British Journal of Psychology (2018)

The British Psychological Society
www.wileyonlinelibrary.com

Invited article

Does cross-frequency phase coupling of oscillatory brain activity contribute to a better understanding of visual working memory?

Paul Sauseng*, Charline Peylo, Anna Lena Biel, Elisabeth V. C. Friedrich and Carola Romberg-Taylor
Department of Psychology, Ludwig-Maximilians-University Munich, Germany

Nesting of fast rhythmical brain activity (gamma) into slower brain waves (theta) has frequently been suggested as a core mechanism of multi-item working memory (WM) retention. It provides a better understanding of WM capacity limitations, and, as we discuss in this review article, it can lead to applications for modulating memory capacity. However, could cross-frequency coupling of brain oscillations also constructively contribute to a better understanding of the neuronal signatures of working memory compatible with theoretical approaches that assume flexible capacity limits? Could a theta-gamma code also be considered as a neural mechanism of flexible sharing of cognitive resources between memory representations in multi-item WM? Here, we propose potential variants of theta-gamma coupling that could explain WM retention beyond a fixed memory capacity limit of a few visual items. Moreover, we suggest how to empirically test these predictions in the future.

Oscillatory brain activity during multi-item working memory processes

Visual working memory (WM) is understood as the function of transiently storing and manipulating visual information, such as the spatial location of visual items or their exact appearance including colour and shape (Baddeley, 2012; Cowan, 2008). Specifically, how this function is implemented in the brain has been investigated with a broad range of neuroscientific methods and approaches (see Slotnick, 2017). Thus far, it has been particularly challenging to identify plausible neuronal signatures for parallel storage and usage of multiple items in WM, as one would need to explain the simultaneous activation of several memory representations as well as binding between them, and temporo-spatial organization of a memory trace. Based on the idea that rhythmical brain activity (Buzsáki, 2006; Fries, 2015; Klimesch, Sauseng, & Hanslmayr, 2007; Mazaheri & Jensen, 2010) and the interaction between slow and fast brain oscillations might be particularly suitable for explaining a temporal code of neural activity (Jensen & Lisman, 1996, 1998; Lisman &

**Correspondence should be addressed to Paul Sauseng, LMU Munich, Leopoldstr. 13, Munich 80802, Germany (email: paul.sauseng@lmu.de).*

DOI:10.1111/bjop.12340

Idiart, 1995; Lisman & Jensen, 2013),[1] several influential models about the underlying mechanism behind WM have been put forward. These models suggest that separate memory items are represented by activity of individual subsets of neurons. Such neuronal subsets form local circuits that tend to get activated in an oscillatory fashion at fast frequencies (in the so-called gamma frequency range [>30 Hz]). Thus, each single memory item is expressed by a transient, fast wave that can be electrophysiologically recorded. As the separate neural circuits storing a memory item could each spatially overlap and even share single neurons, they need to be activated sequentially in order to preserve item identity. According to the models referred to above, this would be achieved by activating the respective neuronal subsets at different phase angles at a slower, global oscillation in the theta frequency range (4–7 Hz). In electrophysiological recordings, this is expressed by a burst of several (individual) gamma waves nested into a slower theta wave. With each new theta cycle, the same sequence of gamma waves is re-activated. This way, multiple memory items still remain distinct from each other but can be actively held in parallel in WM. Another consequence is that, of course, only a limited number of gamma waves can be nested into a theta wave. Therefore, it has been argued that this mechanism could potentially explain limited WM capacity (Jensen & Lisman, 1996; Lisman & Idiart, 1995).

Theta-gamma coupling as basis of multi-item WM in humans

In addition to computational evidence for gamma waves nested into theta cycles as a neural substrate of multi-item WM (Jensen & Lisman, 1996, 1998; Lisman & Idiart, 1995; Lisman & Jensen, 2013), there has been recent electrophysiological evidence shown in humans (Axmacher *et al.*, 2010; Chaieb *et al.*, 2015; Kamiński, Brzezicka, & Wróbel, 2011; Sauseng *et al.*, 2009; Vosskuhl, Huster, & Herrmann, 2015; Wolinski, Cooper, Sauseng, & Romei, 2018). In line with the idea that WM capacity for visual items is around four (Cowan, 2001), it was shown that parietal theta-gamma phase synchronization (as a measure of nested oscillations; Sauseng *et al.*, 2009) increased for a memory load of up to four visual items, and that this phase synchronization increase, in turn, was predictive of memory capacity (Chaieb *et al.*, 2015; Sauseng *et al.*, 2009). In another study, it was demonstrated that an increase in the number of to-be-retained visual items (faces) led to a slowing down of the theta waves into which gamma activity was nested in (Axmacher *et al.*, 2010). This suggests that more memory items, each represented by a gamma wave, require a longer theta cycle to be bound together as a multi-item memory trace. Consequently, this further implies that the length of the theta cycle (i.e., theta frequency) also defines how many items can be transiently held in memory. As evidence for that, Kamiński *et al.* (2011) were able to show that even in a resting state the frequency ratio between coupled theta and gamma oscillations was predictive of memory span. Therefore, relatively slow theta waves coupled to very fast gamma activity would imply that many separate gamma waves were integrated into one theta cycle, and consequently,

