1   Running title: visual working memory and distractibility in schizophrenia

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Unexpected higher resilience to distraction during visual working memory in schizophrenia

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ABSTRACT

Visual working memory (VWM) and distractibility are two core executive functions in human cognition. It has been suggested that schizophrenia (SZ) patients exhibit worse VWM performance and lower resilience to distraction compared with healthy control (HC) subjects. Previous studies, however, have largely investigated these two functions separately. It still remains unclear what are the mechanisms of the deficits, especially the interactions between the two cognitive domains. Here we modify the standard delay-estimation task in VWM and explicitly add distractors in the task so as to examine the two domains simultaneously. We find that SZ indeed exhibit worse performance compared with HC in almost all VWM load and distraction levels, a result consistent with most prior experimental findings. But adding distractors does not selectively impose larger impacts on SZ performance. Furthermore, unlike most previous studies that only focused on behavioral performance, we use the variable precision model to disentangle the distraction effect on different computational components of VWM (resources and resources allocation variability etc.). Surprisingly, adding distractors significantly elevates resources allocation variability—a parameter describing the heterogeneity of resource allocation across different targets—in HC but not in SZ. This counterintuitive result suggests that the internal VWM process in SZ is less interfered by the distractors. However, this unexpected higher resilience to distraction might be associated with less flexible cognitive control mechanisms. In sum, our work demonstrates that multiple cognitive functions might jointly contribute to dysfunctions in SZ and their interactions might manifest differently from merely summing their independent effects.

Keywords: Schizophrenia, Visual working memory, distractibility, Bayesian observer model

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INTRODUCTION

Visual working memory (VWM) is a central cognitive ability that provides temporary storage and manipulation of information[1,2]. VWM deficits have been widely documented in people with schizophrenia (SZ)[3–7]. But the underlying mechanisms still remain unclear. Existing theories propose impaired sensory processing at the encoding stage of working memory as one candidate mechanism of the behavioral deficits[8]. Indeed, our sensory systems are often confronted with an immense amount of information that greatly exceeds the processing capacity[9]. However, working memory capacity is known to be limited[10,11]. The capacity limitation necessities a selection process that prioritizes task-relevant information and filters out task-irrelevant ones in order to optimize performance. This is particularly important when salient distractors are present and interfering with the processing of targets. The interference induced by distractors, so-called "distractibility", has been shown to link with several key cognitive functions, such as working memory[12], endogenous and exogenous attention[13], perceptual and value-based decision[14], response inhibition[15], cognitive control[16]. Moreover, atypical distractibility has been discovered in several psychiatry disorders, including ADHD[17], autism[18], depression[19].

A sizable amount of literature has suggested the aberrant distractibility in SZ [20–24]. One standard approach to study distractibility is to impose distractors in some cue-based attention tasks. However, most studies found no significant deficits in cue-based attention tasks in SZ[25,26]. One possibility is that the cues and instructions in those tasks were quite simple and 100% valid. Simple cues ease the tasks and require less attentional control. By contrast, if probed in high-demanding attention tasks, SZ exhibit deficits in suppressing salient distractors[27,28]. These findings suggest that the distractibility deficits in SZ exist and might be more prominent at the presence of highly salient distractors.

Recent advances in the basic science of VWM demonstrate that behavioral performance in VWM tasks is mediated by multiple factors[29]. It has long been proposed that SZ has lower memory capacity but intact memory precision compared with healthy control (HC) subjects[4,30]. This view has been proposed in the studies that use standard VWM tasks without distractors. It remains unclear whether SZ have deficits in VWM processing when confronted with distractors. From the computational perspective, distractors may reduce memory capacity and/or impair memory precision. Unfortunately, most previous studies on SZ have examined distractibility and VWM deficits separately. Few studies have attempted to combine them and investigate their

74   interaction effect. It remains two unanswered questions: (1) whether SZ have distractibility

75   deficits in VWM; (2) if yes, which VWM component(s) such distractibility deficits will

76   influence.

