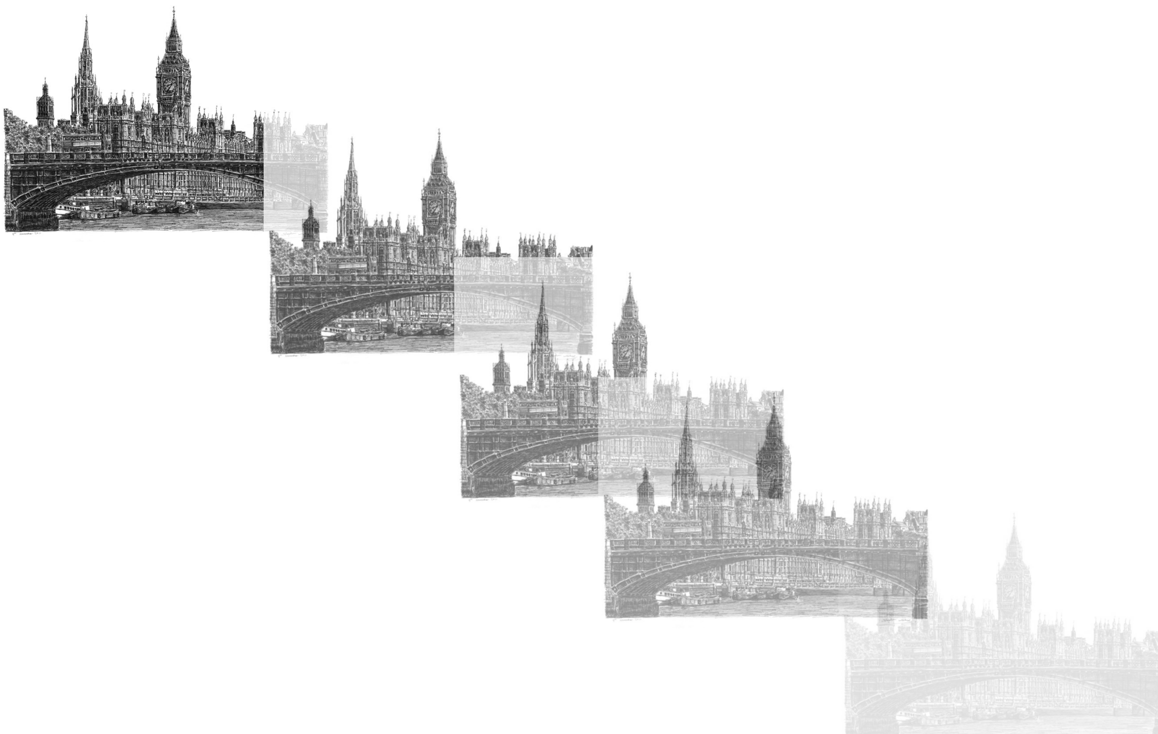
Visual echoes of Iconic Memory



Honours thesis

Author: Ties van Rozendaal
Supervisor: Dr. I.G. Sligte

Submitted: July 3rd 2013

GRANT APPLICATION 2013

1. Applicant

[Omitted]

2. Title

English: Visual echos of Iconic Memory

Dutch: De Echoes van fotografisch geheugen

3. Summary (237 words / max. 250 words)

Some savants can remember images with extreme precision, as if their memory has photographic quality. In fact, all humans have photographic memory, but it only lasts for up to a second and it is called Iconic Memory (IM). Recent research suggests that this memory might work by rhythmic reactivation of the visual image to remember. It was demonstrated that visual stimuli evoke electrical echoes in the brain. These echoes occurred at a very specific frequency (10 Hz; alpha). Many different theories about the function of alpha waves have been proposed, but the current consensus about alpha is that it orients the brain to a more internal state. Low alpha is associated with perception of new information while high alpha is required to focus on internal information. This raises the hypothesis that IM is maintained by echoes at the alpha frequency. To test this hypothesis a new method will be used to estimate the duration and capacity of iconic memory. Experiments using EEG will reveal how alpha oscillations relate to IM. In addition, alpha oscillations will be actively manipulated, using flickering stimuli and a new technique called tACS. tACS is able to modify neural processes by injecting electrical oscillations. We expect that iconic memory will be boosted when the rhythm of stimulation corresponds with the rhythm at which it naturally echoes (alpha frequency). This will prove the hypothesis that alpha echoes are the neural basis of iconic memory.

