Multimodal integration for the representation of space in the posterior parietal cortex

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SUMMARY

The posterior parietal cortex has long been considered an 'association' area that combines information from different sensory modalities to form a cognitive representation of space. However, until recently little has been known about the neural mechanisms responsible for this important cognitive process. Recent experiments from the author's laboratory indicate that visual, somatosensory, auditory and vestibular signals are combined in areas LIP and 7a of the posterior parietal cortex. The integration of these signals can represent the locations of stimuli with respect to the observer and within the environment. Area MSTd combines visual motion signals, similar to those generated during an observer's movement through the environment, with eye-movement and vestibular signals. This integration appears to play a role in specifying the path on which the observer is moving. All three cortical areas combine different modalities into common spatial frames by using a gain-field mechanism. The spatial representations in areas LIP and 7a appear to be important for specifying the locations of targets for actions such as eye movements or reaching; the spatial representation within area MSTd appears to be important for navigation and the perceptual stability of motion signals.

1. INTRODUCTION

The posterior parietal cortex and the hippocampus are areas of the brain considered synonymous with spatial cognition. The classic studies of O'Keefe & Nadel (1978) and their colleagues demonstrated cells in the hippocampus of rats selective for places in the environment. Given the amazing spatial properties of these cells, these authors proposed that the hippocampus contained a cognitive map of space. Likewise, lesions to the posterior parietal cortex of humans and non-human primates produce severe deficits in spatial perception. Thus the posterior parietal cortex has been considered essential for the perception of space. In primates the posterior parietal cortex projects to the presubiculum and parahippocampal gyrus and thus there are strong and rather direct connections between these areas. The loss of spatial memories after lesion of the posterior parietal cortex suggests that these memories are laid down there, with the aid of the hippocampus. In rats the posterior parietal cortex contains cells with properties similar to those of cells found in the hippocampus; this observation again suggests that these two structures play an intimate and associated role in the construction of spatial cognition. In this paper, data on how space is processed in the posterior parietal cortex in the macaque monkey are reviewed. An understanding of the spatial role of the parietal areas, when combined with new data that are emerging from studies of the monkey hippocampus (Uno *et al*. 1993; Satoshi *et al*. 1995; Rolls & Omara

1995), will help in understanding the roles these two structures play in spatial cognition. Likewise, the comparison of primates with rats will determine what spatial functions are similar or dissimilar between the two species.

The posterior parietal cortex lies between the visual, auditory and somatosensory areas of the cortex and has long been envisioned as an area 'associating' these different modalities to form a unified, multimodal impression of space. How this is accomplished has not been appreciated until recently. This paper shows that these different modalities are brought together in a very systematic fashion, using multiplicative gain functions to combine different modalities including vision, audition, somatosensation (neck proprioception), eye position, eye movement, and vestibular information. The gain mechanism for combining these signals forms a distributed representation of space across populations of posterior parietal neurones. This distributed representation has the interesting feature that it can be used to construct multiple frames of reference, which can then be used by other parts of the brain.

2. CORTICAL AREAS

The posterior parietal cortex contains a large number of cortical areas, but this review will concentrate on three: area 7a, the lateral intraparietal area (LIP) and the medial superior temporal area (MST). Although these areas have diverse functions and use a