77   In this study, we aimed to combine the classical distraction and VWM experimental

78   paradigm to simultaneously the two functions in SZ. To do so, we modified a standard VWM

79   task—color delay-estimation task. In the color delay-estimation task, subjects need to memorize

80   the colors of all presented items and after a short delay reproduce the color of one cued item. In

81   our modified version (Fig. 1), subjects were instructed to memorize only a subset of presented

82   items (i.e., targets) and ignore other items (i.e., distractors). We independently manipulated the

83   target size and the distractor size to control VWM loads and distraction levels. Moreover, we

84   employed the Variable Precision (VP) model[31] explicitly estimate three key aspects of VWM—

85   the amount of resources at different target size level, the variability of resource assigned across

86   items, and the variability induced by choice. Therefore, the VP model allows us to quantify the

87   distraction effect in the computational process of VWM.

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91 **MATERIALS AND METHODS**

92 *Subjects*

93 Sixty clinically stable SZ (33 inpatients and 27 outpatients) and sixty-one HC were

94 recruited in this study. All SZ met the DSM-IV criteria for schizophrenia and were receiving

95 antipsychotic medication (2 first-generation, 43 second-generation, and 15 both). The Brief

96 Psychiatric Rating Scale (BPRS), the Scale for the Assessment of Negative Symptoms (SANS)

97 and the Scale for the Assessment of Positive Symptoms (SAPS) were obtained to evaluate the

98 symptom severity. HC were recruited by advertisement. All HC have no current diagnosis of axis

99 1 or 2 disorders, substance dependence or abuse, or family history of psychosis. All subjects are

100 right-handed with normal sight and color perception. Two groups of subjects were matched in

101 age and educational level.

102

103 *Stimuli and Task*

104 The experiment was run on the platform of Matlab 8.1 and Psychtoolbox 3. Subjects were

105 seated at a distance of 50 cm away from an LCD monitor.

106 Each trial started with a fixation cross presented at the center of the screen, lasting for the

107 time randomly chosen from [300, 350, 400, 450, 500 ms]. A set of colored shapes (squares

108 and/or circles) were then shown on the screen on an invisible circle with 4° radius for 500 ms.

109 Four conditions were used in this experiment: target size 1 / 3 × distractor size 0 / 2. Half of the

110 subjects were instructed before the experiment started to remember colored squares (target items)

111 and ignore colored circles (distractors) for the whole experiment and vice versa. Colored squares

112 were $1.5^{o} \times 1.5^{o}$ of visual angles and colored circles were 1.5^{o} of visual angles in diameters. The

113 sample array was shown for 500 ms, followed by a 900 ms delay period with only the fixation

114 cross on the screen for memory retention. Then, an equal number of outlined shapes were

115 presented at the same locations of the items shown in the sample array. One of the outlined

116 shapes was bolded, indicating the target item at this cued location is to be recalled. Meanwhile, a

117 randomly rotated color wheel was shown on the screen, with the inner and outer radius as 7.8^{o}

118 and 9.8^{o} respectively. Subjects were instructed to recall and report the color of the bolded item

119 by clicking on the color wheel using a computer mouse. Precise recall of the color was desired

120 and the response time was unlimited. The 180 colors used in this experiment were selected from

121 a circle (centered at L = 70, a = 20, b = 38, radius of 60) deriving from the CIE L*a*b color

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122   space. All subjects finished one block of 80 trials for each condition. The order of conditions was

