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Slave to the rhythm: Behavioral Consequences of Neural Oscillations

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Rien Sonck
Student number: 01402685

Supervisor(s): Prof. Dr. Tom Verguts, Dr. Mehdi Senoussi

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Abstract

Implementing flexibility mechanically has been a key computational issue in the cognitive control literature. To achieve this, Verguts (2017) developed a model of cognitive control based on oscillatory mechanisms. This model employs “binding by random bursts”, a combination of two principles, namely, communication-through-coherence and noise-induced synchronization. Here, I provide two approaches to further analyze and explore this neural synchrony model. Both approaches make use of empirical data collected from Senoussi, Verbeke, Talsma, & Verguts (2018). The first approach explores the consequences of parameter changes on the behavior of the model, i.e. parameter space partitioning. The second approach tries to estimate parameter values by fitting the model.

Keywords: Cognitive control, neural synchrony, neural oscillations, cognitive modeling

Cognitive control is a set of flexible processes that assist us to (1) suppress or inhibit irrelevant distractors, such as task goals that are no longer relevant, (2) generating new task goals, (3) maintaining current task goals, and (4) modify selective attention based on the representation of the current goal (Gratton, Cooper, Fabiani, Carter, & Karayanidis, 2018). Those processes include task switching, response inhibition, error detection and response conflict, information updating and monitoring, and working memory (Chase, Clark, Sahakian, Bullmore, & Robbins, 2008; Eich, Rakitin, & Stern, 2016; Gianni, Papadakis, & Pirri, 2012; Miyake et al., 2000) and help us to perform well on a wide range of goal-driven tasks (see Gratton, Cooper, Fabiani, Carter, & Karayanidis, 2018 for a review).

A key issue in the cognitive control literature remains how flexibility of cognitive control, such as switching between task rules in the Wisconsin card sorting test, is mechanically implemented. As Fries (2015) noted, an important prerequisite for cognitive flexibility is having effective, precise, and selective communication between the relevant cortical areas, thus, he proposed the communication-through-coherence (CTC) hypothesis, which states that effective communication is mechanically implemented by oscillatory mechanisms, which are fluctuations of rhythmic excitability in the brain. In other words, when a presynaptic neuron wants to communicate effectively with a postsynaptic neuron, both neurons must have coherent excitability, such that excitability of the presynaptic neuron arrives at the excitability peak of the postsynaptic neuron. The phase, which is the position of an oscillation's excitability in time along a waveform circle, of both neurons must be tuned to each other. This results in a temporal coordinated window for effective, precise, and selective communication. As such, there are 'good' windows (i.e., phases) leading to an optimal communication and there are 'bad' windows (i.e., phases) leading to less efficient communication. As illustration, the PFC, which is a key structure for cognitive control (Cavanagh

& Frank, 2014; Helfrich & Knight, 2016; Miller & Buschman, 2013; Sadaghiani et al., 2012; Voloh, Valiante, Everling, & Womelsdorf, 2015) is suggested to act as a central hub, using CTC to interact with its own cortical areas to carry out cognitive control and goal-directed behavior (Helfrich & Knight, 2016). In addition, Cavanagh & Frank (2014) argued that the PFC uses frontal theta frequencies (~ 4-8 Hz), which is the rate of recurrence of a brain oscillation expressed in cycles per second i.e., Hertz, to communicate a need for increased cognitive control to other cortical areas. However, how can the PFC mechanically facilitate CTC on communicating cortical areas? One likely candidate is noise-induced synchronization (Zhou, Chen, & Aihara, 2005).

Verguts (2017) implemented both CTC and noise-induced synchronization in a computational model of cognitive control and called it “binding by random bursts”, see figure 1A. In the model, the lateral frontal cortex (LFC) tags the relevant cortical areas, then, the medial frontal cortex (MFC) sends random frontal theta bursts, signaling a need for increased control, to these areas inducing a timed endogenous phase-reset (see Voloh & Womelsdorf, 2016 for a review), resulting in coherent synchronization between the targeted cortical areas, bringing about a temporal window for effective communication. The model is coherent with the laminar cortical microcircuit structure of the neocortex by including simplified cortical columns, see figure 1B (Douglas, Martin, & Whitteridge, 1989; Schroeder & Lakatos, 2009). Those columns consist out of a rate code neuron and two-phase code neurons (one inhibitory and one excitatory). Rate code neurons receive, process, and transmit information, while phase code neurons coordinate rate code neurons to transmit information to the correct area. Therefore, when the phase-neurons of two areas are coherently synchronized, then, information between those areas is send more efficiently (i.e., CTC). To conclude, Verguts’s model of cognitive control “binding by random bursts” (BRB model) presents us a way in which we can mechanically implement flexible cognitive control using CTC and noise-induced synchronization.