4. Keywords

Iconic Memory, Alpha Rhythms, Reverberation, Internal Representations, Alpha Echoes, Attention.

5. Research topic (832 words / max. 1300 words)

When we close our eyes and try to remember what we just saw, our memory decays very fast. After a few seconds, we are only able to recall the basic elements of this mental image. Initially, our memory is very detailed, almost like photographic memory. This brief yet comprehensive form of visual memory is called Iconic Memory (IM) and it is still a hot topic of research since its discovery in 1960 (Sperling, 1960).

A powerful and often-used paradigm to examine visual memory is the change detection task where subjects have to memorise a briefly shown array of multiple stimuli. After a short retention interval, a probe stimulus is shown one of the positions of the array. This probe stimulus is either the same as the memory stimulus at that position, or different. The detection rate of the change multiplied by the number of the memory array is a measure for memory capacity (Cowan, 2001). Performance at the change detection task is remarkably increased when subjects are instructed about the probe location, even during the retention interval (when the memory array has disappeared). This improvement is most effective when the cue is presented up to 0.5 seconds after disappearance of the memory array (Sligte et al., 2008; Sperling, 1960). However, when the cue is presented after the probe display, it is not effective at all (Landman et al. 2003), since the probe stimulus then overwrites iconic memory. While we know a lot about the dynamics of Iconic Memory, its neural mechanism is still a big mystery.

Iconic memory might be mediated by reverberation of sensory information through a neuronal loop. The thalamo-cortical loop is a very plausible mechanism for reverberation of visual information. The connections of the posterior part of the thalamus, the pulvinar, form a loop with the (visual) cortex (Jones, 1985) and electrical stimulation of anesthetised animals induces echoes of the signal, mainly at alpha frequency (Chang, 1950; Lopes da Silva et al., 1980). Although this is electrophysiological evidence for thalamo-cortical loops at alpha frequency, it does not proof that this is the mechanism of IM. A recent study did demonstrate that visual stimuli cause reverberations at alpha frequency for the first second after their appearance (Van Rullen et al. 2012). Participants viewed flickering stimuli while their EEG was recorded. Cross-correlation of the stimulus signal with the EEG revealed an electrical echo of the visual signal in the EEG, mainly at a delay of 0.5-1 second. Power analysis of this correlation revealed that especially aspects of the stimulus signal within the α-frequency (8-12 Hz) were strongly represented in the EEG. As this delay of 0.5-1 seconds is highly consistent with the duration of iconic memory, reverberation of sensory information at alpha frequency might be a plausible mechanism for iconic memory representation.

The current consensus about alpha is that it orients the brain towards an internal brain state. Perception of subliminal stimuli is correlated negatively with occipital alpha power (Ergenoglu et al., 2004; van Dijk et al. 2008). In addition, alpha power is elevated in a hemisphere that supresses incoming visual information (Sauseng et al. 2009). Alpha is not only associated with decreased perception, but is also elevated during the retention period in memory tasks, suggesting involvement in keeping the information online (Jensen 2002; Busch, 2003). The view of alpha-reverberations as a mechanism of iconic memory is thus consistent with evidence of alpha as a marker of internal oriented brain states.

More causal evidence was obtained by stimulating the visual cortex at different frequencies using rhythmic Transcranial Magnetic Stimulation (rTMS) (Romei et al., 2010). In line with the proposed hypothesis of alpha reverberation, only rTMS at alpha frequency resulted in impaired visual detection while beta and theta did not. Although this is evidence for decreased perception, it does not confirm increased internal processing. Furthermore, effects of TMS are strongly localised, while the alpha rhythm usually affect large parts of visual cortex. An innovative technique to modulate brain activity more globally is transcranial Alternating Current Stimulation (tACS) (Neuling et al., 2012), where an alternating current is applied over the scalp. This technique has recently been developed and already many studies have provided proof of principle. The finding that tACS at certain frequencies results in perception of phosphenes demonstrates that tACS is able to modulate visual processing (Laczo et al, 2012). Furthermore, tACS at alpha frequency enhances alpha power in the EEG (Zaehle, 2010). Using tACS, alpha oscillations in the human brain can be manipulated to investigate their role in iconic memory.

