Published in final edited form as:

J Clin Exp Neuropsychol. 2014 ; 36(2): 186–204. doi:10.1080/13803395.2013.877123.

Disentangling Working Memory Processes during Spatial Span Assessment: A Modeling Analysis of Preferred Eye Movement Strategies

Virginie M. Patt^{1,2}, Michael L. Thomas¹, Arpi Minassian^{1,3}, Mark A. Geyer^{1,3}, Gregory G. Brown^{1,3}, and William Perry¹

¹University of California, San Diego, Department of Psychiatry

²San Diego State University / University of California, San Diego, Joint Doctoral Program in Clinical Psychology

³VA San Diego Healthcare System, San Diego, CA

Abstract

The neurocognitive processes involved during classic spatial working memory (SWM) assessment were investigated by examining naturally preferred eye movement strategies. Cognitively healthy adult volunteers were tested in a computerized version of the Corsi Block-Tapping Task — a spatial span task requiring the short term maintenance of a series of locations presented in a specific order — coupled with eye-tracking. Modeling analysis was developed to characterize eye-tracking patterns across all task phases, including encoding, retention, and recall. Results revealed a natural preference for local gaze maintenance during both encoding and retention, with fewer than 40% fixated targets. These findings contrasted with the stimulus retracing pattern expected during recall as a result of task demands, with 80% fixated targets. Along with participants' self-reported strategies of mentally “making shapes”, these results suggest the involvement of covert attention shifts and higher-order cognitive Gestalt processes during spatial span tasks, challenging instrument validity as single measure of SWM storage capacity.

Keywords

spatial working memory; spatial span; Corsi Block-Tapping Task; eye-tracking; descriptive modeling

Spatial working memory (SWM) is a key brain system that provides temporary maintenance and manipulation of information pertaining to locations and orientation in space (Baddeley & Hitch, 1974; Baddeley, 1986; Cowan, 1999; Della Sala, Gray, Baddeley, Allamano, & Wilson, 1999). SWM is essential for everyday functioning, from way-finding to problem

Virginie M. Patt, M.A. (corresponding author), vpatt@ucsd.edu, San Diego State University / University of California, San Diego Joint Doctoral Program in Clinical Psychology, 9500 Gilman Drive. Mailcode 0738, La Jolla, CA 92093-0738.
Michael L. Thomas, Ph.D., Post-Doctoral Fellow, University of California, San Diego, Department of Psychiatry, 9500 Gilman Drive. Mailcode 0738, La Jolla, CA 92093-0738
Arpi Minassian, Ph.D., Associate Clinical Professor of Psychiatry, University of California, San Diego, Department of Psychiatry, 200 West Arbor Drive, Mailcode 8620, San Diego, CA 92103-8620
Mark A. Geyer, Ph.D., Distinguished Professor of Psychiatry & Neurosciences, University of California San Diego, Department of Psychiatry, 9500 Gilman Drive, Mailcode 0804, La Jolla, CA 92093-0804, USA
Gregory G. Brown, Ph.D., ABPP, Professor of Psychiatry, University of California, San Diego, Department of Psychiatry, 9500 Gilman Drive. Mailcode 0738, La Jolla, CA 92093-0738
William Perry, Ph.D., Professor of Psychiatry, University of California, San Diego, Department of Psychiatry, 200 West Arbor Drive, Mailcode 8620, San Diego, CA 92103-8620

solving and mental calculations (e.g., Passolunghi & Mammarella, 2010), has been linked to genetic susceptibility to serious neuropsychiatric illnesses such as schizophrenia (e.g., Cannon et al., 2000), and may constitute one of the most sensitive impairments in certain dementias (e.g., Cantone, Orsini, Grossi, & DeMichele, 1978; Sullivan, Sagar, Gabrieli, Corkin, & Growdon, 1989).

The cognitive processes and neural correlates underlying SWM have been difficult to resolve, with contributions from oculomotor, attentional, and higher-order cognition processes demonstrated at the earliest stages of spatial information processing (Awh, & Jonides, 2001; D'Esposito, 2007; Repovš & Baddeley, 2006). These complex and overlapping processes have not been disentangled adequately in the assessment of SWM. In fact, in most SWM tasks used in neuropsychological settings, it is often assumed that a single composite ability is measured. For example, classic spatial span tasks wherein individuals are asked to recall a series of locations presented in a specific order – e.g., the Corsi Block-Tapping Task (Corsi, 1972) or the Spatial Span subtest of the Wechsler Memory Scale-Third Edition (WMS-III; The Psychological Corporation, 1997) – have been widely used as a measure of SWM storage capacity, but likely recruit a more complex range of abilities (e.g., Berch et al., 1998).

The present study seeks insight into the neurocognitive processes involved during SWM tasks by examining eye movement strategies naturally utilized by healthy participants as they are attempting to encode and retain a series of locations. A better understanding of these processes is necessary for the development and refinement of assessment instruments (Batchelder, 2010) and to improve identification of specific deficits for targeted treatment strategies (Insel, 2012).

Processes Involved in Spatial Working Memory

Studies across a wide range of fields and modalities have attempted to characterize SWM processes from behavioral accounts to single neuron stimulation. An overview of these findings is essential for considering the variety of neurocognitive and neuroperceptual mechanisms that may be recruited during spatial span assessment.

Oculomotor and attentional processes

Spatial information has been proposed to be represented and retained in working memory (WM) in terms of oculomotor programming; that is, neural activity pertaining to the planning and execution of eye movement (e.g., Baddeley, 1986; Hale, Myerson, Rhee, Weiss, & Abrams, 1996). Similar to the way that subvocal articulatory rehearsal is believed to promote maintenance of verbal information in WM (Baddeley, 1986), eye movement mechanisms have been suggested to promote spatial information maintenance.

Eye movement alone, however, has been insufficient for explaining the representation and maintenance of spatial information. For example, it has been shown that nystagmus — involuntary eye-movement induced by the vestibulo-ocular reflex — does not disrupt SWM (Baddeley, 1986; Postle et al., 2006), and that the retention of spatial information occurs in the absence of eye movement (cf. delayed oculomotor response tasks; Funahashi, Bruce, & Goldman-Rakic, 1989; Fuster & Alexander, 1971). Furthermore, SWM has also been found to be disrupted by voluntary body movement and planning (e.g., Johnson, 1982; Smyth, Pearson, & Pendleton, 1988). These findings suggest that the representation and maintenance of spatial information might not stem solely from oculomotor processes, but likely recruits a more general system also involved in the planning of eye and body movement. Researchers have subsequently proposed that this more general system is attention-based, suggesting that shifts of spatial attention rather than actual eye or body

movements are the underlying mechanism responsible for disrupting information retention during SWM tasks (e.g., Awh, Jonides, & Reuter-Lorenz, 1998; Smyth & Scholey, 1994).

Direct attempts have been made to quantitatively parse oculomotor from attentional contributions in spatial span tasks (Pearson & Sahraie, 2003; Lawrence, Myerson, and Abrams, 2004). Using computerized versions of the Corsi Block-Tapping Task (Corsi, 1972), these studies reported greater performance decline following disruption by eye movement during delay (e.g., alternating gaze between peripheral distractors) compared to disruption by attention shifts. Both studies suggested a crucial role of eye movement over and above covert attention shifts for the rehearsal of spatial information in SWM. However, it has also been shown that the brain circuits involved in preparing saccades play a causal role in directing covert spatial attention (e.g., Chambers & Mattingley, 2005). Therefore, disrupting a person's gaze is also likely to disrupt their attention, rendering experiments based on eye movement disruption inconclusive for distinguishing between those processes.

The role of oculomotor processes during delay has also been examined in terms of their influence on spatial span performance (e.g., Smyth, 1996; Tremblay et al., 2006). Here as well, conflicting conclusions have been reported. Smyth (1996) found no significant difference in spatial span performance depending on whether participants were free or not to move their eyes during delay. After examining video recordings of participants' eyes during delay, Smyth also commented that some subjects seemed to repeatedly retrace a stimulus while others appeared to fixate on the center of the screen and make few, non-repetitive eye movements. In contrast, Tremblay et al. (2006) reported improved performance when fixations were made during delay on two pairs of successive locations compared to one pair and no pair. They thus suggested that eye movement consisting of fixations on successive targets was an efficient form of rehearsal in SWM.

