Title:

Attention samples objects held in working memory at a theta rhythm

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Abstract

Attention samples spatial positions, visual objects or auditory streams rhythmically. This has been reported for tasks where the attended information was perceptually present. Here we tested whether attentional sampling also applies to internal representations held in working memory. Participants memorized four spatial positions that formed the endpoints of two objects, one of which was cued for a delayed match-non-match test. When uncued positions were probed, participants responded faster to those located on the same object as the cued position than to those located on the other object, revealing object-based attention in working memory. Manipulating the interval between cue and probe revealed that object-based attention oscillated at 6 Hz. Moreover, oscillations showed an anti-phase relationship between objects, suggesting that attention sampled them in alternation. The striking similarity between rhythmic sampling of mental representations and perceptual information suggests that attentional sampling is a general mechanism of information processing in human cognition.

At any given moment, both the external world and our nervous systems boast a wealth of information. A hallmark feature of animal and human cognition is that our attention system can select only a fraction of this information for further processing. Recent work has shown that allocation of attention toward information in the environment is not continuous, but perceptual information is sampled rhythmically and discretely in time. For example, participants can be cued to attend a spatial location in order to detect an upcoming target. Across trials, behavioral performance (e.g., target detection rate) then varies over time since cue onset in a rhythmic fashion at frequencies in the theta and alpha ranges (approx. 4-12 Hz) (VanRullen, 2016b). These fluctuations of performance strongly contradict the long held assumption of continuous attentional processing, which would predict constant or increasing performance with time since cue onset. Likewise, the notion of attention as a sampling process is supported by findings of anti-phase performance fluctuations between two simultaneously attended locations, suggesting that both are sampled in alternation (Landau & Fries, 2012). Similar evidence for oscillations of performance has been obtained for a variety for perceptual tasks involving visual or auditory target detection (Dugué, McLelland, Lajous, & VanRullen, 2015; Ho, Leung, Burr, Alais, & Morrone, 2017; Landau & Fries, 2012; VanRullen, Carlson, & Cavanagh, 2007), discrimination (Song, Meng, Chen, Zhou, & Luo, 2014) or priming (Huang, Chen, & Luo, 2015). Moving beyond spatial attention, Fiebelkorn et al. (Fiebelkorn, Saalmann, & Kastner, 2013) demonstrated that attentional sampling also operates in an object-based manner by adapting a perceptual paradigm by Egly and colleagues (Egly, Driver, & Rafal, 1994). They presented pairs of objects and cued the endpoint of one of them as the likely site of an upcoming target. To measure object-based attention independently of visuospatial attention elicited by the cue, they compared performance at the uncued endpoint of the same object as the cued position (i.e., the same-object position) with performance at an endpoint of the other, unattended object (i.e., the different-object position). Consistent with the work on spatial attention, performance oscillated at a theta rhythm and in an anti-phase relationship between both positions. Taken together, these findings indicate that attentional sampling in perception operates equally across different modalities and tasks and applies to both space- and object-based attention.

The ability to select relevant information is however not limited to perception but rather extends to internal information held in working memory (WM). Attention often operates in a very similar way for perceptual and internal information suggesting that those attentional mechanisms constitute general principles of information processing in human cognition (Chun, Golomb, & Turk-Browne, 2011; Gazzaley & Nobre, 2012). For example, both behavioral and neuroimaging studies have shown that spatial attention can also be directed to internally stored locations (Awh, Jonides, & Reuter-Lorenz, 1998) and that attentional shifts in perception and WM involve similar brain regions (Bledowski, Rahm, & Rowe, 2009; Nobre et al., 2004). Recently, we have demonstrated that also the principle of object-based attention is used in WM (Peters, Kaiser, Rahm, & Bledowski, 2015) by adapting the perceptual paradigm of Egly et al. (Egly et al., 1994) to WM. Participants had to memorize the exact location of two objects' endpoints which changed their position across trials. During the retention interval, they were cued to direct attention towards one of these. Consistent with object-based attention, we found shorter reaction times when participants shifted attention to a memory positions located on the currently attended object (i.e., the same-object position) as compared to a memory position on the other, unattended object (i.e., the different-object position). Moreover, multivariate pattern analysis of functional magnetic resonance imaging data revealed increased visuotopic activation in visual and parietal cortices for the uncued same-object position compared to the different-object position. Importantly, as external spatial attention was always directed to the currently cued position, differences between the same- and the different-object position could distinctly be attributed to the effects of internal attention in WM. Our finding of object-based attention in WM thus supported the notion that object-based selection of information is a general mechanism of information processing in human cognition that extends to internal information.