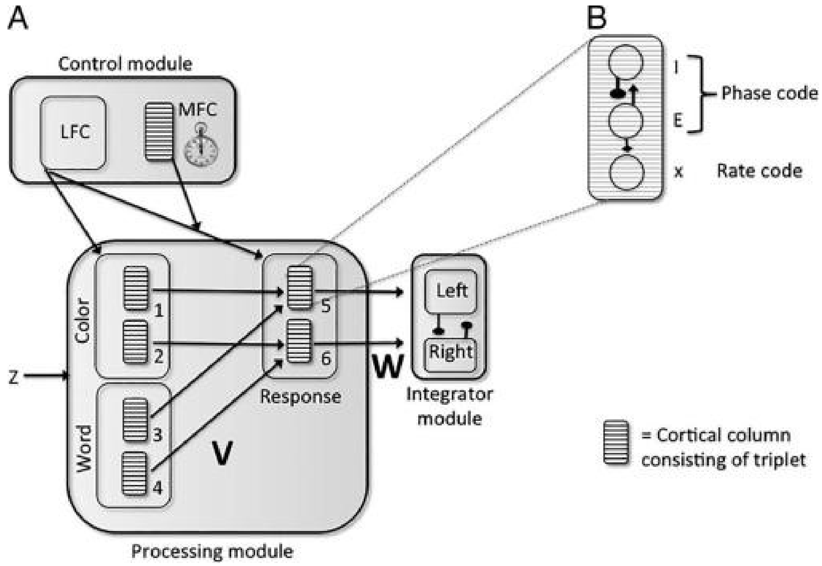

Figure 1: Computational model of cognitive control implemented for the Stroop task (Verguts, 2017).

Present Study

The goal of the current study is to broaden our understanding of the BRB model, therefore, I will use two distinct model analysis approaches to further explore and analyze the behavior of the BRB model. Both approaches use behavioral data from Senoussi, Verbeke, Talsma, & Verguts (2018) 2-AFC task (see figure 2), more information about the task is provided below. It should be noted that by using this dataset it is assumed that the oscillatory patterns in the behavioral data are a result from the underlying oscillatory mechanisms (VanRullen, 2016). First, I will use a global qualitative approach, which aim is to not only learn how representative participant behavior is to the model but also to learn the full range of behaviors that the BRB model exhibits. To achieve this, I will use parameter space partitioning (PSP, Pitt, Kim, Navarro, & Myung, 2006). PSP is a search method that helps to find all possible behaviors (i.e., predicted data patterns) of a model by searching the model's parameter space (the range of permissible values for each model's parameter). PSP allows us to find answers on the following questions: Does the BRB model generate the aggregated and individual behavior found in the behavioral data from the 2-AFC task? If so, how representative are these observed data patterns (i.e., behaviors) to the BRB model? Furthermore, does the BRB model generate any other behaviors besides mimicking the participants behavior? How representative are these behaviors to the BRB model? Second, I will use a local quantitative approach, which aim is to explore and analyze the BRB model's behavior only for its best fitting parameters, in other words, measuring how close the BRB model can mimic participant behavior on the 2-AFC task. To accomplish this, I will use explicit model fitting (see Farrell & Lewandowsky, 2018 for a review). The goodness-of-fit, how well the parameters can describe the observed participant behavior, will be calculated by using the maximum likelihood method (Cam, 2006). This will allow us to answer the following questions: How well can the BRB model mimic the average participant behavior? How well can the BRB model mimic individual behavior? By combining both previous named approaches I can perform a sensitivity analysis, examining how robust the model's behavior is to variations around the model's best fitting parameter values. To conclude, both approaches can assist us in gaining more knowledge about the behavior of the BRB model. Using this knowledge, we can then examine if it is possible to further improve the BRB model, and how we can improve the model. New versions of the BRB model can be tested against the original model by using the following model selection methods: PSP fit (Steegen, Tuerlinckx, & Vanpaemel, 2017), it compares models on their ability to described observed data patterns; AIC criterion (Akaike, 1974) and the BIC criterion (Schwarz, 1978), which estimates the likelihood of the model for a given dataset.

