The strength of attentional biases reduces as visual short-term memory load increases

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Shimi A, Astle DE. The strength of attentional biases reduces as visual short-term memory load increases. J Neurophysiol 110: 12–18, 2013. First published April 10, 2013; doi:10.1152/jn.01098.2012.—Despite our visual system receiving irrelevant input that competes with task-relevant signals, we are able to pursue our perceptual goals. Attention enhances our visual processing by biasing the processing of the input that is relevant to the task at hand. The top-down signals enabling these biases are therefore important for regulating lower level sensory mechanisms. In three experiments, we examined whether we apply similar biases to successfully maintain information in visual short-term memory (VSTM). We presented participants with targets alongside distracters and we graded their perceptual similarity to vary the extent to which they competed. Experiment 3 extended these behavioral findings by demonstrating that the perceptual similarity between target and distracters exerted a significantly greater effect on occipital alpha amplitudes, depending on the number of items already held in VSTM. The trade-off between VSTM load and target-distracter competition suggests that VSTM and perceptual competition share a partially overlapping mechanism, namely top-down inputs into sensory areas.

Attention; EEG; VSTM; biased competition

DESPITE OPERATING IN A RICH visual environment, we are able to achieve our perceptual goals efficiently. This is because despite the richness of the bottom-up sensory input, we can bias or modify our sensory representation in favor of those aspects that are most relevant to the task at hand. These top-down biases are employed in a graded fashion, depending on the extent to which relevant and irrelevant items share receptive fields (Desimone and Duncan 1995); that is, the more similar the neural codes representing relevant and irrelevant items, the more they compete, and thus the greater the top-down bias needed to countermand this bottom-up similarity.

A number of researchers have suggested that these top-down inputs (from domain general areas such as DLPFC and IPS) into sensory areas have a broader function than visual attention per se. These same inputs may underpin short-term storage by preserving sensory items as mental representations (Astle et al. 2012; Awh and Jonides 2001; Chun 2011; Gazzaley and Nobre 2012; Stokes 2011). However, this view is at odds with a relatively large literature that has consistently shown that participants’ ability to engage visual attention, even when targets involve a conjunction of features (thought to be particularly demanding of top-down biases), is not the least influenced by the number of items participants hold in visual short-term memory (VSTM) (Kane et al. 2006; Woodman et al. 2001).

We developed a paradigm that enabled us to quantify the strength of these top-down biases during VSTM maintenance by parametrically varying the degree of perceptual similarity between targets and distracters while participants maintained the targets in VSTM for later recall; the more perceptually similar the distracters to the target (i.e., the greater their shared neural representation), the stronger the top-down bias will need to be to resolve the target-distracter competition. Within a single paradigm (rather than using a dual task methodology) we tested whether participants’ ability to resolve the competition changed as their memory load increased. The paradigm was based loosely on a dot matrix paradigm that requires participants to maintain the location and order of sequential items (Alloway 2007). We accompanied the to-be-remembered targets with graded distracters. We hypothesized that if the same top-down mechanisms are employed for achieving both our perceptual goals and for maintaining items, then the ability to recruit those mechanisms to bias subsequent competition will decrease as the memory load increases; in other words, participants’ ability to achieve their perceptual goals should deteriorate as they are called to maintain more items in memory. We first tested this behaviorally (Experiments 1 and 2). Subsequently, we explored the neural mechanisms by which participants deal with the competition imposed by the relative similarity of distracters. In particular, we looked at alpha band activity (8–15 Hz) using EEG. Alpha band amplitudes over posterior sites have been shown to have a causal role in regulating the efficiency of visual processing (Romei et al. 2010; Thut et al. 2006); i.e., boosting the alpha rhythm with transcranial magnetic stimulation (TMS) assists distracter inhibition (Sauseng et al. 2009), likewise suppression in alpha amplitudes acts to enhance perceptual sensitivity (Thut et al. 2006). We tested whether the recruitment of alpha to resolve the target-distracter interference changed as a function of the number of items held in VSTM (Experiment 3).

METHODS

All experiments were approved by the University of Cambridge Psychology Research Ethics Committee, and participants provided written informed consent. Participants were recruited from the MRC Cognition and Brain Sciences Research Panel and received monetary compensation.

