Maastricht University

In Sync

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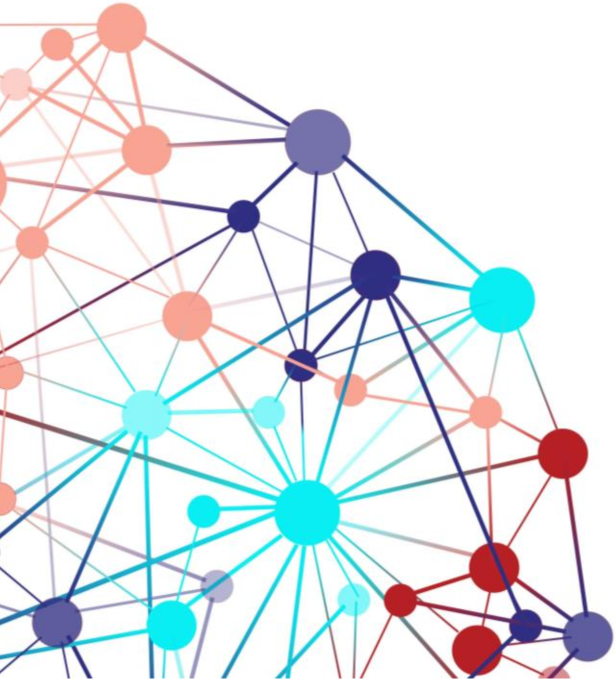


Impacts of studies in the current thesis

Oscillations are a ubiquitous phenomenon in nature, society and technology. In nature, oscillations include predator-prey population cycles (Leconte, Masson, & Qi, 2022), sea surface temperature variations (Knudsen, Seidenkrantz, Jacobsen, & Kuijpers, 2011), and climate oscillations (Mann, Park, & Bradley, 1995). In addition, oscillations play a significant role in living organisms, specifically in human and animal organs. For example, heartbeats (Ryzhii & Ryzhii, 2014), insulin concentration changes in blood (Hellman, Gylfe, Grapengiesser, Dansk, & Salehi, 2007; Lang, Matthews, Peto, & Turner, 2010), and vocal cord vibrations (Titze, 1993) are all oscillatory. Many economic and societal phenomena exhibit oscillations as well. For example, when viewed over long periods of time, prosperity in society and related parameters like unemployment tend to be cyclical (Eeckhout & Lindenlaub, 2019; Mitchell, 1941). Similarly, the development of a circular economy is based on continual recycling between raw materials and derived finished products (Mitchell, 1941). Finally, oscillations are relevant for technology, as many devices and instruments work based on rhythmicity. For example, electrical devices use alternating currents that reverse direction and change their amplitude periodically (Bhargava & Kulshreshtha, 1983). String instruments, like a guitar, produce sound as the result of the vibration in their strings (Perov, Johnson, & Perova-Mello, 2015). Quartz wristwatches, digital clocks, computers and cellphones have electronic oscillator circuits known as crystal oscillators, which keep track of time and stabilize clock signals or frequencies (Matthys, n.d.).

In addition to isolated oscillations, it is also possible to observe systems of coupled oscillators. Whenever a group of oscillators interacts, synchronization can arise (Pikovsky, Rosenblum, Self, & 2001, 2003). This insight occurred to Christiaan Huygens (1629-1695) in the 17th century when he observed that two pendulum clocks suspended from the same beam synchronize (Huygens & Oscillatorium, 1986). Huygens’ observations are in line with the more recently formulated theory of weakly coupled oscillators (TWCO). TWCO describes the rules according to which two or more oscillators interact with each other.