To investigate the hypothesis that alpha reverberations serve as a mechanism for sensory memory, a series of experiments will be conducted. In all these experiments, both capacity and duration of IM will be estimated using a innovative method. To examine the hypothesis, we will first investigate how alpha oscillations change during iconic memory and how these changes relate to capacity and duration. Next, alpha oscillations will actively be manipulated using entrainment and tACS to provide more causal evidence for the proposed hypothesis.

6. Approach (1234 words / max. 1300 words)

General

The basic paradigm used to estimate capacity and duration of IM will be the same in all experiments. In each experiment, 40 subjects will participate. Participants will perform a regular change detection task (Figure 2A) in which set size and cue delay are controlled by performance-fixed staircases.

The data is analysed by plotting the cue latency as a function of the performance (expressed in capacity). A curve will be fit to this scatterplot to estimate the dynamics of IM for each participant in each experimental setting (Figure 1).

The dynamics of this curve can be expressed in terms of two parameters: capacity and duration. Capacity is defined as the capacity at a cue delay of 0 ms (Figure 1A) and the duration is defined as the delay at which the minimum capacity is reached (Figure 1B).

This approach describes the complex dynamics of IM in terms of just two parameters, which are easy to compare between participants and experimental conditions. Next to this, relatively few trials are necessary to estimate them.

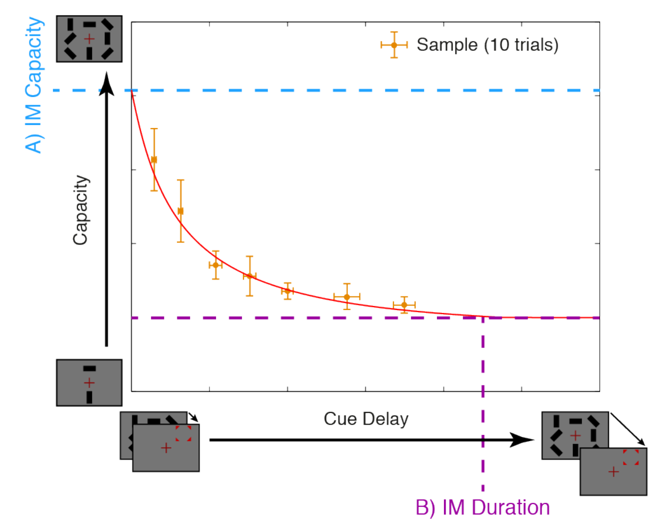


Figure 1: Method to estimate IM capacity and duration. See Figure 2 for the paradigm. Cue delay and set size will be varied according to performance. Each point is a sample of 10 trials. The mean cue delay and capacity are plotted for each sample and an IM function is fitted. Capacity is defined as the IM(0) and duration is defined as min(IM).

According to the hypothesis of alpha reverberations, alpha power will increase after presentation of the memory stimulus, as its representation will now be internal (Figure 2B). After a response has been made, the stimulus will not have to be represented internally anymore and alpha will drop. As high alpha results in low perception of novel information, low pre-stimulus alpha is thought to predict better performance and thus, higher capacity (Figure 2B).

Experiment 1: The dynamic relationship between alpha oscillations and Iconic Memory (EEG)

In the first experiment, the effect of pre- and post-stimulus alpha on IM will be examined to investigate the relationship between alpha power and brain state (internal/external).

EEG will be measured and 500 ms epochs will be used for data analysis (figure 2C). To investigate the effect of alpha power on iconic memory, the relevant epochs will be split into a high alpha and a low alpha group, based on mean alpha power during the epoch. The capacity and duration of IM will be calculated for trials of the high-alpha and low-alpha group separately using the method described above.

It is expected that low pre-stimulus alpha will result in IM with a low capacity, as the brain state during the memory array is less external.

