

# Coordinate transformations in the representation of spatial information

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Coordinate transformations are an essential aspect of behavior. They are required because sensory information is coded in the coordinates of the sensory epithelia (e.g. retina, skin) and must be transformed to the coordinates of muscles for movement. In this review we will concentrate on recent studies of visual-motor transformations. The studies show that representations of space are distributed, being specified in the activity of many cells rather than in the activity of individual cells. Furthermore, these distributed representations appear to be derived by a specific operation, which systematically combines visual signals with eye and head position signals.

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## Introduction

Evidence from recent years has suggested that there are intermediate and abstract representations of space interposed between sensory input and motor output. Intermediate representations of the location of visual stimuli are formed by combining information from various modalities (Fig.1). A head-centered representation refers to a representation in the coordinate frame of the head, and is formed by combining information about eye position and the location of a visual stimulus imaged on the retina (Fig.1b). A body-centered coordinate representation would likewise be achieved by combining head, eye, and retinal position information (Fig.1b). More complicated representations include representations of the stimulus in world-centered coordinates, which can be achieved by combining vestibular signals with eye position and retinal position signals (Fig.1b), or even locations of visual stimuli with respect to parts of the body, such as the arm, which can be accomplished by integrating joint position signals with body-centered representations. There is reason to believe that the brain contains and uses all these representations. The reports discussed in this review will provide a glimpse into the internal operations of the brain that form the basis of our spatial perceptions and actions.

## Head-centered representations

### Area 7a: gain fields rather than receptive fields in space

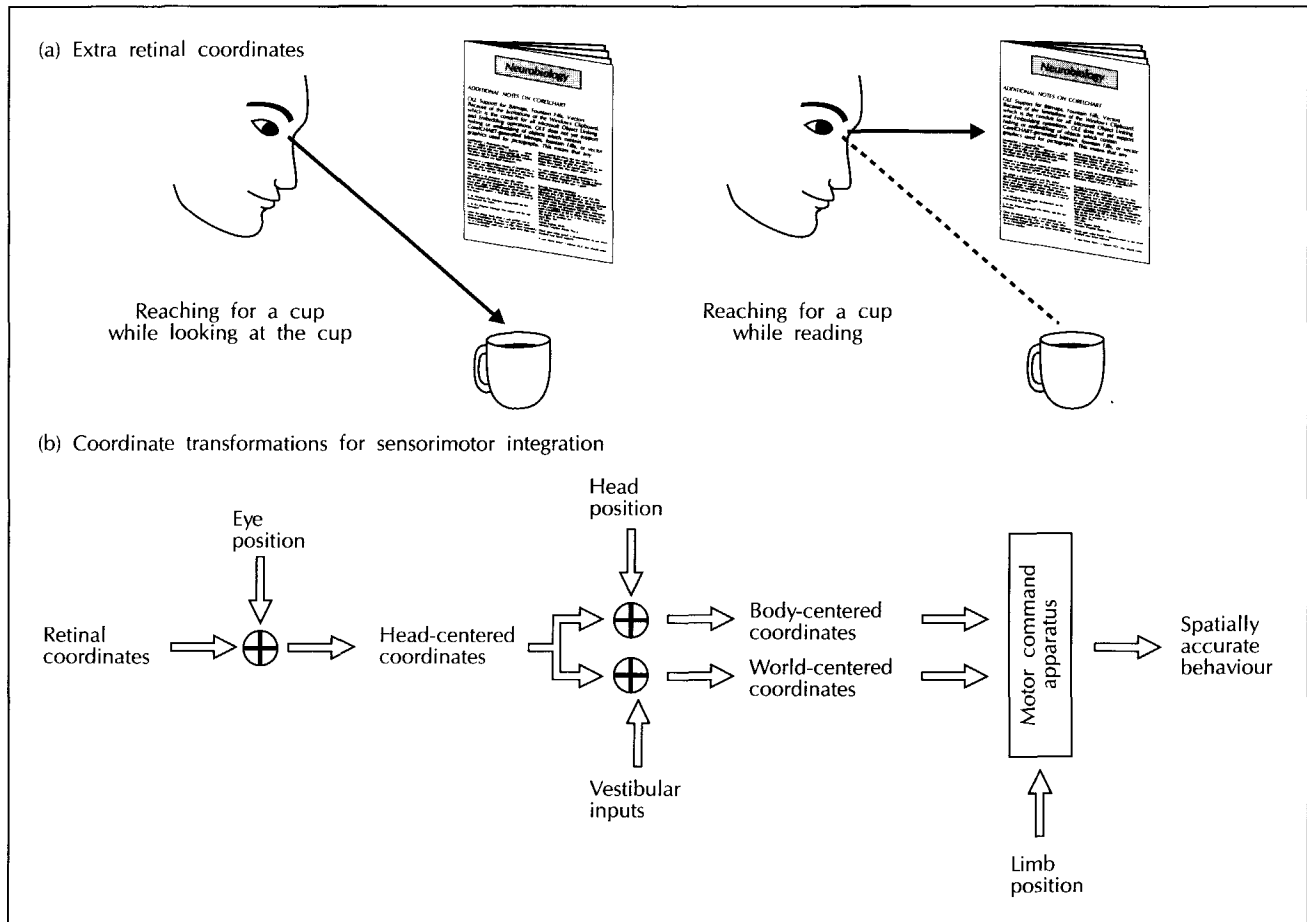
One might have imagined encoding locations in head-centered coordinates using receptive fields similar to retinal receptive fields, but anchored in head-centered, rather than retinal, coordinates. If this were the case, each time