---

[1] *High-frequency rhythmic brain activity (in the so-called gamma frequency range) has been associated with neural activity on local scale but also as a signature of neuronal spiking (Buzsáki, 2006; Buzsáki & Wang, 2012). It is considered that these fast oscillations are generated by short, local circuits in the neocortex (Buzsáki, 2006). Slower brain frequencies, such as the theta rhythm (ranging between approximately 4 and 7 Hz in humans), are considered to be generated by more distributed brain networks (Mitchell, McNaughton, Flanagan, & Kirk, 2008; Raghavachari* et al.*, 2006; Sauseng, Griesmayr, Freunberger, & Klimesch, 2010) that might reinforce neocortical–hippocampal communication (Buzsáki, 2006; Mitchell* et al.*, 2008; Moore, Gale, Morris, & Forrester, 2006).*

WM capacity would be contingently higher. Two recent studies lend causal evidence to the aforementioned idea (Vosskuhl *et al.*, 2015; Wolinski *et al.*, 2018). Transcranial alternating current stimulation (tACS), a non-invasive brain stimulation technique in which weak alternating currents at specific frequencies are applied via relatively large electrodes attached to the scalp, was used to change the speed of theta frequency. Vosskuhl *et al.* (2015) slowed down theta frequency with the idea that this artificial slowing of the theta rhythm would allow an additional gamma wave to be nested into the slower theta cycle. Indeed, compared to placebo stimulation, verbal short-term memory capacity was augmented with the slowing of theta frequency. Therefore, each additional gamma wave, representing one memory item, led to a higher WM capacity. The same underlying logic formed the basis for a recent study conducted by Wolinski *et al.* (2018) using a visuospatial WM task. They delivered tACS at either a slow theta frequency (4 Hz), a fast theta frequency (7 Hz) or in a placebo condition over the right parietal cortex (Figure 1a). Wolinski *et al.* (2018) used a visuospatial WM task in which coloured squares were presented in both visual hemifields; however, in each trial, only items in either the left or the right visual hemifield had to be retained and compared to a probe (Vogel & Machizawa, 2004; Figure 1b). This allowed Wolinski *et al.* (2018) to investigate tACS-specific versus unspecific effects, as right parietal tACS should only have led to effects in trials in which coloured squares in the left visual hemifield (i.e., contralateral to stimulation) had to be retained. Indeed, the authors only report modulation of WM capacity for the visual hemifield contralateral to stimulation: Compared to placebo stimulation, tACS at 4 Hz (and thus, slower theta waves) led to increased WM capacity, whereas 7 Hz stimulation (and thus, faster waves) had a detrimental effect on WM capacity (Figure 1c). In line with the idea of a theta-gamma code as neural substrate for limitations of multi-item WM, a slower theta wave allows for more nested gamma cycles and consequently more items to be retained; faster theta waves, on the other hand, reduce the number of gamma cycles that can be fit into the slow oscillation, hence leading to reduced WM capacity.

Theta-coupled gamma bursts as memory representations

A recent theoretical framework suggests coupling of theta and gamma oscillations as the neural basis for multi-item WM retention as well (Herman, Lundqvist, & Lansner, 2013). However, in contrast to the aforementioned model (Jensen & Lisman, 1996; Lisman & Idiart, 1995), it is not assumed that separate memory items are represented by single gamma waves. Instead, it is suggested that each item is coded by an entire gamma burst, that is, multiple cycles, nested into a theta wave (Herman *et al.*, 2013; Van Vugt, Chakravarthi, & Lachaux, 2014). Consequently, only one item is coded per theta period, with multiple items retained sequentially in different subsequent theta cycles. This would imply that after a certain period of time single items would have to be refreshed (e.g., via a new gamma burst). According to Van Vugt *et al.* (2014), this re-activation of an item sequence after only a few theta cycles could be the mechanism by which WM capacity is limited. However, how could the findings reported by Vosskuhl *et al.* (2015) or those by Wolinski *et al.* (2018) be interpreted within this theoretical framework? Slowing down theta frequency (with each cycle coding one item) would imply that fewer items could be sequentially activated in a certain amount of time. Therefore, one would expect a reduction in WM capacity rather than an increase in capacity, as reported by Vosskuhl *et al.* (2015) and Wolinski *et al.* (2018). How could this divergence be explained? It is true that fewer theta cycles would fit into a certain time span if theta was