Experiment 1: Effect of VSTM Load on the Ability to Bias Competition

Participants. Fifteen healthy right-handed adults (7 female, 1 left-handed, mean age 23.9 ± 4.1 years SD) with normal or corrected-to-normal vision participated in Experiment 1.
Task. The task is presented schematically in Fig. 1A. Participants viewed a sequence of three matrices, each containing a target disc in a particular color (the color of the target was consistent throughout the experiment for each participant). Participants were instructed to remember the location and order of the targets in all three matrices. At the end of each trial, participants viewed a final “probe” matrix with one location highlighted; they responded as to whether a target had occupied the highlighted location in the preceding sequence, and, if so, in which matrix the probed location had been occupied. They responded by pressing keys 1–3 on the numeric keyboard corresponding to the three matrices, respectively, or the fourth button if none of the previous targets had occupied the probed location. For all experiments, we asked participants to make non-speeded reaction times, and instead to attempt to maximize their accuracy.

Targets varied in number depending on the VSTM load condition: for load 3, there was one target disc in each matrix; for load 5, there were two targets in the first and second matrix followed by a single target in the third matrix. Importantly, the third matrix always contained a single target across all load conditions: we were particularly keen to have a common phase of the trial, which was perceptually equated across the two levels of VSTM load (this was particularly important for interpreting the EEG data in Experiment 2). In addition to the target disc(s), each matrix contained distracter discs. There were always two distracters per target, and these are described below.

Stimuli. We varied the perceptual similarity between the targets and the distracters parametrically, to vary the extent to which top-down biases were needed to select targets relative to distracters (Desimone and Duncan 1995). Each disc (0.53° in diameter) was defined in RGB space: the targets were made of a red background (R:255, G:0, B:0) with a blue ring (R:0, G:0, B:255). For each distracter, we then added green in 1% increments from 1 to 255, with the most dissimilar distracter comprising a yellow background (R:255, G:255, B:0) and a cyan ring (R:0, G:255, B:255). This was counterbalanced across participants: for half of the participants, the target comprised the yellow background and cyan ring, with distracters having progressively less green. For each participant, we had a target item and a set of 99 distracters, each of which was progressively more dissimilar to the target (examples of which can be seen in Fig. 1B). Each matrix comprised a 4 × 4 set of boxes, with each matrix spanning 3.08° × 3.08°.

Experimental design. Each matrix appeared for 300 ms and followed the previous one after 700 ms. Finally, after a randomly varied duration of 1,100–1,480 ms, the fourth (probe) matrix appeared. Participants performed 600 trials in a fully randomized order: 300 for each level of VSTM load (load 3 and load 5), with an equal number of seven different levels of distracter dissimilarity across each load (10%, 15%, 20%, 25%, 30%, 40%, and 50% dissimilar, relative to the hue of the target). Participants completed 12 test blocks of 50 trials each, interleaved with self-paced breaks. We imposed the additional constraint that no location could be occupied by either a target or distracter twice on any trial. There was an equal number of trials upon which we probed a target from the first matrix (M1 trials), the second matrix (M2 trials), the third matrix (M3 trials), and trials upon which we probed a non-target location (which was always one of the distracter-occupied locations, evenly distributed across the three matrices). That is, 25% of trials were allocated to each of these four trial types. In all cases, where our data violated the assumption of sphericity, we used the Greenhouse-Geisser correction during the analysis.

Experiment 2: Effect of VSTM Load on the Ability to Bias Competition

Experiment 2 was identical to Experiment 1, except that there were no distracters on the first and second matrix. We carried out this experiment in a different laboratory, with a different population of participants. We observed no significant differences in performance across the two laboratories, and therefore report the data from Experiment 2 as if it were a replication of Experiment 1.
control experiment to test whether the results from Experiment 1 indeed reflected the attentional mechanisms recruited to deal with the perceptual competition on the third matrix, and not the greater intrusion of distracters in the first and second matrix.

Participants. Fifteen healthy right-handed adults (7 females, mean age 23 ± 3.25 years SD) participated in Experiment 2.

Experiment 3: Neural Effects of VSTM Load on Attentional Biases

In Experiment 3, we used a variant of the design used in Experiment 1 while recording EEG. The task was identical to that used in Experiment 1 except for the following differences.

