A distributed common reference frame for egocentric space in the posterior parietal cortex

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[JFS] **Stein** has provided a fair and accurate account of what we know about the posterior parietal cortex (PPC) and its possible functions. He concludes that the evidence points toward multiple reference frames rather than one common reference frame and argues further that there is no need for a single one. In this brief commentary we suggest that the existing evidence does not exclude a common representation for spatial transformations in addition to special purpose ones. A general purpose reference frame, however, does not require topographical maps and is likely to be highly distributed.

Stein argues that perhaps the best candidate for a special purpose reference frame is the one for eye movements. Indeed, retinal position vectors can be converted directly into oculomotor vectors without the need for an intermediate head-centered representation. However, this transformation seems to be performed primarily in the frontal eye field (FEF) (Bruce & Goldberg 1985; Goldberg & Bruce 1990), which has connections with, but is not part of, the PPC. Stein suggests that the lateral intraparietal area (LIP) may be using a similar strategy, that is, a direct transformation; but he misses the fact that in LIP, about 70% of the saccadic neurons are modulated by static eye position (Andersen et al. 1990b), compared to only 2% in the FEF (Bruce & Goldberg 1985; Goldberg & Bruce 1990). As shown by Zipser and Andersen (1988), this suggests that LIP contains a distributed representation of head-centered coordinates. This more general spatial representation allows LIP to integrate cues from different sensory modalities such as audition and vision (Bracewell et al. 1991), unlike FEF, which appears to use only retinal coordinates.

Electrical stimulation experiments also suggest that FEF and LIP use different coordinate systems. Focal stimulation of neurons in LIP lead to saccadic eye movements whose directions and amplitudes are a function of initial eye position, unlike the saccades elicited by stimulations in the FEF, whose characteristics are largely independent of initial eye position, often referred to as fixed vector type (Robinson & Fuchs 1969). In other parietal areas, particularly in the floor of the intraparietal sulcus (IPS) and 7a, the eye movements induced by electrical stimulation are of the convergent type (i.e., the saccades tend to terminate in the same zone of space regardless of initial eye position; Kurylo & Skavenski 1991; Thier & Andersen 1991). These results suggest that the representation of saccadic eye movements is quite different in the PPC from that found in the FEF.

This raises the general issue of why multiple representations of the same sensorimotor transformation exist in different parts of the brain. We agree with **Stein** regarding the usefulness of having many special purpose transformations; however, we suspect that the particular purpose of the representations in the PPC is to integrate these into common representations involving synergies between different sensorimotor transformations. Hence, the egocentric representation found in 7a (Brotchie & Andersen 1991; Thier & Andersen 1991) could be useful for coordinating various kinds of movements, such as eye, head, or even arm movements directed toward the same spatial location. This implies that the same neuronal pool could be used to control many different types of movement. A recent observation by Thier and Andersen (1991) supports this hypothesis, showing that electrical stimulations in 7a and in the floor of IPS can induce simultaneous eye movements as well as shoulder and face muscle movements. A distributed egocentric reference system might not provide the best coordinates for controlling eye movements, but they might be suitable for deciding the extent to which eye movements should be included along with other body movements. Evidence is mounting that there are such representations in the PPC.

A related issue concerns whether the PPC is the first area where a distributed representation of egocentric space can be found. In the visual system, the modulation of responses by static eye position has been observed as early as the lateral geniculate nucleus (Lal & Friedlander 1989), the primary visual cortex area V1 (Trotter et al. 1991; Weyand & Malpeli 1989), and the extrastriate area V3a (Galleti & Battaglini 1989). We have recently shown how these modulatory responses could provide egocentric coordinates for early vision (Pouget et al. 1992). In contrast to the PPC, in the early visual cortex, low-level visual features such as orientation and direction of motion are encoded within retinotopic maps. We have proposed that each location on those retinotopic maps contains a distributed representation of the egocentric positions of these features similar to the one proposed by Zipser and Andersen (1988) for the position of the whole object in the PPC.

The same principle could also apply to other sensory cortices. In the primary auditory cortex, for example, the responses of 62% of the neurons are modulated by the position of the sound source with respect to the head (Ahissar et al. 1992). This is consistent with an early head-centered representation of sound source at early stages of auditory processing.

In summary, we agree with **Stein** that the brain uses specialized sensorimotor transformations. However, these specialized routines are not necessarily implemented in the PPC and may involve other structures such as the FEF. In contrast, the PPC may contain a common reference frame based on distributed representations that would provide a good starting point for mediating and coordinating many sensorimotor routines. Finally, it appears that egocentric transformation might be initiated earlier than previously thought, as early as the primary sensory cortices.