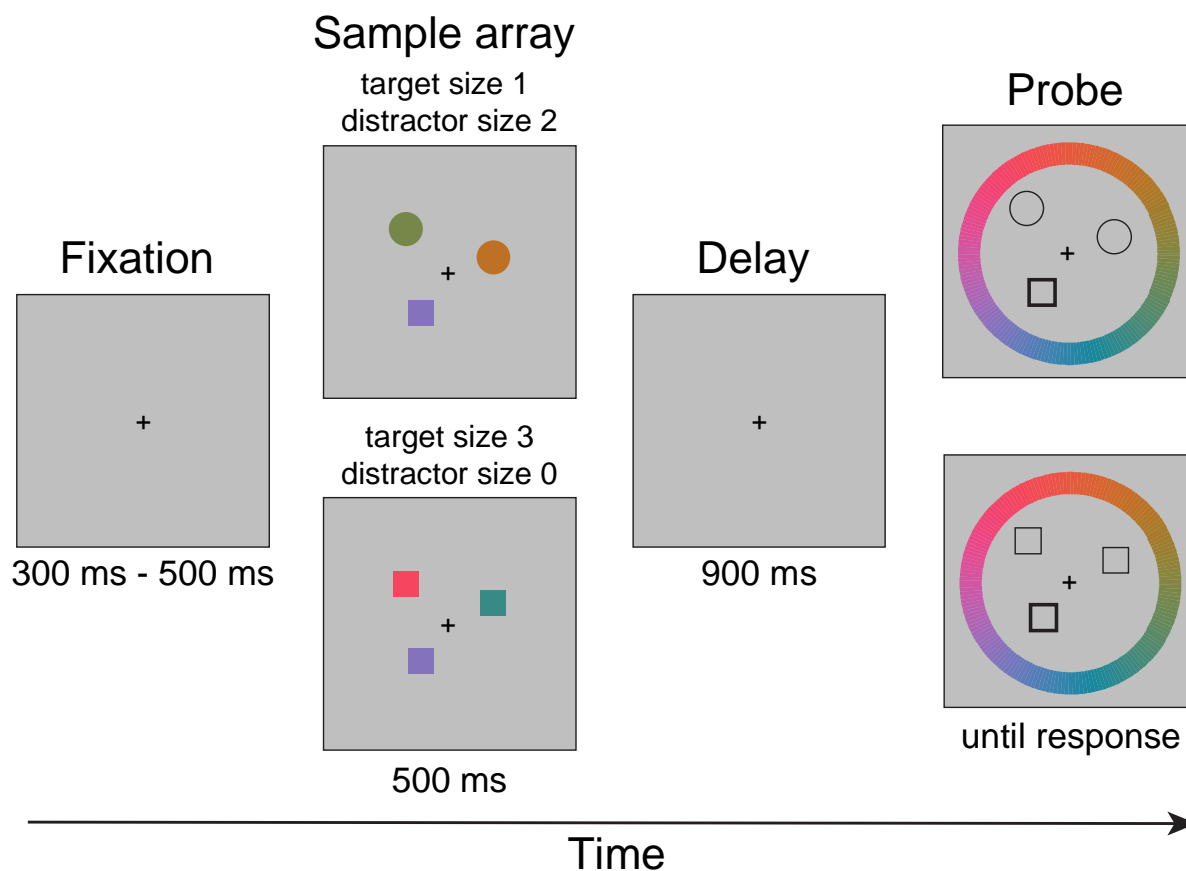123   counterbalanced across subjects.

124

125   Figure 1. The modified color delay-estimation task. This figure illustrates two
126   example trials of the experiment. In the experiment, each trial starts with a fixation
127   point presented for 300ms to 500ms (with a step of 50ms). In the sample array, one
128   or three targets (squares in this example) together with zero or two distractors (circles,
129   a 2×2 design) are displayed on the screen for 500ms. Subjects were instructed to
130   remember the colors of one of the shapes in the sample array. After a 900ms delay,
131   outlines of the items at their original location would appear and one of the cued of
132   target shapes is cued. Subjects are asked to recall and report the color of the target by
133   clicking on the colored wheel using a computer mouse.

134
135   *Data analysis*

136   The data with no distractor has been presented in reference (32)[32]. Comprehensive

137   analysis of the distraction effect in this paper is new.

138   Variable precision model. The variable precision (VP) model was initially proposed by

139   van den Berg *et al*[31,33]. The VP model proposes that the mean VWM resource levels declines as

140   the target size assigned to individual items are not only continuous but also variable across items

141 and trials. This variability in resource assignment results in trial-by-trial response errors.

142 Moreover, the VP model also explicitly isolated the variability of behavior choice (e.g., motor or

143 decision noise), which was ignored by most previous models in VWM.

144 For each item, the memory resources recruited J is defined as Fisher information

145 $J = \kappa \dfrac{I_1(\kappa)}{I_0(\kappa)}$, where I_0 and I_1 are modified Bessel functions of the first kind of order 0 and 1

146 respectively, with the concentration parameter κ. In the VP model, because J varies across

147 items and trials, it is further assumed to follow a Gamma distribution with a mean of $\bar{J}$ and

148 scale parameter τ. Moreover, since the mean VWM resource decreases with target size N (Fig.