Participants. Nineteen healthy right-handed adults (7 females, mean age 25.74 years ± 5.07 SD) participated in Experiment 3.

Task. We included a load 4 condition, in which either the first or second matrix contained two targets. Importantly, it was still the case that the third matrix was identical across the load manipulations. In addition to the target disc(s), each matrix contained three distracter discs, with this number being fixed across all levels of VSTM load.

Stimuli. The distracter stimulus set was identical to that used in Experiment 1. However, for the EEG study, instead of having seven levels of distracter similarity, we assigned two levels of distracter similarity individually for each participant using a staircase procedure. This was done prior to the actual experimental trials, comprised only load 3 trials, and acted as the participants’ practice session. We subsequently refer to these two levels of distracter as “high competition” and “low competition” and we used these two levels for all subsequent experimental trials. During the staircase procedure, we varied the similarity of the distracters such that each participant achieved a performance rate of 95% accuracy (these distracters were used for subsequent low competition trials) and 75% accuracy (these distracters were used for subsequent high competition trials). Throughout the subsequent experimental trials, we continued to adjust the two types of distracter when the accuracy fell below 95% or moved above 75% for the two levels of distracter. This controlled for any practice or fatigue effects that might have changed the degree of competition experienced.

Experimental design. Participants performed 600 trials in a fully randomized order: 100 for each orthogonal combination of VSTM load (load 3, load 4, and load 5) and distracter similarity (low competition, high competition).

EEG recording. EEG activity was recorded continuously using a BrainVision amplifier and actiCAP electrodes mounted on an elastic cap from 66 sites according to the 10–20 system. The montage included 6 midline scalp sites (Fz, Cz, CPz, Pz, Oz, O1 and O2) and 30 scalp sites over each hemisphere (FP1/FP2, AF3/AF4, AF7/AF8, F1/F2, F3/F4, F5/F6, F7/F8, F9/F10, FC1/FC2, FC3/FC4, FC5/FC6, FT7/FT8, FT9/FT10, C1/C2, C3/C4, C5/C6, T7/T8, CP1/CP2, CP3/CP4, CP5/CP6, TP7/TP8, TP9/TP10, P1/P2, P3/P4, P5/P6, P7/P8, PO3/PO4, PO7/PO8, PO9/PO10, O1/O2). AFz served as the ground. Blink and eye movements were monitored with electrodes placed horizontally and vertically around the eyes. Electrode impedances were kept below 20 kΩ. We used a 250-Hz analog-to-digital sampling rate and recorded all frequencies between 0.1 and 124 Hz. The EEG was referenced online to the FCz electrode and then rereferenced offline to the algebraic average of the left and the right mastoids. Bipolar electro-oculogram (EOG) signals were derived by computing the difference between recordings horizontal to each eye and between recordings vertical to the left eye. Subjects were instructed not to move their eyes from central fixation or to blink, and any eye movements and blinks were removed using an independent component analysis (ICA). We applied a 1-Hz high-pass filter and submitted the continuous EEG to a temporal ICA (using EEGLAB) (Delorme and Makeig 2004); we correlated the time course of each IC with our bipolar EOG channels to identify the ICs that corresponded to blinks and eye movements. These were then regressed from the data. We then formed epochs starting 700 ms before and ending 1,700 ms after the onset of the third matrix. Phase and power estimates were extracted for these epochs using a continuous wavelet transform (Tallon-Baudry and Bertrand 1999). This used seven full cycles to establish the phase angles and power estimates, for frequencies between 2 and 40 Hz. We also explored effects in the gamma band (frequencies above 40 Hz) and looked at early visual event-related potentials; however, these did not reveal any significant effects and thus were not included here. In our analyses, we particularly focused on the alpha band amplitudes. Across a number of studies, the alpha rhythm has been shown to regulate sensory mechanisms, leading up to and around the onset of the formation of a perceptual representation. For instance, the alpha rhythm is suppressed by a retinotopically organized fashion depending on the expected spatial location of a to-be-reported target (Gould et al. 2011; Thut et al. 2006); the timing of the alpha suppression is also temporally synchronized relative to the moment that participants expect the onset of a target item (Rohenkol and Nobre 2011); the alpha rhythm is enhanced contralaterally to to-be-ignored distracters (Sauseng et al. 2009; van Dijk et al. 2010). Furthermore, the use of TMS has shown that the alpha rhythm plays a causal role in regulating sensory processing. Its enhancement results in a disruption of sensory processing. Thus, the alpha rhythm offers a clear electrophysiological mechanism by which attentional biases may shape sensory processing; for this reason, we focused on this band here. The amplitudes were log transformed, such that their distribution was closer to normal (Gould et al. 2011). We then trimmed the data to −500 to 1,500 ms relative to the onset of the third matrix, to avoid any edge effects that can result from the time-frequency decomposition.

