et al.*, 2010), consistent with processing having occurred to bring vestibular signals into line with visual signals. In addition, vestibular signals in MSTd are specific to translation and are not affected by orientation relative to gravity (Liu and Angelaki, 2009), unlike otolith afferents.

The presence of both visual and vestibular heading signals in the same neurons suggests that MSTd is involved in the process of integrating multisensory cues relevant to perceptual monitoring of self-motion. In the past decade, this suggestion has been confirmed and elaborated; strong evidence now exists for visual–vestibular integration in macaque MSTd. Gu *et al.* (2006) examined visual and vestibular heading tuning in MSTd neurons in detail. They found that many neurons were tuned to direction of heading in both modalities. When they compared the tuning functions across modalities they found two cell classes that they termed ‘congruent’ and ‘opposite’. Congruent cells had similar heading preferences irrespective of whether heading cues were from inertial motion in darkness or from visual stimulation in the absence of inertial movement. Such cells are clearly well placed to integrate visual and vestibular heading cues. Gu *et al.* (2007) compared behavioural judgements of inertial heading in darkness with tuning in MSTd and found that heading discrimination performance correlated well with neuron performance, consistent with the notion that vestibular information feeds into heading perception at the level of MSTd. Opposite cells had opposite heading preferences for the two modalities. The function of these neurons is less clear, but recent computational work suggests that they could be used for dissociating self-motion and object motion (Kim *et al.*, 2016). Takahashi *et al.* (2007) performed similar physiological experiments to those of Gu *et al.* (2006) but used visual and vestibular rotations (about various axes in three dimensions) as well as linear translations. They found that many neurons were selectively sensitive to specific vestibular rotations (most often head roll). However, the preferred

rotation direction was usually opposite to the preferred visual rotation. The paucity of cells with congruent sensitivities would suggest that MSTd does not integrate multi-sensory cues for best perception of rotation but is more likely using vestibular cues to offset confounding effects of head roll when estimating heading. In short, MSTd may be specialized for analyzing heading during locomotion rather than body-motion in general.

Extensive further work has elaborated our understanding of vestibular responses in MSTd and their integration with visual responses. It has proved useful to study the ability of neurons to discriminate fine differences in heading direction in terms of the slope of the tuning function. In congruent cells, visual and vestibular inputs generally sum linearly and this results in a greater slope, and hence greater potential for discrimination (Gu *et al.*, 2008). The same authors confirmed behaviourally that discrimination performance is indeed superior when both cues are present. Most cells have vestibular and visual heading tuning profiles that favour directions either left or right of centre, such that tuning functions often have steep slopes around straight-ahead (Gu *et al.*, 2010). This property could account for the superior behavioural heading discrimination performance found near straight-ahead (Crowell and Banks, 1993). Reliability-based integration of heading cues has been demonstrated in congruent MSTd cells and quantified (Fetsch *et al.*, 2012; Morgan *et al.*, 2008). Further evidence for direct involvement of MSTd in heading perception comes from the finding that behavioural heading judgements can be predicted from the population of congruent MSTd cells (Fetsch *et al.*, 2012), including the dependence of heading percepts on visual cue reliability. Although microstimulation of MSTd can bias visual heading judgements (Britten and Van Wezel, 1998), it has only modest effects on vestibular heading judgements in darkness (Gu *et al.*, 2012). Thus, MSTd is a site for cue integration but with vision taking the lead; presumably vestibular performance in darkness relies more heavily on other cortical areas, such as PIVC or VPS (Chen *et al.*, 2010, 2011b).

Like macaques, humans are able to integrate visual and vestibular cues to self-motion. Heading judgements can be made with reasonable precision based on inertial motion in darkness (Butler *et al.*, 2010; Telford *et al.*, 1995) and also based on visual heading displays without inertial motion (Butler *et al.*, 2010). When visual simulations and inertial motion are combined, the evidence is limited and mixed but performance may be better than that based on either cue alone, suggesting efficient integration, and there is some evidence that the two cues are weighted dynamically in a way that reflects cue reliability (Butler *et al.*, 2010; Fetsch *et al.*, 2009). It is therefore reasonable to suppose that the two species have similar abilities that operate on similar principles. Unsurprisingly, the neuroanatomical and neurophysiological substrates of these abilities are much less well documented in humans than in macaques.