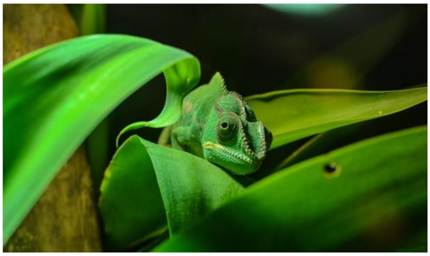
In the present thesis, we used a simple, yet well-defined formulation of TWCO known as the Kuramoto model (Ermentrout, Park, & Wilson, 2019) to study how synchronization arises in neural networks. In particular, we used the Kuramoto model to investigate the factors that determine the size and number of clusters of synchronized (integrated) and unsynchronized (segregated) neuronal groups. We showed that structural characteristics of neural networks (like synaptic strength and conductivity) can interact with the functional segregation of networks and demonstrated how external influences (visual stimuli) affect integration and segregation in behavioural experiments. We found that TWCO was a powerful framework to understand and predict our observations. According to the principles of TWCO, depending on how the oscillations evolve, different functionally segregated networks can form very quickly. Because of this flexibility, oscillations are thought to play a major role in cognition. One's ability to switch quickly from one thought to another may be intimately related to oscillatory mechanisms, and to the ability to quickly change functional networks through synchronization mechanisms. At the same time, specific aspects of the hardware design of the network can influence how likely it is that a large neural network will segregate into smaller ones, all showing their own local synchronization around their own synchronization frequency.

The relationship between oscillations and cognition suggests that aberrations in neural oscillations may be linked to psychiatric disease. Neuroscientific studies have indeed revealed that many mental diseases and disorders, such as major and bipolar depression (Canali et al., 2015; Fitzgerald & Watson, 2018; Linkenkaer-Hansen et al., 2005), obsessive-compulsive disorder (Min, Kim, Park, & Park, 2011), schizophrenia (Canali et al., 2015; Chung, Geramita, & Lewis, 2022; Shin, O'Donnell, Youn, & Kwon, 2011), spatial attentional deficits (Banerjee, Snyder, Molholm, & Foxe, 2011), post-traumatic stress disorder (Popescu et al., 2019; Reuveni et al., 2022) and epilepsy (Lehnertz et al., 2009; Traub & Wong, 1982) are related to abnormalities in ongoing interactions within and between oscillating networks in the brain, which either impede desired synchrony or give rise to undesirable synchronization patterns. The insights afforded by the present thesis may thus not only provide a better understanding of information processing in healthy brains but may also be exploited for clinical applications. In Chapter 2 of the present thesis, we showed that plastic delays can significantly alter the spread of synchrony across a network of oscillators. This might be relevant for computational models of epilepsy that are being used to identify epileptogenic zones of drug-resistant epilepsy patients in order to provide targets for surgery (Jirsa et al., 2017; Olmi, Petkoski, Guye, Bartolomei, & Jirsa, 2019; Proix, Bartolomei, Guye, & Jirsa, 2017; Proix, Jirsa, Bartolomei, Guye, & Truccolo, 2018). The effects of delays on synchrony as well as synchrony-induced changes of delays described in the second chapter provide additional insights that might improve the fidelity of epilepsy models and hence render them more accurate in identifying epileptogenic zones. This might render them safer and thus useful to a larger patient population. Beyond physically removing a source of pathological synchronization, synchronization states can also be modulated by external interventions. Transcranial alternating current stimulation (tACS) (Elyamany, Leicht, Herrmann, & Mulert, 2020) or high-frequency repetitive transcranial magnetic stimulation (rTMS) (Zrenner et al., 2020) can help to treat or control some of the mentioned mental diseases (e.g. major depression, obsessive-compulsive disorder, schizophrenia, spatial attentional deficits). In such treatments, the repetitive synchronization of neural oscillations in selected functional systems with electrical pulses modulates these selected neural networks, which results in plastic changes, of which positive therapeutic outcomes have been documented (Elyamany et al., 2020; Zrenner et al., 2020). Insights gleaned from Chapter 2 may provide a better understanding of plastic changes and their implications.

The previous paragraphs already showed that external influences (e.g. TMS pulses) and ensuing changes in neural network structure modulate neural oscillations and synchrony in the brain to a significant degree. In the present thesis, we focused on a related finding, which is that neural oscillations in the visual cortex depend on visual stimuli in the outside world. Remarkably, stronger stimuli (e.g. moving faster, or having greater contrast) produce faster oscillations in visual neurons. This is an important finding, as it suggests that local contrasts in an image will help in determining which parts in an image belong together and which parts do not. TWCO hence is useful to understand how a figure is perceptually segregated from the background, but, conversely, it can also be used to understand situations in which figure-ground segregation is unsuccessful.

