The modified model:

Each population of neurons (E, I, and M) follow this format:

$$\text{(Rate of change in activity)} = -(\%\text{ in refractory period}) + (\%\text{ at rest}) \times \text{threshold(input)}$$

The excitatory and inhibitory populations (E & I) are biophysically meaningful, so the threshold function has meaningful interpretation and is a paramterized sigmoid. The output value of the modulatory population (M) encapsulates some unknown (linear) way that the brain would manage to define the level of modulatory feedback sent to the modelled region's excitatory population with respect to a "maximum desired" level of activity E_{max}.

The inhibitory population isn't changed from the original model and goes as follows:

$$\tau_i \frac{dI}{dt} = -I + (1 - I)S_i(c_{ei}E - c_{ii}I) \tag{1}$$

With the activation function defined as:

$$S_i(z) = \frac{1}{1 + exp[-2(z - 3.7)]} \tag{2}$$

The excitatory population was changed by the addition of a modulatory term $(1 - c_m M)$ that shifts the sigmoid activation curve making the excitatory population more or less reactive to input depending on the value of the modulation intensity M. It represents, for example, dopamine binding to D1-like receptors and activating adenylyl cyclase (increasing metabolic activity), the effect is expressed here as a lowering of the threshold for the excitatory population. The parameter c_m is just to rescale the input, it defines how much the subcortical structures are able to affect the cortical dynamics:

$$\tau_e \frac{dE}{dt} = -E + (1 - E)S_e(c_{ee}E - c_{ie}I + 1.25, M) \tag{3}$$

$$S_e(z, M) = \frac{1}{1 + exp[-1.3(z - 4(1 - c_m M))]} \tag{4}$$

The dynamics of the modulatory input is defined with a linear threshold function directly proportional to the difference between the "maximum desired" level of activity E_{max} and the current level of activity of the excitatory population (E):

$$\tau_m \frac{dM}{dt} = -M + (1 - M) \cdot (E_{max} - E) \tag{5}$$

The value of τ_m is set very high to replicate the slower time scale at which modulatory (metabotropic receptors) inputs operate. The variable M does not represent a population of neurons directly but rather the output defined by some unknown process that the brain uses to decide how much modulation is needed.

Diagram of the model and table for the free (and fixed) parameters on next 2 pages.

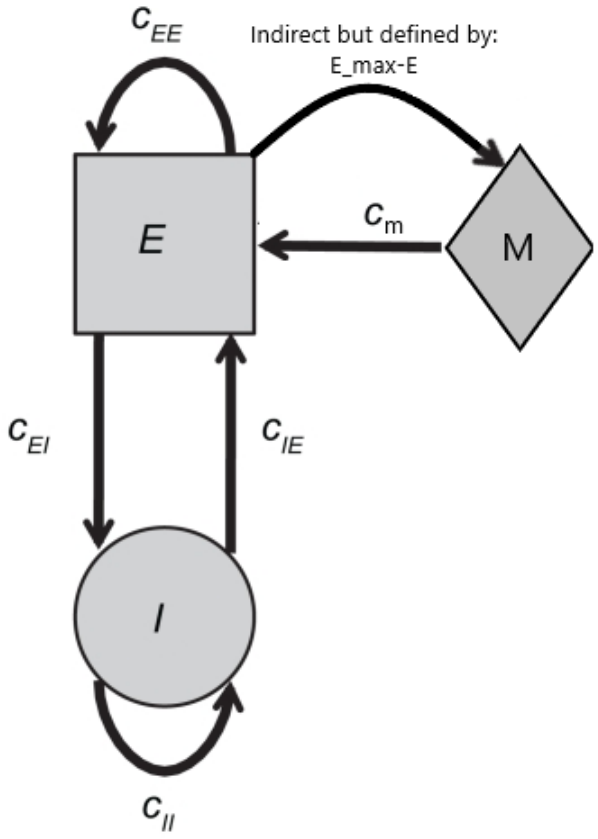

Figure 1: Diagram of the modified model

Parameter	Description
c_{ee}	Excitatory to excitatory coupling coefficient
c_{ei}	Inhibitory to excitatory coupling coefficient
c_{ie}	Excitatory to inhibitory coupling coefficient
c_{ii}	Inhibitory to inhibitory coupling coefficient
τ_e	Excitatory population, membrane time-constant (ms)
τ_i	Inhibitory population, membrane time-constant (ms)
c_m	Modulatory to excitatory coupling coefficient
E_{max}	Value of E that stops Modulatory input
$\tau_m = 100$	Modulatory input time-constant (ms)
$a_e = 1.3$	Value of the maximum slope of the sigmoid function S_e
$b_e = 4$	Sigmoid function threshold
$a_i = 2$	Value of the maximum slope of the sigmoid function S_i
$b_i = 3.7$	Sigmoid function threshold
$\theta_e = 0$	Position of the maximum slope of S_e
$\theta_i = 0$	Position of the maximum slope of S_i
$r_i = 1$	Inhibitory refractory period
$r_e = 1$	Inhibitory refractory period
$k_e = 1$	Maximum value of the excitatory response function
$k_i = 1$	Maximum value of the inhibitory response function
$\alpha_e = 1$	Balance parameter between excitatory and inhibitory masses
$\alpha_i = 1$	Balance parameter between excitatory and inhibitory masses
$P = 1.25$	External stimulus to the excitatory population
$Q = 0$	External stimulus to the inhibitory population

Table 1: Parameters for the modified Wilson-Cowan simulator