Until now, it has remained unclear whether attentional sampling is specific to the selection of perceptual information or whether it constitutes a more general mechanism of information processing in human cognition. Based on the findings of rhythmic fluctuations of object-based attention in a perceptual paradigm (Fiebelkorn et al., 2013) and object-based attention effects in WM (Peters et al., 2015), the present study assessed whether attentional sampling also operates on information that is not externally present but represented internally, in WM. We employed a variant of our previous paradigm (Peters et al., 2015) and varied the interval between attentional cue and probe with a high temporal resolution to study the temporal trajectory of object-based attention in WM. Our specific aim was to focus on purely internal attention to information in WM. Object-based attention is particularly suited for this purpose because performance at the same- and different-object positions is only determined by internal object-based attention and not by external visuospatial attention which is directed towards the cued memorized position. If object-based attention sampling applies to information in WM, reaction times should oscillate at the same- and different-object position over time. Moreover, these oscillations should show an anti-phase relationship between same- and different-object positions.

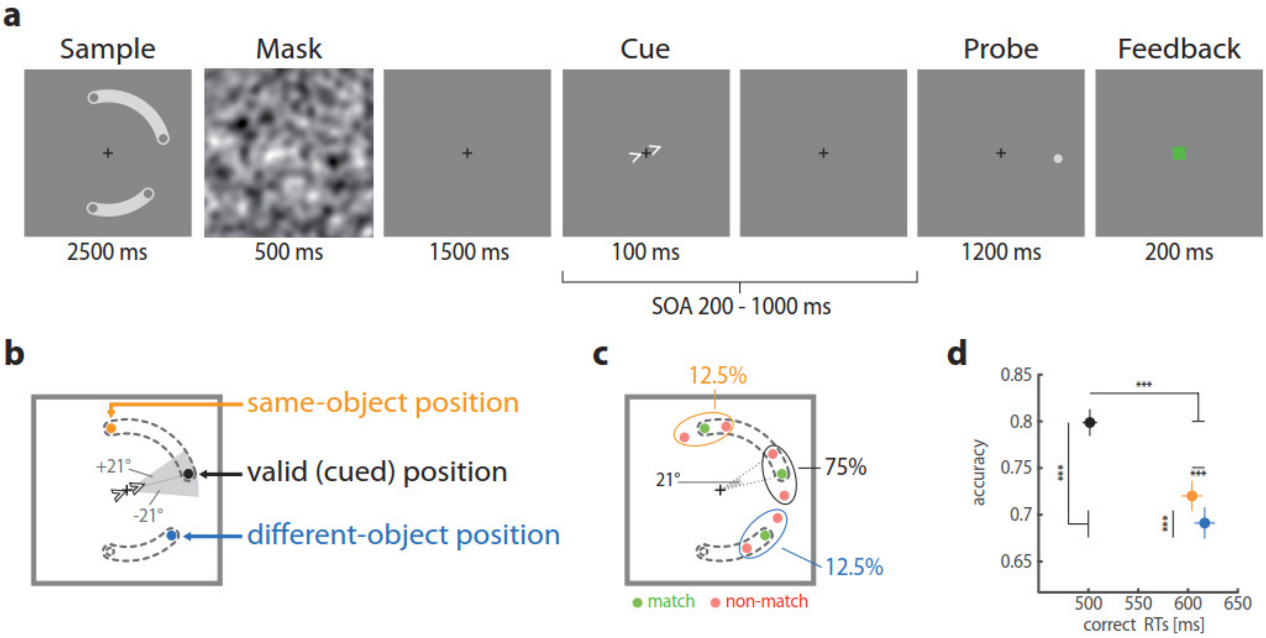

Fig. 1 Experimental paradigm. **a** Participants memorized the exact locations of the endpoints of the two objects. Object-length and position varied randomly across trials. During retention, a spatial cue indicated the endpoint location which would most likely be probed. **b** Memory positions. To ensure that participants selected information from working memory upon cue presentation and to prevent the cue from revealing the memorized position, the cue pointed to the vicinity (±21°) of the cued memory position but was uninformative about the match/non-match decision at the cued position. **c** The cued position (black) was probed in 75%, the same-object position (yellow) in 12.5% and different-object position (blue) in 12.5% of all trials. Probes were either matching the corresponding memory position (green) or displaced by ±21° (red). **d** Accuracy and reaction times (RTs) of correct responses for the three probe conditions. Lines indicate standard error of the mean. SOA stimulus-onset-asynchrony. *** $p < .001$, paired t-test.

Results