In Chapters 3 and 4, we have experimentally investigated the effects of the stimulus-dependence of oscillations on visual perception. We used a computational model rooted in TWCO to predict which areas in a stimulus would be perceived as separate from others in figure-ground segregation experiments. The computational model consisted of a network of connected oscillators, in which each oscillator corresponds to a small pool of neurons receiving input from a given receptive field (RF). In this computational model, we used additional knowledge about V1, specifying that more distant neurons have weaker connections, and specifying that RF stimuli would produce higher-frequency oscillations the higher the local contrast of the stimuli. Second, we used the TWCO principles specifying that neuronal populations (oscillators) that can influence each other more effectively (coupled by stronger connections) and neuronal populations (oscillators) that are stimulated with stimuli generating more similar oscillation frequencies, would be more likely to reach synchronization. This computational network, which incorporated V1 architectural knowledge and TWCO principles, was able to predict whether human observers would be able to see one specific texture as different from another texture in experimental stimuli. Specifically, whenever the V1 neural network model converged to two different synchronization states in response to different areas in a large texture stimulus, human observers would also *perceive* these texture differences.

This view on figure-ground segregation, aside from providing insight into a set of mechanisms giving rise to the distinct perception of objects in the visual field, provides an interesting perspective on visual tricks in nature, such as camouflage. Camouflage in prey or predator animals is a functional form of unsuccessful figure-ground segregation that can be understood in the TWCO framework. Many animals use camouflage to merge with their background and to hide from their predators and/or prey[39,40]. Our findings suggest that animals can blend in with their surroundings because neuronal groups whose receptive fields fall on the animal will synchronize with those neuronal groups whose receptive fields fall on the surroundings because they receive highly similar low-level features. A deeper understanding of the contribution of oscillations and synchrony to successful and unsuccessful figure-ground segregation may thus prove relevant not only to vision neuroscientists but also to evolutionary ecologists interested in the competing evolutionary drives for better camouflage and the ability to see through this camouflage.



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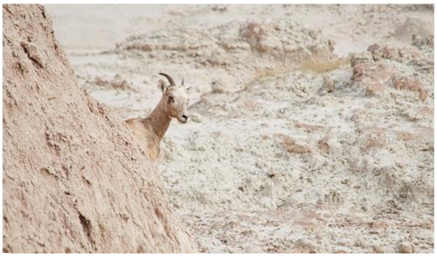

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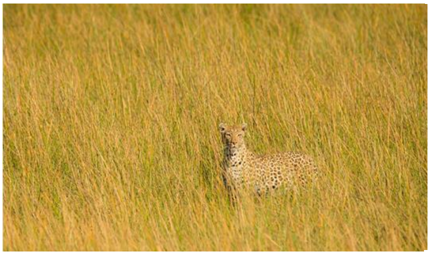

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Animal camouflage

Insights from the third and fourth chapters on how oscillations and synchrony contribute to figure-ground segregation (a form of image segmentation) are not only relevant for biological but also for computer vision. There is a growing interest in neuromorphic, and in particular, oscillation-based computing (Csaba & Porod, 2020). In particular, spin-torque nano-oscillators (STNOs) are a developing technology for oscillation-based computing that is very energy efficient, noise tolerant and has promising applications in technologies that heavily rely on computer vision, such as in self-driving cars. The reliability of self-driving cars depends on the accuracy and time-efficiency of decision-making processes, which, in turn, depend on the precision of information received by sensors of the surrounding environment. Visual signals comprise a large proportion of this information. Hence, self-driving cars need to perform fast and efficient analysis of visual signals while minimizing battery use. In particular, self-driving cars need to continuously perform segmentation on the stream of incoming images (Sellat et al., 2022). The results of Chapters 3 and 4 provide insights into how image segmentation may be achieved by networks of oscillators that may prove relevant for the development of networks of coupled STNOs specifically dedicated to this task. Importantly, the present thesis also provides insights on how a form of (tri-factor) biological reinforcement learning can be utilized to improve figure-ground segregation and, by extension, image segmentation. These insights might be exploited for the development of systems that are capable of continuously adjusting their performance based on past experience.

To summarize, oscillations and synchronization are essential to normal cognition and perception and understanding the precise role of these phenomena may pave the way for new technological developments. Furthermore, tracking as well as manipulation of oscillations and synchronization in the brain may help in alleviating pathology in brain function and mental disease. Novel insights gained from the results presented in the present thesis have the potential to contribute to further improvement of both brain-inspired technology and healthcare.

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