Although the role of overt eye movement for retaining information during delay in spatial span tasks has been studied, its role for encoding information has yet to be examined. Indeed, none of the aforementioned spatial span experiments studied eye movement during stimulus presentation. This omission perhaps reflects the implicit but heretofore untested assumption that examinees would uniformly move their gaze from target to target as they were presented. However, as previously noted, results from delayed oculomotor response tasks have shown that spatial information can be encoded and retained in the absence of eye movement. Testing this implicit assumption is essential to gaining better insight into encoding processes during spatial span assessment.

Higher-order cognitive processes

In addition to closely intertwined attentional and oculomotor programming, SWM has also been shown to involve higher-order cognitive processes, such as executive functioning, at the earliest stages of information processing. This involvement has been demonstrated in several studies using dual task paradigms (e.g., Ang & Lee, 2008; Vandierendonck, Kemps, Fastame, & Szmalec, 2004). For example, Vandierendonck et al. (2004) found that spatial span performance, although unaffected by finger tapping in fixed intervals, was disrupted by random interval generation which recruits higher executive loads. Furthermore, depending on task requirements, and thus on planning, different neural substrates have been shown to be activated for the representation and retention of the same spatial information in WM. In one study, for example, instructions to saccade to a remembered location "A" led predominantly to activation of the frontal eye field, whereas instructions to saccade to a different but not yet known location, despite also requiring remembering "A", led predominantly to activation in and around the intra parietal sulcus (Curtis, Rao, & D'Esposito, 2004). Task requirements for inhibition have also been shown to influence the coding of spatial information in WM. For example, in the same way that saccades were

shown to curve away from visible to-be-ignored stimuli, Theeuwes, Olivers, and Chizk, (2005) found that saccades also curved away from no longer visible stimuli held in WM, suggesting representations of to-be-ignored information in terms of inhibited saccade programming. Thus, depending on strategies elaborated and task demands, the same spatial information may be represented in WM by different patterns of activation in the brain. This view is consistent with a model of WM arising from the interaction between higher-order cognitive top down processes governed by the prefrontal cortex and stimulus specific brain regions (d'Esposito, 2007). Therefore, when considering the brain processes that might be activated during SWM assessment, one has to consider not only the stimulus properties and paradigm instructions, but also the strategies that might be elaborated by participants. These considerations are especially important in spatial span tasks, as stimuli, although presented in the form of a serial series of locations, may also have underlying configural properties (Berch et al., 1998).

Study Goals and Hypotheses

In this study, we sought to gain insight into neurocognitive processes used by healthy participants during classic SWM assessment by characterizing naturally preferred (i.e., unconstrained) eye movement strategies. This goal was accomplished by using eye-tracking during the encoding, retention, and recall phases of a computerized version of the Corsi Block-Tapping Task.

Two potential eye movement strategies were expected during encoding and retention, with perhaps different implication for underlying SWM processes: stimulus retracing (i.e., fixations on successive targets) and local gaze maintenance (i.e., fixations contained in one area). We suggest that preference for a stimulus retracing strategy may be consistent with the encoding and retention of spatial information as a series of discrete items. By contrast, preference for a local gaze maintenance strategy may be consistent with dominant involvement of Gestalt mechanisms (Wertheimer, 1923); that is, the encoding and retention of spatial information in the form of an overall picture. Such a strategy may then imply activation of higher-order cognitive processes to facilitate the integration into a whole of information presented as a series of discrete locations.

To characterize patterns of eye movement during each paradigm phase, we developed a novel method based on descriptive modeling. Previous spatial span studies have analyzed eye-tracking data by examining fixations on specific stimulus features (e.g., Tremblay et al., 2006). Such analyses have required the construction of possibly arbitrary boundaries around those features. In this study, we utilized a more nuanced modeling approach allowing geometric characterization of fixation distributions in a two dimensional continuum. Modeling has been applied previously for analyzing eye movements, with accumulator models developed to fit saccade latency distributions and characterize decision-making processes in inhibition of return tasks (Carpenter & Williams, 1995; Ludwig, Farrell, Ellis, & Gilchrist, 2009). These models, however, did not address the characterization of eye movement strategies. Our descriptive modeling method was tested using simulations and is described in detail in the Method section and Appendix.

Method

Participants

Participants were 25 normal adult volunteers recruited on college campuses by means of flyers. The mean age was 24 ($SD = 5.7$, range = 18 to 43) and 14 subjects (56%) were female. Mean years of education was 15 ($SD = 1.8$, range = 13 to 20). All participants had normal or corrected-to-normal vision, did not meet criteria for a psychiatric diagnosis, and

had a negative urine toxicology test. Written informed consent was obtained, and the study was reviewed and approved by the University of California, San Diego Human Research Protections Program and San Diego State University Institutional Review Board.

Paradigm and Procedure

Participants were administered a computerized SWM task as part of a larger battery of tests. Participants were seated at a 29 inch viewing distance of a 17 inch computer screen with a 1024 × 768 resolution. During the experiment, eye movements were monitored by eye-tracking (see below), and head movements were constrained by a chinrest and forehead bar. The chair's height was adjusted for comfort prior to the beginning of the experiment.

The computerized SWM task was designed based on the Corsi Block Tapping Task (Corsi, 1972; Milner, 1971) using the Matlab™ Psychtoolbox (Brainard, 1997). The paradigm consisted of 4 practice and 24 test trials, each divided into three phases: encoding, retention, and recall (see Figure 1). During encoding, the computer screen displayed ten circles on a white background. Each circle was white with a black outline and measured 50 pixels in diameter. Among these circles, a sequence of 4, 6, or 8 circles (the targets) changed from white to gray, one at a time, at a rate of one per 1.5 seconds (1 second black, 0.5 second white). The three target number conditions (i.e., 4, 6, and 8) were chosen so as to limit fatigue effects while covering the range of spatial span reported in the literature, varying between 4.9 and 7.1 in different samples of healthy subjects (Corsi, 1972; Farrell Pagulayan, Busch, Medina, Bartok, & Krikorian, 2006; Kessels, van Zandvoort, Postma, Kappelle, & de Haan, 2000; Orsini et al. 1986).

After the last target was presented, a retention period followed, randomly varied between 5 or 20 seconds, with the ten background circles remaining displayed on the screen to allow rehearsal. Because decline in visual working memory has been shown to begin between 4 and 10 seconds in healthy adults (Zhang & Luck, 2009), delays of 5 and 20 seconds were chosen at both ends of that range so as to force active rehearsal. An immediate recall condition was not included as it would not have permitted eye-tracking observation. Participants knew that a delay would take place but did not know in advance the duration of the delay, thus promoting onset of similar strategies at the beginning of the interval. To indicate the end of the retention period, a blue frame appeared around the edge of the screen. Participants then used a computer mouse to click on the circles in the same order that they had previously changed from white to gray, and were instructed to click on a button marked "Done" when finished.

For each trial, a new set of circles was randomly generated to avoid long-term memory formation, with the constraints that any two circles would be separated by a distance of at least 150 pixels to avoid overlap. Total path length and angle sharpness were also controlled: locations of consecutive targets were generated such that their distance would be between 300 and 500 pixels, with an average distance of 400 ± 25 pixels when considering all pairs of consecutive targets, and such that angles between three consecutive targets would always be greater than 45 degrees. These constraints were chosen to limit confounding effects of stimulus geometry, shown to affect recall on similar SWM tasks (e.g., Parmentier, Elford, & Maybery, 2005). Although the same overall series of trials was administered to every participant, the order of the trials was randomized using a Latin square design to distribute practice effects over stimulus conditions (i.e., number of targets and delay condition). At the end of task administration, a short 5-minute interview was carried out, asking participants about their preferred strategy to remember the series of targets.

Materials

Eye movements were monitored using an ISCAN® (Cambridge, MA) eye-tracking system. Calibration was conducted at the beginning of the experiment by requiring participants to successively fixate on five evenly distributed-points on the stimulus computer screen. Data, recorded in terms of pupil and corneal reflection, were sampled at a 60Hz-rate, with 12-bit resolution and 0.3 degree eye-position accuracy (per manual). Eye movement monitoring was initiated and terminated automatically by the stimulus display program, so that each recording period would correspond exactly to a trial phase (i.e., encoding, retention, or recall).