In the case of MSTd, a human homologue has been proposed, referred to as hMST (human MST). A complex of cortical visual areas that are highly responsive to motion is readily identifiable with fMRI, located in lateral occipital cortex. This has been referred to as the MT complex, or hMT+, on the assumption that it corresponds loosely to the group of motion-sensitive areas in the posterior/dorsal portion of the macaque superior temporal cortex, including MT and MSTd. A key property of MSTd neurons is that their receptive fields are large, usually include the fovea and are not restricted to the contralateral visual field but commonly extend across the midline to include part of the ipsilateral field (e.g., Komatsu and Wurtz, 1988). This is not the case in MT, where sensitivity is largely confined to the contralateral hemifield. Applying the fMRI equivalent of this criterion to human cortex, it is possible to divide hMT+ into two zones, a posterior portion where responses are elicited mainly by contralateral moving stimuli and an anterior portion where strong ipsilateral drive also occurs (Dukelow *et al.*, 2001; Huk *et al.*, 2002). By analogy with macaque MT and MSTd, these areas have become known as hMT and hMST.

Various studies have delivered artificial vestibular stimulation (either galvanic or caloric) during fMRI scanning to map the vestibular regions of the human brain (e.g., Bucher *et al.*, 1998; Lobel *et al.*, 1998; Stephan *et al.*, 2005). Galvanic vestibular stimulation (GVS) involves passing a controlled current between two electrodes located over the mastoid bones behind the two ears, to stimulate the eighth cranial (vestibulocochlear) nerve that carries signals from the inner ear to the brainstem (Fitzpatrick and Day, 2004). Caloric vestibular stimulation, on the other hand, involves inducing a temperature differential between the two ears with warm and/or cold water irrigation, inducing endolymph flow primarily in the horizontal canals and thus causing an imbalance in neural activity (Gernandt, 1949; Barnes, 1995). Studies employing these methods reveal a prominent region of activity in and around the posterior insula, widely regarded as the homologue of macaque parieto-insular vestibular cortex (PIVC) and given the same name. Various other vestibular hotspots have also been identified (see particularly Stephan *et al.*, 2005) but lateral occipital cortex is not prominent among them, although vestibular activity in the vicinity of MT+ is apparent in the data of Bense *et al.* (2001) and Fasold *et al.* (2002). In a study specifically targeted at hMT+, Smith *et al.* (2012) localised hMT and hMST in their participants with the method of Huk *et al.* (2002) and then delivered galvanic vestibular stimulation during fMRI in darkness. They were careful to control for somatosensory activity arising from the electrode site (where a tingling sensation is typically experienced), a precaution lacking in some earlier studies. When regions of interest were defined corresponding to hMT and hMST and activity within each region was averaged, vestibular activity was clearly seen in hMST but no such activity

was found in hMT. Thus, the activity previously seen in MT+ arises entirely in hMST. Smith *et al.* observed that vestibular activity was not spread evenly throughout hMST but was consistently confined to an anterior portion of it. This confirms earlier suspicions, based mainly on knowledge of macaque cortex rather than human fMRI data, that hMST is not a single visual area but contains at least two subregions, only one of which exhibits vestibular responsiveness. Smith *et al.* (2012) referred to the two areas as hMSTa and hMSTp (anterior and posterior).

The mere presence of vestibular activity in hMSTa does not reveal the nature of the interactions with visual signals that occur there. Indeed, it does not necessarily indicate that the two signals interact at all. A few studies have presented visual and vestibular stimuli together during scanning and documented the brain regions that are responsive (Della-Justina *et al.*, 2015; Deuschländer *et al.*, 2002). However, demonstrating and characterizing interactions between the two signals with imaging techniques is extremely difficult because inertial motion cannot be used and the scope for parametrically manipulating artificial vestibular stimulation is extremely limited. Ideally, one would wish to vary vestibular heading direction and study interactions with simulated visual heading, as has been done in macaques. This is simply not possible with current techniques. Nonetheless, an attempt to quantitatively assess visual–vestibular interactions has been made by Billington and Smith (2015). In this study, galvanic vestibular stimulation was applied while the participant lay supine in an MRI scanner and the resulting head roll sensation was measured psychophysically by nulling it with simulated visual roll. Once the magnitude of visual motion needed for nulling was known, it was used in fMRI experiments in which simulated vestibular and visual roll cues of equal magnitude were presented together, either in the same direction, so that they were experienced as summed, or in opposite directions, so that they cancelled and no roll was experienced. The two combinations elicited about equally strong responses in hMSTa, showing that hMSTa activity reflects the physical stimulus, not the perceptual outcome which was very different in the two cases. Two recent caloric vestibular stimulation studies (Frank *et al.*, 2014; Roberts *et al.*, in press) have also failed to find a difference in hMST response magnitude between congruent and opposite motion, although the use of stimuli that were not matched for motion magnitude across the two senses limits the sensitivity of such analyses. Using multi-voxel pattern analysis, Billington and Smith (2015) were able to predict, or classify, the stimuli based on the responses they elicited in hMSTa, suggesting that congruent and opposite stimulus combinations drive different neuronal populations, at least to some extent. This raises the possibility that two distinct neuron populations exist, tuned for the congruent and opposite directions of roll and potentially used for estimating and discounting head roll signals, respectively. However, roll is a rotation and

given that macaque MSTd neurons mainly have opposite rather than congruent rotation preferences (Takahashi *et al.*, 2007), an alternative interpretation could be that decoding is possible because one stimulus drives opposite cells and the other drives only neurons that are indifferent to the cross-modal direction relationship: decoding requires only that the two conditions activate non-identical neuron populations. Whether neurons with congruent or opposite preferences for translation (heading) exist in hMSTa is unknown.