Phil. Trans. R. Soc. Lond. B (1997) **352**, 1421–1428
Printed in Great Britain

1421

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variety of sensory modalities, they have in common the ability to process information about spatial relations. One of the best-understood posterior parietal areas is area LIP, which plays a direct role in the processing of saccadic eye movements. This area has strong anatomical connections to other saccade centres (Lynch *et al*. 1985; Asanuma *et al*. 1985; Blatt *et al*. 1990), the neurones have presaccadic responses (Andersen & Gnadt 1989; Mountcastle *et al*. 1975; Andersen *et al*. 1987) and electrical stimulation of the area evokes saccadic eye movements (Shibutani *et al*. 1984; Kurylo & Skavenski 1987; Thier & Andersen 1996). Area MST has neurones selective for complex patterns of motion, including 'optical flow' motion produced during self-motion, and many of its cells are also activated by vestibular stimuli and during smooth pursuit eye movements (Sakata *et al*. 1985; Tanaka *et al*. 1986; Duffy & Wurtz 1991; Graziano *et al*. 1994; Newsome *et al*. 1988; Thier & Ericksen 1992; Bradley *et al*. 1996). This constellation of inputs suggests that it is important for navigation using motion information. This area may also play a more general role in the perception of patterns of motion (Graziano *et al*. 1994; Geesaman & Andersen 1996) and their stable localization in space during eye and head movements (Bradley *et al*. 1996). Area 7a is also a largely visual area, but also has connections with areas of the cortex associated with the highest cognitive functions, including structures associated with the hippocampus (Andersen *et al*. 1990). Although adjacent to area LIP, area 7a does not appear to play a direct role in saccades (Barash *et al*. 1991*a*). Unlike LIP, which has relatively smaller and contralateral visual receptive fields (Blatt *et al*. 1990), area 7a has large, bilateral fields (Motter & Mountcastle 1981). Area 7a, similar to area MST, has cells sensitive to vestibular inputs. All of the areas listed above are strongly interconnected via corticocortical projections. As will be seen in this review, one of the likely consequences of this interconnectivity is that even areas like LIP and MST, which seem on the surface to be a unimodal visual areas, can reveal their multimodal nature when probed with the right set of tasks.

3. REPRESENTATION OF SPACE
(*a*) *Combining visual and eye-position signals*

Areas 7a and LIP receive a convergence of visual and eye-position signals (Andersen & Mountcastle 1981; Andersen *et al*. 1985); this convergence produces cells with retinal receptive fields that are modulated by the orbital position of the eyes. This modulation produces a 'gain field' because the eye position determines the gain of the visual response. To represent the location of a visual target with respect to the head requires a combining of both eye- and head-position information. One might imagine that an area representing space in a head-centred reference frame would have receptive fields that are anchored in space with respect to the head. The cells in LIP and 7a do not appear to use a head-anchored encoding scheme. Although each neurone receives both necessary input signals, its response for head-centred stimulus location

is ambiguous at a single-cell level, because its activity can be varied by changing either the eye position or the retinal location of the stimulus. However, the activity across a population of cells with different eye-position and retinal-position sensitivities will have a unique pattern of firing for each head-centred location. Thus the code of head-centred location in the posterior parietal cortex can be carried as a distributed, population code. When neural networks are trained to transform retinal signals into head-centred coordinates by using eye position signals, the middle layer 'cells' that are responsible for the transformation develop gain fields similar to those of the cells found in the parietal cortex (Zipser & Andersen 1988). This model shows that the gain-field mechanism can be used to code head-centred spatial locations, and that this representation occurs naturally for learning coordinate transformations.

(*b*) *Head position*

A knowledge of the orientation of the head with respect to the body is required for coding locations of stimuli in body-centred coordinates. It has recently been shown that approximately half of the 7a and LIP cells that have eye-gain fields also have gain fields for the head (Brotchie *et al*. 1995). Monkeys were trained to orient their direction of gaze with either head movements or eye movements. Interestingly, the eye- and head-gain fields were found to be the same for individual cells; this result indicates that the modulation of the visual signals is a function of gaze direction, independent of whether the head or the eyes are used to direct gaze.

