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Behavioral and computational signatures of visual working memory deficits in adolescents with anxiety disorder

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Abstract

Pathological anxiety is one of the most common mental health problems in adolescents. It is well documented that working memory, a core cognitive function, is often impaired in individuals with anxiety disorders. However, the computational mechanisms underlying these deficits in adolescents with anxiety disorder remain elusive. We used the classic delay-estimation visual working memory (VWM) task to assess the performance of adolescents with anxiety disorders ($N=39$) and healthy controls ($N=41$). Using a computational psychiatry approach, we tested 14 computational models established in basic research of VWM. Model comparison results identified the variable precision model as the best-fitting model for both groups, suggesting that the two groups share a qualitatively similar VWM process in completing the task. Subsequent analyses of the parameter estimates pointed to atypically reduced memory resources as the primary determinant of impaired VWM performance in adolescents with anxiety disorder. Crucially, the estimated memory resources in the anxious group predicted the severity of anxiety symptoms. Our results demonstrate that the reduced memory sources are the key factor mediating working memory deficits in adolescents with anxiety disorders, and this factor may also serve as a potential behavioral marker for future clinical interventions.

Keywords Anxiety disorder · Adolescents · Visual working memory · Computational modeling

Introduction

Maintaining mental health during adolescence is critical for lifelong psychological well-being (Kieling et al., 2011). Anxiety is one of the most common types of emotional problems among adolescents worldwide (Freeman, 2022). In the U.S., for example, the most recent epidemiological report reported ~9.11% (6 million) adolescents suffering from the anxiety disorders under the ICD-10-CM diagnosis (Barr et al., 2022). Dysfunctions in cognitive development severely disrupt adolescents' psychological status, social life, and academic performance, resulting in long-lasting negative effects that may persist throughout life (Sanders, 2013).

A number of previous studies have shown that anxiety impairs several cognitive functions (for review, see Refs. Castaneda et al., 2008; Eifert, 1992; Eysenck et al., 1987; Ferreri et al., 2011). Working memory (WM), defined as the process of temporarily maintaining information for immediate subsequent use, is one of the central cognitive functions that enables various forms of mental operations in

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daily life. WM is also a predictor of performance in a variety of functional domains, such as fluid intelligence (Jaeggi et al., 2008) and academic performance (Titz & Karbach, 2014). WM impairments are associated with several psychiatric disorders, including schizophrenia (Forbes et al., 2009; Zhao et al., 2021), major depressive disorder (Rose & Ebmeier, 2006), autism spectrum disorder (Williams et al., 2005), and anxiety disorders (Owens et al., 2008).

Previous research has shown a clear association between the severity of anxiety symptoms and poorer WM performance on several types of memory span tasks, including complex span (Turner & Engle, 1989), simple span (Darke, 1988), and dynamic span tasks (Vytal et al., 2012). A meta-analysis of 177 studies and 22,061 individuals supports the association between anxiety symptoms and poorer WM performance (Moran, 2016). The similar association has also been found for spatial and verbal working memory tasks (Vytal et al., 2013). Taken together, these studies have documented the convergent findings of WM deficits in people with anxiety disorders across different forms of behavioral tasks. Despite the well-established poorer WM performance in patients with anxiety disorders, the exact underlying computational explanations for the impact of anxiety disorders on visual working memory (VWM) have not been explicitly specified.