Blinks were removed, and saccades and fixations were calculated using a program developed in Matlab™. Saccades were extracted from the data via identification of eye-acceleration patterns, a method that was shown to be advantageous compared to using velocity thresholds (Behrens & Weiss, 1992), and fixations were identified in the remaining portions of the data where eye movement remained within a 1 degree-cone for at least 100 milliseconds (Salvucci & Goldberg, 2000; Widdel, 1984).

Data Analysis

Descriptive modeling—Two descriptive models were developed to characterize and contrast eye movement strategies during the encoding, retention, and recall phases of the spatial span task. This novel analysis method allows geometric characterization of fixation distributions in a two-dimensional spatial continuum, thus bypassing the constraints of past eye-tracking studies that often had to construct arbitrary boundaries around stimulus features.

The first model, which we termed the ON-TARGET model, assumes that fixations are made on the targets to be remembered. This model focused on the overall spatial distribution of the fixations and did not penalize eye movement patterns where targets were not fixated in a specific order. The second model, which we termed the ZONE model, assumes that participants spend most of their allocated time fixating in one area, presumably attending to all presented targets without actual overt eye movements.

For both models, geometric distributions of fixations were modeled using likelihood functions calculated by building two-dimensional Gaussians over hypothesized features of interest (see Figure 2). That is, the degree to which participants' fixations landed on particular features of interest were quantified using symmetric and continuous distributions around those features. We suggest that this method has notable advantages over classical eye-tracking analyses, where regions of interest are often established with sharp boundaries and arbitrary sizes. Here, by using continuous distributions, fixations could be examined along a continuum, without having to set arbitrary thresholds. Likelihood scores were allocated for each fixation with values decreasing following a Gaussian shape depending on distance to predetermined features of interest.

Model fit required parameter estimation, with the free parameters of two-dimensional Gaussians being vectors of means and standard deviations. Estimation of these parameters differed between models. In the ZONE model, the likelihood function was characterized by one unique two-dimensional Gaussian (see Figure 2), with parameterized means (central coordinates; x_c , y_c) and standard deviations set equal to the same value in both dimensions (σ). In the ON-TARGET model, several identical two-dimensional Gaussians were constructed centered on each of the targets to be remembered (Figure 2). For example, if six targets were presented during encoding, six Gaussians were built centered on the xy-coordinates of each target's center. Because the central coordinates of these Gaussians were

predetermined based on target locations, the only free parameter of the ON-TARGET model's maximum likelihood estimation was the standard deviation common to all constructed Gaussians (σ). The likelihood function of the ON-TARGET model was determined by examining two properties of the fixation distributions: 1) the distances of each fixation to the closest possible target; and 2) the overall evenness of the fixation distribution around the targets to be remembered. The second factor was calculated by decomposing the 2D-space according to a Voronoi diagram (Devadoss & O'Rourke, 2011) and by using a multinomial distribution (Evans, Hastings, & Peacock, 2000). Effectively, this factor introduced a penalty for the ON-TARGET model if some targets were fixated excessively compared to others. Further details, including equations supporting the construction of these models, are presented in the appendix.

Maximum likelihood estimation of parameters was carried out by fitting all the participants' data simultaneously, using an unconstrained nonlinear optimization method (Lagarias, Reeds, Wright, & Wright, 1998). For each stimulus, three parameters were estimated in the ZONE model (x_c , y_c , and σ) and a unique parameter in the ON-TARGET model (σ). Model fits were compared using the Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC), measures of relative goodness of fit taking into account penalty terms for the model's number of parameters (Farrell & Lewandowsky, 2001). Relatively lower AIC and BIC values indicate better fit.

Simulation studies—To validate our novel modeling approach, we used computer simulation to generate multiple hypothetical datasets and test the correct behavior of the ON-TARGET and ZONE models.

The first two hypothetical datasets were generated to represent ideal cases of the ON-TARGET and ZONE models (see Figure 3): fixations were either evenly distributed around the targets (Simulation 1) or distributed around one location (Simulation 2). Both simulations were computed assuming 30 hypothetical participants, each performing a number of fixations randomly selected between 1 and 30. Each fixation location was randomly selected within 2D-Gaussian distributions with standard deviation $\sigma_{\text{sim}} = 75$ pixels.

Model fits were carried out on the simulated data using both the ON-TARGET and ZONE models. As expected, Simulation 1 was best fitted by the ON-TARGET model and Simulation 2 by the ZONE model (see Figure 4). Confirming the absence of bias toward one model in ideal data configurations, identical likelihood functions were found as a function of model fit parameter (σ) for the fits of Simulation 1 by the ON-TARGET model and Simulation 2 by the ZONE model. In both configurations, maximum likelihood was found for fit parameter $\sigma = 75$ pixels, showing good restitution of the characteristics of the original simulation distributions.

Two additional simulations were generated to verify good model functioning in extreme cases (see Figure 3). For these simulations, fixations were either all distributed around one single target in a 2D-Gaussian distribution (Simulation 3), or were flatly and randomly distributed over the 2D-space (Simulation 4). As expected, Simulation 3 – essentially designed as Simulation 1 but centered on one of the targets – was also fitted ideally by the ZONE model but not by the ON-TARGET model. The difference between model fits in this case illustrates an extreme case of the penalty that can be assigned to the ON-TARGET model due to some targets being excessively fixated compared to others (see Appendix). Finally, Simulation 4 was better fitted by the ON-TARGET model compared to the ZONE model. These results were also expected since an even distribution of data points through space should be better represented by several Gaussians distributed on the screen (ON-TARGET model) rather than by one Gaussian alone (ZONE model). All run simulations

thus confirmed the good functioning of the models' algorithms in describing the intended eye movement strategies.

Proportion of targets fixated—Finally, in order to support results from the modeling approach, an additional parameter was extracted from the data to characterize preferred eye movement strategies: the percentage of targets that were fixated at least once by each participant during encoding, retention, or recall. By focusing on target salience rather than on the entire fixation distribution, this parameter brings information complementary to descriptive modeling. For example, data from participants who glanced quickly once at each target but systematically brought their gaze back to one location, might be better fit by the ZONE model, while having fixated 100% of the targets at least once.

To determine whether a target was or was not fixated, circular regions of 150 pixels in diameter were drawn around each target, three times larger than the targets themselves and corresponding to a visual angle of about 4 degrees. The size of these regions was chosen conservatively based on eye physiology (i.e., it represents twice the visual angle of foveal vision where acuity is maximum; Rayner, 1995), and on stimulus constraints (150 pixels was the minimal distance allowed between targets during stimulus generation). A target was considered as fixated at least once by a participant, if any of his or her fixations fell within that target's circular region. Comparison between the proportions of targets fixated during the encoding, retention, and recall phases of the paradigm was carried out using repeated measure multivariate analyses of variance (RM-MANOVAs). The repeated-measure independent variable was paradigm phase, and the dependent variables (DVs) were the proportions of targets fixated during stimulus 1 (DV_1), stimulus 2 (DV_2), and so forth. Separate analyses were conducted for each delay configuration (5 versus 20 seconds during retention) so as to limit the number of dependent variable in each analysis, and to examine whether different effects of phase might be present depending on delay. For each analysis, the significance value was set at .025 (Bonferroni correction).

Results

Modeling Analysis of Eye Movement Strategies

Descriptive modeling revealed marked differences in eye movement strategies utilized during encoding and retention compared to recall. In each of the 24 stimulus configurations (see Figure 5 – upper panel), the ZONE-model provided a better fit of the data in the encoding phase, $BIC_{ZONE} = 609$ to 652 , $BIC_{ON-TARGET} = 630$ to 710 , and in the retention phase, $BIC_{ZONE} = 595$ to 654 ; $BIC_{ON-TARGET} = 646$ to 750 , whereas the ON-TARGET model provided a better fit during recall, $BIC_{ZONE} = 635$ to 690 , $BIC_{ON-TARGET} = 536$ to 600 . Maximum likelihood parameter estimates for each stimulus (σ_{ML}) were also different in the encoding and retention phases compared to recall (see Figure 5 – lower panel). During encoding and retention, σ_{ML} values had wide overlapping distributions depending on stimulus, ranging from 84 to 152 pixels for the ZONE model and 44 to 122 pixels for the ON-TARGET model. By contrast, during recall, σ_{ML} distributions did not overlap between models; they were characterized by a wide distribution of higher values ranging between 126 and 217 pixels for the ZONE model and by a tighter distribution of lower values ranging between 45 and 72 pixels for the ON-TARGET model. These σ_{ML} distributions imply tight distributions of fixations around targets during recall, contrasting with more diffuse fixation distributions during encoding and retention. Examples of fixation distribution data are presented in Figure 6, representative of trials with 4, 6, and 8 targets to remember. The differences in eye-movement strategies were visually apparent, with diffuse local gaze maintenance during encoding and retention, compared to evenly distributed fixations on targets during recall.