149 3A), we assume that the relationship between $\bar{J}$ and N can be written in a power-law fashion

150 $\bar{J} = \bar{J_1} * N^{-a}$, where $\bar{J_1}$ is the initial resources when only 1 item ($N = 1$) should be remembered in

151 VWM and α is the decay exponent.

152 The model also assumes that the subject' internal representations of stimuli are noisy and

153 follow a von Mises distribution. Thus, the distribution of sensory measurement (m) given the

154 input stimulus (s) can be written as:

$$p(m \mid s) = \frac{1}{2\pi I_0(\kappa)} e^{\kappa \cos(m-s)} \equiv VM(m;s,\kappa), \qquad [1]$$

156 and we further assumes that subjects' reported color ($\hat{s}$) shat also follows a von Mises

157 distribution with the choice variability κ_r:

$$p(\hat{s} \mid m) = \frac{1}{2\pi I_0(\kappa_r)} e^{\kappa_r \cos(\hat{s}-m)} \equiv VM(\hat{s};m,\kappa_r). \qquad [2]$$

159 Taken together, there are four free parameters: $\bar{J_1}$, α, τ and κ_r in the VP model.

160

161 *Model fitting*

162 We fit the model separately for each subject. Because J is a variable across items and

163 trials, we sampled it for 10000 times from the Gamma distribution with mean $\bar{J}$ and scale

164 parameter τ. We then used all these samples to calculate response probability in each trial.

165 We used the BADS optimization toolbox in MATLAB to search the best fitting

166 parameters that maximize the likelihood of responses. To avoid the issue of local minima, we did

167 the optimization process for 20 times with 20 different initial seeds. The parameters with the

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168   maximum likelihood were used as the best fitting parameters for a subject and were further used

169   in the statistical process.

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RESULTS

SZ make larger recall errors than HC

We set four experimental conditions (target size 1/3 x distractor size 0/3) for each group. In the modified color delay-estimation task, performance in a trial, denoted as "response error", was defined as the distance between the true color and the reported color of the cued item in the circular color space. For each subject, circular standard deviations (CSD) of response errors in each experimental condition were calculated separately as indexes of VWM performance.

A $2 \times 2 \times 2$ ANOVA was performed with the CSDs as the dependent variable (Fig. 2), target size (1/3) and distractor size (0/3) as the within-subject variables, and group (SZ/HC) as the between-subject variable. We observed the main effects of target size ($F(1,119) = 935.650$, $p < 0.001$, partial $\eta^2 = 0.887$) and distractor size ($F(1,119) = 8.909$, $p = 0.003$, partial $\eta^2 = 0.070$), indicating that behavioral performance in both groups declined as the memory load and the distraction level increased. These results also suggest that our experimental manipulation successfully induced the classical load effect and the distraction effect. A group difference was also found ($F(1,119) = 12.716$, $p < 0.001$, partial $\eta^2 = 0.097$) and we confirmed a general worse VWM performance of SZ than HC, a result consistent with many previous studies showing the VWM deficits in schizophrenia[3–6]. We also found a significant interaction between target size and distractor size ($F(1,119) = 4.486$, $p = 0.036$, partial $\eta^2 = 0.036$). Post hoc analysis showed that the distractors worsened VWM performance ($p = 0.004$) in the high target size (i.e., target size = 3) condition, whereas no distraction effect was detected in the low target size (i.e., target size = 1) condition ($p = 1.000$).

The key question we asked here was whether the distractors selectively impaired VWM processing in SZ. If yes, we should expect an interaction effect between distractor size and group as adding distractors might impose stronger performance deteriorations in SZ compared with HC. However, we did not find such interaction effect ($F(1,119) = 0.820$, $p = 0.367$, partial $\eta^2 = 0.007$), indicating that adding distractors worsened performance in both groups and such distraction effect was not specific to SZ. Moreover, previous studies have suggested that distractibility deficits in SZ might be more prominent when the task becomes more challenging (e.g., higher memory load). However, no other significant interaction effect was noted with respect to the group variable (target size × group, $F(1,119) = 0.139$, $p = 0.710$, partial $\eta^2 = 0.001$; target size × distractor size × group ($F(1,119) = 0.137$, $p = 0.712$, partial $\eta^2 = 0.001$). These

202 results were consistent with the previous studies[25,26,34] showing that SZ exhibit generally worse