Task design. On every trial, participants (N = 30, two of whom were excluded because of poor performance, see *Participants*) memorized four positions located at the endpoints of two objects (Fig. 1). During the retention interval, a cue indicated the memorized position that would most likely be probed in a delayed match-to-sample decision at the end of the trial. The cue pointed only near the memorized position. This ensured that participants were required to retrieve the exact position from WM (Fig. 1b). The cued memory position was probed in most of the trials (75%, valid condition) to direct the participants' internal and external visuospatial attention towards the cued endpoint (Fig. 1c). By design, responses at the cued position were therefore influenced by a mixture of several factors such as focal visuospatial attention, the spatial uncertainty of the cue, and internal object-based attention. Thus, to solely test the effects of internal attention, in the remaining 25% of the trials, either the uncued memory position that was located on the same object (same-object position) or the uncued memory position on the other object (different-object position) adjacent to the cued position were probed. Hence, object-based attention in WM was measured by a direct contrast between the reaction times (RT) for correct responses at the same object position (12.5% of trials) and the different-object position (12.5%). To test the time-course of object-based attention in WM, we presented the probe at different temporal lags after cue presentation with a high temporal resolution (stimulus onset asynchrony, SOA: 200 ms, 267 ms, 333 ms and subsequently in steps of 33 ms up to 1000 ms).

Attention selects the entire object. First, we tested whether participants followed the instruction and directed their focal spatial attention to the cued memory position. This was the case as participants showed faster RTs ($t_{27} = 20.96$, $p < .001$) and higher accuracy ($t_{27} = 15.27$, $p < .001$) for the cued memory position compared to the two uncued memory positions (Fig. 1d). Moreover, we found that RTs were faster to a probe presented at memory positions located on the currently attended object compared with equidistant positions on the unattended object ($F_{1,27} = 17.42$, $p < .001$, $\eta_p^2 = .39$, mean difference $\Delta t = 13$ ms, Fig. 1d). This replicated our previous finding of object-based attention in WM (Peters et al., 2015), indicating that attention spread across the entire object even though the cue pointed to only one memorized position of the object.