Taken together, the results of human fMRI studies and macaque neurophysiology are consistent with a homology between a portion (MSTd) of macaque MST and a portion (hMSTa) of human hMST, both of which receive vestibular as well as visual afferents. However the exact correspondence, if one exists, between subregions of macaque and human MST is extremely uncertain. Most fundamentally, the composition of hMST in terms of subregions is uncertain and so comparison between its subregions and those of macaque MST (and perhaps neighbouring areas such as FST) is, for the moment, precluded. At least two attempts have been made to refine the composition of hMT+. The first (Amano *et al.*, 2009) used retinotopic mapping and identified two maps of the contralateral hemifield that were referred to as TO-1 and TO-2. The authors did not make an empirical comparison with the above hMT/hMST distinction but they speculated that TO-1 corresponds to hMT. TO-2, located broadly where hMST is expected, bordered TO-1, had a mirror-image field map with receptive field size estimates similar to TO-1 and a shared foveal representation with TO-1. These properties are suggestive of a homology not with MSTd but instead with the lateral/ventral subdivision of macaque MST, MSTl (also called MSTv). The location of any MSTd homologue is therefore left open. In such a scheme, it would be expected to lie adjacent to TO-2 but the very large receptive fields of macaque MSTd make it unlikely that a human homologue could be located with retinotopic mapping. Using similar retinotopic mapping methodology, Kolster *et al.* (2010) described four visual areas arranged in a pinwheel arrangement with a shared foveal representation. Using labels from the macaque literature, they refer to them as MT/V5, pMSTv, pV4t and pFST. The first two likely correspond to TO-1 and TO-2 respectively. The arrangement is similar to that demonstrated by the same group with fMRI in macaques (Kolster *et al.*, 2009). Use of the same methods in both species is invaluable in testing homologies and, in this instance, suggests strong correspondence between the two species but, unfortunately for our purposes, this does not extend to MSTd. The use of structural MRI markers for MT+ has not so far shed any further light: the only study to attempt this shows a high level of variability in the overlap between structural (based on estimates of myelin concentrations) and functional MRI definitions (Large *et al.*, 2016).

To summarize a rather complex situation, there are good reasons to believe that some kind of macaque-human homology exists in relation to MT. The fact

that hMT does not respond during galvanic stimulation (Smith *et al.*, 2012) and macaque MT neurons do not respond during inertial motion (Chowdhury *et al.*, 2009) is consistent with this proposed homology. There are also some grounds to postulate a homology in relation to MSTl (MSTv). It is plausible that one also exists in relation to MSTd. TO-2 is immediately anterior to TO-1 (hMT) suggesting that TO-2 might correspond to hMSTp of Smith *et al.* (2012). hMSTa, where vestibular activity is found, is immediately anterior to hMSTp and such a location is plausible for an MSTd homolog. Such an arrangement would apparently leave human MSTd without the border with MT that is described in the macaque literature (Desimone and Ungerleider, 1986) but that border is at the representation of the far periphery of the visual field and might become evident with a sufficiently large visual stimulus. Currently an MSTd–hMSTa homology is a good guess but may prove incorrect.

4. VIP/hVIP

The macaque ventral intraparietal area, VIP (Colby *et al.*, 1993), is a polysensory area in the fundus of the intraparietal sulcus that encodes visual, vestibular, auditory and somatosensory stimuli. It is particularly sensitive to visual stimuli located near the observer in depth (Bremmer *et al.*, 2013; Colby *et al.*, 1993; Yang *et al.*, 2011) and to air puffs on the face (Avillac *et al.*, 2005), suggesting that it may be specialised for encoding nearby objects such as reach targets and/or obstacles during locomotion. There is evidence not only for visual–vestibular integration (discussed below), but also for visual–auditory (Schlack *et al.*, 2005) and visual–somatosensory (Avillac *et al.*, 2007) integration.

Most VIP neurons respond well to at least one type of optic flow (Bremmer *et al.*, 2002a; Schaafsma and Duysens, 1996), some preferring expansion or contraction, some rotation and some translation. Of those that prefer expansion, most are sensitive to heading direction, indexed by the location of the focus of expansion. As in MSTd, they are quite broadly tuned, but selective enough to support perceptual heading judgements (Zhang and Britten, 2010). Indeed, responses to optic flow in VIP appear similar to those in MSTd in most respects (Chen *et al.*, 2011a). VIP is connected with MST (Boussaoud *et al.*, 1990), which may be a key source of visual input and account for the similarity of its visual response properties, although response latencies are similar in the two areas consistent with parallel inputs from some other source (Chen *et al.*, 2011c).