203 VWM performance than HC but the memory load and distraction effect manifest similarly in
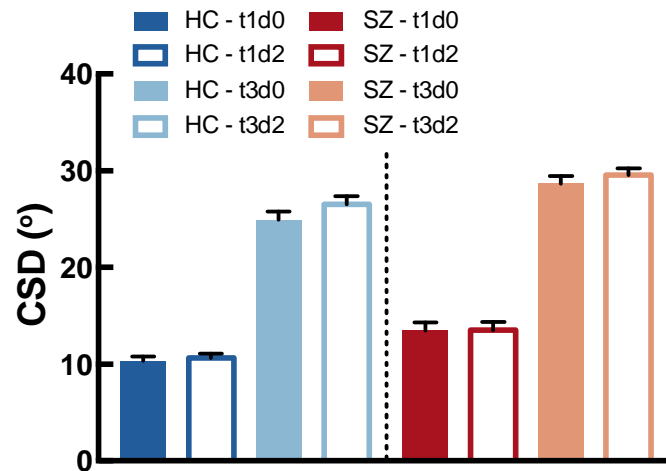
204 both groups.

205

206 Figure 2. General memory load and distraction effects on both groups. A higher CSD
207 indicates worse performance. Increasing the memory load and the distractor level
208 worsen performance in both groups. Also, SZ showed generally worse VWM
209 performance than HC. Moreover, distractors only impact VWM performance at high
210 memory load (target size = 3). Error bars represent ±SEM across subjects. The letter
211 "t" in the legend means "target size" and "d" means "distractor size". For example,
212 "t1d0" indicates target size = 1 and distractor size = 0.

213

214 ***Distractors elevate resource allocation variability in HC but not in SZ***

215 Above analyses only focused on CSD—a summary statistics describing the variance of recall

216 error distributions in each experimental condition. To further scrutinize the data, we employed

217 the VP model (see Methods)—a Bayesian observer model describing the generative process of a

218 behavioral choice in the delay-estimation task. The VP model has two major strengths. First,

219 unlike the CSD as a summary statistical variable, the VP model is a probabilistic model that can

220 utilize the data in every trial without losing any information. Second and more importantly, the

221 VP model explicitly defines some key VWM components and characterizes the full generative

222 process of the VWM task. Therefore, we can quantify the distraction effect on these VWM

223 components.

224 We elaborated the details of the VP model here. First, the VP model estimates the initial

225 resources when only one target is present. Second, the memory resources decline as a power

226 function of target size and this decreasing trend can be described by the decay exponent. Third,

227   the power function only specifies the mean resource at each target size level. The actual

228   resources assigned to each item vary and follow a Gamma distribution with the variance as

229   resource allocation variability. The amount of resources assigned to each item determines the

230   precision of sensory measurement (i.e., memory representation) of the item. Forth, given the

231   noisy representation, there exists choice variability describing the uncertainty from internal

232   sensory representation to the outcome behavioral choice. We estimated the four parameters (i.e.,

233   initial resources, decay exponent, resource allocation variability and choice variability) on each

234   subject and separately on two distractor size levels.

235   We performed a 2×2 ANOVA with distractor size as the within-subject variable, group

236   as the between-subject variable, and the four estimated parameters of the VP model as the

237   dependent variables. We observed a main effect of group in resource allocation variability

238   ($F(1,119) = 9.863$, $p = 0.002$, partial $\eta^2 = 0.077$), showing an overall higher resource allocation

239   variability in SZ compared to HC (Fig. 3D). This result is consistent with our earlier work[32]. The

240   main effect of group was not significant in the other three parameters. Particularly, we did not

241   observe a significant main effect of initial resource and decay exponent, two factors that control

242   the amount of memory resources. Intuitively, these results suggest that SZ might have the same

243   amount of memory resources, but they distributed the resources across targets in a very

244   heterogeneous manner.

245   We also found a main effect of distractor size on initial resource ($F(1,119) = 5.559$, $p =$

246   0.020, partial $\eta^2 = 0.045$) and a marginal significant main effects on decay exponent ($F(1,119) =$

247   3.882, $p = 0.051$, partial $\eta^2 = 0.032$). We speculate that adding distractors greatly enhanced the

248   task difficulty and consequently forced subjects to internally utilize more resources to memorize

249   targets. There were no main effects of distractor size on choice variability ($F(1,119) = 3.528$, $p =$

250   0.063, partial $\eta^2 = 0.029$) and resource allocation variability ($F(1,119) = 2.862$, $p = 0.093$, partial

251    $\eta^2 = 0.023$). Note that these main effects manifest in both groups not specific for SZ.