Amplitude (power) analyses. For our amplitude analyses, we used a nonparametric cluster-based analysis (Maris and Oostenveld 2007) examining the effect of competition (high vs. low) across our two extremes of VSTM load. The calculation of the cluster-based statistic started with calculating a t-test for each electrode and each sample within the epoch. T statistics greater than T < 0.01 were then forming into clusters (across neighboring electrodes or time samples); each resulting cluster was defined in terms of its summed T value. A probability distribution of cluster size was then created using a permutation procedure on the data, with 5,000 iterations, whereby the experimental conditions were intermixed within each participant. We then compared our clusters to this distribution and we report those whose extent exceeded T < 0.05. This controls for the false alarm rate for all clusters (Maris and Oostenveld 2007). To isolate the effect of target-distracter competition, we subtracted alpha activity on low competition from high competition trials. We tested whether participants’ ability to bias the competition at the onset of M3 (which was perceptually identical across the different load conditions) was influenced by the number of items participants were already holding in VSTM. To do this, we compared the relative competition effects across our two extremes of VSTM load (load 3 vs. load 5) during the post-stimulus period for M3 onset (0–300 ms).

RESULTS

Experiment 1: Effect of VSTM Load on Attentional Precision

We submitted the accuracy data from Experiment 1 to a three-way repeated measures ANOVA, with the within-subjects factors of load, competition, and serial order (whether we probed the 1st, 2nd, or 3rd item in the array). Accuracy increased with serial order [F(2, 26) = 20.457, P < 0.001] and decreased with increasing load [F(2, 13) = 122.394, P = 0.001], and when distracters were more similar to targets [F(2, 26) = 17.030, P < 0.001], with the effect of load being significant when a target from M1 [F(1, 13) = 48.045, P < 0.001] or M2 [F(1, 13) = 49.011, P < 0.001] was probed, but
not when the final item was probed [F(1, 13) = 0.022, P = 0.884]. (This interaction is very difficult to interpret, since the first two matrices were not perceptually identical across the different load conditions.) There was also a significant interaction between serial order and competition [F(4.84, 62.91) = 2.627, P = 0.034], with there being a linear interaction between the levels of distracter similarity and serial order [F(1, 13) = 13.787, P = 0.003]. This was because the linear effect of our seven levels of similarity decreased with increasing serial order [M1: F(1, 13) = 55.204, P < 0.001; M2: F(1, 13) = 19.395, P = 0.001; M3: F(1, 13) = 12.688, P = 0.003].

In addition to analyzing the raw accuracy scores, we also tested for graded changes in participants’ ability to distinguish targets and distracters. To do so, we used a polynomial function to identify the level of distracter similarity at which participants reached asymptotic performance, for each level of the other two factors (VSTM load and serial order). This was done by approximating each participant’s performance with a function that allowed for two turning points, with the second corresponding to the point at which they reached asymptotic performance. We then submitted these values to an ANOVA. There was a main effect of load [F(1, 13) = 11.516, P = 0.005], with larger differences in target-distracter similarity needed for participants to perform optimally when they were performing a load 3 trial relative to when they were performing a load 3 trial. There was also a main effect of serial order [F(1, 13) = 3.793, P = 0.036], with there being a significant change in asymptote between M1 and M2 [F(1, 13) = 10.125, P = 0.007], and marginally so between M1 and M3 [F(1, 13) = 3.447, P = 0.086], but there was no difference between M2 and M3 trials [F(1, 13) = 0.047, P = 0.832]. Importantly, there was an interaction between these two factors [F(2, 26) = 3.727, P = 0.038]: there was no effect of VSTM load at M1 [t(13) = 0.510, P = 0.618] or at M2 [t(13) = 1.604, P = 0.133], but there was at M3 [t(13) = 3.861, P = 0.002]. This interaction can be seen in Fig. 1C, as can the asymptotes for the two VSTM loads on M3 trials.