To examine the dynamics of alpha power during iconic memory, pre-stimulus alpha is compared with post-stimulus and post-response alpha. It is expected that post-stimulus alpha is elevated compared with pre-stimulus and post-response alpha (Figure 2B).

To examine the effect of alpha dynamics on IM performance, the '*alpha response'* is calculated by dividing post-stimulus alpha with pre-stimulus alpha for each trial. The alpha response trials will be split into a high and low alpha response group, and capacity and duration are calculated.

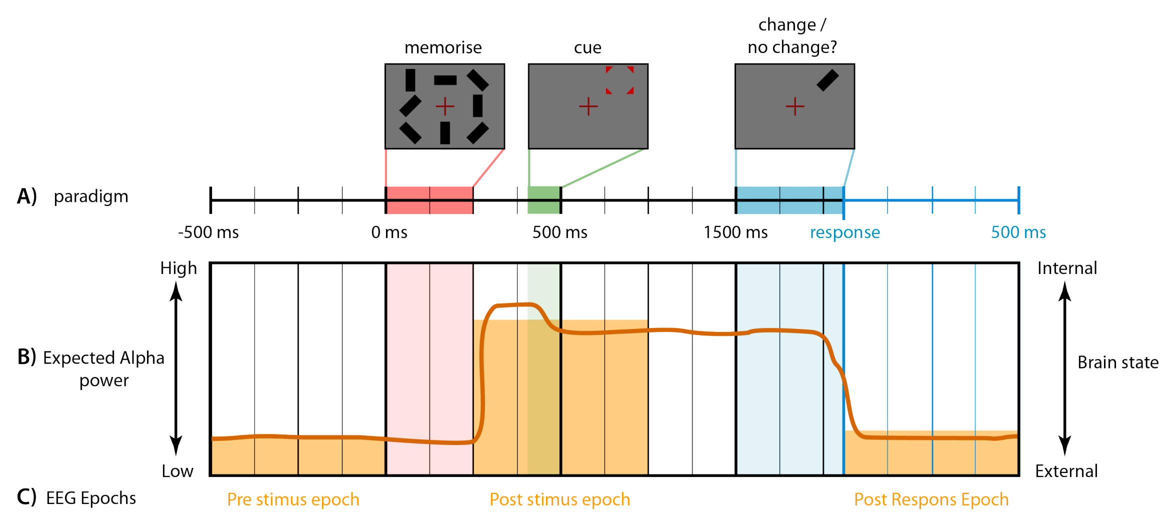


Figure 2: Basic Paradigm and expected results. The orange line indicates expected alpha power for efficient IM with a high capacity and duration. The EEG Epochs illustrate the 500 ms epochs used in experiment 1. It is expected that low pre-stimulus alpha, and high post stimulus alpha will result in IM with a high capacity and duration.

It is expected that a high alpha response will result in a high capacity and duration of IM.

Finally, we will test if there is a correlation between alpha response and IM capacity or duration. It is expected that both capacity and duration will correlate positively with alpha response as an increased alpha response strengthens the internal representation.

Experiment 2: The effect of timing of alpha stimulation on Iconic Memory (behavior)

To investigate the causality of the effect of alpha on Iconic Memory, alpha power will be manipulated by flickering frames. The frames will be used to entrain specific frequencies and will be presented 2 seconds before or after the memory stimulus (similar to the EEG epochs of experiment 1). A frame containing flicker in the alpha band (8-12 Hz) will be used to entrain alpha rhythms. To control for the general effect of flickering frames, a random-noise condition is included, containing flicker of all frequencies (figure 3A). This random-noise stimulus also contains alpha flicker and vanRullen et al. (2012) demonstrated that it is these alpha aspects of random noise, that are best picked-up by the brain (figure 3B). Therefore, a second control condition will be introduced, alpha-free random noise. The frame in this condition will flicker at all conditions except at alpha frequency (similar to vanRullen et al., 2012 figure 3).

The use of these three conditions creates the possibility to proof both necessity of alpha (alpha-free random noise vs. random noise) and the sufficiency (alpha vs. random noise) of alpha for a good iconic memory.