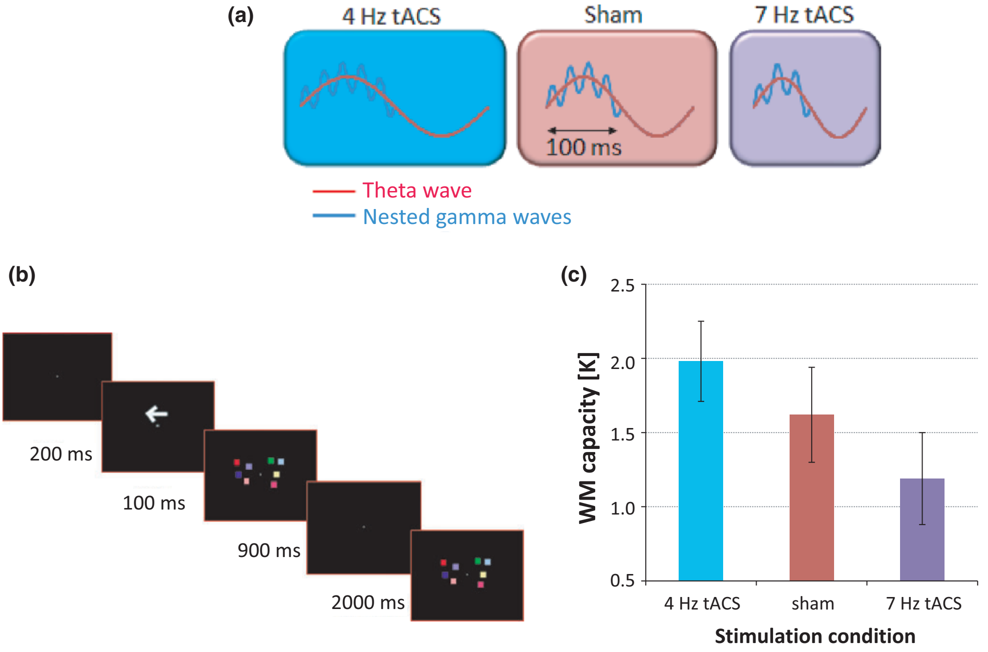

Figure 1. Modulating speed of theta oscillations leads to changes in working memory (WM) capacity. Wolinski *et al.* (2018) applied transcranial alternating current stimulation (tACS) over the right parietal cortex. (a) Slowing of theta oscillations by tACS was predicted to lead to an increase in the number of gamma waves that could be nested in a theta wave, and thus, to an increase in WM capacity when compared to a placebo stimulation. Speeding-up theta frequency, on the other hand, should have the opposite effect. (b) Visual WM was tested in a delayed match-to-sample task in which only an effect in trials that required retention of items presented in the visual hemifield contralateral to tACS (i.e., left hemifield) was expected. (c) As predicted by the idea of a theta-gamma code of multi-item WM, memory capacity was increased with slow theta tACS but decreased with fast theta stimulation compared to placebo stimulation.

slowed down. However, lengthier theta cycles would also mean a longer duration of gamma bursts. This should lead to a stronger (re-)activation of the memory item (compare Figure 2a,b).

Consequently, an increase in WM capacity as reported by Vosskuhl *et al.* (2015) or Wolinski *et al.* (2018) would mean that the gain in memory fidelity due to a stronger activation with the longer gamma burst would supersede the memory decay rate incurred by the slowing down of theta waves (causing longer intervals between phases of re-activation). In other words, the greater reliability of a given memory representation offsets the memory decay caused by the longer time intervals between re-activation of memory items (Figure 2c). However, the exact relation between these two mechanisms still remains to be empirically tested.

Working memory capacity: A discrete number or a flexible resource?

The literature discussed above and neuronal substrates of multi-item WM presented so far might suggest that WM capacity is set at a discrete, fixed number of items. This reiterates