252   More importantly, to examine the distraction effect, the key is to examine the interaction

253   effect between group and distractor size. If SZ have deficits in distractibility, we should expect

254   that adding distractors imposes significantly larger interferences on VWM processing in SZ but

255   compared with HC. We indeed observed a significant interaction effect between group and

256   distractor size (F(1,119) = 5.062, p = 0.026, partial $\eta^2 = 0.041$) (Fig. 3D) in resource allocation

257   variability. However, post hoc analysis suggested that adding distractors only increased the

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258   resource allocation variability in HC ($p = 0.036$) but had little impact on SZ ($p = 0.999$). This is

259   surprising since elevated distractibility has long been proposed as a core executive function

260   deficit in SZ. On the contrary, we found a more prominent distraction effect in HC rather in SZ,

261   indicating a relatively higher resilience to distraction in SZ. We did not find such interaction

262   effect in all other three parameters (initial resource, $F(1,119) = 2.042$, $p = 0.156$, partial $\eta^2 =$

263   0.017; decay exponent, $F(1,119) = 0.236$, $p = 0.628$, partial $\eta^2 = 0.002$; choice variability,

264     $F(1,119) = 0.430$, $p = 0.513$, partial $\eta^2 = 0.004$).

265   These results also suggest the critical role of resource allocation variability since we did

266   not find the interaction effect of group and distractor size, as well as their interaction on other

267   three VP model parameters (see full statistical results in Supplementary Materials note 1).

268   Resource allocation variability is a relatively new concept in VWM and has increasingly been

269   regarded as one of the key determinants for VWM performance[31]. Also, our earlier work

270   confirmed its contribution to schizophrenic pathology[32]. Recent studies have shown that it is not

271   only a key component in VWM but might be also a very general property in sensory processing[35].
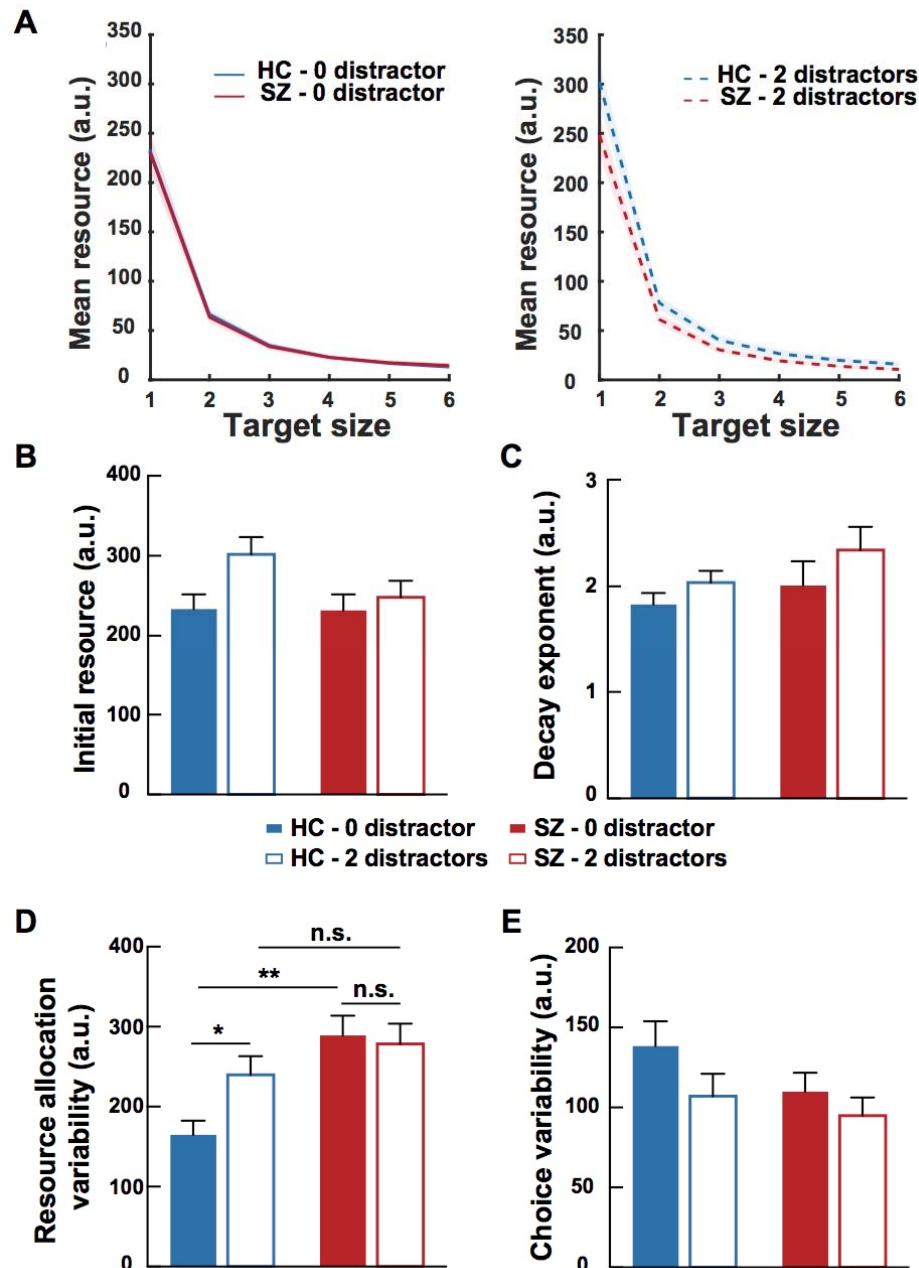
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Figure 3. Effects of group, target size and distractor size on the four fitted parameters of the VP model. Panel A illustrates the mean resources as a function of the target size, which are generated by fitted initial resource (panel B) and decay exponent (panel C) values. Panels D and E illustrate the fitted resource allocation variability and choice variability respectively. The main group effect was only found in resource allocation variability (panel D). Precisely, SZ showed overall larger resource allocation variability than HC and adding distractors only elevated the resource allocation variability in HC but not SZ, indicating that SZ have stronger resilience to distraction than HC. No group × distractor size interaction was observed in initial resource, decay exponent and choice variability. Shaded areas in panel A and error