In short, as VSTM became fuller, the distracters needed to be more perceptually distinct from targets in order for participants to reach asymptotic performance. This is shown in Fig. 1C by the steeper climb to asymptote along the x-axis in the load 3 condition, relative to the load 5 condition (asymptote is reached at 30% target-distracter similarity for load 3, and at 39% for load 5). This result cannot stem from perceptual differences between load 3 and load 5 trials; the final item was perceptually identical across the levels of VSTM load, and this final item showed the most marked effect of VSTM load on the distracter similarity function. Furthermore, this result cannot stem from ceiling effects influencing the asymptotes differentially across the load conditions; despite the differences in asymptote, our raw accuracy results showed no overall effect of VSTM load on trials on which the final item was probed.

**Experiment 2: Effect of VSTM Load on Attentional Precision**

The goal of Experiment 2 was to replicate the significant effect of VSTM load on the level of distracter similarity at which participants reach asymptotic performance. As with Experiment 1, asymptotic performance was reached at a significantly higher level of dissimilarity on load 5 trials, relative to load 3 trials [t(12) = 2.179, P = 0.050]. There were no distracters in the previous two matrices, so any effect of VSTM load on the level of asymptote on M3 trials cannot stem from the differential intrusion of distracters across the two load conditions, which might be adding to the load effects. The reduction in the number of distracters in Experiment 2 made the task substantially easier as indicated by the close-to-ceiling performance in most participants (mean accuracy was 90% across the different conditions, indeed two participants reached ceiling and could not be included). Nonetheless, the difference between targets and distracters still needed to be larger when participants retained more items in VSTM.

**Experiment 3: Neural Effects of VSTM Load on Attentional Biases**

Experiments 1 and 2 indicated that participants’ ability to bias competition was reduced when more items had to be maintained in VSTM; this suggested that targets and distracters need to be more perceptually distinct, in order for participants to achieve the same performance level as the number of items held in VSTM increases. Experiment 3 sought to explore the neural mechanisms that underpin these changes in biased competition.

**Behavioral data from the EEG session.** Because there were fewer conditions in the EEG experiment, we were able to detect accurately the proportion of false alarms within each condition, and so we calculated d’ prime scores (normalized false alarms subtracted from normalized correct hits). These were submitted to a within-subject ANOVA with load, serial order, and competition as factors. As in Experiment 1, performance became gradually worse with increasing load [F(2, 36) = 59.587, P < 0.001], increasing serial position [F(1.27, 22.93) = 53.990, P < 0.001], and increasing similarity between targets and distracters [F(1, 18) = 85.838, P < 0.001]. Furthermore, there was a significant interaction between competition and load [F(2, 36) = 3.278, P = 0.049]; when targets were very similar to distracters, there was less of a load effect [F(2, 36) = 20.590, P < 0.001] than when the targets were very distinct from distracters [F(2, 36) = 44.935, P < 0.001] (see Fig. 2A). Load and serial position also interacted [F(2.39, 42.96) = 9.034, P < 0.001], with VSTM load having the largest effect on M2 trials [F(1.49, 26.78) = 53.884, P < 0.001], relative to M1 [F(2, 36) = 35.294, P < 0.001] and M3 trials [F(2, 36) = 6.368, P = 0.004] (see Fig. 2B). (As in Experiment 1, this load by order interaction is difficult to interpret since the first two matrices were not perceptually equated across the load conditions). In all cases, there was a significant difference between each level of load at each level of serial order [Ts > 2.709, Ps < 0.014] apart from between load 3 and load 4 on M3 trials [t(18) = 0.999, P = 0.331]. Finally, there was also an interaction between competition and serial order [F(2, 36) = 4.638, P = 0.016], with there being a larger serial order effect when targets and distracters were very similar [F(1.22, 21.95) = 53.635, P < 0.001] than when they were more distinct [F(2, 36) = 31.590, P < 0.001] (see Fig. 2C). In summary, there were two important interpretable results from these behavioral data: making targets and distracters more similar reduced the overall load effect, but increased the serial order effect.