For descriptive comparison of model fit across stimulus features, log-likelihood values of trials with same target number and delay were added (see Table 1). This operation required that we assume local independence of the data across trials after accounting for eye movement strategy. Fit results obtained during retention suggested fixation distributions that were similar across delay conditions, independent of whether information had to be retained for 5 or 20 seconds. Delay conditions were thus collapsed. The impact of the number of targets on differences between model fits (ΔBIC) was then examined (see Figure 7). ΔBIC increased markedly with number of targets during encoding and retention, but remained nearly constant during recall. These variations of ΔBIC with the number of targets supports the presence of ZONE-like strategy during encoding and retention, and the presence of on-target-like strategy during recall. That is, based on model definitions, ZONE-like fixation distributions are expected to be fitted equally well by the ZONE model independently of the number of targets, but to yield increasingly worse fits (i.e., increasing BIC) by ON-TARGET models defined by more targets. By contrast, fixation distributions evenly distributed around increasing numbers of targets (i.e., increasingly spread out) are expected to lead to increasingly worse fits by the ZONE model. They should also lead to somewhat worse fits by ON-TARGET models due to increased potential for noise in the calculation of evenness when the number of targets that define the model increases.

Comparison of fit results between the encoding and retention phases suggests consistent although subtler differences (see Figure 7). In particular, the difference in fit between the ON-TARGET and ZONE models were found to be consistently smaller during encoding, $\Delta\text{BIC} = 270, 425$, and 580 for 4, 6, and 8 targets, respectively, compared to retention, $\Delta\text{BIC} = 431, 696$, and 738 . We attribute this difference to the fit of the ON-TARGET model being relatively better during encoding compared to retention, suggesting local gaze maintenance that was more diffusely and evenly distributed during target presentation than during retention.

Proportion of Targets Fixated

RM-MANOVAs revealed a significant effect of paradigm phase on the proportion of targets fixated for all trials (see Figure 8), whether they featured a 5-second delay, $F(24,76)=7.29$, $p < .001$, $\eta^2 = .70$, or a 20-second delay, $F(24,76)=5.29$, $p < .001$, $\eta^2 = .63$. In both configurations, there were significantly fewer targets fixated during encoding and retention compared to recall (Figure 9). Notably, on average, only 37% of the targets were fixated during encoding, a number twice lower than the number of targets fixated during recall ($M = 78\%$). These results are congruent with the previous model fit results, suggesting diffuse gaze maintenance in one area during encoding and retention, compared to eye movements carried out in the close vicinity of the targets during recall.

The proportion of targets fixated at least once was significantly smaller during retention (25%) compared to encoding (37%) when the delay lasted 5 seconds, $F(12,13)=5.41$, $p = .002$, $\eta^2 = .83$, but not when the delay lasted 20 seconds, $F(12,13)=1.61$, $p = .202$, $\eta^2 = .60$. Upon closer examination of trials with a 5-second delay, differences between encoding and retention were only significant for conditions with 6 targets, $F(4,21)=10.57$, $p < .001$, $\eta^2 = .67$, and 8 targets, $F(4,21)=15.02$, $p < .001$, $\eta^2 = .74$, but not for conditions with 4 targets, $F(4,21)=3.76$, $p = 0.019$, $\eta^2 = .42$ (Bonferroni correction, $\alpha = .004$). In other words, it appears that when individuals had to remember a series of 6 or 8 locations, they fixated on fewer targets during the first 5 seconds of retention (1.2 and 1.6 targets) than they did on average during encoding (2.4 and 2.7), but given enough time, resumed eye movements to as many targets during retention (2.2 and 2.8) as during encoding.

These results must be interpreted in the context of presentation times associated with the 4, 6, and 8 targets encoding phases. Indeed, RM-MANOVAs carried out on the rates of targets

fixated at least once, revealed no significant difference between the encoding and 5-second retention intervals, whether participants had to remember 4 targets, $F(4,21) = 3.09$, $p = .038$, $\eta^2 = .37$, 6 targets, $F(4,21) = 2.27$, $p = .096$, $\eta^2 = .30$, or 8 targets, $F(4,21) = 4.22$, $p = .012$, $\eta^2 = .45$ (Bonferroni correction, $\alpha = .004$). Rates of targets fixated at least once ranged between .24 and .29 targets per second during encoding and between .23 and .31 targets per second during the 5-second delay.

Self-Reported Strategies

In post-experiment interviews, 22 out of 25 subjects reported linking targets in their mind with imaginary lines and “making shapes”. Five out of 25 participants reported mentally counting the targets, one described giving themselves verbal instructions such as “up, down, right, left”, one reported making locations mentally correspond to audio tones, and one reported retracing the stimuli on their leg with their fingers.

Discussion

The goal of this study was to identify and characterize naturally preferred eye movement strategies during the encoding, retention, and recall phases of a classic spatial span task, a computerized version of the Corsi Block-Tapping Task. Two analyses, descriptive modeling and comparison of fixated target proportion, revealed strategies that were markedly different during encoding and retention as compared to recall. We found that, during encoding and retention, fixations were distributed diffusely in one area of the screen, often centrally located, with fixations on less than 40% of the targets; whereas during recall, fixations were evenly distributed in the vicinities of each target, falling on close to 80% of the targets.

The results suggest that there is a natural preference for local gaze maintenance when remembering a series of locations during stimulus presentation and delay, contrasting with stimulus retracing patterns during recall. These findings are novel in that they report unconstrained eye movement strategies across all phases of a spatial span task, including stimulus presentation. Our results are discussed in terms of SWM processes, including considerations of rehearsal, oculomotor versus attentional processes, and involvement of higher-order cognition at the earliest stage of information processing. Implications for the neuropsychological assessment of SWM are discussed.

Eye Movement Strategies across Task Phases

Encoding—There is a marked absence of past work examining natural eye movements during the encoding phase of spatial span tasks. In absence of previous measurement and quantification of eye movement strategies during the encoding phase, one might assume that the eyes would follow targets that are presented serially, in a pattern similar to that observed during the recall phase. Our results demonstrate that this is not the case, and preference for local gaze maintenance with fixations on less than half of the targets is consistently identified during stimulus presentation.

Retention—In relevant literature, retention (or delay) is by far, the phase most studied with eye tracking. Some authors have suggested that stimulus retracing with the eyes is a means for rehearsal; for example, Tremblay et al. (2006) defined “rehearsal” as a measure of whether pairs of targets were consecutively fixated by participants. In contrast, our findings show consistent preference for local gaze maintenance during the retention phase, with eye movement to less than 40% of the targets. Our results are consistent, however, with previous observations noting a surprising limitation or absence of eye movement during delay (Smyth, 1996; Pearson & Sahraie, 2003). Furthermore, despite an ultimately different conclusion on the role of eye movement in SWM, our findings are also consistent with

numerical results in Tremblay et al. (2006), where only a limited portion of the stimulus was shown to actually be “visually rehearsed”. For example, out of six possible target pairs, the authors reported successive fixations on only one or no pair in two thirds of all trials collapsed across participants.

Preference for local gaze maintenance during delay could also suggest an alternative explanation for past findings. Smyth (1996) showed that spatial span performance did not differ between delay conditions when participants had to maintain central fixation versus delay conditions when they were free to move their eyes. While it was concluded that performance was not affected by fixation, our findings suggest that gaze maintenance in a centrally located area, even in the unconstrained condition, may be the preferred and presumably more adaptive strategy for retaining spatial locations in WM.

Recall—Eye tracking data during the recall phase suggested eye movement strategies that retraced the stimuli, consistent with task demands of clicking on targets. These expected results do not allow direct inferences on cognitive processes, but provide further validation that our novel measures, descriptive modeling and fixated target proportion, characterize eye movement patterns adequately. They especially serve as a comparison point for the encoding and retention results, supporting the finding that eye movement strategies differed from stimulus retracing during those two phases of the task.