Three possible sources for the head position signal are an efference copy of the command to move the head, a vestibular signal generated by the head movement, and a neck proprioceptive signal generated by the change in the orientation of the head on the body. It was found that even when the head was moved passively to different orientations the head-gain fields were still present (Brotchie *et al*. 1995). Thus efference copy is not the only source of the head-position signal. To test the possible involvement of vestibular signals, the animal's entire body was rotated in a vestibular chair. In this experiment the head remained at the same orientation on the body, but the direction of gaze was shifted by rotating the animal. Rotations were performed in the dark, to remove visual landmarks and optic flow cues. Twenty-eight per cent of cells tested in this manner exhibited vestibularly derived head-gain fields (Snyder *et al*. 1997). In a second experiment, designed to test for proprioceptive (somatosensory) cues, the animal's body was rotated under the head, with the head fixed relative to the world. In this case there is no vestibular cue, only a neck proprioceptive cue. Forty-nine per cent of cells tested in this paradigm showed proprioceptive gain fields (Snyder *et al*. 1997). A third test was run in which cells were tested for both proprioceptive and vestibular gain fields. Of 17 cells with gain fields, none had gain modulation for both signals; eight were proprioceptive only and the remaining nine were vestibular only. This is an important result: it indicates that two potential coordinate

frames are segregated at a single-cell level. Proprioceptive signals provide information about the location of the head relative to the body and thus can code locations in a body-centred coordinate frame. Vestibular signals indicate the location of the head in space and thus can participate in coding locations in world-centred coordinates. It would be difficult to interpret the presence of both neck proprioceptive and vestibular signals for single parietal neurones; the finding that they do not co-occur fits well with the above scenario. Moreover, the cells with neck proprioceptive signals were found in LIP and the cells with vestibular signals were found in 7a, suggesting that these two areas represent space in different coordinate frames. Area LIP is strongly connected to oculomotor and motor areas and thus a body-centred representation makes good sense in terms of motor control. On the other hand, area 7a projects to the presubiculum and parahippocampal gyrus. Recordings in rats and monkeys have suggested that cells in the hippocampal formation carry information related to place in the world; a world-centred coordinate coding in area 7a is consistent with these observations.

An additional effect was found in the course of these experiments. Some cells showed no gain fields in the vestibular experiment when the monkey was rotated in the dark. However, if the animal was rotated in the light and then tested in the dark, some neurones were found to have gain fields. This finding suggests that memory of the locations of landmarks in the room, or optic flow generated by the movement, was used to produce the gain fields. This result is of course reminiscent of 'place fields' in the hippocampus of the rat: these also use landmarks in the environment to encode the location of the animal.

(c) *Combining auditory and visual information*

When a bird sings we perceive the source of the song and the image of the bird as spatially coincident. The multimodal perception of space occurs so effortlessly that we do not recognize what a formidable task it is to bring auditory and visual stimuli into the same coordinate frame. Visual information arrives in the cortex in the coordinates of the retina (eye); auditory stimulus locations are computed into a head-centred reference frame by using intraural time, intraural intensity, and spectral cues arriving at the two ears. How auditory signals are combined with visual signals in the posterior parietal cortex, with special emphasis on how the mismatch in coordinate frames of the two modalities is resolved, has been investigated.

Until recently area LIP was believed to be strictly a visual area involved in processing saccadic eye movements to visual targets. It was recently examined whether LIP would also play a role in processing saccades to auditory targets. It was found that when a monkey is required to memorize the location of an auditory target in the dark, and then make a saccade to it after a delay, neurones in area LIP are active during the presentation of the auditory stimulus, and during the delay period. The LIP cells are multimodal

in this task, and the auditory and visual response direction preferences are usually the same; these results suggest that the auditory and visual receptive fields and memory fields overlap one another.

In the experiments outlined above, the animal was fixating straight ahead with its head oriented in the same direction; as a result, the eye and head coordinate frames are aligned and cannot be distinguished. To determine the coordinate frame of the auditory signals in LIP, the auditory fields were mapped with the animal fixating in different directions with respect to the head (Stricanne *et al.* 1996). In these conditions the eye and head coordinate frames are moved apart. The animals performed saccades in darkness to the remembered locations of auditory sounds, and the activity was measured in the delay period between the offset of the sound and offset of the fixation light triggering the saccade. Forty-four per cent of the auditory-responding cells in LIP were found to code the auditory location in eye-centred coordinates during the delay period; in other words, these auditory memory fields actually moved with the eyes. Thirty-three per cent of the cells coded in head-centred coordinates and the remaining 23% were intermediate between the two coordinate frames. Cells of all three types also had gain fields for the eye. The occurrence of cells with eye-centric auditory fields and eye-gain fields suggests that at least this group of LIP neurones shares a common, distributed representation for both auditory and visual signals.