2-AFC task. Senoussi et al. (2018) used a 2-alternative forced choice (2-AFC) orientation discrimination task, see figure 2. During this task, two letters (R and/or L) were shown above and below a fixation cross. The letter above the fixation cross indicated to which grating the participants had to respond (either left grating or the right grating) and the letter at the bottom of the fixation cross indicated with which hand the participants had to respond (either left hand or the right hand). Next, an interstimulus interval (ISI) followed from 1700 to 2200ms, then, two sinusoidal gratings were simultaneously shown at both sides of a fixation cross and the participants had to respond using the correct hand. Furthermore, depending on the orientation of the grating clockwise or counterclockwise they had to respectively respond with the index or the middle finger of the correct hand. The results showed an oscillatory pattern of accuracy and reaction time across the ISIs. Additionally, they found that high performers showed a ~7.3 Hz theta oscillation in their accuracy across time while low performers showed a ~6 Hz theta oscillation in their accuracy across time.

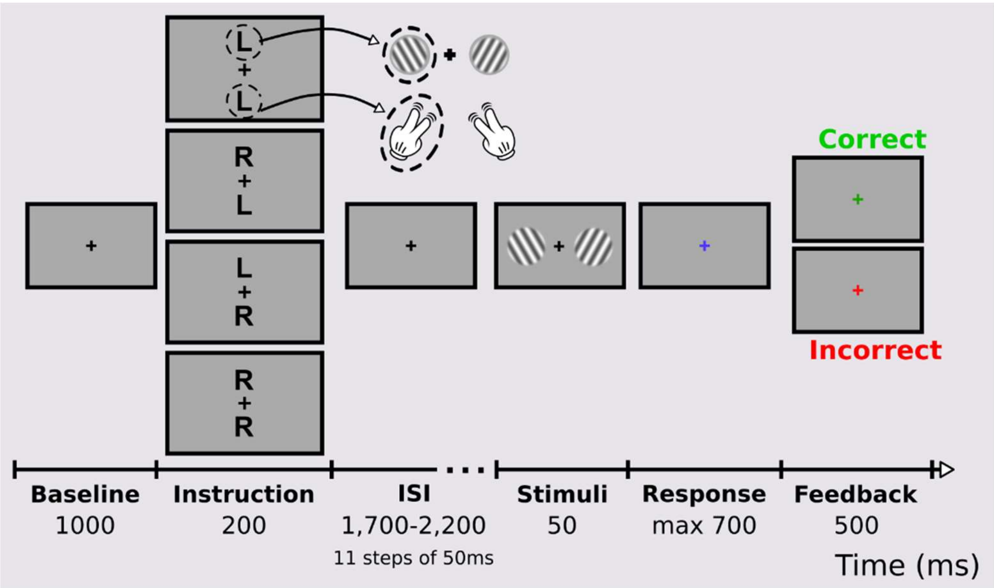

Figure 2: 2-AFC task from Senoussi et al. (2018)

Methods

Sample

The sample from Senoussi et al. (2018) contains thirty-five (18-32 years old; 25 females). They excluded six participants due to poor behavioral performance and/or excessive eye-movements.

Procedure

The BRB model is implemented using the Python programming language (https://www.python.org/), for more detailed information about the model and the upcoming formulas, see Verguts (2017).

