The thinking around long-range horizontal connections has been dominated by their first-order statistics and its peak at zero orientation offset. However, the nonmonotonicity of the variance was first reported almost a decade ago (Fig. 3d in Malach et al., 1993) and we have further confirmed it from the more detailed measurements in Bosking et al. (1997) as was illustrated in Figure 3a. Since neither collinearity nor association field models can explain this aspect of the physiological data, even if much noise is allowed, it is necessary to consider whether this and the other subtle properties of the pooled data reflect genuine functional properties of long-range horizontal connections. We therefore developed a geometric model of projection patterns and examined quantitatively both pooled connection statistics and connectivity patterns of individual cells generated by it. Since many findings suggest that long-range horizontal connections are primarily excitatory, especially those extending beyond one hypercolumn (Ts'o et al., 1986; Gilbert & Wiesel, 1989; Kapadia et al., 1995; Kisvárday et al., 1997; Buzás et al., 1998; Sincich & Blasdel, 2001), our model concentrates on this class of connections.

2 From Differential Geometry to Integration Models

Curve integration, the hypothesized functional role ascribed to long-range horizontal connections, is naturally based in differential geometry. The tangent, or the local linear approximation to a curve, abstracts orientation preference, and the collection of all possible tangents at each (retinotopic) position can be identified with the orientation hypercolumn (Hubel & Wiesel, 1977). Formally, since position takes values in the plane $\mathbb{R}^2$ (think of image coordinates x, y) and orientation in the circle S^1 (think of an angle θ varying between 0 and 2π), the primary visual cortex can be abstracted as the product space $\mathbb{R}^2 \times S^1$ (see Figure 4). Points in this space represent both position and orientation to abstract visual edges of given orientation at a particular spatial (i.e., retinotopic) position. It is in this space that our modeling takes place.

Since any single tangent is the limit of any smooth curve passing through a given (retinotopic) point in a given direction, the question of curve integration becomes one of determining how two tangents at nearby positions are related. (Collinearity, for example, asserts that the tangent orientation hardly changes for small displacements along the curve.) In general terms, the angular difference between RFs captures only one part of the relationship between nearby tangents; their relative spatial offset also must be considered. Thus, in the mathematical abstraction, relationships between tangents correspond to relationships between points in $\mathbb{R}^2 \times S^1$. Physiologically, these relationships are carried by the long-range horizontal connections, with variation in retinotopic position corresponding to $\mathbb{R}^2$, and variation along orientation hypercolumns corresponding to S^1 (see Figure 5). Determining them amounts, in mathematical terms, to determining what is called a con-