the eyes would move, the receptive field would change the location on the retina from which it derives its input, in order to code the same location in space.

Early investigations of area 7a of the posterior parietal cortex showed that locations in head-centered coordinates could be coded in an entirely different format, however [1]. The receptive fields of the neurons did not change their retinal locations with eye position. Rather the visual and eye position signals interacted to form 'planar gain fields' in which the amplitude of the visual response was modulated by eye position. The gain fields were said to be planar because the amplitude of the response to stimulation of the same patch of retina varied linearly with horizontal and vertical eye position [2].

Thus, spatial locations were not represented explicitly at the single cell level using receptive fields in space. However, the location of a target in head-centered coordinates could still be easily determined if the activity of several area 7a neurons was examined together; in other words the representation of head-centered space is distributed within this relatively small cortical area.

Looking at the behavior of single cells as components of a much larger distributed network has been critical in advancing our understanding of how the brain computes locations in space. Neural networks trained to convert inputs of eye position and retinal position into locations in head coordinates at the output, develop a distributed representation in the 'hidden layer' interposed between the input and output layers [3]. This distributed representation appears to be the same as that found in area 7a, with the 'hidden' units exhibiting planar gain fields. A mathematical analysis of this network indicates that the planar gain fields are the basis of an algorithm for adding eye and retinal position vectors to a distributed network (PR



**Fig. 1.** (a) Demonstration of why representations of space in extraretinal coordinates are required for accurate motor behaviors. The term 'extraretinal' refers to the encoding of visual stimuli in higher level coordinate frames than simple retinal coordinates. In the sketch on the left, the person is fixating the cup and it is imaged on the foveas, whereas on the right she/he is fixating the newspaper and the cup is imaged on a peripheral part of the retinas. In both cases the subject is able to localize the cup with a reaching movement. As different parts of the retinas are stimulated in the two conditions, information about eye position must also be available to accurately determine that the cup was at the same location in space. (b) Schematic showing how extraretinal coordinate frames can be computed from retinal coordinates. Visual stimuli are imaged on the retinas, and are inputted to the brain in retinal coordinates. Eye position signals can be added to form representations in head-centered coordinates, and body-centered coordinates can be formed by also adding head position information. One way of forming world coordinates is to add vestibular signals, which code where the head is in the world, to a head-centered coordinate frame. The figure shows these signals being added sequentially for illustrative purposes. It is presently not known if there is a hierarchical organization of extraretinal coordinate frames in the brain, or if several of these signals come together at once to immediately form body- or world-coordinate frames. The motor command apparatus can use the body- and world-coordinate frames, combined with information about limb position derived from proprioceptive inputs, to encode accurate reaching movements.