Parameter Space Partitioning (PSP). Before using the PSP method, I will identify the model parameters that are relevant for the behavioral performance (accuracy and reaction time) on the 2-AFC task. Next, I will use PSP to examine the full range of behaviors caused by these parameters and how representative these are to the model, see Pitt et al. (2006) for a formal description of the PSP algorithm. Two parameters have already been identified by completing a parameter search. A restricted range has been imposed on the values of both parameters, see table 1, in order to be consistent with the Verguts's model. First, the noise level parameter (σ_{noise}) of the integrator module, see equation 1 and figure 3.

$$\mathrm{d}\mathbf{y}_{\boldsymbol{i}}(\mathrm{t}) = \mathbf{W}\mathbf{x}(\mathrm{t}) + \mathbf{W}_{\boldsymbol{inh}}\mathbf{y}(\mathrm{t}) + \sigma_{noise}N(t) \tag{1}$$

Second, the theta wave coupling parameter (C_t) of the MFC phase code neurons, each cortical column contains one inhibitory (I) and one excitatory (E) phase neuron, see equation 2 and 3 and figure 4.

$$dE_i(t) = -C_t I_i(t) - DJ(r > r_{min})E_i(t) + B_i(t) \tag{2}$$

$$dI_i(t) = C_t E_i(t) - DJ(r > r_{min})I_i(t) \tag{3}$$

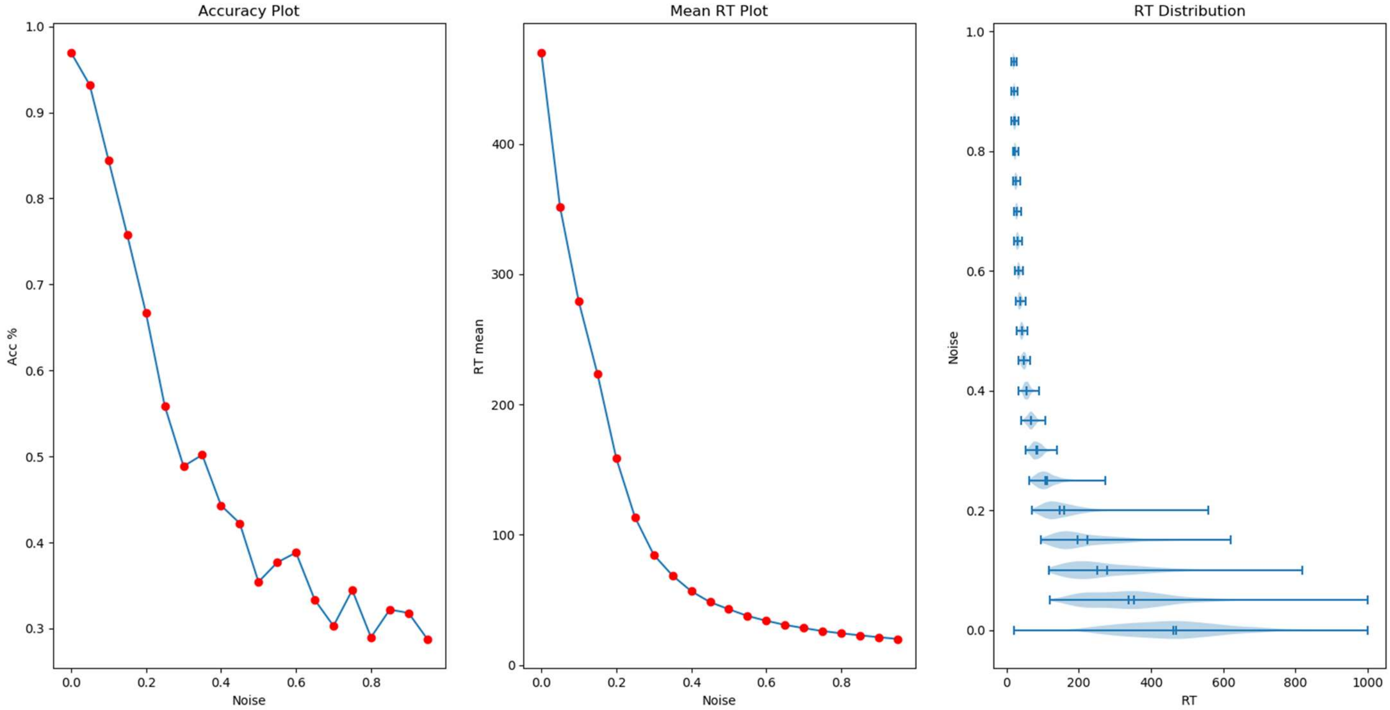

Figure 3: Parameter search for the noise level parameter (σ_{noise}), see equation 1. The plot shows the accuracy and the reaction time for a specific noise level (0.00 – 1.0) value on the 2-AFC task.