The co-occurrence of head, eye and intermediate coordinate frames also suggests that area LIP is at the source of, or participates in, the transformation from head- to eye-centred coordinates. Further bolstering this view is the finding that all three types of cell are also gain-modulated by eye position. Modelling experiments from the author's laboratory have shown that eye-gain fields can also accomplish the transformation of coordinates from head- to eye-centred; that is, in the opposite direction to the previous examples mentioned above (Xing *et al.* 1995).

(i) *Dynamic integration of auditory and visual signals*

The finding of auditory responses in LIP is quite novel. In early studies Hyvärinen (1982) and Mountcastle *et al.* (1975) tested posterior parietal neurones with auditory stimuli and found no response. Because area LIP had not been described at that time it is possible that the neurones tested were outside LIP. In the early phases of experiments in LIP neurones were also tested with auditory stimuli and no response was found (R. A. Andersen, unpublished observation). On the other hand, several authors (Koch & Fuster 1989; Sakata *et al.* 1973; Seal *et al.* 1983) have reported auditory responses for neurones in the posterior parietal cortex. These responses were found only when the auditory stimuli were cues for movement. These observations prompted a re-examination of the auditory responsiveness of LIP neurones in two conditions; when the auditory stimuli were irrelevant to the animal, and when they were the targets of eye movements.

Recordings were made from LIP neurones during presentation of auditory and visual stimuli in animals trained to fixate a fixation point for their reward and ignore the presentation of these stimuli (Linden *et al*. 1996). LIP neurones were very responsive to the visual stimuli and absolutely unresponsive to the auditory stimuli. This shows that area LIP is a 'default' visual area. The auditory responsiveness seen in the previous experiments with an auditory memory saccade task could result from training the animals; alternatively, auditory signals could be switched into area LIP when the animals are required to use them for planning saccades. These two possibilities are currently being tested. If the latter, switching operation turns out to be the case, this switching may be required to use area LIP to transform auditory signals into eye-movement coordinates. This model would propose that area LIP is 'multimodal' in a dynamic sense, being auditory only when an auditory saccade is required. This switch would be much more absolute than previously reported attentional phenomenon. Attentional modulation typically changes the gain of sensory responses (Maunsell 1995; Desimone & Duncan 1995), but with the responses still present, and is rarely changed by more than half. The proposed switch would be essentially all-or-nothing. In other words, the decision to make a saccade to an auditory target switches auditory signals into LIP.

If such a gating mechanism for auditory signals is found, it poses the interesting question of why LIP would need to keep out auditory signals so absolutely, except under conditions where the animal requires these signals for saccades. In addition, what is the neural mechanism that can account for such an absolute gating? Finally, will non-spatial, cognitive signals also have gated access to LIP for particular eye movements? For instance, if during driving I wonder if there is enough petrol to get home, I will make a saccade to foveate the petrol gauge. Perhaps LIP receives many signals from numerous parts of the brain for particular, learned eye movement behaviours. The simultaneous input of all these signals may overwhelm the LIP machinery, requiring dynamic switching of specific signals based on the particular task at hand. Moreover, gain mechanisms may be learned for transforming coordinates under a variety of conditions; limiting the 'pathways' into LIP to only a few at a time may allow very specific learning for making the correct coordinate transformations.