It is expected that random noise entrainment will have similar effects as alpha entrainment, as both conditions amplify alpha.

Pre-stimulus alpha entrainment is expected to orient the brain state more internally and result in a decreased IM capacity (due to decreased perception) with respect to alpha-free entrainment. Post-stimulus alpha entrainment, on the other hand, is thought to mediate internal processing resulting in a higher IM capacity and duration with respect to alpha-free entrainment.

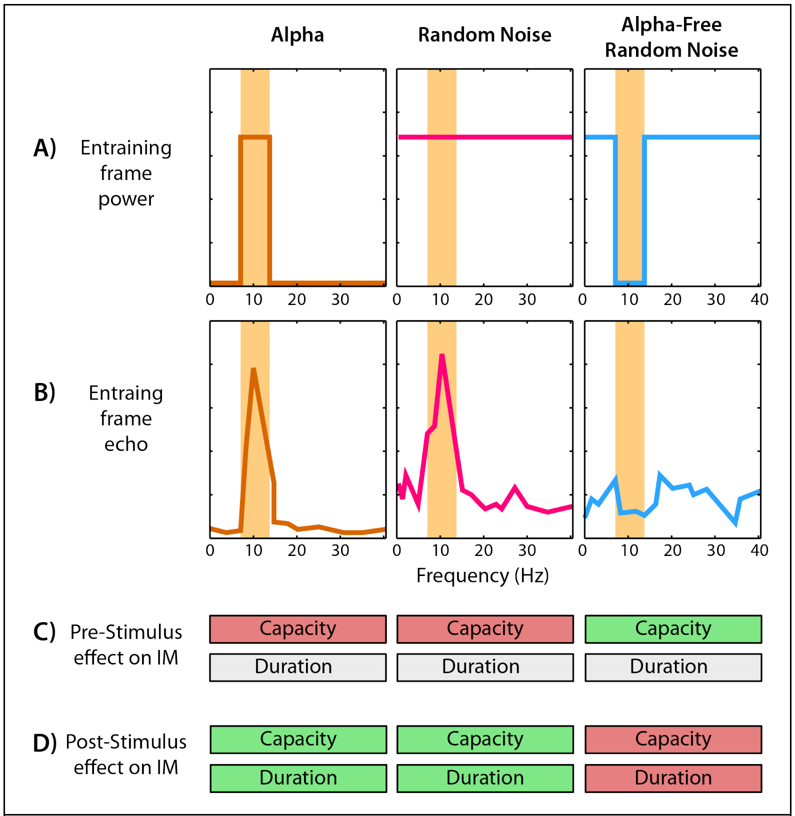


Figure 3: The Frequencies of the entraining frames (A), their expected electrophysiological echoes in the brain (B) and their expected effects on IM (C/D).

Experiment 3: The global effect of alpha stimulation on Iconic Memory (tACS)

To investigate the global effect of alpha stimulation on Iconic Memory, alpha power will be manipulated using tACS. Subjects will perform 6 blocks of the change detection task while they receive tACS at different frequencies. Sham and Theta tACS will be used as a control for frequency-unspecific effects and will be compared to sham. It is expected that alpha tACS will increase duration (due to increased post-stimulus alpha) and decrease capacity (due to increased pre-stimulus alpha) compared with theta and sham.

Experiment 4: The effect of timing of alpha stimulation on Iconic Memory (tACS)

To further explore the effects of tACS found in experiment 3, the effect of pre-stimulus alpha and post-stimulus alpha stimulation on IM will be examined. Alpha or sham stimulation will be applied for 2 seconds either pre-stimulus or post-stimulus (Figure 2C). The stimulus presentation software will trigger the tACS device. It is expected that post-stimulus alpha stimulation will enhance capacity and duration of IM compared with post-stimulus sham stimulation. For pre-stimulus stimulation, it is expected that alpha stimulation will result in decreased capacity compared with sham and will not affect duration.