There is strong evidence for visual–vestibular integration in macaque VIP. Vestibular drive was first demonstrated in VIP by Bremmer *et al.* (2002b) who observed that visual and vestibular responses of heading-selective neurons were typically tuned for the same axis of translation. As in MSTd, some

cells have congruent heading preferences and some opposite (Chen *et al.*, 2011c; Schlack *et al.*, 2002). In congruent cells, heading sensitivity is similar to congruent MSTd cells and it is greater during bimodal stimulation than with either stimulus alone, suggesting cue combination (Chen *et al.*, 2013a). As in MSTd, optic flow tuning is in eye-centred coordinates (Chen *et al.*, 2013b). In contrast, vestibular translation tuning is organized within a head-centred reference frame (Chen *et al.*, 2013b). About half of VIP neurons are able to encode heading and eye rotation (including that arising from smooth pursuit eye movements) in a separable manner (Sunkara *et al.*, 2016).

A polysensory cortical region has also been identified in the fundus of the human intraparietal sulcus. The initial description (Bremmer *et al.*, 2001) showed clearly with fMRI that visual, auditory and somatosensory responses are present; vestibular sensitivity was not tested. Strong grounds for considering this region homologous with macaque VIP were claimed and accordingly, we refer to this region as hVIP (human VIP). Selectivity for motion that arises from self-motion is greater in hVIP than in hMST, as evidenced by comparing the response to a large optic flow pattern with that to an array of nine flow patterns, each of which could be interpreted as self-motion but only when considered alone (Wall and Smith, 2008). In hVIP, the response is reduced by about half when the stimulus is made incompatible with self-motion in this way. In hMST, the response is also reduced, but much less. In a recent macaque fMRI study using the same stimuli (Cottureau *et al.*, 2017), a similar pattern of results was found: about 50% reduction in VIP activity for a nine-patch array but a smaller reduction in MSTd, consistent with the VIP homology claimed by Bremmer *et al.* (2001) and also with a homology at the level of MSTd.

The vestibular status of hVIP is less clear than that of hMST. In a study that measured vestibular activity in regions of interest defined with visual localisers (Smith *et al.*, 2012), there was a hint of vestibular activity in visually defined hVIP, but it was small and not significantly different from zero. The region examined was at a very similar location to hVIP of Bremmer *et al.* (2001). Based on this study, vestibular activity is seemingly weaker in hVIP than in macaque VIP, or even absent. A logical possibility is that hVIP has vestibular sensitivity but that this does not include sensitivity to the head roll that dominates the sensation induced by galvanic stimulation. However, a similar weakness of hVIP activity is present in the data of Frank *et al.* (2016a) who used caloric stimulation, which induces primarily a sensation of yaw rotation or horizontal translation. They were able to find vestibular activity in hVIP only when a very liberal threshold was used (personal communication). Although there is thus no clear and direct demonstration of vestibular activity in hVIP, less direct evidence comes from the results of Billington and Smith (2015), described above in connection with hMST. These authors were able to decode congruent and opposite roll motions in hVIP as well as in hMSTa (and

in PIC, see below). Although they did not test vestibular stimulation in darkness, this result shows indirectly that vestibular sensitivity must exist in hVIP. Moreover, vestibular responses have been reported (Stephan *et al.*, 2005) at a location described as inferior parietal lobule but with coordinates that were close to the expected location of hVIP. If this is indeed hVIP, which is uncertain, the elusive nature of hVIP vestibular activity in the only study to use a region-of-interest approach (Smith *et al.*, 2012) is unexplained and possibly due simply to limitations of measurement sensitivity. At best, roll sensitivity is demonstrable; unfortunately it is not possible to configure galvanic stimulation to induce forward motion of the kind needed to test for heading responses. If vestibular heading signals do exist then it becomes likely that they interact with visual signals in the way that occurs in macaque VIP, but this is untested.

Although the convergence of visual, auditory, somatosensory and possibly vestibular responses in hVIP does suggest a homology with macaque VIP, care is needed because the organization of the intraparietal sulcus is different in the two species. In humans, there are several more visual areas in and around the sulcus than are thought to exist in macaques (Orban *et al.*, 2006; Swisher *et al.*, 2007). It remains possible nonetheless that one of them corresponds to VIP and that a straightforward functional homology exists. An additional reason for caution is that the preference for near visual stimuli found in macaque VIP is apparently absent in hVIP (Quinlan and Culham, 2007). The failure to find it could reflect methodological limitations but the same study successfully found such a preference in the parieto-occipital sulcus.