It was also verified that the observed encoding and retention eye movement patterns could be validly attributed to willful strategies and not to paradigm time constraints or physiological limitations. Based on physical properties of fixations and saccades (Salvucci & Goldberg, 2000), we found that there was always enough time for making fixations on all presented targets. For example, the 5 second delay was calculated to be sufficient for saccades and fixations to about 6 to 16 targets. Additionally, the proportion of targets fixated was noted to remain fairly constant during encoding with respect to number of targets presented (41% for 4, 35% for 6, and 34% for 8 targets), perhaps suggesting the existence of an optimal proportion of targets to be fixated within an overall local gaze maintenance strategy when remembering a series of locations.

Rehearsal Mechanisms

Descriptive modeling and fixated target proportion revealed eye movement strategies that were similar during encoding and retention. Significant differences between the number of targets fixated during encoding and retention were only found when the delay was shorter than presentation time (i.e., stimuli of 6 and 8 targets with a 5-second delay). This observation suggests effects of time constraints rather than differences in preferred eye movement strategies between encoding and retention in those cases. Indeed, examination of the data in terms of rates of fixated target proportion revealed no difference between encoding and the 5-second retention interval. In addition, even when extra time was allowed during retention compared to encoding – such as in the 20-second delay configuration – this extra time was not used to make fixations on additional targets. Taken together, these results suggest reproduction of similar eye movement strategies during retention compared to encoding, with fixations mostly distributed in a local area and saccades performed at a specific rate to a portion of the stimulus targets. These findings support the theory of information rehearsal during retention (Baddeley & Hitch, 1974) and are consistent with the suggestion that information is maintained in WM in the same way it was encoded, i.e., in its original representation (D’Esposito, 2007).

Nonetheless, small differences were noted between encoding and retention. The ON-TARGET model provided slightly better results during encoding compared to retention, while the ZONE model had superior and equivalent fits across both of these phases of the

task (Figure 7). These observations suggest eye movement patterns that were more diffuse during encoding compared to retention, perhaps reflecting the uncertainty intrinsically associated with serial stimulus presentation. Indeed, during encoding, not knowing the location of the next target likely brings need for gaze adaptability, with the production of eye movements that may not be optimal for remembering a stimulus. By contrast, during retention, the stimulus has already been revealed, thus promoting a reliance on the more optimal eye movement strategy; that is, local gaze maintenance.

Oculomotor and Attentional Processes

The consistently observed preference for local gaze maintenance during stimulus presentation suggests perception of most targets using peripheral vision, and thus reliance on covert attention shifts rather than overt eye movement for encoding at least a portion of the stimulus.

Our findings appear to contrast with previous work suggesting that overt eye movement contribution supersedes that of attention shifts in SWM (Tremblay et al., 2006, Pearson & Sahraie, 2003; Lawrence et al., 2004). The conclusions of those studies were supported by a greater decline in spatial span performance observed following disruption by eye movement during delay – alternating gaze between peripheral distractors – compared to disruption by attention shifts. In light of the present findings, however, the eye movement strategy that was affected by the disruption during delay was likely local gaze maintenance, not overt eye movement rehearsal. Moreover, if gaze maintenance provides an optimal anchor point for attention shift rehearsal, then disruption by eye movement may have actually disrupted attention before affecting performance. This explanation is supported by findings that oculomotor circuits play a causal role in directing covert spatial attention (e.g., Chambers & Mattingley, 2005). In fact, it might not be possible to move one's gaze without producing an attention shift. Indeed, in the aforementioned studies, although participants were asked to shift their attention to specific stimuli while maintaining gaze, they were never instructed to move their eyes while maintaining attention to a fixation point.

In light of these considerations and of our results, we suggest that covert attention shifts are a preferred mechanism over overt eye movement for encoding and retaining serial spatial information in SWM. This proposal does not exclude activation at the neural level of circuitries that are also involved in the planning of eye movement. In fact, neural circuitries governing spatial attention and oculomotor planning have been shown to closely overlap in the brain (Awh & Jonides, 2001). For example, they are so similar in the frontal eye fields that distinction is only made at the single-neuron level (Awh et al., 2006). Thus, if our findings suggest a behavioral preference for covert attention shifts for remembering a series of locations in WM, the representation and maintenance of these locations in the brain likely involve activation of neural circuits that subserve both attentional and oculomotor functions.

Higher-Order Cognitive Processes

Beyond the use of covert attention shifts, the consistent preference demonstrated for local gaze maintenance may also suggest involvement of Gestalt mechanisms for encoding and retaining a series of locations in WM. Indeed, gaze maintenance in a stimulus-central location promotes attendance and mental retention of all presented targets at once, making it possible to construct mental representations of the stimulus as a whole. Post-experiment interviews supported this proposition, with 22 out of 25 subjects reporting linking targets in their mind with imaginary lines and “making shapes”. In other words, it appears that instead of encoding targets mentally as a series of discrete locations, participants actively used higher-order cognitive processes to integrate them into shapes. Such strategy is consistent with previous literature showing that integrating pieces of discrete information into wholes,

a process known as chunking (Miller, 1956), is an efficient approach for increasing the amount of information retained in memory.

These findings also suggest a close collaboration between SWM and visual WM (i.e., WM for shapes and color) during spatial span tasks, with series of locations being potentially encoded and maintained using visual WM processes. This collaboration between SWM and visual WM is consistent with recent findings demonstrating the partnership in the other direction; that is, the involvement of SWM processes for retaining color stimuli (Williams, Pouget, Boucher, & Woodman, 2013).

Besides “making shapes”, which was by far the most frequently cited self-aware approach, a wide diversity of strategies was also reported by some participants, including mentally counting the targets, giving themselves verbal instructions (e.g., “up down left right”), retracing the stimuli on their leg with their fingers, or even making locations mentally correspond to audio tones. These post-experiment interviews illustrate a wealth of higher-order strategies that involved encoding serial spatial information into different modalities, including visual, verbal, auditory, and motor modes.

The involvement of higher-order cognition and encoding of serial spatial information in different modalities are consistent with the WM framework proposed by D’Esposito (2007). Contrasting with Baddeley (1986) who initially proposed a model of WM based on independent units, each specializing in the storage and rehearsal of information in a specific modality and controlled by an overarching attentional system, D’Esposito (2007) viewed WM as stemming from the interaction between the prefrontal cortex (PFC) with the rest of the brain. Thus in essence, instead of a finite number of storage units governed by the central executive, D’Esposito (2007) suggested a potentially infinite number of overlapping circuits that can be activated for the representation and maintenance of a piece of information, with selection depending on stimulus characteristics and top-down processes (e.g., task demands or strategy elaborated). Consistent with D’Esposito’s interactive WM framework, our findings support a key role of higher-order cognitive processes and the potential activation of a wide variety of circuitries for the representation and maintenance of serial spatial information during spatial span tasks.

Implications for Neuropsychological Testing

The results of the present study and above discussion highlight the complexity of processes that underlie performance on spatial span tasks. Consistent with the WM framework of D’Esposito (2007), these functions likely involve higher-order cognitive processes (e.g., integrating information into chunks, or strategy devising) interacting with stimulus-specific neural codes (e.g., oculomotor and spatial attention programming, as well as association areas such as those dedicated to shape perception and, in some cases, verbal, auditory, and motor-related circuitries).

The apparent complexity and number of processes involved in spatial span tasks challenge the construct validity of current SWM assessments. Indeed, instead of solely measuring SWM storage capacity as often assumed (e.g., Farrell Pagulayan et al. 2006, Kessels et al. 2000), spatial span performance might also represent a person’s capacity for attention or their ability to integrate information into shapes, depending on task demands and individual style. For adequate assessment of SWM, we suggest the necessity of developing a process approach for parsing and evaluating the various abilities involved during spatial span tasks (Kaplan, 1988). We propose that this approach should be devised in future work using computational modeling (Farrell & Lewandowsky, 2001) and cognitive-psychometrics (e.g., Batchelder, 2010; Brown, Turner, Mano, Bolden, & Thomas, 2013; Thomas et al., 2013),

simultaneously taking into account participants' abilities and stimulus spatial and implicit configural properties.

Limitations and Future Work

First, our participant sample consisted mostly of college students, and was therefore not representative of the general population in terms of age and education. This homogeneous population was nonetheless chosen for the present SWM study for its high intelligence and motivation, making them likely to devise elaborate and effective strategies for performing spatial span tasks.