Planning

Experiment 1	
Experiment 2	
Experiment 3	
Experiment 4	

First Year	1	2	3	4	5	6	7	8	9	10	11	12
Pilot Testing												
Data collection and analysis												
Prepare Manuscripts												
Second Year	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Pilot Testing												
Data collection and Analysis												
Prepare Manuscripts												
Third Year	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Pilot Testing												
Data collection and Analysis												
Prepare Manuscripts												
Fourth Year	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Data collection and Analysis												
Prepare Manuscripts												
Control Experiments / finalisations												

7. Requested support (max. € 250.000,- in total)

A. Personnel:			**€225.000**
PhD student	*4 years*	*fulltime*	*€175.000*
Research assistant	*4 years*	*2 days/ week*	*€50.000*
B. Subjects:			**€3.600**
	compensation	*participants*	*Cost*
Experiment1	€30	*40*	*€1200*
Experiment2	€20	*40*	*€800*
Experiment3	€20	*40*	*€800*
Experiment4	€20	*40*	*€800*
C. Consumables			**€2.200**
Electrodes and Gel:			€200
EEG Sessions			€2000
D. Equipment			**€12.740**
tACS Device:			€8000
Computer equipment			€2500
Stimulus presentation Software			€240
Analysis software			€2000
Total Requested Support			**€243.540**

8. Concise justification of requested support for personnel, animals and consumables

In order to finish the data collection of all the projects in time, a research assistant is needed 2 days a week. The university will provide a PhD student with matching. Participants get paid €10 per hour.

9. Aspects relevant for a DEC (animal experiments) or a MEC (human subjects)

Transcranial Direct Current Stimulation (tDCS) and transcranial Alternating Current Stimulation (tACS) are forms of electrical neurostimulation. Two or more electrolyte sponges are placed on the skull, and a current will flow between the two electrodes, modifying ongoing electrical and chemical activity in the brain. Tingling and burning sensations as well as nausea and mild to severe headaches are reported side effects. An important factor for side effects is the current density and skin conductance. When one of these two is high, subjects will feel a burning sensation. When both are low, subjects will feel virtually nothing. The skin conductance is dependent of skin- and hair type and cannot be changed. The current density is defined as the current divided by the surface of the electrodes. The current density we will use in this experiment is 42,9 μA/cm2, which is well below the average of 65,38 μA/cm2. Only two other experiments with tACS of 1,5 mA were conducted. However, subjects reported no side effects in one experiment, (Feurra et al., 2011) and only mild headaches in the other (Laczo et al., 2012).

Application of tDCS results in altered neurotransmitter concentrations (Stagg et al. 2009) and has effects up to 13 min (Nitsche et al, 2001). tACS has only recently been used but no other side effects than tDCS are known and the measured effects disappear quickly after offset of stimulation.

10. Signature of the applicant

[omitted]

11. Popular abstract for lay people (in Dutch, max 250 words)If granted, this description will be used for communication in Dutch, also to non-specialists.

Mensen met een fotografisch geheugen kunnen als ze één keer iets zien, dit tot in detail onthouden. Wat veel mensen niet weten is dat iedereen over zo’n fotografisch geheugen beschikt! Het heet iconisch geheugen, en duur maar heel kort, een seconde ongeveer. Er is niet veel bekend over hoe dit fascinerende geheugen werkt, maar recent onderzoek lijkt te suggereren dat het beeld wat we zien als het ware door ons hoofd heen echoot. Om deze theorie te testen worden de hersenen gestimuleerd met ritmische elektrische pulsen. Als iconisch geheugen inderdaad door een visuele echo tot stand komt, betekent dit dat we dit geheugen kunnen verbeteren. Door het ritme van de elektrische pulsen overeen te laten komen met dat van de echo word het geheugen als het ware versterkt en blijft je fotografische geheugen langer door werken. Want zeg nou zelf, een fotografisch geheugen, dat wil toch iedereen!