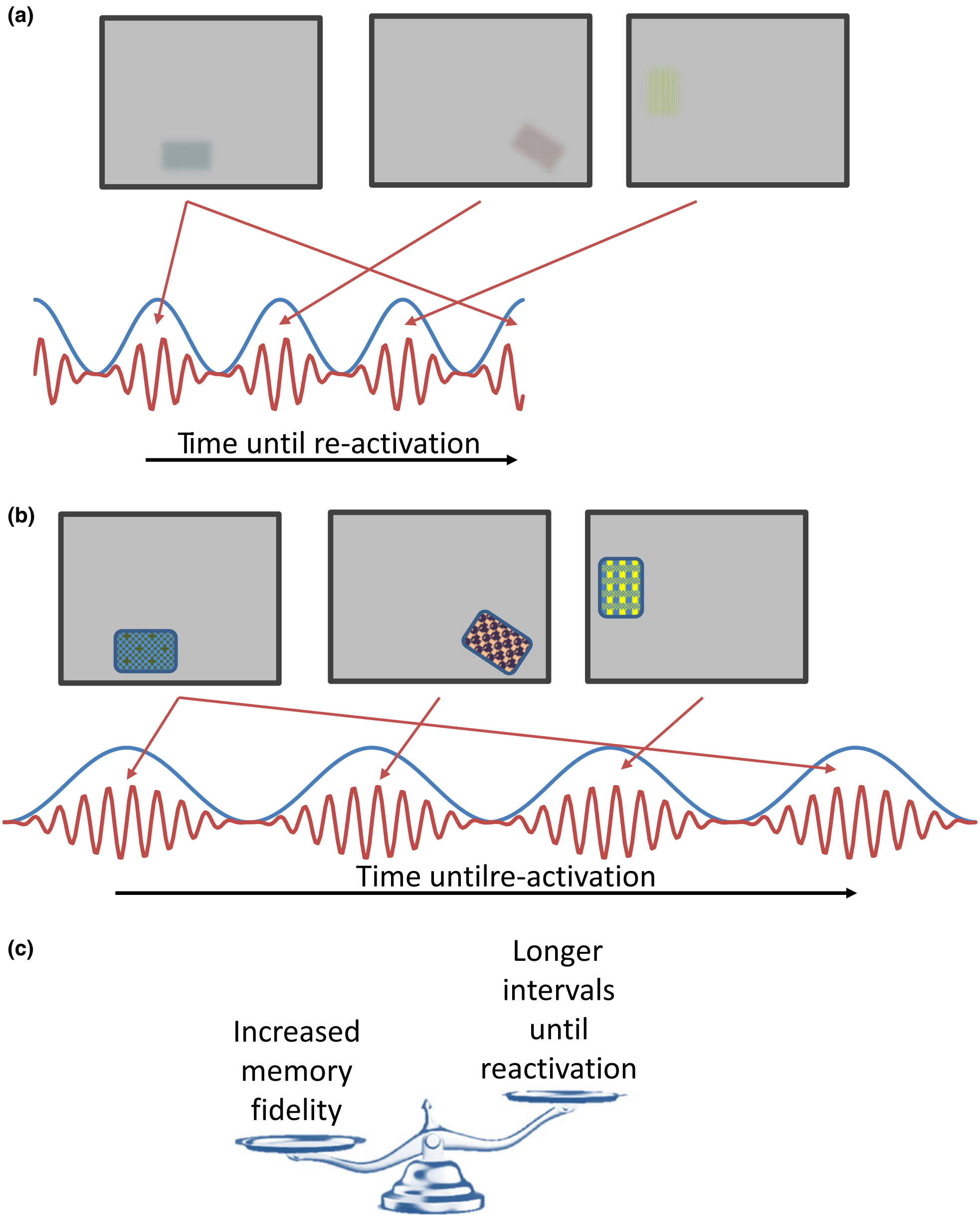

Figure 2. Theta frequency determines the length of gamma bursts and fidelity of memory items. (a) If single visual items are neuronally represented by entire gamma bursts nested into theta waves, fast theta waves will lead to relatively short gamma bursts. Consequently, representation of single items will be rather fuzzy. (b) Slow theta waves, on the other hand, will result in longer lasting gamma bursts which will lead to memory representation of high fidelity. Unfortunately, slower theta waves will need more time until all (multiple) memory items are represented and can be re-activated in a new sequence. (c) Increased memory capacity by slowing down theta waves can, consequently, only be interpreted by increased memory fidelity due to longer gamma bursts outweighing a slower rate of memory re-activation.

the classic view on WM limitations (Cowan, 2001; Miller, 1956). Indeed, there has been electrophysiological and neuroimaging evidence that seemingly supports the idea of a strict visual WM capacity limit at three to four items (Jost, Bryck, Vogel, & Mayr, 2011; Todd & Marois, 2004; Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005). However, there is an appealing theoretical framework suggesting that WM is not limited in its absolute number of items to be retained but rather in the amount of general cognitive resources that can be attributed to WM retention (also referred to as 'shared resource model'; Bays & Husain, 2008; Ma, Husain, & Bays, 2014). According to this approach, cognitive resources in multi-item WM are distributed across items. Consequently, if only two items were to be retained, the cognitive resources allocated per item would be far more than if the resources were to be shared amongst multiple items (e.g., 10 items). The prime message would therefore be that theoretically, even ten items could be retained in memory (i.e., WM is not only limited to three to four items as suggested by the 'slot model' which assumes that there is a discrete number of slots that can be filled with item information; Adam, Vogel, & Awh, 2017; Luck & Vogel, 1997; Zhang & Luck, 2008). Assuming that ten items need to be remembered, each of the ten items would receive only a small portion of cognitive resources, and thus, they would be retained at a rather low precision or low fidelity (Bays & Husain, 2008). There are compelling theories explaining how such a shared resources model might be neuronally implemented (Bays, 2015; Ma *et al.*, 2014); however, we will not address those in this review article.

Can theta-gamma coupling code for flexible, shared resources?