Brotchie, RA Andersen, S Goodman, unpublished data) [4]. Thus, the method of integrating these two signals is not random, but is systematic and requires the gain fields to be planar.

One of the neural network models for area 7a in the paper by Zipser and Andersen [3] was trained to produce output units with receptive fields in head-centered coordinates. The middle layer of this model produced gain fields similar to those found in area 7a, suggesting that gain fields are an intermediate stage between retinal and spatial receptive fields. A possible objection to this model is that cells resembling its output (receptive fields in space) are not routinely found (although they may be present in the frontal lobe [5•]). Zipser and Andersen [3] trained a second network, with an output representation similar to the activity found in oculomotor structures and motor centers in general. In this

format activity varies monotonically as a function of location with respect to the head. Andersen *et al.* [6] and Goodman and Andersen [7] have shown that such a network can be trained to make eye movements, and have argued that receptive fields in space are an unnecessary method of encoding spatial location. Instead, cells with planar gain fields appear to represent an intermediate step in the transformation from visual to motor coordinates.

#### Other areas with gain fields

Recently gain fields have been found in several areas besides 7a. Modulation of retinal visual signals by eye position has been found in monkeys in cortical area V3a [8], cortical area LIP [6], the inferior and lateral pulvinar [9], and premotor and prefrontal cortex [10•], and

in cats in the superior colliculus (CL Peck, JA Baro, SM Warder: *ARVO Abstr* 1992, 33:1357). In the cases where data were collected for a sufficient number of eye positions, the gain fields were usually linear for horizontal and vertical eye positions. These results suggest that gain fields are a typical format for the representation of spatial information in many areas of the brain.

It is interesting that the more recent data listed above show that planar gain fields appear to be the predominant method of representing space and performing coordinate transformations. A clue to the predominance of this form of representation comes from Mazzoni *et al.* [11•]. They found that networks with multiple hidden layers trained to make coordinate transformations have gain fields in all of these layers. The planar gain field is an economical method for compressing spatial information [4]. An analogy can be made with orientation tuning, which is found in many cortical areas and is a parsimonious method of compressing form information.

There is, nonetheless, a suggestion that receptive fields in space may also exist in some cortical areas [12•,13,14]. These studies are presently preliminary and it will be interesting to see more complete reports by these groups.

#### Distance

The data above indicate that there are representations with respect to the head in the dimensions of elevation and azimuth. Recent experiments suggest that the third dimension of distance from the head is also contained within these representations, and that the method of encoding distance is in the form of gain fields. Trotter *et al.* [15••] found disparity-tuned cells in area V1 whose responsiveness, but not disparity tuning, is affected by viewing distance (these experiments used a technique that could not determine whether accommodation or vergence was the critical variable). Gnadt and Mays have found LIP neurons in which the vergence angle modulates the magnitude of the visually-evoked responses, but not their disparity tuning (JW Gnadt, LE Mays: *Soc Neurosci Abstr* 1991, 17:1113) [16]. These types of gain fields are also predicted by neural network models similar to the Zipser-Andersen model, but trained to localize in depth [17].

The finding of Trotter *et al.* [15••] offers the rather surprising possibility that eye position effects, at least for vergence, may be present very low in the visual cortical pathway. One possible role for this early convergence may be in the perception of three-dimensional shape from stereopsis. Cumming and colleagues [18••] have found that changing vergence angle produces systematic changes in the perceived shape of random dot stereograms, suggesting that knowledge of the vergence angle is used to scale horizontal disparities for shape perception. Pouget [19•] has modeled early encoding of visual features in head-centered coordinates using gain fields, but within retinotopic maps, an organization he refers to as a retinospatiotopic representation.

#### Evidence from lesions

Nadeau and Heilman [20•] have studied a patient with a lesion of the right occipital and temporal lobes who demonstrated a hemianopia for the left retinotopic visual field when fixating straight ahead, but showed a nearly complete recovery of the left visual field when the subject's eyes were deviated 30 degrees to the right. These results are consistent with damage to an area of cortex representing space in head-centered coordinates, leaving only the part of the map representing contralateral space intact.