Existing theories suggest that anxiety consists of two dimensions: anxious apprehension (or worry) and anxious arousal (Barlow et al., 1996; Heller et al., 1997a, b; Nitschke et al., 2001). Worry refers to the mental rumination about the possible negative outcomes in the future; arousal refers to the uncontrolled psychological or physiological hypertension (Watson et al., 1995). It has been suggested that worry, especially verbal rumination, consumes additional cognitive resources, and thus interferes with task-relevant processes (Eysenck & Calvo, 1992). Similarly, task-irrelevant arousal may impose additional cognitive costs and thus interfere with the task-relevant processes (Zhu et al., 2024; Sohail & Zhang, 2024; Sarason, 1988). Taken together, theories on both dimensions suggest that anxiety may limit the capacity or reduce the resources of working memory. On the surface, this view is supported by the well-established finding that a reduced memory span is typically associated with patients with anxiety disorders (Moran, 2016). However, as discussed below, behaviorally measured WM span is the result of several complex cognitive processes, involving not only capacity or resources, but also other cognitive factors and their interactions. It remains unclear what specific mechanism contributes to the poorer WM performance in anxiety disorders. For example, is poorer WM performance associated with fewer memory resources or less efficient resource allocation or their interaction? Elucidating the mechanisms of how anxiety affects WM is imperative because intervention strategies (e.g., cognitive-behavioral therapy) rely heavily on our understanding of the hidden processes that cause and maintain the cognitive deficits in anxiety disorders.

Using computational modeling, recent work in basic research has significantly deepened our understanding of VWM and revealed several new factors that may mediate WM performance. For example, there exists an ongoing debate as to whether WM resources are maintained as a continuous value or as discrete chunks (Bays & Husain, 2008; Ma et al., 2014; Zhang & Luck, 2008). These two theories can be distinguished by comparing corresponding computational models. In addition, empirical evidence now shows that memory resources and capacity, two seemingly similar concepts, may play fundamentally different roles in WM (van den Berg et al., 2014; van den Berg et al., 2012). Researchers have also found that poor memory performance can arise from either reduced memory capacity (i.e., the maximum number of items that can be held in memory) and/or reduced memory precision (i.e., how well each individual item can be represented) for an item (van den Berg et al., 2014). These studies using computational modeling can accurately quantify the various factors that contribute to performance outcomes. Applying such a nuanced approach in clinical research has helped to identify specific deficits in psychiatric disorders, such as schizophrenia (Chey et al., 2002; Zhao et al., 2021). Recent studies have also used computational models to elucidate the mechanisms of anxiety (Gillan et al., 2021; Hitchcock et al., 2022; Zainal et al., 2023). These examples highlight the use of computational models developed in basic science to disentangle the theories of psychiatric disorders. The computational investigations may provide new insights into the targets of behavioral treatments (Geng et al., 2022).

In this study, we took advantage of the well-developed paradigm and classical computational models in basic VWM research to elucidate the computational substrates of memory deficits in adolescents with anxiety disorder (AAD). We used the delay-estimation VWM paradigm and systematically assessed subjects' memory errors as memory load increased. In this task, an observer views and memorizes the colors of several squares on the screen, and, after a short delay, chooses the color of a cued target on a continuous color spectrum. The discrepancy between the true target color and the chosen color can be used to quantify and model VWM abilities. Most importantly, we evaluated a thorough list of mainstream computational models of VWM to explore the underlying factors of atypical VWM performance. Through model comparisons and model parameter analyses, we were able to identify which of the following factors best explain the impaired VWM functions in AAD: (1) fewer memory resources, (2) smaller memory capacity, or (3) low resource allocation efficiency. In contrast to previous behavioral findings, we identified reduced memory resources rather than reduced memory capacity or abnormal resource allocation efficiency as the key determinant of VWM deterioration in AAD. Furthermore, estimated memory resources can predict individual differences in anxiety symptom severity. Our findings highlight the lack of working memory resources as a key mechanism in AAD.

Methods and materials

Ethics and participants

All experimental protocols were approved by the institutional review board of Nankai University. All research was conducted in accordance with relevant guidelines and regulations. Informed written consent was obtained from all participants. 45 adolescents with anxiety disorder (AAD) were recruited for this study. All participants were recruited from the Department of Adolescent at the Tianjin AnDing Psychiatric Hospital. The outpatients who met the criteria were informed about the experiments. All 45 AADs were clinically diagnosed by clinical psychiatrists according to ICD-10 without structured interviews. In particular, all AADs had already been diagnosed with an anxiety disorder according to ICD-10. Here, an anxiety disorder is described as "emotional disorders with onset specific to childhood", according to the subcode F93 in ICD-10. We did not further differentiate the exact symptoms of anxiety and treated F93 as a unity. 6 subjects were excluded because their depression scores were greater than 24. Similarly, 45 healthy controls were also recruited. 4 subjects were excluded because their depression scores were greater than 24 and/or their anxiety scores were greater than 35. All participants were not paid but received the feedback on their questionnaire results.