A theta-gamma code as possible mechanism for WM retention has only been discussed in the light of the more 'classic view', the slot model (Freunberger, Werkle-Bergner, Griesmayr, Lindenberger, & Klimesch, 2011; Jensen & Lisman, 1996, 1998; Lisman & Idiart, 1995; Turi, Alekseichuk, & Paulus, 2018). The idea of gamma waves coding for multiple WM items and being organized into theta cycles seemingly opposes the idea of shared resources (see above) as suggested by Bays and Husain (2008). How could variable memory representations with variable fidelity (dependent on the number of items that are stored) be explained by theta-gamma coupling? Could the previously introduced idea (of single memory representations coded by an entire gamma burst each) instead (Herman *et al.*, 2013) offer a solution? As discussed earlier, one could expect that the longer a gamma burst, and thus, the slower the respective theta wave, the higher the fidelity of this item's memory representation. Consequently, retaining only two items should lead to relatively slow theta waves into which gamma bursts of longer duration are nested (see Figure 3a), whereas when, for example, four items are retained in each theta cycle, the length of the cycle (and consequently the length of the gamma burst) should be much shorter (see Figure 3b). This could then lead to lower fidelity of single items when memory load is high, but a better resolution (i.e., fidelity) when only few items are retained (see Figure 3). If this was true, the prediction would be rather clear: Increased memory load combined with lower precision of memory items should lead to faster theta waves (possibly even beyond the usually defined frequency range for theta) to which gamma burst are coupled.

However, Axmacher *et al.* (2010) report exactly the opposite pattern. They presented between one and three human faces that had to be retained for a short period of time. Oscillatory activity from the hippocampus was recorded, and it was found that during the retention period, there was an increase in theta phase to gamma amplitude coupling. With increasing memory load (i.e., number of faces), however, the theta frequency to which

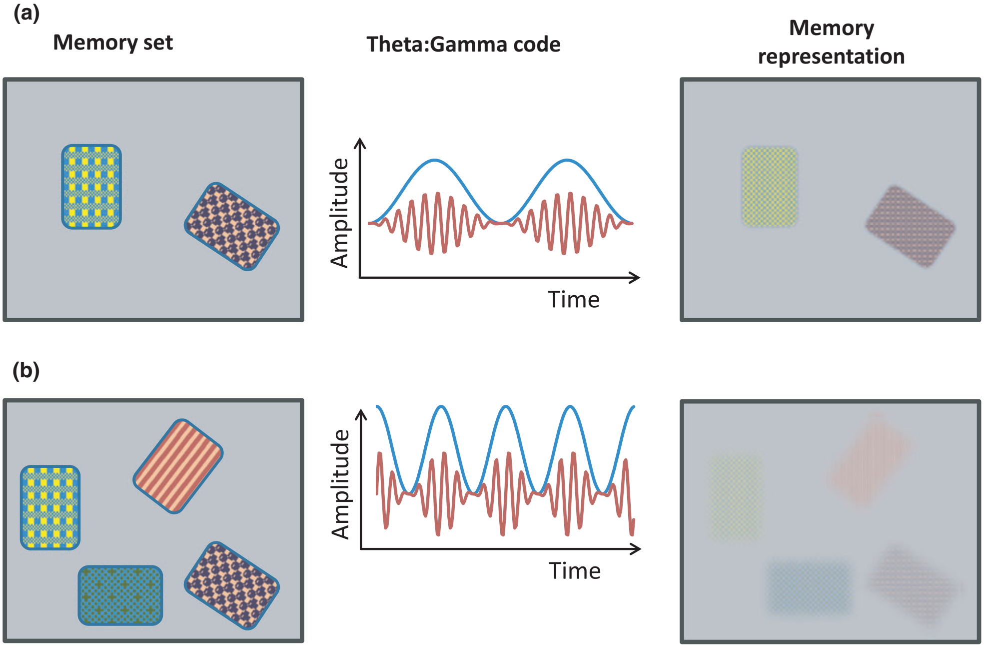

Figure 3. Cognitive resources shared between multiple memory items, each represented by a gamma burst of variable duration. (a) If memory load is low within a defined time interval, the brain can allow relatively long-lasting gamma bursts, each representing one memory item. These would be nested into theta waves that would be consequently slow. Longer gamma bursts per item, however, would lead to a more stable neuronal representation and, therefore, to higher fidelity of memory representations. (b) Parallel retention of many items would lead to gamma bursts of short duration nested into faster theta waves. This would lead to less stable representations and low item fidelity.

gamma amplitude was locked became slower. This result supports the idea that single memory representations are coded by separate gamma cycles (as originally suggested by Lisman & Idiart, 1995) instead of entire gamma bursts. Nonetheless, faces might entail very specific encoding processes that are not entirely representative of visual information in general. It also has been pointed out that there is a possibility that hippocampal activity during WM retention more likely reflects associated long-term memory processes rather than pure WM functions (Slotnick, 2017). Therefore, the above-presented hypothesis that sharing of cognitive resources between representations in multi-item WM could potentially be reflected by modulation in theta frequency and associated gamma burst duration still needs to be empirically tested rigorously.