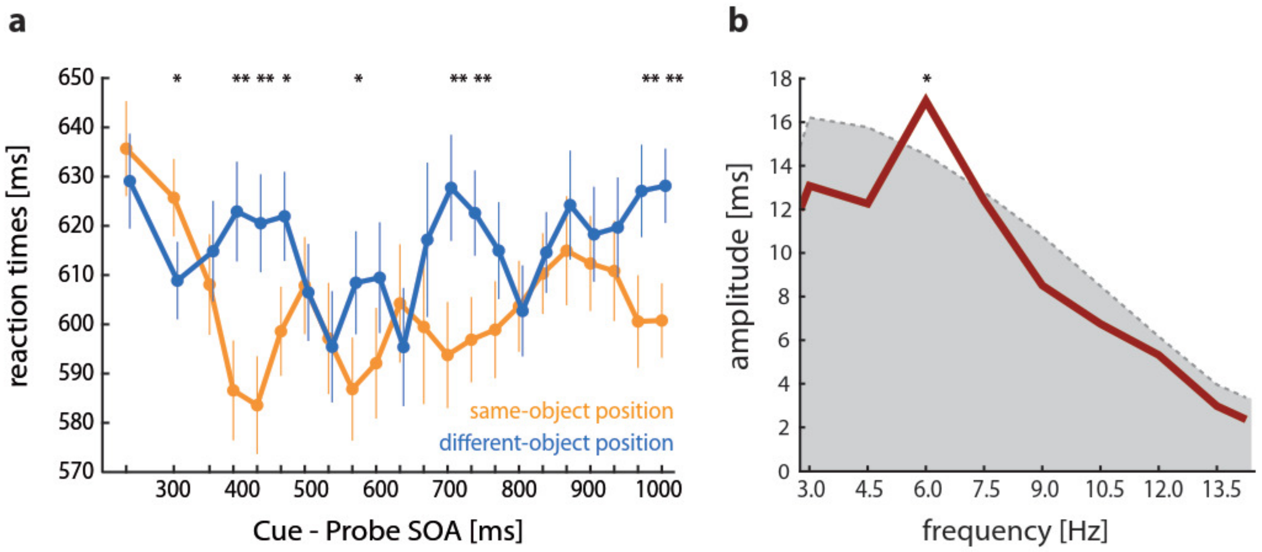

Fig. 2 Results. **a** Reaction times (RTs) to the probe as a function of time after the onset of the attentional cue (SOA: stimulus-onset-asynchrony) for the same-object position (yellow) and the different-object position (blue). Lines indicate within subject standard errors (Morey, 2008) * $p < .05$, ** $p < .01$. **b** Fourier decomposition of the time-course of object-based attention (RTs of different-object condition minus same-object condition), shaded area represents 95th percentile of permutation null-distribution * $p <. 05$, FDR-corrected (Benjamini & Hochberg, 1995).

Rapid allocation of object-based attention in WM. To assess the temporal dynamics of object-based attention in WM, we calculated the attentional benefit at each of the temporal lags between cue and probe using a sliding time window approach(Fiebelkorn et al., 2013) with a window size of 66 ms. The attentional benefit in WM varied as a function of the time between cue and probe (interaction: time × condition: $F_{21,567} = 2.35$, $p < .001$, $\eta_p^2 = .08$). It emerged at approximately 383 ms after cue onset ($t_{27} = 3.59$, uncorrected $p < .01$, $\Delta t = 36$ ms), indicating that, by this time, object-based attention in WM had co-activated the same-object position (Fig. 2a).

Object-based attention oscillates in WM. Concerning the central question of our study, we found clear evidence for attentional sampling in WM. In particular, after the initial build-up of the same-object benefit in WM at 383 ms, it vanished at 483 ms ($t_{27} = 0.14$, $p = .89$, $\Delta t = 1$ ms) and subsequently re-occurred periodically with peaks at 550 ms, 683 ms, and 950 ms (Fig. 2a). This shows that object-based attention in WM oscillated in time even though the probability of a target appearance was identical for both uncued memory positions throughout the cue-probe interval. Fluctuations of object-based RT benefits across time in WM were further supported by a significant interaction between time and condition even when the first three temporal lags, during which object-based attention was in the process of building up, were excluded ($F_{18,486} = 1.89$, $p < .05$, $\eta_p^2 = .07$). Moreover, to quantify the temporal frequency of these fluctuations, we submitted the time course of the object-based benefit, i.e., the RT difference between the different-object and same-object conditions for the equidistant temporal lags of 350 ms to 983 to a Fourier transformation. The amplitude spectrum of frequencies from 1.5 Hz to 13.5 Hz (Fig. 2b) showed a significant peak at 6 Hz ($p < .05$, FDR corrected). This indicates that the observed fluctuations of object-based attention in WM may be driven by an oscillatory mechanism in the theta range, corroborating the sampling frequency observed in perception.

Objects in WM are sampled in alternation. If attention can only sample one object at a time, the speed of access for the cued and uncued object should be anti-correlated, as previously shown for visual spatial and object-based attention (Fiebelkorn et al., 2013; Landau & Fries, 2012). To test whether attention in visual WM similarly samples objects in alternation, we extracted the Fourier coefficients at 6 Hz from the time-course of RTs in the same- and different-object condition and computed the phase-locking value of both oscillations (Lachaux, Rodriguez, Martinerie, & Varela, 1999). Both 6 Hz rhythms were significantly phase-locked (phase-locking value = .40, $p = .011$) and the mean phase angle difference between the two memory conditions was 159° (95% confidence interval from 119° to 199°, Fig. 3). The anti-phase relationship of both oscillations supports the assumption that attention samples objects in WM in alternation.

