

are thought to facilitate contour integration (Field, Hayes, & Hess, 1993). However, there is no direct physiological evidence that these connections *only* support curve integration, while there also remains much ambiguity about the precise connections required to support the integration of curves. Our goal in this article is to address both of these concerns.

1.1 Biological Data and Integration Models. The argument that associates long-range horizontal connections with curve integration begins with the realization that the finite spatial extent of RFs and their broad orientation tuning lead to significant uncertainties in the position and the local orientation measured from visual stimuli. This causes a further uncertainty in determining which of the many nearby RFs signal the next section of a curve (see Figure 1a).

All of these uncertainties underlying curve integration can be reduced by interactions between neurons whose RFs are close in retinotopic coordinates. Starting with Mitchison and Crick (1982) and their hypothesis about interactions between iso-oriented RFs, physiological and anatomical findings have been accumulating to suggest a roughly collinear interaction. The main evidence supporting this conclusion is based on the distribution of angular differences between preferred orientations of connected cells. These distributions are computed by taking the orientation difference between a target cell and every other cell it is connected to with a long-range horizontal connection. Indeed, as is exemplified in Figure 1b, these distributions have been shown to be unimodal on average, with maximal interaction between iso-oriented RFs (Ts'o, Gilbert, & Wiesel, 1986; Gilbert & Wiesel, 1989; Weliky, Kandler, Fitzpatrick, Katz, 1995; Schmidt, Goebel, Löwel, & Singer, 1997; Buzás, Eysel, Kisvárdy, 1998; Bosking, Zhang, Schofield, & Fitzpatrick, 1997; Malach, Amir, Harel, & Grinvald, 1993; Sincich & Blasdel, 2001; Schmidt & Löwel, 2002). Furthermore, direct anatomical studies reveal long-range interactions between coaxial cells (Bosking et al., 1997; Schmidt et al., 1997) and indirect psychophysical experiments report a general association field (Field et al., 1993; Kapadia, Ito, Gilbert, & Westheimer, 1995; Kapadia, Westheimer, & Gilbert, 2000) which emphasizes straight or slowly varying continuations while allowing some support for more rapidly varying continuations as well (see Figure 2a).

With the accumulation of these data, however, are a growing number of observations that are difficult to reconcile with the intuition that neural spatial integration is based on collinearity or that it serves only curve integration. Facilitory interaction between cells of significant orientation difference (Kapadia et al., 1995) short-range coaxial inhibition (Polat & Sagi, 1993), iso-orientation side facilitation (Adini, Sagi, & Tsodyks, 1997), and strong correlations between iso-oriented, nonoverlapping, and parallel receptive fields (Ts'o et al., 1986) are functionally inconsistent. Evidence of cross-orientation (Matsubara, Cynader, Swindale, & Stryker, 1985; Kisvárdy, Tóth, Rausch, & Eysel, 1997) and nonaxial (Gilbert & Wiesel, 1989) connections, plus roughly