All healthy control (HC) participants were recruited from the Tianjin No.19 Middle School. The two groups were matched in gender ($\chi^2 = 2.847$, $p = 0.092$). We defined healthy control participants as those adolescents: (1) who have no past or current diagnosed psychiatric disorders, major physical disabilities, and substance abuse; (2) whose Child Depression Inventory (CDI) scores were not greater than 24, a threshold defined as the two standard deviations from the norm documented in Yu and Li (2000); (3) whose Screen for Child Anxiety Related Emotional Disorders (SCARED) scores were not greater than 35, a threshold defined as the two standard deviations from the norm documented in Wang et al. (2002). In particular, to exclude the possible confounding effect of comorbid depression, we recruited only adolescents with anxiety disorder and without clinically confirmed comorbidity with depression. All demographic information is summarized in Table 1.

For age matching, we specifically recruited the healthy adolescents at the age of 14, which is equivalent to the mean age of the AAD groups. However, due to the small age variance in the HC group, the AAD group was slightly older than the HC group (14.64 ±1.693 vs. 13.39 ±0.494, t(82) =4.694, $p < 0.001$, Cohen's $d = 1.027$).

Table 1 Demographics and clinical information of adolescents with anxiety disorder (AAD) and healthy control (HC) subjects

	AAD ($N = 39$)		HC ($N = 41$)	
	Mean	SD	Mean	SD
Age	14.64	1.693	13.39	0.494
range	11–18	n/a	13–14	n/a
Female/Male	27/12	n/a	20/21	n/a
Inpatient/Outpatient	5/34	n/a	n/a	n/a
CDI scores	29.00	11.287	8.97	5.364
SCARED scores	48.43	16.141	17.415	9.516

CDI: Children's Depression Inventory (Helsel & Matson, 1984)

SCARED: The Screen for Child Anxiety Related Emotional Disorders (Birmaher et al., 1999)

Power analysis

Before the experiment, we calculated the sample size based on the estimated between-group difference effect size of 0.70, which is considered medium to large (Cohen, 2013). Based on a two-sided test with an alpha of 0.05, a power of 80%, and an estimated effect size of 0.70, we needed at least 34 patients in each group. The above power analysis was conducted using G-Power 3.1.

Questionnaires

In this study, we used the Screen for Child Anxiety Related Emotional Disorders (SCARED) and the Children's Depression Inventory (CDI) to measure anxiety and depression symptoms, respectively.

The SCARED was originally developed by Birmaher et al. (1999). SCARED can be used for clinical diagnosis, basic research, and epidemiological studies. The SCARED parallels the classifications of anxiety disorders in DSM-IV and has good internal consistency and validity. We used the Chinese version of SCARED (translated and revised by (Wang et al., 2002)), which has good internal consistency and validity (α =0.43–0.89, according to (Wang et al., 2002)). This version contains 41 items representing five factors—somatization/panic (10 items), generalized anxiety (12 items), separation anxiety (8 items), social phobia (7 items), and school phobia (4 items). Each item can be scored 0 (no problem at all), 1 (sometimes), and 2 (frequent) points to indicate the severity.

The CDI is a self-evaluation questionnaire that was originally developed by Kovacs (1992) based on the Beck Depression Inventory. The CDI is suitable for children or adolescents aged 7–17 years, and has high reliability and validity. We used the Chinese version of CDI, which has good internal consistency and validity (α = 0.85 according to (Yu & Li, 2000)). This version contains 27 items that comprise five subscales: anhedonia (8 items), negative mood (6 items), negative self-esteem (5 items), ineffectiveness (4 items), and interpersonal problems (4 items). Each item can be assigned to one of three choices indicating increasing levels of severity. The CDI requires no strong reading abilities and can be completed within 15 min. The CDI is currently the most widely used self-evaluation depression questionnaire for children and adolescents.

