Inhomogeneous retino-cortical mapping is supported and stabilized with correlation-learning during self-motion

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Abstract

In primates, the area of primary visual cortex representing a fixed area of visual space decreases with increasing eccentricity. We identify visual situations to which this inhomogeneous retino-cortical mapping is well adapted and study their relevance during natural vision and development. We assume that cortical activations caused by stationary objects during self-motion along the direction of gaze travel on average with constant speed across the cortical surface, independent of retinal eccentricity. This is the case if the distribution of objects corresponds to an ellipsoid with the observer in its center. We apply the resulting flow field to train a simple network of pulse coding neurons with Hebbian learning and demonstrate that the density of learned receptive field centers is in close agreement with primate retino-cortical magnification. In addition, the model reproduces the increase of receptive field size and the decrease of its peak sensitivity with increasing eccentricity. Our results suggest that self-motion may have played an important role in the evolution of the visual system and that cortical magnification can be refined and stabilized by Hebbian learning mechanisms in ontogenesis under natural viewing conditions.

1. Introduction

The spatial resolution of the representation of the visual field in primate primary visual cortex decreases strongly with increasing eccentricity (e.g., Daniel and Whitteridge, 1961) in parallel with the increase of receptive field (RF) sizes of retinal, thalamic and cortical neurons (Hubel and Wiesel, 1974; Dow et al., 1981; Croner and Kaplan, 1995; Xu et al., 2002). A large number of cortical neurons process stimuli near the fovea, while relatively few represent the periphery. This inhomogeneous mapping keeps the number of retino-cortical connections relatively low, but requires eye movements over larger areas of the visual field for perception at high spatial resolution. The inhomogeneous retino-cortical mapping is to a large part determined genetically, but development of theories on its underlying principles and its shaping during ontogeny may help to understand fundamental coding mechanisms in the visual system. We investigate whether visual situations exist to which the inhomogeneous retino-cortical mapping is well adapted and ask how relevant these situations are during natural vision and development. Because vision plays an important role during navigation, visual processing should be well adapted to self-motion. Thus, it is reasonable to hypothesize that self-motion plays a

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role in determining retino-cortical mapping and magnification. Virsu and Hari (1996) showed that cortical magnification can be estimated by linear self-motion in a world, idealized as a sphere, under the assumption that cortical activations, caused by stationary objects, travel at constant cortical speed, independent of eccentricity. We take the complementary approach and investigate which average geometrical arrangement of static objects in the environment is best suited to predict cortical magnification from flow fields arising during self-motion along the direction of gaze. Furthermore, we demonstrate that a RF distribution, whose density is consistent with cortical magnification, can be learned in a basic network model of spiking neurons by training with flow fields similar to those experienced during self-motion.

2. Relating cortical magnification to self-motion

The dependence of RF density of neurons in primary visual cortex on retinal eccentricity can be quantitatively described by the linear cortical magnification factor M (Daniel and Whitteridge, 1961; Van Essen et al., 1984), which is defined as the cortical distance corresponding to one degree of visual angle. M depends strongly on the retinal eccentricity α and can be approximated as

$$M(\alpha) = \frac{C_2}{C_1 + \alpha}, \tag{1}$$

where C_2 is a scaling factor and the quotient C_2/C_1 is the cortical magnification in the fovea ($\alpha = 0$).

We make the assumption that cortical magnification has the effect that during self-motion along the line of gaze, representations of static objects shift on average the same cortical distance, independent of eccentricity. This would have the important advantage that the neuronal modules, concerned with the processing of motion, can be identical in their spatial and temporal properties across the representation of the whole visual field.

For convenience, we introduce the inverse cortical magnification factor M^{-1}, which has the form:

$$M^{-1}(\alpha) = \frac{C_1}{C_2} + \frac{1}{C_2}\alpha, \tag{2}$$

M^{-1} specifies the change in visual angle that corresponds to a fixed cortical distance. Thus, cortical activations travel at constant speed, if the angular velocity $\omega(\alpha)$ of the corresponding retinal activations is proportional to the inverse cortical magnification factor

$M^{-1}(\alpha)$ for all eccentricities:

$$\omega(\alpha) \overset{!}{\propto} M^{-1}(\alpha). \tag{3}$$

In the following, we neglect the term C_1 of the cortical magnification factor ($C_1 \ll \alpha$), which cannot be explained by linear self-motion along the direction of gaze (Virsu and Hari, 1996), because a finite C_1 corresponds to non-zero retinal velocities in the fovea. One possibility to explain a non-vanishing value of C_1 would be to assume velocity jitter across the visual field, due to eye and body-motion. However, we will show (Section 3) that even a vanishing retinal velocity in the fovea can lead to a magnification factor with $C_1 \neq 0$, due to the finite size of the retinal receptive fields.

According to the experimentally estimated linear cortical magnification factor (Eq. (1), for $C_1 \ll \alpha$), angular velocity increases linearly with eccentricity for the condition of constant velocity across the visual cortical representation:

$$\omega(\alpha) \propto \alpha. \tag{4}$$

In the next step, we determine the geometrical arrangement of objects surrounding an observer which leads to angular velocities increasing linearly with eccentricity. The retinal speed of objects depends on their distance, their eccentricity, and the velocity of self-motion. Therefore, we have to derive a mathematical expression for the angular velocity of an object at a given position in visual space during self-motion of an observer with velocity v. We assume rotational symmetry around the axis of fixation, which allows us to solve the problem in the horizontal plane. We choose a coordinate system that originates in the observer's eye, with positive y-direction in the direction of gaze. The distance r of an object in the horizontal plane at position $P = (x, y)$ from the observer is

$$r = \sqrt{x^2 + y^2}, \tag{5}$$

and its retinal eccentricity is

$$\alpha = \arctan \frac{x}{y}. \tag{6}$$

To obtain the angular velocity $\omega(\alpha)$ of the object we differentiate α with respect to t:

$$\omega(\alpha) = \frac{\dot{x}y - \dot{y}x}{r^2}. \tag{7}$$

We examine the case of the observer moving with velocity v in the positive y-direction. The coordinates of an object which is initially ($t = 0$) at position $P = (x_0, y_0)$