A static object-based benefit in accuracy. In accordance with object-based attention allocated to the cued object, accuracy at the same-object position was significantly higher than at the different-object position ($F_{1,27} = 24.2$, $p < .001$, $\eta_p^2 = .47$, Fig. 1d). However, there was neither a main effect of time ($F_{21,567} = 0.9$, $p = .62$, $\eta_p^2 = .03$) nor a significant modulation of the object-based accuracy benefit across time (time × condition interaction $F_{21,567} = 0.96$, $p = .52$, $\eta_p^2 = .03$), suggesting that the spatial positions were stably encoded in WM throughout the task. Moreover, there was no significant peak in the Fourier spectrum (uncorrected $p > .07$ for all frequencies). Thus, while attentional sampling affected the latency of accessing memorized positions in WM, we found no evidence for a modulation of their fidelity.

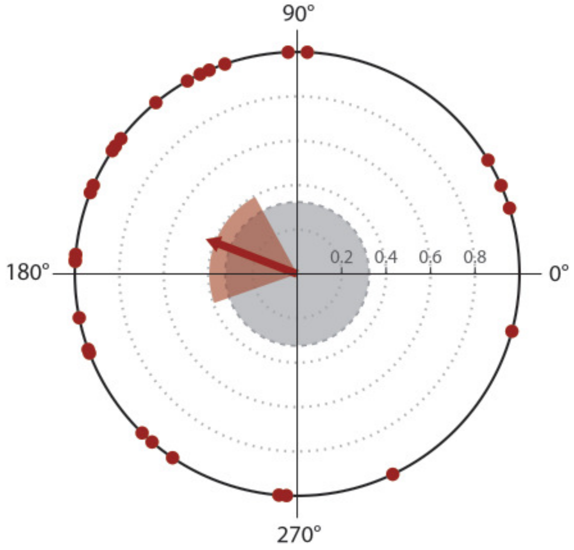

Fig. 3 Phase relationship of 6Hz oscillations for the same- and different-object condition. Dots indicate participants' individual phase differences plotted on the unit circle. Length of the resultant vector corresponds to the phase-locking value (PLV). Red shaded area indicates 95% confidence interval of the phase difference. Gray shaded area indicates 95th percentile of the permutation null distribution of PLVs.

Discussion

The present study demonstrated that attentional sampling can also be observed for information that is not physically present but retained internally in visual WM. We replicated the general object-based advantage with shorter average RTs to uncued memorized positions on the attended object (Peters et al., 2015), that is, object-based attention in WM. More importantly, tracking the time course of object-based attentional selection by varying the interval between attentional cue and probe revealed that RT oscillated rhythmically at a rate of 6 Hz. Moreover, object-based attention sampled the two memorized objects in alternation, as evidenced by an anti-phase relationship of reaction time oscillations at the attended and unattended object. These findings of attentional sampling in WM suggest that attentional sampling extends beyond perception and is a general mechanism of information processing in human perception and cognition.

We assessed object-based attention by RT to probes at positions either on the same object as the cued position or on the other object. This task therefore is particularly well suited to study effects of attention in WM. As both of these positions were uncued (and hence unlikely probe positions) visuospatial attention was not directed to these critical positions but only to the cued position. In the perceptual domain, this procedure has been used to dissociate external visuospatial attention from external object-based attention (Egly et al., 1994; Fiebelkorn et al., 2013). Here, this procedure dissociated external visuospatial attention from internal object-based attention in WM. In contrast, if a cued memory position was tested directly, both visuospatial (external) as well as internal attention would be confounded at the same location precluding an unambiguous interpretation of performance at this position as reflecting the effect of internal attention.