A different possibility on how theta-gamma synchronization could still be understood as a neural signature of WM retention within the framework of dynamic shared cognitive resources is that gamma instead of theta frequency could define the resolution of multiple memory items. First, we must take into account that gamma oscillations are generated on a more local scale compared to lower frequencies (Buzsáki, 2006; Buzsáki & Wang, 2012; von Stein & Sarnthein, 2000) and that the larger and more distributed a cell assembly, the slower the oscillation it generates (von Stein & Sarnthein, 2000). Let us now consider a small number of items to be retained in WM. Each item will receive a large amount of cognitive resources, or in other words, we can afford a large assembly of neurons to code for each of the few items (see Figure 4a). Therefore, again using the idea that single WM items are represented by separate gamma cycles nested into a theta wave (Lisman & Idiart, 1995), those few gamma (or possibly even beta) cycles would be relatively slow (Figure 4a). Only very few gamma cycles (e.g., two in Figure 4a) would be nested into a theta wave with relatively constant frequency. If we now increase memory load, the same pool of neurons will have to be distributed amongst a larger number of items (four in the case of Figure 4b). Consequently, smaller cell assemblies with fewer neurons will code each item. This will lead to faster gamma cycles being nested into a theta wave and less precise memory representation of each single item (Figure 4b).

If that holds true it should be possible to determine fidelity or precision of memory representation based on the specific frequency of gamma activity coupled to theta waves during WM retention. However, this is rather difficult to test empirically given the limitations in signal processing of neuronal activity. First, it is difficult to acquire gamma activity with a very high signal-to-noise ratio non-invasively on a single trial basis. Thus, to test the predictions above, most likely, one would need to record intracranially in patients with implanted electrodes. Second, and a more severe issue, is that in order to quantify the frequency of gamma activity, it is necessary to apply time-frequency analysis algorithms of some kind. All of these come with a time-frequency trade-off; that is, if the temporal resolution of the analysis is high (which is required when investigating gamma cycles on a scale of a few milliseconds), frequency resolution will be poor (thus, it will be difficult to distinguish gamma activities at slightly different frequency). And third, cognitive

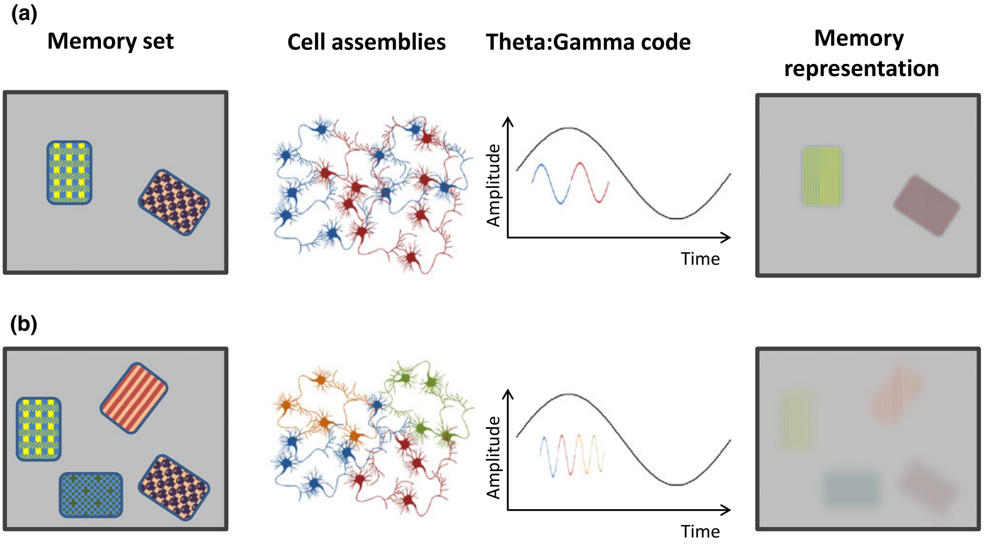

Figure 4. Sparse but local neural representation of multiple working memory items leads to faster gamma activity nested into theta waves. (a) If a discrete neuronal pool is used for coding of memory items, retaining only two items will lead to relatively large local networks with many neurons storing each of the items, respectively. These larger circuits would oscillate at a slower gamma frequency with each cycle representing one item with relatively high fidelity. (b) If the same pool of neurons is required to store, for example, four items, the cell assemblies coding for each of these items will be smaller, the circuit more local, and the produced gamma waves will be faster. A larger number of faster gamma waves will be nested into a theta cycle, and memory representations will be at a poor resolution.

resources could potentially be distributed unequally amongst memory items (van den Berg, Shin, Chou, George, & Ma, 2012). If this is the case one would expect that nested within one theta wave, there could be several gamma waves, each associated with their corresponding item. This would be particularly hard to quantify. Nevertheless, new signal processing approaches might make it possible to test the predictions stated in the future.

Conclusion

In this review article, we argued that synchronization between cortical theta and gamma oscillations is a plausible candidate for a neural substrate of memory representations in multi-item WM. We discussed electrophysiological and neurostimulation literature suggesting multiple items being represented by fast brain waves that are nested within slow oscillatory cycles. These phenomena have mainly been discussed within the theta-gamma coding framework suggested by Lisman and colleagues (Jensen & Lisman, 1996; Lisman & Idiart, 1995; Lisman & Jensen, 2013) and have often been used as evidence for a slot model of WM, where a discrete number of items can be stored in a fixed number of memory slots. Here, we tried finding possible theta-gamma coupling phenomena that are compatible with alternative WM models such as a shared resource model (Bays & Husain, 2008) or hybrid WM models (van den Berg *et al.*, 2012). However, the predictions that can be made from these considerations are yet to be thoroughly empirically tested. So, in the end, does cross-frequency coupling of oscillatory brain activity contribute to a better understanding of visual WM? It definitely does by providing a plausible neural process that can explain several facets of multi-item WM retention. It also provides electrophysiological evidence for more classical models of how multi-item WM information might be retained. However, there are hypothetical approaches that could, if thoroughly tested, also be well integrated into newer, alternative models of visual WM retention.