(*d*) *Stabilization of motion signals: integration of retinal motion stimuli with eye pursuit and head pursuit*

The brain needs to take into account moving as well as static stimuli when forming stable representations of space. This problem is particularly acute when using optical flow signals for navigation. As outlined below, smooth movements of the eyes during locomotion generate motion signals on the retinas that must be subtracted from the motion signals due to translation in space to determine the path of movement. Human subjects perform this task effortlessly. Another

important task is to perceive accurately the locations of motions in the world during eye movements; for instance, the world moves on our retinas when the eyes move yet we perceive the world as stationary and not moving. Whether these two perceptual consequences of integration of retinal motion and extraretinal signals use the same or different neural pathways is not known and will be discussed in more detail below. However, it is now clear that cells of area MSTd, which are sensitive to motion stimuli, shift their tuning properties spatially to compensate for eye movements (Bradley *et al*. 1996). This compensation is produced by an extraretinal eye-movement signal, which appears to operate through a gain-field mechanism similar to that of other parietal areas.

(i) *Heading computation by area MSTd*

Gibson (1950) proposed that the focus of expansion of the retinal image can be used to determine the direction of heading during observer motion. The focus of expansion corresponds to the direction of heading if the eyes and head do not move. If the eyes are moving, as would occur while fixating a feature on the ground, then a roughly laminar motion (which is opposite in direction to the eye movement) is added to the expansion. In scenes with very little depth variation the retinal-expansion focus is shifted in the direction of eye movement.

Two general methods could be used to compensate for eye movements during observer translation; one uses *retinal cues* in the image, such as motion parallax, and the other uses *extraretinal cues* such as a signal related to pursuit eye movements. Psychophysical experiments have shown that it is largely extraretinal signals that account for compensation during pursuit eye movements (Royden *et al*. 1992).

Area MSTd is a likely candidate for a cortical area involved in heading computation. Cells in this area have been found to respond to rotations, expansions and contractions, and laminar motion. (Sakata *et al*. 1985; Tanaka *et al*. 1986; Duffy & Wurtz 1991; Graziano *et al*. 1994; Lagae *et al*. 1994). The receptive fields of the expansion-selective neurones are also tuned to the location of the expansion focus; this observation provides support for the idea that MSTd plays a role in navigation from optic flow (Duffy & Wurtz 1995). Several studies have documented activity in MST related to the direction of smooth pursuit eye movements (Mountcastle *et al*. 1975; Lynch *et al*. 1977; Komatsu & Wurtz 1988*a,b*; Newsome *et al*. 1988). This coincidence of optic-flow selectivity and pursuit selectivity in MSTd suggests that this area plays a role in heading computation. Area MST also receives angular-rotation vestibular signals, which would result as a consequence of head pursuit (Kawano *et al*. 1980, 1984; Thier & Erickson 1992). The vestibular component during head-pursuit has been measured with a VOR cancellation task in which the monkey maintains fixation on a stimulus that is attached to a rotating vestibular chair in which the animal is seated. The preferred direction of activity during a VOR cancellation task was found to be similar, in individual neurones, to the preferred

eye-pursuit direction; this result suggests that the cells are coding smooth gaze movements independently of whether eye or head rotations are used for the gaze pursuit. These results hint that area MSTd may also provide heading compensation during head movements.

The simple condition of an observer moving toward a wall with or without eye movements has recently been examined (Bradley *et al*. 1996). Compensation for pursuit in this condition has been shown to occur when subjects are making eye movements, but not under simulated pursuit conditions where the retinal stimulus is the same but the eyes are not moving. If MSTd is involved in heading computation, then it would be expected that the focus-tuning curves of the expansion-sensitive cells would shift during pursuit eye movements to continue to code the correct heading direction with the eyes moving. It would also be expected, from the human psychophysical results, that movement compensation would not be present when the same retinal stimulus was generated as in the pursuit condition, but without eye movements. Both of these predictions were found to be true; this result provided evidence that area MSTd may play a direct role in heading computation. Moreover, many neurones shifted completely to compensate for the eye movement and showed no shift with the simulated condition. However, other cells shifted only partly and some did not shift at all. In addition, many of the non-shifting cells (as well as shifting cells) showed strong gain modulations of their activity caused by the eye-pursuit signal.