### Body-centered coordinates in the posterior parietal cortex

The experiments described above tested the interaction of eye position and retinal position signals for animals with their heads mechanically immobilized. As a result, head-centered representations could not be distinguished from body-centered representations. With this in mind, Brotchie *et al.* (PR Brotchie, RA Andersen, S Goodman, unpublished data) have examined the effect of head position on the visual response of cells in the posterior parietal cortex. Neural network simulations performed before the experiments suggested that posterior parietal neurons should have gain fields for head position as well as eye position if they are representing space in body-centered coordinates. Furthermore, the eye and head gain fields of individual parietal neurons should have the same gradients (two-dimensional slopes), even though the gradients of different cells may vary considerably. The recording experiments from areas 7a and LIP bore out these predictions. About half of the cells with eye position gain fields were also found to have similar head position gain fields. These results suggest that there may be two representations of space in the posterior parietal cortex, one in head-centered coordinates (units with gain fields for eye position) and the other in body-centered coordinates (units with gain fields for eye and head position).

The possibility that two representations of space can co-exist in the same cortical area suggests that one or the other could be used depending on the requirements of a particular task. Such a possibility is strongly suggested by the psychophysical experiments of Soechting *et al.* [21], who found that human subjects use a head-centered reference frame when asked to point to locations relative to the head, and a shoulder-centered reference frame when asked to point to locations relative to the shoulder. As the shoulder is fixed to the body, the shoulder-centered coordinate frame in this study differed from the body-centered frame only by a constant offset.

The apparent existence of both head and body reference frames in the posterior parietal cortex also raises the question of whether there is a serial order in processing, with the body-centered representation derived from the head-centered representation. This hierarchy has been proposed in a model by Flanders *et al.* [22••]

to explain their psychophysical results from normal and brain-damaged subjects.

One possible source of the head position effects in posterior parietal cortex may be proprioceptive signals derived from the neck muscles. Biguer *et al.* [23], Roll *et al.* [24•], and Taylor and McCloskey [25•] have found that vibration of muscles in the neck, which activates muscle spindle afferents in a similar way to head rotation, produces the illusion of motion in stationary visual stimuli. When asked to point to the stimulus after vibration, subjects mispoint in the perceived direction of movement [23,24•].

The saccade system also appears to have access to a head position signal. Gnadt *et al.* [26•] have found that the constant component of error for saccades to memorized locations is significantly affected by head position as well as by eye position. A likely location in the brain for this integration is area LIP, which has both saccade-related, head-position, and eye-position signals. One possible reason for this convergence is to ensure proper coordination of eye and head movements during gaze shifts.

The problem of not knowing whether deficits are in a head- or body-centered frame, unless the eye and head positions are varied, also exists clinically. Karnath *et al.* [27•] have studied the effect of head and body orientation on saccadic reaction times in brain-damaged patients. Typically, reaction times are greatly increased for saccades into the left visual field after right parietal lesions, and this defect has been used as a probe for hemispatial neglect. They found that turning the patients' trunks to the left, so that both right and left saccades in their task were to locations in space to the right side of the body, compensated for the hemineglect. The results have been interpreted as indicating that the neglected contralateral space in parietal patients is in body-referenced coordinates.

### Arm-centered coordinates

Caminiti and colleagues [5•,28] have examined the directional selectivity of motor and premotor cortical units when monkeys make movements of similar directions but in different parts of the work space. Although results from individual cells could vary considerably, as a population there was a systematic shift in direction tuning roughly equal to the angular shift in the work space. These data imply that the motor and premotor cortices transform target location into an arm-centered frame of reference. This transformation is not in the distributed form found in the posterior parietal cortex and other areas outlined above; if it were, then only the magnitude of activity and not the direction tuning of the cells would change with changes in initial arm position. As the motor and premotor cells change their direction tuning in parallel with arm movements, they appear to encode spatial receptive fields in arm-centered coordinates. The signals from posterior parietal cortex representing body-centered coordinates in a distributed format (PR

Brotchie, RA Andersen, S Goodman, unpublished data) could be combined with shoulder joint position signals to produce cell responses like those in motor cortex. One possible pathway for this process would be the projection from LIP and 7a to area 7b, which also receives inputs conveying limb position, and from 7b to premotor cortex. On the other hand, Burnod *et al.* [29•] have published a neural network model which makes a more direct transformation. This model receives inputs of the retinal positions of the target and the hand, and proprioceptive information about the initial position of the limb, and computes at the output the desired limb trajectory. This model can bypass the head-centered stage, but apparently works only if both the hand and target are simultaneously visible before reaching.