It is a long-standing notion that the continuous stream of sensory information is sampled discretely by the perceptual system (VanRullen, 2016b). Recently, a series of psychophysical studies have demonstrated attentional sampling in tasks including visual target detection (Dugué et al., 2015; Landau & Fries, 2012; VanRullen et al., 2007), discrimination (Song et al., 2014), and priming (Huang et al., 2015), as well as auditory target discrimination (Ho et al., 2017). Until now, these studies have considered attentional sampling as a phenomenon that operates on perceptual representations and may serve a particular behavioral purpose. For instance, attentional sampling could serve to segregate the continuous stream of perceptual input into discrete "events" that form the basis of cortical processing. Alternatively, sampling may periodically disengage attention from particular stimuli and locations (Buschman & Kastner, 2015) and thus constitute a mechanism to balance exploration and exploitation behavior. The present results demonstrate that attentional sampling can be observed even in the absence of a continuous perceptual input and without the presence of perceptual objects that necessitate attentional disengagement in the service of visual exploration. Instead, attentional sampling was also present for information that is retained internally, i.e., in WM. This suggests that attentional sampling constitutes a more general mechanism of information selection and processing in the human brain.

What are the potential neuronal mechanisms responsible for attentional sampling? It has been suggested that sampling may be a consequence of communication between different cortical areas that is temporally aligned to specific phases of ongoing low-frequency oscillations (Bonnefond, Kastner, & Jensen, 2017; Fries, 2015). The 6-Hz attentional modulation in WM perfectly matches the range of theta frequencies observed in perceptual studies of attentional sampling. The ubiquity of theta rhythms in the human brain (Canolty et al., 2006) and their suspected role in inter-areal brain communication (Bonnefond et al., 2017; Solomon et al., 2017) suggest a direct link of behaviorally observed attentional sampling rhythms and low frequency neural rhythms. In perceptual attention, fronto-central (Busch & VanRullen, 2010) as well as posterior sites in the primate visual cortex (Landau, Schreyer, Van Pelt, & Fries, 2015; Spyropoulos, Bosman, & Fries, 2017) have been identified to convey neural theta oscillations. These theta rhythms are modulated by attention (Spyropoulos et al., 2017) and their phase predicts behavioral performance in visual detection tasks (Busch & VanRullen, 2010; Landau et al., 2015). This suggests that similar neural substrates may be involved in the generation of the theta-rhythmic sampling that we observed in WM. Specifically, theta-mediated fronto-parietal attention may have sampled the two object representations putatively stored in posterior regions. On the other hand, neural theta oscillations in several cortical areas and the hippocampus as well as theta coherence modulations between different regions have been linked to WM maintenance (Axmacher et al., 2010; Canolty et al., 2006; Fuentemilla, Penny, Cashdollar, Bunzeck, & Düzel, 2010; Jensen & Tesche, 2002; Liebe, Hoerzer, Logothetis, & Rainer, 2012; Palva, Kulashekhar, Hämäläinen, & Palva, 2011; Sauseng et al., 2009), possibly reflecting the highly distributed nature of WM maintenance (Christophel, Klink, Spitzer, Roelfsema, & Haynes, 2017). Thus, the involvement of theta-oscillations may not be specific to a particular cortical area but may represent a general principle of neural processing. For example, one influential theory suggests that items in WM may be encoded as individual gamma-bursts that are maintained by sequential reactivation within the cycle of a theta-oscillation (Lisman & Idiart, 1995). Indeed, theta-rhythmic re-activation of WM items has been shown to emerge as an intrinsic dynamic within a recurrent neuronal network of biologically plausible integrate- and fire neurons (Mongillo, Barak, & Tsodyks, 2008). This suggests that the theta rhythm may arise from the biophysical constraints of neural ensembles that store and process the memorized objects in WM. In sum, different lines of research indicate that the theta rhythm is an intrinsic and stable property of neural circuits. However, several questions remain unresolved. For example, some have proposed that individual objects are sampled at a fixed theta rhythm (VanRullen, 2016a) while others suggest that the whole ensemble of relevant objects is sampled within one theta cycle (Lisman & Jensen, 2013), leading to diverging and testable predictions for the sampling frequency when the number of relevant objects is increased in WM (see Holcombe & Chen, 2013, for perception).