284   bars in panels B to E denote ±SEM across subjects. Significance symbol conventions
285   are *: $p < 0.05$; **: $p < 0.01$; n.s.: non-significant.
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287

288 **DISCUSSION**

289 Visual working memory and distractibility have long been recognized as core executive

290 functions. Despite the widely documented behavioral deficits of SZ in these two domains, little is

291 known with respect to the computational mechanisms underlying these deficits. This arises from

292 two major obstacles: (1) few studies have attempted to integrate two cognitive functions within

293 the same experimental paradigm; (2) the computational models that describe the internal

294 processes have been lacking. To circumvent these, we modified the classical VWM delay-

295 estimation task to deliberately incorporate distractors and employed the VP model to distinguish

296 several VWM key components. We set two distractor conditions (distractor size 0/3) and used

297 the VP model to estimate the VWM components separately under these two conditions. We

298 made two major observations: (1) the variability of allocation memory resources was generally

299 larger in SZ ; (2) adding distractors enlarged the resource allocation variability in HC but had

300 little impact on that in SZ. These results highlight the significance of resource allocation

301 variability in mediating VWM performance and demonstrate an unexpected higher resilience to

302 distraction during VWM in SZ.

303 The finding of enhanced resource allocation variability is of unique significance for

304 understanding VWM deficits in SZ. This finding has been systematically evaluated in our prior

305 work[32]. In that study, we compared several influential models in VWM literature and compare

306 results between SZ and HC. We found that the only difference between the two groups lies in

307 resource allocation variability not the amount of memory resources. This result suggests that SZ

308 have the same amount of mean resources as HC at each target size level, but the resources

309 assigned to individual items exhibit larger variability around this mean value. For example,

310 assume that, given three targets, both SZ and HC have r units of mean resource across three

311 targets. But the actual resources assigned to each item vary around this mean value (i.e., $r+0.1$, $r-$

312 0.2). SZ exhibit overall larger variability (e.g., $r+3$, r-2) than HC (e.g., $r+0.3$, $r-0.2$). Note that

313 this mechanism is fundamentally different from elevated attentional lapse or general deficits in

314 filtering distraction. Elevated attentional lapse will lead to more guessing trials and the general

315 deficits in filtering distraction will allow more resources assigned to distractors. Therefore, these

316 mechanisms predict that the mean resources will be overall reduced in SZ. However, we did not

317 observe the significant group differences in memory resources (Fig. 3A).