Acknowledgements

This research was supported by the German Research Council DFG (grant SA 1872/2-1) to PS. We want to thank Sheila Steiner and Zhen Chen for language editing.

References

Adam, K. C. S., Vogel, E. K., & Awh, E. (2017). Clear evidence for item limits in visual working memory. *Cognitive Psychology*, *97*, 79–97. https://doi.org/10.1016/j.cogpsych.2017.07.001

Axmacher, N., Henseler, M. M., Jensen, O., Weinreich, I., Elger, C. E., & Fell, J. (2010). Cross-frequency coupling supports multi-item working memory in the human hippocampus. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 3228–3233. https://doi.org/10.1073/pnas.0911531107

Baddeley, A. (2012). Working memory: Theories, models, and controversies. *Annual Review of Psychology*, *63*, 1–29. https://doi.org/10.1146/annurev-psych-120710-100422

Bays, P. M. (2015). Spikes not slots: Noise in neural populations limits working memory. *Trends in Cognitive Sciences*, *19*, 431–438. https://doi.org/10.1016/j.tics.2015.06.004

Bays, P. M., & Husain, M. (2008). Dynamic shifts of limited working memory resources in human vision. *Science*, *321*, 851–854. https://doi.org/10.1126/science.1158023

Buzsáki, G. (2006). *Rhythms of the brain*. Oxford, UK: Oxford University Press. https://doi.org/10.1093/acprof:oso/9780195301069.001.0001

Buzsáki, G., & Wang, X.-J. (2012). Mechanisms of gamma oscillations. *Annual Review of Neuroscience*, *35*, 203–225. https://doi.org/10.1146/annurev-neuro-062111-150444

Chaieb, L., Leszczynski, M., Axmacher, N., Höhne, M., Elger, C. E., & Fell, J. (2015). Theta-gamma phase-phase coupling during working memory maintenance in the human hippocampus. *Cognitive Neuroscience*, *6*(4), 149–157. https://doi.org/10.1080/17588928.2015.1058254

Cowan, N. (2001). The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *The Behavioral and Brain Sciences*, *24*(1), 87–114; discussion 114–185. https://doi.org/10.1017/s0140525x01003922

Cowan, N. (2008). What are the differences between long-term, short-term, and working memory? *Progress in Brain Research*, *169*, 323–338. https://doi.org/10.1016/S0079-6123(07)00020-9

Freunberger, R., Werkle-Bergner, M., Griesmayr, B., Lindenberger, U., & Klimesch, W. (2011). Brain oscillatory correlates of working memory constraints. *Brain Research*, *1375*, 93–102. https://doi.org/10.1016/j.brainres.2010.12.048

Fries, P. (2015). Rhythms for cognition: Communication through coherence. *Neuron*, *88*(1), 220–235. https://doi.org/10.1016/j.neuron.2015.09.034

Herman, P. A., Lundqvist, M., & Lansner, A. (2013). Nested theta to gamma oscillations and precise spatiotemporal firing during memory retrieval in a simulated attractor network. *Brain Research*, *1536*, 68–87. https://doi.org/10.1016/j.brainres.2013.08.002

Jensen, O., & Lisman, J. E. (1996). Novel lists of 7 ± 2 known items can be reliably stored in an oscillatory short-term memory network: Interaction with long-term memory. *Learning & Memory*, *3*(2–3), 257–263. https://doi.org/10.1101/lm.3.2-3.257

Jensen, O., & Lisman, J. E. (1998). An oscillatory short-term memory buffer model can account for data on the Sternberg task. *The Journal of Neuroscience*, *18*, 10688–10699. https://doi.org/10.1523/JNEUROSCI.18-24-10688.1998

Jost, K., Bryck, R. L., Vogel, E. K., & Mayr, U. (2011). Are old adults just like low working memory young adults? Filtering efficiency and age differences in visual working memory. *Cerebral Cortex*, *21*, 1147–1154. https://doi.org/10.1093/cercor/bhq185

Kamiński, J., Brzezicka, A., & Wróbel, A. (2011). Short-term memory capacity (7 ± 2) predicted by theta to gamma cycle length ratio. *Neurobiology of Learning and Memory*, *95*(1), 19–23. https://doi.org/10.1016/j.nlm.2010.10.001

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition-timing hypothesis. *Brain Research Reviews*, *53*(1), 63–88. https://doi.org/10.1016/j.brainresrev.2006.06.003