These presumed mechanisms may explain why the two memorized objects were sampled in alternation at a theta rhythm. However, additional assumptions have to be made in order to account for the behavioral oscillations observed in the present WM task. Behavioral oscillations could only be observed if the phase of the underlying theta oscillation as well as the order with which both objects were sampled was consistent across trials. This implies that theta oscillations had to be reset or initiated by one of the elements in the task (e.g., the attentional cue) in each trial (Landau & Fries, 2012). The order with which objects are reactivated within a theta cycle has been proposed to depend on their behavioral priority (O. Jensen, Bonnefond, & VanRullen, 2012). This provides an explanation why the cued object was on average sampled first within the theta cycle as it was probed in most of the trials (87.5%, combining the cued memory position and same-object position) compared to the other, non-cued object.

Similar to perception, information in working memory can be selected for prioritized processing (Cowan, 1999; Garavan, 1998; Oberauer, 2002). Directing internal attention towards one of several items stored in WM via a “retro-cue” during the retention interval of a working memory task leads to faster reaction times for the cued as compared to the uncued item(s) (Griffin & Nobre, 2003; Landman, Spekreijse, & Lamme, 2003). In line with our finding, several studies have shown that attention is fully deployed approximately 300 to 500 ms after the onset of an attentional retro-cue (Gressmann & Janczyk, 2016; Schneider, Mertes, & Wascher, 2016; Souza & Oberauer, 2016; Tanoue & Berryhill, 2012; van Moorselaar, Gunseli, Theeuwes, & N. L. Olivers, 2015). Until now, it has been assumed that attention is allocated stably after its initial deployment (Souza & Oberauer, 2016). Testing with higher temporal resolution than previous studies and using a paradigm that allowed us to dissociate object-based attention in WM from visuospatial attention at the cued position, we have demonstrated for the first time that attention in WM is not stably allocated but oscillates rhythmically between objects in WM.

Beyond the present study, our results therefore suggest the intriguing possibility that many effects in WM may reveal an oscillatory structure when tested at a fine-grained temporal level, which could inform current debates in WM research. For example, attentional sampling might be particularly beneficial when multiple items in WM can potentially become behaviorally relevant. In the present case, both objects in WM could be the target of a subsequent probe, and alternating attentional sampling may have provided the means to sustain priority across both of those objects. Indeed, some researchers have argued that attention selects only a single object at a time in WM (Makovski & Jiang, 2007; Oberauer, 2002; Oberauer & Hein, 2012; Olivers, Peters, Houtkamp, & Roelfsema, 2011) while others have proposed that attention can be distributed across multiple objects in WM (Cowan et al., 2005; Matsukura, Luck, & Vecera, 2007; Matsukura & Vecera, 2015). Attentional sampling in WM may reconcile these views depending on the temporal frame of view. While sampling only a single object at a time, rapid attentional fluctuations may serve to maintain a state of elevated priority simultaneously for both objects. Whether attentional sampling indeed constitutes a viable mechanism to prioritize an object over a prolonged time-interval remains to be tested, e.g. by comparison to an irrelevant object.

The finding of attentional sampling in working memory suggests that it may reflect a general information processing mechanism in the human brain. This opens the possibility that attentional sampling may provide an algorithmic explanation also for other cognitive phenomena. For instance, a striking observation is that reaction time speed in simple perceptual tasks is closely associated with intelligence (Eysenck, 1967; Hick, 1952). On the other hand, working memory function is strongly linked to intelligence (Engle, Tuholski, Laughlin, & Conway, 1999), serving as a “mental blackboard” for higher cognition. Up to now, the mechanism that links simple perceptual processing speed with higher cognitive abilities has remained unclear. The rate with which a common attentional mechanism samples external and internal information may determine both perceptual reaction time distributions as well as the efficiency of internal information processing and therefore provide a hitherto missing link between perceptual processing speed and intelligence (A. R. Jensen, 2006).

To summarize, we provided evidence for a basic mechanism of human cognition that samples information about objects in alternation at a theta rhythm, regardless whether these objects are physically present or held as internal representations in memory.

Methods

Participants

Participants (N = 30, 16 female; mean age = 22.1 years, SD age = 2.6 years) with normal or corrected-to-normal vision were recruited from the Goethe-University Frankfurt and the Fresenius University of Applied Sciences Frankfurt and gave written informed consent. Two subjects were excluded because of behavioral performances below 60% correct responses (remaining 28 participants percent correct: 77.8%, SD = 7.8%) yielding a final sample of N = 28. Participants were either remunerated or received course credit. The study was approved by the local ethics committee.