References

- Busch, N. A., & Herrmann, C. S. (2003). Object-load and feature-load modulate EEG in a short-term memory task. *Neuroreport*, *14*(13), 1721-1724.
- Chang, L. C., & Read, T. A. (1950). *PLASTIC DEFORMATION AND DIFFUSIONLESS PHASE CHANGES IN METALS THE BOLD-CADMIUM BETA PHASE* (No. NYO-755). Columbia University.
- Cowan, N. (2001). The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and brain sciences*,*24*(1), 87-114.
- Ergenoglu, T., Demiralp, T., Bayraktaroglu, Z., Ergen, M., Beydagi, H., & Uresin, Y. (2004). Alpha rhythm of the EEG modulates visual detection performance in humans. *Cognitive Brain Research*, *20*(3), 376-383.
- Feurra, M., Bianco, G., Santarnecchi, E., Del Testa, M., Rossi, A., & Rossi, S. (2011). Frequency-dependent tuning of the human motor system induced by transcranial oscillatory potentials. *The Journal of Neuroscience*, *31*(34), 12165-12170.
- Jensen, O., Gelfand, J., Kounios, J., & Lisman, J. E. (2002). Oscillations in the alpha band (9–12 Hz) increase with memory load during retention in a short-term memory task. *Cerebral Cortex*, *12*(8), 877-882.
- Jones, E. G. (1985). *The thalamus* (p. 935). New York: Plenum Press.
- Laczó, B., Antal, A., Niebergall, R., Treue, S., & Paulus, W. (2012). Transcranial alternating stimulation in a high gamma frequency range applied over V1 improves contrast perception but does not modulate spatial attention.*Brain Stimulation*, *5*(4), 484-491.
- Landman, J., Venkatesh, R., Lee, D., Vanlangendonck, R., Morissey, K., Andriole, G. L., ... & Sundaram, C. P. (2003). Renal hypothermia achieved by retrograde endoscopic cold saline perfusion: technique and initial clinical application. *Urology*, *61*(5), 1023-1025.
- Lopes da Silva, F. H., Vos, J. E., Mooibroek, J., & Van Rotterdam, A. (1980). Relative contributions of intracortical and thalamo-cortical processes in the generation of alpha rhythms, revealed by partial coherence analysis.*Electroencephalography and clinical neurophysiology*, *50*(5), 449-456.
- Neuling, T., Wagner, S., Wolters, C. H., Zaehle, T., & Herrmann, C. S. (2012). Finite-element model predicts current density distribution for clinical applications of tDCS and tACS. *Frontiers in Psychiatry*, *3*.
- Ng, S. C., Hart, A. L., Kamm, M. A., Stagg, A. J., & Knight, S. C. (2009). Mechanisms of action of probiotics: recent advances. *Inflammatory bowel diseases*, *15*(2), 300-310.
- Nitsche, M. A., Nitsche, M. S., Klein, C. C., Tergau, F., Rothwell, J. C., & Paulus, W. (2003). Level of action of cathodal DC polarisation induced inhibition of the human motor cortex. *Clinical Neurophysiology*, *114*(4), 600-604.
- Romei, V., Gross, J., & Thut, G. (2010). On the role of prestimulus alpha rhythms over occipito-parietal areas in visual input regulation: correlation or causation?. *The Journal of neuroscience*, *30*(25), 8692-8697.
- Sauseng, P., Klimesch, W., Heise, K. F., Gruber, W. R., Holz, E., Karim, A. a, Glennon, M., et al. (2009). Brain oscillatory substrates of visual short-term memory capacity. *Current biology : CB*, *19*(21), 1846–52. doi:10.1016/j.cub.2009.08.062
- Sligte, I. G., Scholte, H. S., & Lamme, V. A. (2008). Are there multiple visual short-term memory stores?. *PLOS one*, *3*(2), e1699.
- Sperling, G. (1960). The information available in brief visual presentations.*Psychological monographs: General and applied*, *74*(11), 1.
- Van Dijk, H., Schoffelen, J. M., Oostenveld, R., & Jensen, O. (2008). Prestimulus oscillatory activity in the alpha band predicts visual discrimination ability. *The Journal of Neuroscience*, *28*(8), 1816-1823.
- VanRullen, R., & Macdonald, J. S. P. (2012). Perceptual echoes at 10 Hz in the human brain. *Current biology : CB*, *22*(11), 995–9. doi:10.1016/j.cub.2012.03.050
- Zaehle, T., Rach, S., & Herrmann, C. S. (2010). Transcranial alternating current stimulation enhances individual alpha activity in human EEG. *PLoS One*, *5*(11), e13766.