The nature of nurture: the role of gene-environment interplay in the development of intelligence

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APPENDIX A

MATHEMATICAL DESCRIPTION OF THE TWO-CELL MODEL

Van Oss and van Ooyen (1997) model neuronal activity as:

$$\frac{dx}{dt} = -x + (1-x)wf(x) - (h+x)wpf(y) \ (1)$$

and

$$\frac{dy}{dt} = -y + (1-y)wpf(x) \ (2)$$

where

$$f(u) = \frac{1}{1+e^{(\theta-u)/\alpha}} \ (3)$$

The variable x is interpreted as the average membrane potential of a population of excitatory neurons, and y that of inhibitory ones. The cells outputs are taken their mean firing rates, which are a sigmoid function f of their membrane potentials. The function f has two parameters: α, the steepness of the function, and θ, the firing threshold. In equation 1 and 2, w represents the connection strength between cells. Furthermore, $w = w_{xx}$, $w_{xy} = w_{yx}$, $w_{yy} = 0$ (See Figure 2.1). Parameter h represents the relative inhibitory saturation potential (the finite maximum membrane potential) compared to the excitatory saturation potential, and p represents the relative strength of the inhibitory connection ($p = w_{xy} / w_{xx}$).

The dynamics of w are governed by the equation:

$$\frac{dw}{dt} = q(\varepsilon - bw^2 - x) \ (4)$$

where q determines the outgrowth rate of neurons. Finally, b stands for the degree of saturation, while ε stands for the membrane potential at which the cell neither retracts nor extends its neurites (i.e., at which neurite outgrowth is 0).

In this model the dynamics of the connection strength are considerably slower compared to the dynamics of neuronal activity. Hence, variables x and y can be displayed in a *(w, x)* or *(x, y)* -plane as a function of w (as depicted in Figure A.1). In such a diagram one can observe a characteristic S-shaped curve, which van Oss and van Ooyen (1997) call the slow manifold. The set of points defined by dw/dt = 0, is called the null-cline. Intersections of the slow manifold with the w-nullcline are the equilibrium points of the system. Variables x and y are able to show transient behavior jumps from the one to another trajectory. In addition, as w changes x and y can either end up in a point attractor or in a stable or unstable limit cycle, depending on the w-nullcline.

By means of bifurcation analysis van Oss and van Ooyen (1997) distinguished different regions in the parameter plane *(ε, p)*. These regions are characterized by the number and stability of equilibrium points. Furthermore, three types of limit cycles appeared to exist: 1) 'relaxation oscillations' (very slow oscillations in x, y, and w with high amplitude), 2) 'bursting oscillations' (a single fast oscillation in x and y, and w almost non-oscillating), 3) 'fast oscillations' (a relatively high amplitude in x and y, and low amplitude in w). Subregions are defined as having equal number and stability of equilibrium points, but having different types of limit cycle attractors. Figure A.2 displays the parameter regions, subregions, and bifurcation lines within the parameter plane *(ε, p)*. Multistability can occur in (sub)regions 1b, 2b, 4d, 5b, 6, 7, 9, 10, 11, and 12.

In most cases of multistability, there exist a point attractor at low values of connectivity (*w*) and either a second point attractor or an additional limit cycle of type 2 or 3 for high values of connectivity. At intermediate values there exists an unstable equilibrium (unstable node or limit cycle). However, for values of $p > 0.43$ - in some cases - the second attractor can be reached even for low values of *w*. Switching from the first attractor to the second is possible when *w* is decreased, *x* is chronically decreased, or *y* is chronically increased. Reversely, if *w* is increased, x chronically increased, or *y* chronically decreased, a switch from the second to the first attractor can be accomplished.

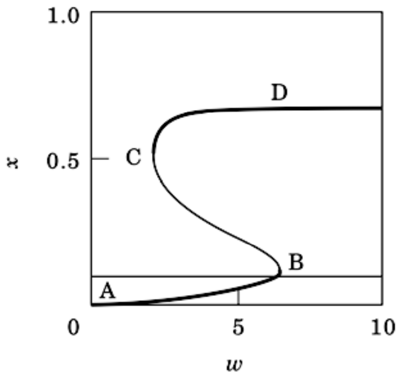

Figure A.1 Copy of Fig. 2b in van Oss and van Ooyen (1997): An S-shaped curve and the w-nullcline (horizontal line). Bold lines indicate stable equilibrium points with respect to x, when w is regarded as a parameter.

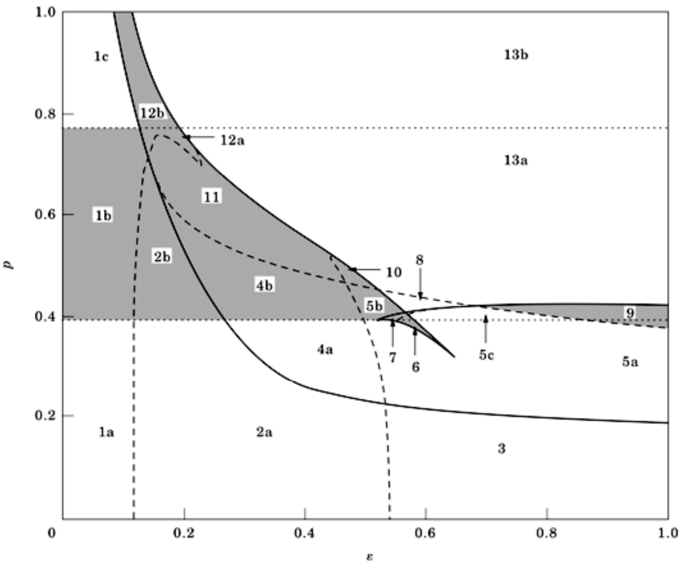

Figure A.2 Copy of Fig. 1 in van Oss & van Ooyen (1997): Regions and subregions in the (ε, p)-parameter plane. In the grey regions multistability can occur; between the dotted lines oscillations can occur. Continuous lines represent fold lines; dashed lines represent Hopf lines.