Stimuli and design

During encoding (2500 ms), participants were presented with four gray dots (size in visual angle: 0.37°) that were grouped to form the endpoints of two objects (Fig. 1). Spatial positions and objects were presented on an invisible circle with a radius of 8° visual angle. Neighboring memory positions were separated by 60°, 90°, or 120° angular distance on the invisible circle. The location of the gray dots and the groupings varied randomly across trials. After encoding, a visual mask was presented for 500 ms. The mask was generated by convolving random pixel-wise luminance (uniformly distributed) with a Gaussian (kernel standard deviation 0.5° visual angle). The central cue presented for 100 ms during the retention interval pointed to a position in the vicinity of one of the four memory positions. This was done to avoid revealing the exact memory position. The cue's direction was drawn from a uniform distribution (-21° to +21°, centered on the cued memory position). Cue-probe SOAs were equidistant from 300 ms to 1000 ms in steps of 33.3 ms (two frames on a 60-Hz monitor). In addition, two shorter SOAs (200 ms and 267 ms) were used to obtain behavioral performance measures before any attentional selection had occurred. Matching probes were presented at the exact spatial location as the respective memory position during encoding. Non-matching probes were displaced from the probed memory position either clockwise or counterclockwise by 21°. Participants gave their response via left (match) or right (non-match) mouse button click. Probes were presented for 1200 ms. Hereafter, performance feedback was presented for 200 ms that consisted of either a green (correct and in time) or red (incorrect or RT > 1200 ms) central box. Trials were separated by an inter-trial interval of 2000 ms.

Procedure

The probe could appear either at the cued position, at the uncued position on the same object or at the spatially nearest position on the uncued object. Each participant conducted 60 trials of the valid probe condition, 10 trials of the same-object condition, and 10 trials of the different-object condition for each of the 23 SOAs. The resulting 1840 trials were separated into 46 blocks of 40 trials each that were performed in four separate session within two weeks. Sessions lasted approximately 1.5 h each and were always conducted on separate days.

Analysis

All data were analyzed using MATLAB R2016b (The Mathworks) and the CircStat Toolbox (Berens, 2009). Mean correct RTs and accuracies were compared by either paired-sample t-tests or repeated-measures ANOVAs with the factors SOA and condition (same- or different-object condition). To reduce noise in the data, reaction times to correct responses were averaged in adjacent time bins using a sliding time window approach for the analysis of the time courses (see (Fiebelkorn et al., 2013)). To obtain the frequency spectrum of the time course of object-based attention we analyzed the difference of RTs in the same-object condition and different-object condition for the SOAs with equidistant temporal spacing (excluding the first two SOAs). Each participant's difference time-course was detrended using a second order polynomial and subsequently Fourier transformed (using the fast Fourier transform). Amplitude values at frequencies from 1.5 Hz to 13.5 Hz (in steps of 1.5 Hz) were then averaged across participants to obtain the mean amplitude spectrum. To obtain the phase relationship of the 6-Hz oscillations at the same- and different-object position, we performed the Fourier transform for the same- and different-object conditions separately as described above. We then computed the angular difference between the phase angles of the 6-Hz oscillations of each condition. The angular difference was then projected onto the unit circle in the complex plane and averaged across participants. The length and the angle of the resulting vector then corresponded to the phase-locking value (PLV (Lachaux et al., 1999)) and the mean phase difference, respectively. We obtained non-parametric estimates of the probability of the observed data under the null hypothesis. For each of 5000 permutation samples, each participant's individual time-course was shuffled before entering the analysis as described above. This resulted in one mean amplitude spectrum for the object-based attention effect, one PLV, and one mean phase difference between the same- and different-object condition for each permutation sample. Individual frequency *p*-values in the amplitude spectrum were corrected for number of frequency bins to control the false discovery rate at 5% (Benjamini & Hochberg, 1995).

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Author contributions

B.P., B.R., and C.B. designed the experiment. B.P. analyzed the data. B.P., B.R., J.K., and C.B. wrote the manuscript.