By means of cross-correlation techniques it was found that the average shift of the population of cells recorded from was $18° \pm 3°$ when the pursuit and simulated pursuit conditions were compared. This was approximately a 60% compensation for a focus that was shifted $30º$ during pursuit under the experimental conditions. The fact that many MSTd neurones shift their focus tuning by the right amount, whereas others only shift partly or not at all, suggests two possibilities: (i) only a portion of the MSTd neurones (those with complete compensation) are involved in heading computation and the others are involved in some other function (these being the ones that do not compensate); or (ii) the distribution of shifts reflects the *transformation* from retinal to heading coordinates. In the latter case, the cells with different amounts of compensation would be considered to be at different stages of the transformation process and the output would be derived from the completely shifted group. However, it is also possible that the heading judgment is based on the average shift of all cells; this partial compensation is consistent with psychophysical experiments showing that subjects may only partly correct for pursuit eye movements in heading judgment tasks.

(ii) *Gain-field effects and a model for the pursuit-compensation mechanism*

As indicated above, a fraction of cells in MSTd do not have focus-tuning shifts with pursuit. However, most of these cells do show modulation of their amplitude tuning by pursuit, by an average of $25 \pm 3\%$ for the cells in the sample studied. This finding suggests that shifting may be accomplished by gain modulation. A compensation model has been made, which uses two first-stage neurones whose focus tunings are offset and whose activity is summed by a second-stage neurone, which shifts its focus tuning during pursuit (Bradley *et al*. 1996). The first-stage cells have non-shifting focus-tuning fields whose gains are modulated by a pursuit signal. The receptive fields were modelled as sine functions; the amplitude, frequency and phase of the receptive fields, as well as two gain parameters that are applied during each of the opposed pursuits, were the parameters of the model that were adjusted and compared to the recording data. For the 36 neurones that clearly shift their focus tuning during pursuit, the fits were extremely good for such a simple model $(r^2 = 0.72 \pm 0.03)$ and much better than those found in single-stage models, which use nonlinear pursuit modulations of the focus-tuning curves (sigmoids, exponentials, thresholded linear functions) (Bradley *et al*. 1996).

The above model shows how MSTd could correct for the motions due to eye pursuit. However, neither this model, nor the experimental results, can determine in what coordinate frame MSTd represents heading: in the experiments (and model) the position of the eyes, head and body were all aligned. Additional experiments will be needed to dissociate these different coordinate frames by performing the experiments with the eyes, head and body in different positions relative to one another. At some point in the nervous system, heading direction will be represented in body and world coordinates in order to be able to walk or drive through the world, but we do not know if MSTd is yet at the stage where heading is taken out of eye-centred coordinates.

(iii) *Heading compensation for head rotations*

The previous section shows that an eye-velocity signal is required to compensate for heading judgments during eye movements, but it is not known whether a head-velocity signal would also compensate for gaze movements that are performed by moving the head. Current research in the author's laboratory is examining whether human subjects can perceive heading direction during pursuit head movements; it has been found that head-pursuit compensation is present. There are at least three potential sources for the head-movement signal: efference copy, the vestibular system, and neck proprioception. Experiments so far have shown that vestibular signals alone do not lead to compensation. This result is interesting in the light of the observation that simulating the retinal image that would occur if the eyes rotated during observer translation produces a stimulus very similar to what is generated during self motion on a curved path. When subjects view these eye rotation or translation simulations they in fact perceive that they are moving on a curved trajectory; they do not perceive that they are moving on a linear path and rotating their eyes. Such a curved path trajectory would produce vestibular stimulation in the absence of proprioceptive or

efference copy signals. Therefore, the psychophysical observation that vestibular stimulation alone does not produce compensation is consistent with the curved-path interpretation made by the subjects: compensation would produce a linear path percept.