5. VPS/PIC

The core vestibular region in the macaque cerebral cortex is thought to be PIVC. PIVC receives direct vestibular input from the vestibular nuclei through the thalamus and is sometimes regarded as primary vestibular cortex. PIVC is not a likely candidate for visual–vestibular integration because most PIVC neurons do not exhibit excitatory visual responses (Chen *et al.*, 2010). However, immediately posterior to PIVC lies a separate cortical region that, like PIVC, responds to both rotations and translations in darkness. This region is distinguishable from PIVC in that it also responds well to optic flow (Chen *et al.*, 2011b). These authors refer to this area as VPS (visual posterior Sylvian) but in earlier literature (e.g., Guldin *et al.*, 1992) it was called the parieto-temporal association area T3. It is strongly connected with PIVC, from which it presumably receives vestibular signals, and also receives a projection from MSTd, a likely source of optic flow signals (Guldin and Grüsser, 1998). Many VPS neurons respond selectively to heading direction in both modalities. As in MSTd and VIP, their preferred translation axes usually align between the two modalities and both congruent and opposite heading preferences are found.

However, opposite preferences strongly dominate. Consequently, VPS may prove to be a key site for some forms of visual–vestibular interactions but perhaps not for optimizing perception of self-motion trajectory.

PIVC has the same status in humans, with direct subcortical vestibular inputs recently characterised in detail (Kirsch *et al.*, 2016). Moreover, a likely human homolog of VPS has been identified in humans (Frank *et al.*, 2014; Frank *et al.*, 2016a). Several imaging studies had previously identified visual responses at a location very close to PIVC, so close that sometimes such responses were misinterpreted as visual responses in PIVC itself. The region was named PIC (posterior insular cortex) by Sunaert *et al.* (1999) based on responsiveness to visual motion. Confirmation that PIVC and PIC are distinct comes from a recent diffusion tensor imaging study (Wirth *et al.*, *subm.*) showing different connectivity patterns: PIC exhibits predominant connectivity to superior temporal sulcus (STS), to the supramarginal gyrus, and to the intraparietal cortex, whereas PIVC exhibits predominant connectivity to areas in the anterior insula and precuneus. It was recently shown that engaging in a visual task enhances visual activity in PIC compared to passive viewing of the same stimuli (Frank *et al.*, 2016b). It has also recently become clear that PIC responds to vestibular stimuli. Frank *et al.* (2014) identified PIC with a visual localiser and then sought vestibular responses within it by delivering caloric vestibular stimulation during fMRI scanning. They found robust vestibular responses in near-darkness, as well as responses to optic flow in the absence of vestibular stimulation. Both stimuli were then presented together in two arrangements: caloric stimulation usually causes left-right movement sensations and they therefore added visual left-right flow. Combining the two stimuli in either congruent or opposite directions yielded responses of similar magnitude. Although opposite motion gave slightly larger responses, as would be predicted if there was a preponderance of opposite cells as in VPS, the difference was not significant. However, Billington and Smith (2015) were able to decode congruent and opposite visual–vestibular roll combinations in PIC, suggesting orderly visual–vestibular interactions. Thus far, the evidence for a homology between VPS and PIC is encouraging.

6. FEFsem

One further cortical area in macaques has been shown to contain multisensory visual–vestibular neurons like those in MSTd and VIP that show tuned responses and matched preferences: FEFsem, the division of the frontal eye fields associated with the control of smooth pursuit eye movements. Many FEFsem cells show significant heading sensitivity in both modalities and again, both congruent and opposite heading preferences are present (Gu *et al.*, 2016). Given that FEFsem is regarded as having oculomotor rather than

perceptual functions, it is likely that visual–vestibular interactions exist in the region for motor rather than perceptual purposes. More specifically, Gu *et al.* (2016) suggest that FEFsem may play a prominent role in coordinating volitional eye movements during self-motion.