Second, eye movement strategy was characterized using descriptive modeling, a novel method proposed here for analyzing eye-tracking data. As in all modeling analysis, this approach required making choices for model construction, which might have influenced the results. Our models were, however, exercised in a series of simulations that showed performance as expected, with the models' relative fits showing adequate sensitivity for capturing relevant variations in fixation distributions. We also supported and supplemented our descriptive modeling results with another measure, fixated target proportion, which offered complementary insight into eye movement strategy. On one hand, descriptive modeling provided characterization of entire distributions of fixations in a two dimensional continuum, bypassing classic needs for defining arbitrary boundaries around regions of interest. On the other hand, fixated target proportion focused on target salience, discarding the number of fixations performed on or around each target. Fixated target proportion thus provided either confirmation of the descriptive modeling results (e.g., data better fitted by the ON-TARGET model also have high fixated target proportion) or complementary information (e.g., data better fitted by the ZONE model can have either low or high fixated target proportion).

The present work proposed a novel approach to the study of SWM mechanisms by examining naturally preferred eye movement strategies during a spatial span task. We acknowledge, however, that this approach is essentially descriptive, and the gap between preferred eye movement strategy and neurocognitive processes requires further bridging. For example, it may be possible to retain information in discrete pieces while maintaining gaze in one area, or to build up gestalt representations while fixating individual objects. To span this gap, complementary work is clearly needed, perhaps examining the relationship between eye movement strategy and performance, or using neuroimaging to confirm involvement of proposed neural networks – e.g., the activation in visual association areas dedicated to shapes during stimulus presentation and delay. Nonetheless, based on a wealth of evidence that healthy brains are adaptable (e.g., Bruel-Jungerman, Davis, & Laroche, 2007; Klingberg, 2010), we argue that there is value in observing and characterizing strategies naturally utilized by healthy individuals, without constraint. Further, by providing the first direct observation and characterization of where people look during stimulus presentation in spatial span tasks, this study may contribute to the end of decades of untested assumptions.

Acknowledgments

This work was sponsored by the Department of Health and Human Services, National Institute on Drug Abuse (NIDA), grant 5T32DA007315-09/10, and National Institute of Mental Health (NIMH), grant R01MH071916. The contents are solely the responsibility of the authors and do not necessarily represent the views of the Department of Health and Human Services NIDA, or NIMH. We also thank Anna Legenkaya and Anvay Ullal for their help with paradigm administration.

Appendix

Mathematical construction of the ZONE model

In the ZONE model, probability scores were allocated to each fixation following a two dimensional Gaussian equation,

$$f(x, y) = \frac{1}{2\pi\sigma^2} e^{-\frac{(x-x_c)^2 + (y-y_c)^2}{2\sigma^2}}, \quad (1)$$

where (x, y) are the coordinates in pixels of the fixations, (x_c, y_c) are the coordinates of the Gaussian's center, and σ is a measure of the Gaussian's width (equivalent to its standard deviation). The ZONE model's likelihood function L is then calculated by multiplying probability scores for every participant's fixation distribution. To give equal importance to each participant in the calculation of the likelihood function and address the differences in number of fixations between participants, the geometric mean in likelihood scores was calculated for each participant's set of fixations. This technique allowed limiting the contributing weight of every participant to one fixation, while taking into account the geometrical distribution of all fixations.

$$L = \prod_{i=1}^N \left(\prod_{j=1}^{n_i} f(x_{ij}, y_{ij}) \right)^{\frac{1}{n_i}}, \quad (2)$$

where N is the total number of participants and n_i the number of fixations made by participant i . Maximum likelihood modeling was then carried out on the (x_{ij}, y_{ij}) fixation data, using x_c , y_c , and σ as model fit parameters.

Mathematical construction of the ON-TARGET model

The likelihood function of the ON-TARGET model was calculated as the product of two terms, representing the probability that each fixation be close to at least one of the presented targets (L_D) and the evenness of the overall fixation distribution around these targets (C_E):

$$L = L_D \times C_E. \quad (3)$$

First, the term L_D was calculated using Equations (1) and (2) by replacing (x_c, y_c) for each fixation by the coordinates of its closest target. Second, to calculate C_E , the 2D-space was first decomposed into target-bins using a Voronoi diagram (Devadoss & O'Rourke, 2011), and the number of fixations made by each participant in each of these bins were counted (i.e., the number of fixations N_j closest to target T_j). The coefficient C_E , effectively introducing a penalty for the ON-TARGET model if some targets were fixated excessively compared to others, is expressed as follows:

$$\left\{ C_{Ei} = \left(\frac{C_{Ei} = \prod_{i=1}^N C_{Ei}}{p(N_{1i}, N_{2i}, \dots, N_{Ki})} \right)^{\alpha} \right\} \quad (4)$$

where C_{Ei} represents the coefficient of evenness of participant i ; K is the total number of presented targets; $p(N_{1i}, N_{2i}, \dots, N_{Ki})$ is the simultaneous probability of finding N_{1i} fixations in the T_1 -bin, N_{2i} fixations in the T_2 -bin, ..., and N_{Ki} fixations in the T_K -bin; N_{Fi} is the number of fixations of participant i in each bin, and α is a sensitivity coefficient allowing fine tuning between the ON-TARGET and ZONE model. Division by the term $p(N_{Fi}, N_{Fi}, \dots, N_{Fi})$ allows identical likelihood functions for the ON-TARGET and ZONE models when fitting datasets ideally verifying each model's respective hypothesis. The terms $p(N_{1i}, N_{2i},$

..., N_{Ki}) and $p(N_{Fi}, N_{Fi}, \dots, N_{Fi})$ were expressed using a multinomial distribution (Evans et al. 2000),

$$p(N_{1i}, N_{2i}, \dots, N_{Ki}) = \frac{1}{K^{N_{1i} + N_{2i} + \dots + N_{Ki}}} \frac{(N_{1i} + N_{2i} + \dots + N_{Ki})!}{N_{1i}! N_{2i}! \dots N_{Ki}!}, \quad (5)$$

leading simplification of Equation (4) to

$$C_{Ei} = \left(\frac{\bar{N}_{Fi}!}{N_{1i}!} \times \frac{\bar{N}_{Fi}!}{N_{2i}!} \times \dots \times \frac{\bar{N}_{Fi}!}{N_{Ki}!} \right)^\alpha. \quad (6)$$

To allow comparison of data from trials with different recording times as well as equal contribution across individuals, percentages of fixations in each target-bin were used instead of raw fixation numbers. The sensitivity coefficient α was chosen so that the maximum log-likelihood value of the ON-TARGET model diminishes by a third of its value in the extreme case where all the fixations are located in the same target-bin (see Simulation 3 in Figure 3). Simulations confirmed that this value allowed the likelihood functions of the ON TARGET and ZONE models to lie within similar ranges, thus providing sensitive and meaningful comparison between models.

References

- Ang SY, Lee K. Central executive involvement in children's spatial memory. *Memory*. 2008; 16:918–933. [PubMed: 18802804]
- Awh E, Jonides J, Reuter-Lorenz PA. Rehearsal in spatial working memory. *Journal of Experimental Psychology: Human Perception and Performance*. 1998; 24:780–790. [PubMed: 9627416]
- Awh E, Jonides J. Overlapping mechanisms of attention and spatial working memory. *Trends in Cognitive Sciences*. 2001; 5:119–126. [PubMed: 11239812]
- Awh E, Armstrong KM, Moore T. Visual and oculomotor selection: links, causes and implications for spatial attention. *Trends in Cognitive Sciences*. 2006; 10:124–130. [PubMed: 16469523]
- Baddeley, AD.; Hitch, GJ. Working memory. In: Bower, GH., editor. *The psychology of learning and motivation: advances in research and theory*. New York, NY: Academic Press; 1974. p. 47-89.
- Baddeley, A. *Working memory*. New York, NY: Oxford University Press; 1986.
- Batchelder, WH. Cognitive psychometrics : Using multinomial processing tree models as measurement tools. In: Embretson, SE., editor. *Measuring psychological constructs : Advances in model-based approaches*. Washington, DC: American Psychological Association; 2010. p. 71-93.
- Berch DB, Krikorian R, Huha EM. The Corsi block-tapping task: Methodological and theoretical considerations. *Brain and Cognition*. 1998; 38:317–338. [PubMed: 9841789]
- Behrens F, Weiss L-R. An algorithm separating saccadic from nonsaccadic eye movements automatically by use of the acceleration signal. *Vision Research*. 1992; 32:889–893. [PubMed: 1604857]
- Brainard DH. The psychophysics toolbox. *Spatial Vision*. 1997; 10:433–436. [PubMed: 9176952]
- Brown GG, Turner T, Mano QR, Bolden K, Thomas ML. Experimental manipulation of working memory model parameters: An exercise in construct validity. *Psychological Assessment*. 2013; 25:844–858. [PubMed: 23815108]
- Bruel-Jungerman E, Davis S, Laroche S. Brain plasticity mechanisms and memory: a party of four. *Neuroscientist*. 2007; 13:492–505. [PubMed: 17901258]
- Cannon TD, Huttunen MO, Lönqvist J, Tuulio-Henriksson A, Pirkola T, Glahn D, Finkelstein J, Hietanen M, Kaprio J. The inheritance of neuropsychological dysfunction in twins discordant for schizophrenia. *American Journal of Human Genetics*. 2000; 67:369–382. [PubMed: 10880296]
- Cantone G, Orsini A, Grossi D, Demichele G. Verbal and spatial memory span in dementia. *Acta Neurologica*. 1978; 33:175–183. [PubMed: 654979]