Graziano and Gross (MSA Graziano, CG Gross: *Soc Neurosci Abstr* 1992, 18:593) [30] have reported cells with visual activity modulated by movement of the limbs in premotor cortex, as well as in the putamen in anesthetized monkeys. They interpret the receptive fields as being related to 'body parts'. They have found that the receptive fields are either gated on or off with limb movements, or that one edge of a receptive field moves when the limb is moved. The receptive fields in this preliminary report were not mapped in enough detail to determine if they were receptive fields in limb coordinates, or exhibited limb gain fields (MSA Graziano, personal communication); however, the results bear a close resemblance to those of Caminiti *et al.* [5•], and it is quite possible that the cells will be found that code explicit locations in arm-centered coordinates.

### World-centered coordinates

Information about the position of the head in space can be derived from otolith and vestibular inputs. These signals, when combined with eye and retinal position information, can code locations in world-based coordinates (also often referred to as allocentric coordinates). Recent psychophysical studies show that human subjects can accurately localize using vestibular and otolith cues [31•,32].

'Direction-tuned' cells, which are active for particular orientations of the whole body, have been found in the posterior parietal cortex, dorsal presubiculum of the hippocampal formation, and the retrosplenial cortex of rats (for a review, see [33•]). It is thought that these cells encode an integrated vestibular signal, as the signals are present in the dark, and the best directions of individual neurons can be changed by slow rotations, which are presumably below the sensitivity of the vestibular apparatus. McNaughton *et al.* [33•] have recently proposed a theory to explain how animals are able to use directional (vestibular) signals and visual landmarks to form and update internal representations of space in world-centered coordinates.

It would be interesting to determine whether there are integrated vestibular signals in the posterior parietal cor-

tex of monkeys, which provide information about orientation of the head in space. One possibility worth testing is whether there are vestibular gain fields, in which visual signals are linearly modulated by vestibularly-derived body position signals. These gain fields could form the basis of a distributed world-centered representation.

Eye motion and head motion signals also appear to be combined in some areas of the brain to compute the velocity of the eye in space. Thier and Erickson [34••] have found that individual MST cells receive eye and head velocity signals that are usually tuned to the same direction of movement. These cells are reminiscent of the posterior parietal neurons which have the same direction tuning for eye and head gain fields. Recent psychophysical experiments on navigation using optical flow, in which area MST is often believed to play a role, have suggested that extra-retinal eye and head movement signals are important for extracting direction of heading [35••].

## Conclusions

The experiments reviewed here are shedding light on the nature of abstract representations of space. Spatial representations are derived by integrating visual signals with information about eye, head and limb position, and movements. Most regions of the brain where these signals are brought together appear to form a specific representation of space, which is typified by linear gain fields.

One issue for further research is whether the different representations of space, outlined above, share the same neural circuits. Area LIP is fascinating in that it appears to be an example of such an area. Cells in LIP integrate eye and head position with retinal signals to code space in head- and body-centered coordinates. Many cells in this area also carry vergence and disparity signals, enabling the representation of distance with respect to the body, and have activity related to auditory stimuli, if those stimuli are targets for eye movements (RM Bracewell, S Barash, P Mazzoni, RA Andersen: *Soc Neurosci Abstr* 1991, 17:1282).

A related issue is whether the coordinate transformations proceed in a hierarchical fashion. For instance, are the body-centered cells of the posterior parietal cortex constructed by adding head position signals to the head-centered representation? Alternatively, the entire representation could be body-centered, with some cells exhibiting only retinal and eye position signals within this highly distributed representation (training networks to code in body-centered coordinates often generates some hidden units which carry only eye and retinal signals). Is information about shoulder position added to the body-centered representation of space in areas 7a and LIP to generate arm-referenced representations like those found in the motor cortex? Are there further representations of visual targets which code with respect to the hand? These and many other questions should make this an interesting area of research in the future.

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