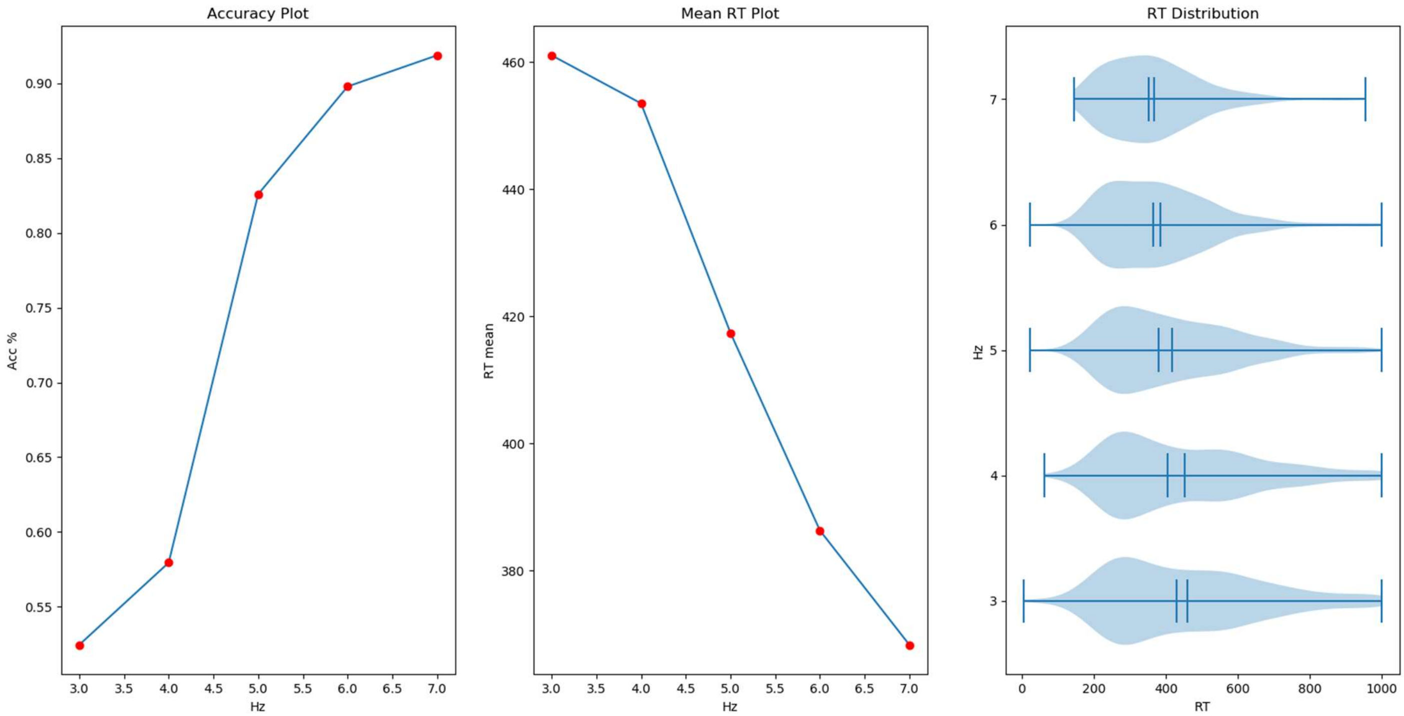

Figure 4: Parameter search for the theta wave coupling parameter (C_t), see equation 2 and 3. The plot shows the accuracy and the reaction time for a specific theta wave coupling value (3Hz – 7Hz) on the 2-AFC task.

Model fitting. The identified model parameters from the first approach, see parameter space partitioning, will be fit to the data from Senoussi et al. (2018). This will be done for each individual participant and for the aggregated data across participants. Finding the best fitting values for each parameter will be achieved by using a negative log-likelihood method, which describes the probability for the current parameter values to achieve a similar behavioral outcome as the participant(s). The log-likelihood function will be minimized using the scipy Python toolbox (https://www.scipy.org/). For each model fitting forty simulations will run, each consisting out of thirty trials (Verguts, 2017).

Table 1. Default Parameter Range of Each Identified Parameter

Parameter	σ_{noise}	C_t
Value	0.0 – 1.0	0.03-0.07 (3Hz – 7Hz)

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