- Carpenter RHS, Williams MLL. Neural computation of log likelihood in the control of saccadic eye movements. *Nature*. 1995; 377:59–62. [PubMed: 7659161]
- Chambers CD, Mattingley JB. Neurodisruption of selective attention: insights and implications. *Trends in Cognitive Sciences*. 2005; 9:542–550. [PubMed: 16214388]
- Corsi, PM. Doctoral dissertation. McGill University; 1972. Memory and the medial temporal region of the brain.
- Cowan, N. An embedded-processes model of working memory. In: Miyake, A.; Shah, P., editors. *Models of working memory: Mechanisms of active maintenance and executive control*. Cambridge, UK: Cambridge University Press; 1999. p. 62-101.
- Curtis CE, Rao VY, D'Esposito M. Maintenance of spatial and motor codes during oculomotor delayed response tasks. *The Journal of Neuroscience*. 2004; 24:3944–3952. [PubMed: 15102910]
- de Berg, M.; van Kreveld, M.; Overmars, M.; Schwarzkopf, O. *Computational Geometry: Algorithms and Applications*. 3rd ed. Berlin, Germany: Springer-Verlag; 2008. p. 147-172.
- Della Sala S, Gray C, Baddeley AD, Allamano N, Wilson L. Pattern span: a tool for unwinding visuo-spatial memory. *Neuropsychologia*. 1999; 37:1189–1199. [PubMed: 10509840]
- D'Esposito M. From cognitive to neural models of working memory. *Philosophical Transactions of The Royal Society B*. 2007; 362:761–772.
- Devadoss, SL.; O'Rourke, J. *Discrete and Computational Geometry*. Princeton, NJ: Princeton University Press; 2011.
- Evans, M.; Hastings, N.; Peacock, B. *Statistical Distributions*. New York: Wiley; 2000.
- Farrell Pagulayan K, Busch RM, Medina KL, Bartok J, Krikorian R. Developmental normative data for the Corsi Block-tapping task. *Journal of Clinical and Experimental Neuropsychology*. 2006; 28:1043–1052. [PubMed: 16822742]
- Farrell, S.; Lewandowsky, S. *Computational Modeling in Cognition: Principles and Practice*. Thousand Oaks, CA: Sage publications; 2001.
- Funahashi S, Bruce CJ, Goldman-Rakic PS. Mnemonic coding of visual space in the monkey's dorsolateral prefrontal cortex. *Journal of Neurophysiology*. 1989; 61:331–349. [PubMed: 2918358]
- Fuster JM, Alexander GE. Neuron activity related to short-term memory. *Science*. 1971; 173:652–654. [PubMed: 4998337]
- Hale S, Myerson J, Rhee SH, Weiss CS, Abrams RA. Selective interference with the maintenance of location information in working memory. *Neuropsychology*. 1996; 10:228–240.
- Insel TR. Next-generation treatments for mental disorders. *Science Translational Medicine*. 2012; 4:155s19.
- Johnson P. The functional equivalence of imagery and movement. *The Quarterly Journal of Experimental Psychology A*. 1982; 34:349–365.
- Kaplan, E. A process approach to neuropsychological assessment. In: Boll, T.; Bryant, BK., editors. *Clinical neuropsychology and brain function: Research, measurement, and practice*. Washington, DC: American Psychological Association; 1988. p. 127-167.
- Kessels RPC, van Zandvoort MJE, Postma A, Kappelle LJ, de Haan EH. The Corsi Block-Tapping Task: standardization and normative data. *Applied Neuropsychology*. 2000; 7:252–258. [PubMed: 11296689]
- Klingberg T. Training and plasticity of working memory. *Trends in Cognitive Sciences*. 2010; 14:317–324. [PubMed: 20630350]
- Lagarias JC, Reeds JA, Wright MH, Wright PE. Convergence Properties of the Nelder-Mead Simplex Method in Low Dimensions. *SIAM Journal of Optimization*. 1998; 9:112–147.
- Lawrence BM, Myerson J, Abrams RA. Interference with spatial working memory: An eye movement is more than a shift of attention. *Psychonomic Bulletin and Review*. 2004; 11:488–494. [PubMed: 15376800]
- Ludwig CJH, Farrell S, Ellis LA, Gilchrist ID. The mechanism underlying inhibition of saccadic return. *Cognitive Psychology*. 2009; 59:180–202. [PubMed: 19520369]
- Milner B. Interhemispheric differences in the localization of psychological processes in man. *British Medical Bulletin*. 1971; 27:272–277. [PubMed: 4937273]

- Miller G. The Magical Number Seven, Plus or Minus Two: Some Limits on Our Capacity for Processing Information. *The Psychological Review*. 1956; 63:81–97.
- Orsini A, Chiacchio L, Cinque M, Cocchiari C, Schiappa O, Grossi D. Effects of age, education and sex on two tests of immediate memory: a study of normal subjects from 20 to 99 years of age. Perceptual and motor skills. 1986; 63:727–732. [PubMed: 3808855]
- Parmentier FBR, Elford G, Mayberry M. Transitional information in spatial serial memory: path characteristics affect recall performance. *Journal of Experimental Psychology. Learning, Memory, and Cognition*. 2005; 31:412–427.
- Passolunghi MC, Mammarella IC. Spatial and visual working memory ability in children with difficulties in arithmetic word problem solving. *European Journal of Cognitive Psychology*. 2010; 22:944–963.
- Pearson DG, Sahraie A. Oculomotor control and the maintenance of spatially and temporally distributed events in visuo-spatial working memory. *The Quarterly Journal of Experimental Psychology A*. 2003; 56:1089–1111.
- Postle BR, Idzikowski C, Della Sala S, Logie RH, Baddeley AD. The selective disruption of spatial working memory by eye movements. *The Quarterly Journal of Experimental Psychology*. 2006; 59:100–120. [PubMed: 16556561]
- Rayner, K. Eye movements and cognitive processes in reading, visual search, and scene perception. In: Findlay, JM.; Walker, R.; Kentridge, RW., editors. *Eye movement research: mechanisms, processes, and applications*. Amsterdam, the Netherlands: Elsevier Science B.V.; 1995. p. 3-22.
- Repotš G, Baddeley AD. The multi-component model of working memory: explorations in experimental cognitive psychology. *Neuroscience*. 2006; 139:5–21. [PubMed: 16517088]
- Salvucci, DD.; Goldberg, JH. *Proceedings of the Eye Tracking Research and Applications Symposium*. New York: ACM Press; 2000. Identifying fixations and saccades in eye-tracking protocols; p. 71-78.
- Smyth MM, Pearson NA, Pendleton LR. Movement and working memory: Patterns and positions in space. *The Quarterly Journal of Experimental Psychology A*. 1988; 40:497–514.
- Smyth MM, Scholey KA. Interference in spatial immediate memory. *Memory & Cognition*. 1994; 22:1–13. [PubMed: 8035679]
- Smyth MM. Interference with Rehearsal in Spatial Working Memory in the Absence of Eye Movements. *The Quarterly Journal of Experimental Psychology A*. 1996; 49:940–949.
- Sullivan EV, Sagar HJ, Gabrieli JDE, Corkin S, Growdon JH. Different cognitive profiles on standard behavioral tests in Parkinson's disease and Alzheimer's disease. *Journal of Clinical & Experimental Neuropsychology*. 1989; 11:799–820. [PubMed: 2592525]
- The Psychological Corporation. *WAIS-III—WMS-III technical manual*. San Antonio: Harcourt Brace & Co.; 1997.
- Theeuwes J, Olivers CNL, Chizk CL. Remembering a location makes the eyes curve away. *Psychological Science*. 2005; 16:196–199. [PubMed: 15733199]
- Thomas ML, Brown GG, Gur RC, Hansen JA, Nock MK, Heeringa S, Ursano RJ, Stein MB. Parallel psychometric and cognitive modeling analyses of the Penn Face Memory Test: Test score validity in the Army Study to Assess Risk and Resilience in Servicemembers. *Journal of Clinical and Experimental Neuropsychology*. 2013; 35:225–245. [PubMed: 23383967]
- Tremblay S, Saint-Aubin J, Jalbert A. Rehearsal in serial memory for visual-spatial information: Evidence from eye movements. *Psychonomic Bulletin & Review*. 2006; 13:452–457. [PubMed: 17048730]
- Vandierendonck A, Kemps E, Fastame MC, Szmalec A. Working memory components of the Corsi blocks task. *British Journal of Psychology*. 2004; 95:57–79. [PubMed: 15005868]
- Wertheimer M. Untersuchungen zur Lehre von der Gestalt II. *Psychologische Forschung*. 1923; 4:301–350.
- Widdel, H. Operational problems in analyzing eye movements. In: Gale, AG.; Johnson, F., editors. *Theoretical and Applied Aspects of Eye Movement Research*. New York: Elsevier; 1984. p. 21-29.
- Williams M, Pouget P, Boucher L, Woodman GF. Visual-spatial attention aids the maintenance of object representations in visual working memory. *Memory & Cognition*. 2013; 41:698–715. [PubMed: 23371773]