**Alpha amplitude analysis.** We focused our EEG analyses around the onset of the final matrix, as this time window is
perceptually identical across all levels of VSTM load. Our subsequent analyses focused on the alpha band. We calculated the difference between high and low competition trials to isolate the relative competition effect within the alpha band (8–15 Hz) and compared this across the two extremes of load (load 5 vs. load 3) during the perceptual processing of the stimuli (0–300 ms). There was a significant effect of VSTM load on this peristimulus alpha competition effect [T_cluster = 11.8972, P_cluster = 0.0304], with the cluster comprising P6, PO8, and PO10. The time course of the competition effect (high vs. low competition) for these electrodes, across the three VSTM load conditions, can be seen in Fig. 3A. The topographical distributions for the effect at each level of VSTM load can be seen in Fig. 3B.

To rule out the possibility that this result reflects changes in the evoked response, even though the events were perceptually equated across the load conditions, we carried out the same comparison as detailed above on the event-related potentials (ERPs) themselves. There was no effect [P_cluster = 1], meaning that the result we observed in the alpha band does not reflect the ERP. The topographical distributions of the ERPs, calculated in the same way as the alpha topographical plots, are shown in Fig. 3C.

In addition to this within-subject contrast, we also examined between-subject effects across the time window and electrodes...
revealed by our within-subject comparison. Our staircasing procedure ensured that each participant had an individually titrated competition level, and we examined the extent to which these between-subject differences in competition might be manifested in peristimulus alpha. To do this, we selected the high competition trials (as we reasoned that these are where the individual differences ought to be most apparent) and performed a regression analysis to examine whether the amplitude of peristimulus alpha differed across participants depending on the degree of competition that they were experiencing. We found a quadratic relationship between the level of competition and alpha amplitude at each level of VSTM load \[ load 3: t = 2.269, P = 0.038, R^2 = 0.332; \] \[ load 4: t = 2.295, P = 0.037, R^2 = 0.332; \] \[ load 5: t = 2.406, P = 0.029, R^2 = 0.365 \]. In short, peristimulus alpha amplitudes varied systematically depending on the perceptual competition experienced by the participants (although this relationship was not linear). The relationship between competition level and alpha amplitude, at each level of VSTM load, can be seen in Fig. 3D.

**DISCUSSION**

We examined whether increasing the number of items held in VSTM influences the attentional mechanisms recruited while processing perceptually competing items. Previous studies have demonstrated that the load of VSTM has no effect on the efficiency of visual search (He and McCarley 2010; Woodman et al. 2001). This result is important as it suggests that there is no shared mechanism between visual attention and VSTM, and it is therefore inconsistent with theories proposing a close link between attention and VSTM maintenance (Awh and Jonides 2001; Gazzaley and Nobre 2012; Stokes 2011). In our paradigm, we manipulated visual attention in a different way: we varied the degree of perceptual similarity between targets and distractors, and we were thus able to manipulate the extent to which they competed with one another, and the extent to which top-down attentional mechanisms were needed to bias this competition (Desimone and Duncan 1995). We found that when participants held four items in VSTM, the fifth item then needed to be more perceptually distinct from its accompanying distractors, compared with when only two items were already held in VSTM (Experiments 1 and 2). In short, there was a trade-off between the number of items that participants held in VSTM and their ability to bias subsequent competition between targets and distractors. We propose that this is because both of these functions rely, at least in part, on a common mechanism, i.e., on top-down inputs into sensory areas (Gazzaley and Nobre 2012). In one context, these inputs can act to resolve competition between relevant and irrelevant material, thereby having an attentional effect; in another context, these inputs can act to insulate or protect the fading sensory representations of previously seen items, thereby ensuring that their representation survives the onset of subsequent memoranda or probe items. The greater the number of items to be maintained, the more these top-down inputs are recruited, and thus the less scope there is for using them to bias subsequent competition.

There are a number of possibilities for why our result contradicts previous studies demonstrating a lack of attention/VSTM trade-off. One possibility is that we probed a different aspect of attention than the one tapped in pure visual search. Another possibility is the use of different methodology; here we did not use a dual task methodology, whereas, to our knowledge, all previous studies of the interaction between attention and VSTM have manipulated these two mechanisms in separate tasks (e.g., participants retained items in VSTM for use in a subsequent recognition task, while performing a separate visual search during the VSTM maintenance period). In a dual task setup, it may be possible for participants to divide their resources strategically between the VSTM and search tasks, and this may mask any interaction between VSTM load and search efficiency.