As mentioned above, vestibular as well as eye-pursuit signals have been recorded in area MSTd. In preliminary experiments in which animals are rotated in a vestibular chair, evidence has been found that many cells show focus-tuning compensation during head movement as well as during eye movement (Shenoy *et al.* 1996). This result brings up two possibilities. The first is that neurones in area MSTd that compensate for vestibular signals alone are not the final stage for perceiving the path of self motion. Rather, sites downstream from these vestibular-compensating neurones, either within MSTd or in other cortical areas, would be this final site. Thus the computation could be made, but not used if the right set of other stimuli and efference copy signals were not present. The alternative possibility is that area MSTd is not involved in heading computation but rather is computing the head- or body-centred location of motion stimuli in the world and that this computation takes place in a separate network. It is also possible that area MSTd is very general in always compensating for gaze shifts, and that this compensation can be used for either heading computation or egocentric motion perception.

(iv) *Rotation, spiral and contraction patterns*

Area MSTd contains neurones selective for rotation, contraction, laminar flow and spiral motions. During self motion these various motion patterns can be present, depending on the structure of the environment and the movement of the eyes. For example, when fixating a location forwards and to the side on the ground plane while translating forwards, the motion around the fixation point is in the form of a spiral. Thus stimuli other than just expansion could potentially provide information for computing heading. However, like expansion stimuli, the rotation, contraction and spiral stimuli will shift their retinal focus during pursuit movements. However, these shifts are not in the direction of the eye movement as is the case for expansion. A rotation focus will move orthogonally to the direction of pursuit; a contraction focus will move opposite to the direction of pursuit; and spiral foci will move in oblique paths that depend on the rotation and expansion–contraction components producing the spiral.

In the above experiments, only expansion stimuli were discussed. However, the effects of pursuit eye movements on rotation and contraction neurones have also been investigated. These cells also showed focus-tuning curves and compensated the focus tuning in the correct directions (orthogonal to pursuit for rotation and opposite pursuit for contraction). The cross-correlation results on the population data also showed that the degree of compensation was nearly identical for all three patterns of motion (averaging $18 \pm 3\%$ for expansion, $15 \pm 3\%$ for contraction and $17 \pm 4\%$ for rotation) (Bradley *et al.* 1996).

That pursuit compensation also occurs for rotation- and contraction-sensitive neurones has interesting implications for the role of area MSTd in perceptual functions. Fixation straight ahead while moving over a ground plane leads to expansion on the retina. Tracking points on the ground that are eccentric to the direction of heading leads to rotation in the stimulus, with greater rotation the more eccentric the gaze direction. Thus outward spirals are generally seen (expansion + rotation) when translating while fixating locations on the ground plane. The focus of these spirals can in principle tell us the direction of heading, but only if their locations are corrected for eye velocity. The same arguments pertain to contraction and inward spiral stimuli when looking in directions opposite to the direction of motion. Therefore, the correction of the focus tuning of MSTd neurones for motion patterns other than expansions during eye movements is consistent with the hypothesis that they also assist in heading computation.

A second important perceptual function may be served by compensation for multiple patterns of motion stimuli. The shifts in focus tuning for all flow stimuli may indicate a more general phenomenon of perceptual stability in the face of retinal image motions due to pursuit eye movements. For example, when the eyes track across a spinning umbrella, the umbrella does not appear to move up or down. This idea has recently been tested directly in psychophysical experiments; results showed that subjects do adjust the focus of rotation by using an extraretinal pursuit signal (J. A. Crowell, M. Maxwell, D. C. Bradley and R. A. Andersen, unpublished observation). Thus MSTd may play a general role in compensating for smooth pursuit eye movements by means of extraretinal signals. One important outcome of this compensation may be the ability to compute heading direction, but another may be the perceptual stability of motion in the environment.

4. CONCLUSIONS

The posterior parietal cortex combines signals from many different modalities to create an abstract representation of space. The modalities involved include vision, audition and somatosensation (neck proprioception), as well as signals derived from the vestibular apparatus and signals indicating eye position and eye velocity. All these signals are combined in a systematic fashion by using the gain-field mechanism. This mechanism can represent space in a distributed format, which is quite powerful, allowing inputs from multiple sensory systems with discordant spatial frames and constructing outputs to other parts of the brain in different coordinate frames. It is possible that humans' unitary impression of space, independent of sensory modality, may be embodied in this abstract and distributed representation of space in the posterior parietal cortex.

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