The existence of human frontal eye fields is well established and has been confirmed with fMRI, although human FEF has been studied (e.g., Corbetta *et al.*, 1998; Kimmig *et al.*, 2001; Luna *et al.*, 1998) and compared to macaque FEF (Koyama *et al.*, 2004) mainly in the context of saccades rather than smooth pursuit. It has however been shown to be active during smooth pursuit (Tanabe *et al.*, 2002). Direct comparison between activations associated with saccades and pursuit have been made (Petit *et al.*, 1997), suggesting that pursuit is associated with more ventral locations of activation in the FEF. However, Berman *et al.* (1999) point to a high overlap in the patterns of activations evoked by saccades and pursuit. Differences in the results of these two studies could be related to the frequency of small ‘catch-up’ saccades evoked during pursuit, which serve to re-centre the fovea on the pursuit target (Haller *et al.*, 2008). Kimmig *et al.* (2008) compared fMRI activations during passive viewing of a moving single dot with activation when subjects pursued a single dot. Appropriate contrasts compared the oculomotor, sensory and combined effects on fMRI activation in the FEF, the supplementary eye fields (SEF), posterior parietal cortex (PPC), MSTd, and primary visual cortex (V1). Combined visual–motor stimulation led to the most pronounced activations in all of these areas. In summary, there is some support for a subdivision of the human frontal eye fields in the control of saccadic and smooth pursuit eye movements. However, this evidence is not particularly strong. Vestibular activity in human FEF has been reported in fMRI studies involving artificial vestibular stimulation (Bense *et al.*, 2001, Stephan *et al.*, 2005), although this activity could be related to the reflexive eye movements that are induced by vestibular stimulation, rather than to the analysis of self-motion. Responses to visual motion have been observed in FEF (e.g., Frank *et al.*, 2016b) but specificity for self-motion has not been documented. It is thus uncertain whether human FEF performs highly developed visual–vestibular interactions akin to those that have been observed in macaque FEFsem.

7. CSv

In the human cortex, a new focus of self-motion processing has recently emerged (Wall and Smith, 2008): the cingulate sulcus visual area (CSv). This region responds well to optic flow stimuli but not to random motion (Antal *et al.*, 2008), with one study claiming that it is actually suppressed by random motion and also by static visual stimuli (Pitzalis *et al.*, 2013a). Indeed, even with an optimal optic flow stimulus, the excitatory response is quite small as

measured with fMRI. The strongest responses are obtained with dynamically changing optic flow, such as a stimulus that cycles through spiral space from expansion to rotation and back (Wall and Smith, 2008) or a heading stimulus in which the direction of heading is continuously changing (Furlan *et al.*, 2014). Responses to unchanging flow such as continuous expansion or continuous horizontal translation are dramatically smaller in CSv. Despite the weakness of the response in comparison to, say, hMST or hVIP, CSv has a striking feature. When the paradigm of replacing optic flow with an array of optic flow patches is applied (see hVIP above), the response in CSv is almost completely abolished (Wall and Smith, 2008; Cardin and Smith, 2010). An array of optic flow patches is apparently met with the same indifference as random motion, the feature the two have in common being that neither indicates that self-motion is occurring. Other areas (hVIP, hV6 and to a limited extent hMST) show signs of this behaviour but CSv shows it much more strongly than any other area examined and, if the interpretation is correct, CSv is therefore much more sensitive to whether a given motion stimulus arises from self-motion.

In addition to these visual responses, compelling vestibular activity has been demonstrated in CSv with artificial vestibular stimuli applied in conjunction with fMRI (Smith *et al.*, 2012). CSv is therefore potentially a site of visual–vestibular interaction. Interestingly, however, the evidence for interaction, such as it is, is negative. Attempts to decode congruent and opposite visual–vestibular combinations (Billington and Smith, 2015) show a complete failure to do so in CSv, despite good success in hMST, hVIP and PIC in the same study. Thus CSv is undoubtedly bi-sensory in humans but evidence for integration of signals is so far lacking. A recent study of the connectivity of CSv (Smith *et al.*, in press) has revealed strong connectivity with nearby cingulate motor areas and also with more distal motor areas including the supplementary motor area. Connectivity with sensory cortex is relatively weak, although PIC and hVIP both emerge as possible sources of sensory afferents. This, together with the near-silence of CSv in the presence of visual motion that does not reflect self-motion, suggests that the role of CSv may be to feed information about self-motion into the motor system. The apparent lack of integration could indicate that disparate sensory signals are merely marshalled for that purpose, rather than integrated, in CSv. There is no particular reason to think that activity in CSv influences conscious perception, although it is possible. There are parallels here with hV6 (see below), which also probably has the primary role of guiding action, but quite different parts of the motor system are involved in the two cases.

Macaque neurophysiology has not yet identified a counterpart of CSv. Neurophysiological exploration of the cingulate cortex in general has been limited, at least partly because of the technical difficulty of recording so deep in the brain without causing damage. A few studies have reported visual activity in

posterior cingulate regions that could possibly correspond to CSv (Dean *et al.*, 2004; Olson *et al.*, 1993). One study (Guldin *et al.*, 1992; see also Guldin and Grüsser, 1998) has identified a vestibular cingulate region in squirrel monkey. It is possible that this region also has visual sensitivity and constitutes a squirrel monkey counterpart of CSv but this is far from certain. Very recently, the use of fMRI in macaques has tentatively identified a macaque homologue of CSv (Cottureau *et al.*, 2017). In this study, the 1-patch and 9-patch stimuli of Wall and Smith (2008) were presented to fixating monkeys during fMRI and the responses contrasted. A quite similar set of cortical regions emerged to that seen in humans, including differential activity in a small region of the cingulate sulcus that the authors refer to as pmCSv (putative macaque CSv). As in humans, the response in this region to a large changing flow field is reduced almost to zero when the stimulus is replaced by an array of changing flow stimuli. Whether pmCSv also possesses vestibular sensitivity is unknown; to the best of our knowledge no macaque fMRI studies have used vestibular stimulation. Uniquely among the cortical areas reviewed here, human work is more advanced than macaque in the case of CSv.