**Neural Correlates of the Trade-Off Between VSTM Load and Attentional Bias**

Previous studies have demonstrated that alpha has a causal and mechanistic role in shaping the incoming perceptual information, possibly by influencing the anticipatory tuning of retinotopically organized areas (Thut et al. 2006). Indeed, during maintenance, rhythmic alpha TMS has been shown to enhance VSTM by boosting the inhibition of competing distractors in the contralateral hemifield (Sauseng et al. 2009). Subsequently, Romei et al. (2010) demonstrated that alpha suppression can act to enhance item processing and conversely that alpha enhancement acts to suppress item visibility. In our data, we observed an increase in alpha power for targets accompanied by similar distractors relative to those accompanied by dissimilar distractors. We suggest, in line with previous studies, that this increase in alpha power for similar distractors has the result of disrupting their visual processing, thereby reducing their interference with target detection, encoding, and maintenance. Importantly, despite being perceptually identical across the load conditions, this relative competition effect increased depending on how many items were already being held in VSTM; even though the distractors were perceptually identical across the load conditions, more disruption was required if more items were being held in VSTM. Some studies have shown that the early visual-evoked response may reflect stimulus-evoked changes in alpha and theta amplitude and phase (Gruber et al. 2005; Klimesch et al. 2004). We did not replicate our alpha band effects in an ERP analysis, so at least in this case we do not think that our result reflects changes in the evoked response per se.

An interesting supplementary finding was that there was a nonlinear relationship between the amplitude of these peristimulus alpha rhythms and the level of competition that subjects were experiencing. A similar parabolic relationship between alpha amplitude and sensory detection was shown by Linkenkaer-Hansen et al. (2004). They suggested that the relationship, in their case between these rhythms and a tactile stimulus detection task, may reflect poor performance stemming from the top-down activation of a too-small or a too-large neuronal population. This is a possible explanation for our result. Participants’ task was to detect targets within distractors. Given that participants still needed to process the target while resisting distraction, simply boosting alpha amplitudes maximally may not result in optimal performance. Our result may reflect the relative tuning of these amplitudes in order for the particularly well-performing participants to detect targets even when these are presented alongside very similar distractors. A further possible interpretation of our data is that as distractors become more target-like, participants mistake them...
for targets and thus they exert a VSTM load effect. Of course, this is possible, and it is difficult to rule out, but we do not think that it can account for, or undermine, the particular effects that we report here for three reasons. First, the effect of VSTM load on the target-distracter discrimination function (Experiment 1) might be exacerbated by these distracter intrusions; however, this does not undermine our conclusion. Whether targets are stored correctly or erroneously (in the case of distracters), the number of items held in VSTM prior to the onset of the final matrix influences participants’ ability to distinguish the target from the distracters. Second, Experiment 2 was included to test for this exact effect. There were no distracters in the first two matrices in Experiment 2 and yet we found the same result as in Experiment 1; increasing VSTM load earlier in the trial resulted in poorer target-distracter discrimination for the final matrix. Third, this possible account cannot explain the EEG result. In the EEG experiment (Experiment 2), the number of distracters was identical across the different VSTM load conditions. If participants erroneously store distracters when they become more target-like, then this ought to have an equivalently detrimental effect across the different load conditions and thus it doesn’t provide a compelling explanation for the load by similarity interaction that we observed.

In conclusion, the same target needs to be more perceptually distinct from accompanying distracters depending on how many items participants are already holding in VSTM. This is mirrored by an increased distracter-related amplitude effect in the alpha band; that is, the same distracters elicit greater alpha amplitudes if participants are already holding more items in memory. In short, our ability to use top-down attention to achieve our perceptual goals reduces with increasing VSTM maintenance demands. A number of studies have suggested competing explanations for these effects is that biased competition and VSTM maintenance share a common mechanism, top-down inputs into sensory areas.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

A.S. and D.E.A. conception and design of research; A.S. performed experiments; A.S. and D.E.A. interpreted results of experiments; A.S. and D.E.A. drafted manuscript; A.S. and D.E.A. edited and revised manuscript; A.S. and D.E.A. approved final version of manuscript; D.E.A. analyzed data; D.E.A. prepared figures.

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