318   The unexpected enhanced resilience to distraction in resource allocation variability
319   provides a new perspective for understanding distractibility in SZ. We confirmed that behavioral
320   performance of SZ is in general worse than HC, a well-established finding in many previous
321   studies[3–6]. However, in the analyses of behavioral performance, we indeed observe significant
322   effects of memory load and distraction but both effects manifest similarly in both groups. There
323   was no stronger distraction effect specific for SZ. Most previous studies employed a similar
324   approach and only focused on behavioral performance. We made a further stride here and
325   examined the distraction effect on individual VWM computational components. Results showed
326   that adding distractors only significantly raise the resource allocation variability in HC but not in
327   SZ. This is the key contribution of our work. Our approach allows us to provide a deeper
328   mechanistic interpretation rather than only reporting the quantitative behavioral deficits in SZ.
329   Note that our approach here is to fit the VP model separately to the data at two distraction
330   conditions and then examine the differences in the estimated parameters. An alternative approach
331   is to directly incorporate the distraction effect into the generative process, which has been
332   recently pursued in Ni & Ma[36] and Shen & Ma[35]. The latter approach permits to compare
333   different computational models so as to ground different theories. Future work might continue to
334   explore this line of research.

335   At first glance, higher resilience to distraction in the VWM resource allocation suggests a
336   cognitive advantage in SZ. However, this might also imply less flexible cognitive control in SZ.
337   For example, there has been shown that SZ tend to allocate their VWM resources more intensely
338   and narrowly than HC[37], a phenomenon called "hyperfocusing". If SZ distribute too many
339   resources on a small set of visual objects, they may have trouble in flexibly switching to new
340   objects. Hyperfocusing might be particularly problematic in VWM tasks since one of the key
341   features of VWM is to flexibly and dynamically maintain representations of multiple objects.
342   The hyperfocusing mechanism might explain both the elevated resource allocation variability
343   and higher distraction resilience in SZ. In our task, hyperfocusing on a subset of targets avoids
344   the interference of distractor. Again, note that the "side effect" of hyperfocusing might be the
345   lack of ability to flexibly switch to different sources of information [38]. Also, the atypical ability
346   in task switching has also been discovered in other special populations, such as aging[39,40],
347   ADHD[41].

348   What are the neural mechanisms underlying VWM deficits and distraction effects in SZ?

349   A recent study has identified the superior intraparietal sulcus (IPS) as the cortical region

350   controlling resource allocation variability [42]. SZ patients have also been found the atypical neural

351   processing in this region[43]. On the other hand, the distraction effect on neural processing has

352   been broadly found in attention and cognitive control networks[44]. Especially, SZ exhibited

353   abnormal neural processing when distractors are present and cortical activity in high-level brain

354   regions (i.e., dorsolateral prefrontal cortex) is correlated with negative symptoms[45]. However, no

355   study has combined the VWM and distractors paradigm and measured neural activity in SZ. Also,

356   it is unclear how other computational components of VWM are implemented in the brain. Future

357   studies might need to combine computational modeling, neural measurements and behavioral

358   testing to systematically address this issue.

359   Taken together, in this study we combined the standard VWM and distractor paradigms

360   to examine the distraction effect during VWM in both SZ and HC. We replicated the standard

361   memory load and distraction effects in both groups. We also found general worse VWM

362   performance in SZ. But we did not observe a significant higher distraction effect in SZ. Further

363   modeling analyses revealed that distractors elevate resource allocation variability during VWM

364   in HC but not in SZ. This unexpected higher resilience to distraction in SZ provides new

365   evidence for the cognitive deficits of SZ. Such unexpected higher resilience and less flexible

366   cognitive control might be two sides of the same coin.

367

368 **ACKNOWLEDGMENTS**

374

375 **AUTHOR CONTRIBUTIONS**

376 YZ, RZ, & YK developed research idea and study concepts; YZ & YK design the experiment;

377 XR and LZ collected the data; RZ & YZ performed the data analyses and modeling; RZ&YZ

378 wrote the manuscript.

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380 **COMPETING INTERESTS**

381 The authors report no biomedical financial interests or potential conflicts of interest. ☐

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