8. STP/STSms

In macaques, a superior temporal polysensory area (STP) has been identified where neurons may respond to visual, auditory and somatosensory stimuli (Bruce *et al.*, 1981; Hikosaka *et al.*, 1988). It is connected with MST (Bous-saoud *et al.*, 1990) and many neurons respond well to optic flow, often with a clear preference, most commonly for expansion (Anderson and Siegel, 1999). However visual heading sensitivity in STP neurons has not received the detailed treatment accorded to MSTd, VIP and VPS. In humans, a polysensory region has been identified in the superior temporal sulcus (STS) that may well be homologous with macaque STP (Beauchamp *et al.*, 2004, 2008). It responds to visual, auditory and tactile stimuli and is referred to by Beauchamp's group as STSms (STS multisensory).

Macaque STP, although certainly multisensory, is not known as a vestibular area. However, human STSms responds strongly to artificial vestibular stimulation (Smith *et al.*, 2012) and appears to be well connected to PIVC and PIC (Wirth *et al.*, *subm.*). Responses to optic flow are sometimes seen but are more elusive, suggesting that vestibular inputs may be stronger than visual. In humans, STSms is therefore a potential site of visual–vestibular interaction. It is not known whether macaque STP has vestibular inputs that have been overlooked or, alternatively, whether their absence reflects a species difference.

9. Mono-Sensory Areas Involved in Encoding Self-Motion

Two further cortical regions are known to be responsive to sensory cues to self-motion but apparently do not receive both visual and vestibular afferents. The first is PIVC, already discussed. PIVC is well documented in primates and is prominent in almost every human imaging study that involves artificial vestibular stimulation. It is a core vestibular area and it is likely that there is a broad homology between macaque and human. However, it does not exhibit excitatory responses to visual stimuli in either species and so it cannot be considered a site of visual–vestibular integration. Indeed, imaging studies suggest that visual stimulation causes neural suppression in human PIVC (Brandt *et al.*, 1998; Frank *et al.*, 2016a) and recently it has been shown that when participants perform a visual-motion tracking task, suppression in PIVC scales with the demands of the task (Frank *et al.*, 2016b). These findings are consistent with generalized and attention-dependent suppressive competition between the two senses.

The second and less obvious region in this category is V6, located in the parieto-occipital sulcus (POS). Earlier neurophysiological work had identified visual responses in this vicinity but macaque V6 was fully characterised relatively late in the history of visual neuroscience. It forms a discrete retinotopically organised visual region with high sensitivity to moving stimuli and strong direction selectivity on the anterior bank of the sulcus (Galletti *et al.*, 1991, 1999). Human V6, located on the posterior bank of the POS but thought to be functionally homologous because of its sensory properties, is also retinotopically organised. Like its macaque counterpart (Colby *et al.*, 1988), it emphasises the peripheral visual field and it requires wide-field stimulation for optimal activation (Pitzalis *et al.*, 2006). Like many motion-sensitive cortical regions it is more responsive to coherent motion than to motion noise (Pitzalis *et al.*, 2010) and indeed is part of a much smaller set of regions (the others being VIP, CSv and PIC) that are more responsive to wide-field optic flow than to an array of optic flow patches (Cardin and Smith, 2010). Human V6 responds well to large expanding, rotating and spiralling optic flow patterns but also responds well to translation (Pitzalis *et al.*, 2013a). The sensitivity of macaque V6 neurons to optic flow stimuli has been examined only recently. Most cells respond well to optic flow and are selective for heading direction, much like those found in MSTd and VIP (Fan *et al.*, 2015). Overall, there is a very good case for a homology between macaque and human V6. A key shared property contributing to this view is that V6, uniquely among cortical visual areas specialised for encoding optic flow, does not respond to vestibular stimulation in either species. Macaque V6 neurons do not respond during inertial motion in darkness even though they mostly respond well to optic flow (Fan *et al.*, 2015) while galvanic vestibular stimulation does not elicit activity in human

V6 (Smith *et al.*, 2012). Unless something important has been missed, V6 is not a site of visual–vestibular integration in either species. It is apparently a purely visual area that is maximally sensitive to stimuli in near space (Quinlan and Culham, 2007) and it is sensitive to the stereoscopic depth structure (only useful for nearby stimuli) of optic flow (Cardin and Smith, 2011). It may therefore process self-motion in order to aid perception of objects (Pitzalis *et al.*, 2013b), rather than to facilitate perception of the self-motion itself. Its location, close to parietal regions concerned with motor functions such as reaching and pointing, suggests that it may feed visual information about nearby objects into the motor system, either for reaching or for object-avoidance during locomotion, probably via adjacent area V6A (Galletti *et al.*, 1996; Pitzalis *et al.*, 2013c).