Lisman, J. E., & Idiart, M. A. (1995). Storage of 7 ± 2 short-term memories in oscillatory subcycles. *Science*, *267*, 1512–1515. https://doi.org/10.1126/science.7878473

Lisman, J. E., & Jensen, O. (2013). The θ-γ neural code. *Neuron*, *77*, 1002–1016. https://doi.org/10.1016/j.neuron.2013.03.007

Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature*, *390*, 279–281. https://doi.org/10.1038/36846

Ma, W. J., Husain, M., & Bays, P. M. (2014). Changing concepts of working memory. *Nature Neuroscience*, *17*, 347–356. https://doi.org/10.1038/nn.3655

Mazaheri, A., & Jensen, O. (2010). Rhythmic pulsing: Linking ongoing brain activity with evoked responses. *Frontiers in Human Neuroscience*, *4*, 177. https://doi.org/10.3389/fnhum.2010.00177

Miller, G. A. (1956). The magical number seven plus or minus two: Some limits on our capacity for processing information. *Psychological Review*, *63*(2), 81–97. https://doi.org/10.1037/h0043158

Mitchell, D. J., McNaughton, N., Flanagan, D., & Kirk, I. J. (2008). Frontal-midline theta from the perspective of hippocampal 'theta'. *Progress in Neurobiology*, *86*(3), 156–185. https://doi.org/10.1016/j.pneurobio.2008.09.005

Moore, R. A., Gale, A., Morris, P. H., & Forrester, D. (2006). Theta phase locking across the neocortex reflects cortico-hippocampal recursive communication during goal conflict resolution.

International Journal of Psychophysiology, *60*, 260–273. https://doi.org/10.1016/j.ijpsycho.2005.06.003

Raghavachari, S., Lisman, J. E., Tully, M., Madsen, J. R., Bromfield, E. B., & Kahana, M. J. (2006). Theta oscillations in human cortex during a working-memory task: Evidence for local generators. *Journal of Neurophysiology*, *95*, 1630–1638. https://doi.org/10.1152/jn.00409.2005

Sauseng, P., Griesmayr, B., Freunberger, R., & Klimesch, W. (2010). Control mechanisms in working memory: A possible function of EEG theta oscillations. *Neuroscience and Biobehavioral Reviews*, *34*, 1015–1022. https://doi.org/10.1016/j.neubiorev.2009.12.006

Sauseng, P., Klimesch, W., Heise, K. F., Gruber, W. R., Holz, E., Karim, A. A., . . . Hummel, F. C. (2009). Brain oscillatory substrates of visual short-term memory capacity. *Current Biology*, *19*, 1846–1852. https://doi.org/10.1016/j.cub.2009.08.062

Slotnick, S. D. (2017). *Cognitive neuroscience of memory*. Cambridge, UK: Cambridge University Press. https://doi.org/10.1017/9781316026687

Todd, J. J., & Marois, R. (2004). Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature*, *428*, 751–754. https://doi.org/10.1038/nature02466

Turi, Z., Alekseichuk, I., & Paulus, W. (2018). On ways to overcome the magical seven item limit of working memory. *PLoS Biology*, *16*, e2005867. https://doi.org/10.1371/journal.pbio.2005867

van den Berg, R., Shin, H., Chou, W.-C., George, R., & Ma, W. J. (2012). Variability in encoding precision accounts for visual short-term memory limitations. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 8780–8785. https://doi.org/10.1073/pnas.1117465109

Van Vugt, M. K., Chakravarthi, R., & Lachaux, J.-P. (2014). For whom the bell tolls: Periodic reactivation of sensory cortex in the gamma band as a substrate of visual working memory maintenance. *Frontiers in Human Neuroscience*, *8*, 696. https://doi.org/10.3389/fnhum.2014.00696

Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature*, *428*, 748–751. https://doi.org/10.1038/nature02447

Vogel, E. K., McCollough, A. W., & Machizawa, M. G. (2005). Neural measures reveal individual differences in controlling access to working memory. *Nature*, *438*, 500–503. https://doi.org/10.1038/nature04171

von Stein, A., & Sarnthein, J. (2000). Different frequencies for different scales of cortical integration: From local gamma to long range alpha/theta synchronization. *International Journal of Psychophysiology*, *38*, 301–313. https://doi.org/10.1016/S0167-8760(00)00172-0

Vosskuhl, J., Huster, R. J., & Herrmann, C. S. (2015). Increase in short-term memory capacity induced by down-regulating individual theta frequency via transcranial alternating current stimulation. *Frontiers in Human Neuroscience*, *9*, 257. https://doi.org/10.3389/fnhum.2015.00257

Wolinski, N., Cooper, N., Sauseng, P., & Romei, V. (2018). The speed of parietal theta frequency drives visuospatial working memory capacity. *PLoS Biology*, *16*, e2005348. https://doi.org/10.1371/journal.pbio.2005348

Zhang, W., & Luck, S. J. (2008). Discrete fixed-resolution representations in visual working memory. *Nature*, *453*, 233–235. https://doi.org/10.1038/nature06860

Received 9 March 2018