Zhang W, Luck SJ. Sudden death and gradual decay in visual working memory. *Psychological Sciences*. 2009; 20:423–428.

Figure 1.

Time sequence for a typical trial of the spatial span paradigm, divided into three phases: 1) Encoding, where ten circles were displayed on the computer screen, and a subset of 4, 6, or 8 circles changed serially from white to gray in a specific order; 2) Retention, where the white background circles remained displayed for durations of 5 or 20 seconds, and 3) Recall, where participants were instructed to click on the targets in the same order that they were presented. The onset of recall was indicated by the appearance on the screen of a blue box, a “Done”-button, and a cursor.

Figure 2.

Example of construction of the ON-TARGET and ZONE models for a stimulus where 6 targets had to be remembered. The likelihood function of the ON-TARGET model (top panel) was characterized by 6 two-dimensional Gaussians with identical parameterized standard deviation (σ) built above the to-be-remembered targets (T1–T6); and by a multinomial coefficient representing the evenness of the fixation distribution with respect to a target-based Voronoi space decomposition. The ZONE model (bottom panel) was characterized by a unique two-dimensional Gaussian with parameterized central coordinates (x_c , y_c) and standard deviation (σ).

Figure 3.

Hypothetical datasets generated in four simulations to test the good functioning of the ON-TARGET and ZONE models. These simulations assumed a randomly generated stimulus configuration where 6 targets, T1 to T6, had to be remembered. Hypothetical datasets were generated assuming 30 virtual participants, each performing a random number of fixations between 1 and 30. Fixation locations were randomly selected within specific two-dimensional distributions, defined by 6 two-dimensional Gaussians ($\sigma_{\text{sim}}=75$ pixels) centered on targets T1 to T6 for Simulation 1; by a unique Gaussian ($\sigma_{\text{sim}}=75$ pixels) centered on the middle of the screen for Simulations 2; by a unique Gaussian ($\sigma_{\text{sim}}=75$ pixels) centered on target T3 for Simulation 3; and by a flat distribution, covering the screen evenly for Simulation 4. Maximum likelihood parameters resulting from each model's best fit are illustrated in the form of circles of radius the estimated standard deviations (σ): black dotted circles centered on targets T1 to T6 for the ON-TARGET model, and gray dotted circles with estimated (x,y) centers for the ZONE model.

Figure 4.

Fit results for the four simulated datasets generated to test the good functioning of the ON-TARGET and ZONE models. For each simulation, Log-Likelihood functions are presented for the ON-TARGET model (solid line) and ZONE model (dashed line) with dependence on the Gaussian's standard deviation parameter (σ).

Figure 5.

Descriptive modeling results for the fixation distribution data, calculated separately for each of the 24 stimuli (x-axis) and paradigm phase (encoding, retention, and recall). Modeling results are presented for the ON-TARGET (black squares) and ZONE (light gray diamonds) models in terms of maximum log-likelihood, a measure of goodness of fit (upper panels), and in terms of estimated parameter σ_{ML} , i.e., the Gaussians' standard deviation at maximum likelihood (lower panels). The 24 stimuli, which were presented in a different order during paradigm administration for each participant, are re-ordered on the graphs based on stimulus characteristics, i.e., target number and delay duration.

Figure 6.

Fixation distribution data obtained during encoding, retention, and recall for 3 representative stimuli, where 4, 6, and 8 targets had to be remembered and with a retention delay of 5 seconds. Data are presented in the form of heat maps with darker color corresponding to higher fixation density. Model fit parameter results are illustrated on the graphs in the form of circles of radius the estimated Gaussians' standard deviation at maximum likelihood (σ_{ML}): black dotted target-centered circles for the ON-TARGET model and gray solid circles with centers estimated by model fit for the ZONE model.

Figure 7.

Goodness of fit modeling results presented in terms of Bayesian Information Criterion (BIC) for fixation distributions recorded during encoding, retention, and recall. Combined BIC scores are provided by summing maximum log-likelihood values for stimuli with same target number, assuming data independence across trials after accounting for eye movement strategy. BIC results are presented separately for the ON-TARGET (black) and ZONE (gray) models, and model fit differences (ΔBIC) are presented in gray bar-graphs.

Figure 8.

Proportion (upper panel) and number (lower panel) of targets fixated by participants during encoding, retention, and recall, calculated separately for each of the 24 stimuli (x-axis). The 24 stimuli are ordered in the graphs based on stimulus characteristics, i.e., target number and delay duration.

Figure 9.

Proportion of targets fixated for trials with delays of 5 seconds (left panel) or 20 seconds (right panel), combining trials with same target number. Differences between encoding, retention, and recall that reached significance per the result of the repeated measure MANOVAs are indicated with asterisks.

Goodness of fit of the ON-TARGET and ZONE models applied to eye movement recorded during encoding, retention, and recall. Indices of goodness of fit are provided in terms of Maximum Log-Likelihood (MLL), Akaike Information Criterion (AIC), and Bayesian Information Criterion (BIC).

Table 1

	4 Targets			6 Targets			8 Targets		
	MLL	AIC	BIC	MLL	AIC	BIC	MLL	AIC	BIC
Encoding	ON-TARGET	-2,618	5,239	5,240	-2,676	5,355	5,356	-2,747	5,496
	ZONE	-2,480	4,966	4,970	-2,460	4,927	4,931	-2,454	4,914
Retention	ON-TARGET	-2,663	5,329	5,330	-2,789	5,581	5,582	-2,836	5,674
	ZONE	-2,444	4,895	4,898	-2,438	4,883	4,886	-2,464	4,934
<i>5 sec</i>	ON-TARGET	-1313	2628	2630	-1377	2756	2757	-1444	2891
	ZONE	-1204	2414	2417	-1250	2507	2511	-1249	2504
<i>20 sec</i>	ON-TARGET	-1350	2702	2703	-1413	2827	2828	-1392	2785
	ZONE	-1241	2487	2491	-1188	2382	2385	-1215	2436
Recall	ON-TARGET	-2,245	4,492	4,493	-2,297	4,595	4,596	-2,318	4,638
	ZONE	-2,570	5,145	5,149	-2,604	5,214	5,217	-2,647	5,301

Notes: Numbers corresponding to the better fitting model are presented in bold.