10. Why so Many Cortical Regions?

It might be expected that a single cortical area specialised for visual–vestibular integration would be sufficient to account for self-motion perception, but it is apparent from the above discussion that there are at least four such areas in both the macaque and human brains. A possible interpretation is that these areas are specialised for different purposes, in which case we would expect this to be reflected in different response properties. However, at least in macaque, a number of response properties that have been examined appear to be rather similar across areas. Heading tuning is similar in MSTd, VIP, PIVC and VPS and this is true for visual, vestibular and combined stimulation (Chen *et al.*, 2011a, 2011b, 2013a). A few identifiable differences exist, however. The simplest lies in the relative dominance of the two senses in each area. In MSTd, visual responses are stronger than vestibular. In VPS, vestibular responses are stronger and in VIP they are relatively balanced. Another difference lies in the frame of reference in which vestibular signals are encoded. In MSTd, vestibular heading tuning, measured in the coordinates of the external world, is influenced by head-on-body position, such that most MSTd neurons signal vestibular heading in a head-centred reference frame (Fetsch *et al.*, 2007). In VIP, vestibular heading tuning is affected by neither eye nor head position, such that heading is represented in body-centred (or perhaps world-centred) coordinates (Chen *et al.* 2013c; Zhang *et al.*, 2004). Arguably, therefore, some aspects of processing are more evolved in VIP than in MSTd. VIP is also more multisensory than MSTd, showing somatosensory and auditory responses that appear to be absent in MSTd. Another difference among areas involves the dynamics of vestibular heading signals. Whereas PIVC neurons show response dynamics that primarily reflect acceleration of the head, MSTd neurons predominantly represent velocity, with VIP being intermediate (Chen *et al.*, 2011a). However, the differences in vestibular dynamics between

these cortical areas are modest compared to the substantial transformation that occurs from otolith afferents to the vestibular nucleus (Laurens *et al.*, 2017).

An interesting recent discovery is that MSTd and VIP differ in terms of the effect of inactivation on heading perception. When MSTd is reversibly inactivated with muscimol, visual heading judgements are substantially affected but vestibular heading sensitivity is only modestly disrupted (Gu *et al.*, 2012), suggesting that MSTd may play a greater role in visual heading perception (see also Britten and Van Wezel, 1998). Surprisingly, perhaps, inactivation of VIP results in neither visual nor vestibular heading perception deficits (Chen *et al.*, 2016), despite the fact that VIP neurons show much stronger choice-related activity than MSTd neurons (Chen *et al.*, 2013a). This suggests that VIP may not be involved in perception of heading *per se*, and may be consistent with the view that VIP is more concerned with obstacles and objects in near-space, for motor rather than perceptual purposes. The strongest effects of inactivation on vestibular heading perception have been found in area PIVC (Chen *et al.*, 2016).

While the existing literature from macaque studies suggests some functional differences between areas, a complete understanding of the respective roles of these cortical areas in self-motion perception remains elusive. This may result, at least in part, from our incomplete understanding of how neural representations of self-motion account for object motion, as well as eye and head movements of the observer. These present substantial computational challenges, and it seems likely that self-motion signals need to be combined with other sensory and motor signals, in a variety of ways, to generate representations of self-motion that are robust in natural environments.

In humans, less information is available about differences between areas. Sensitivity to optic flow structure has been demonstrated in hMST with fMRI adaptation (Wall *et al.*, 2008) but no fMRI studies have so far addressed heading tuning in this or any other area. hMST is more responsive to visual than vestibular stimuli, as in macaques, but this is also true in hVIP (Smith *et al.*, 2012) whereas in macaques the balance is more even. Limited data on the pathways connecting the various visual/vestibular areas are available from recent studies on the connectivity of CSv (Smith *et al.*, in press) and PIC/PIVC (Wirth *et al.*, *subm.*). The former study suggests that CSv is strongly connected with PIC and hVIP and that these two areas are therefore likely sources of visual and vestibular afferents. Area hV6 is an additional likely source of visual information. The latter study suggests that PIC is more connected to visual and posterior parietal areas, whereas PIVC shows connectivity that is more pronounced in anterior insula and premotor cortex. Beyond this, little is known.

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