As expected, the AAD had severer anxiety and depression problems than the HC (SCARED: $t(73) = 9.239$, $p < 0.001$, Cohen's $d = 2.178$; CDI: $t(71) = 9.606$, $p < 0.001$, Cohen's $d = 2.312$). Detailed demographic information is summarized in the Table 1.

Stimuli and task

All experimental data from the adolescents with AAD were collected in a quiet room at the Tianjin AnDing Psychiatric Hospital. All participants were recruited from the Department of Adolescents at the Tianjin AnDing Psychiatric Hospital. All AADs first received a clinical diagnosis. The patients who met our criteria were further informed about our experiment, and the patients could voluntarily choose to participate or not. A participant was further escorted to the experimental room. All HC participants were also tested in a quiet room at the Tianjin No.19th Middle School. All participants first completed the behavioral task and then the questionnaires.

All stimuli were generated using Matlab 8.1 and Psychtoolbox 3 and presented on an LCD monitor. The viewing distance was kept to 50 cm. In the color delay-estimation task (Fig. 1A), a fixation circle with a radius of 0.25° was first presented at center-of-gaze, and the fixation lasted for a duration randomly selected from a sequence of 300, 350, 400, 450, and 500 ms. Participants were instructed to maintain their fixation on the fixation circle throughout the whole experiment. Next, a set of squares with different colors were presented at an eccentricity of 4°. Each square covered a visual angle of 1.5° × 1.5°. The number of squares was defined as the set size in this trial. Their positions were randomly selected from 8 predefined positions that formed an invisible circle with a radius of 4°. Their colors were randomly selected from the 180 colors that are equally spaced along the wheel representing the CIE L*a*b color space. The color wheel was centered at (L = 70, a = 20, b = 38) with a radius of 60 in the color space. The square array was followed by a 1000 ms black period for working memory retention. After the blank period, an equal number of outlined colorless squares were shown at the same positions as the previous colored squares. One of the squares were bold and served as the target. A 360° colorwheel with a random starting color was displayed. The inner and outer radius of the colorwheel were 7.8° and 9.8°, respectively. Participants were instructed to select the memorized color of the bold target square by clicking on the corresponding position on the colorwheel. Participants were asked to select the color as precisely as possible, and reaction time was not restricted. Each participant completed 30 trials for set sizes 1 and 8, and 50 trials for set sizes 3 and 6, respectively. For most computational models, trials at medium difficulty levels (i.e., set sizes 3 and 6) provide the most valuable data for constraining model parameters. As a result, we did not evenly distribute the trials across all set sizes, but instead focused more heavily on the medium difficulty levels.

Computational modeling

The mathematical details of all 14 models are documented in the Supplementary Information. All models used here embody several important theoretical underpinnings discussed in basic research of VWM. First, there exists a long-standing debate as to whether memory resources can be formulated as a continuous quantity (Bays & Husain, 2008) or as discrete chunks (Zhang & Luck, 2008). Second, it has also been suggested that memory capacity can be an infinite (Zhang & Luck, 2008) or a fixed value (van den Berg et al., 2012). Third, previous work also suggests that subjects may inadvertently recall the color of the wrong item rather than the cued target, a phenomenon referred to as the swapping error (SE) (Bays, 2016). We emphasize that memory resources and memory capacity have independent definitions here. Memory resources are formulated either a continuous quantity and or discrete chunks. However, memory capacity is defined as an integer, which represents the maximum number of items can be encoded into memory. For example, if memory capacity of an individual is four and five squares are presented, memory resources can only be allocated to the maximumly four items. Thus, memory capacity and the total amount of memory resources are independent.

We summarize all models in Table 2 and provide detailed mathematical descriptions in Supplementary Information Note 1. A total of 14 distinct computational models were constructed, each identified by a combination of acronyms. The item-limit (IL) model assumes a direct mapping between input stimuli and behavioral responses, as well as a fixed capacity. The mixture (MIX) model posits that

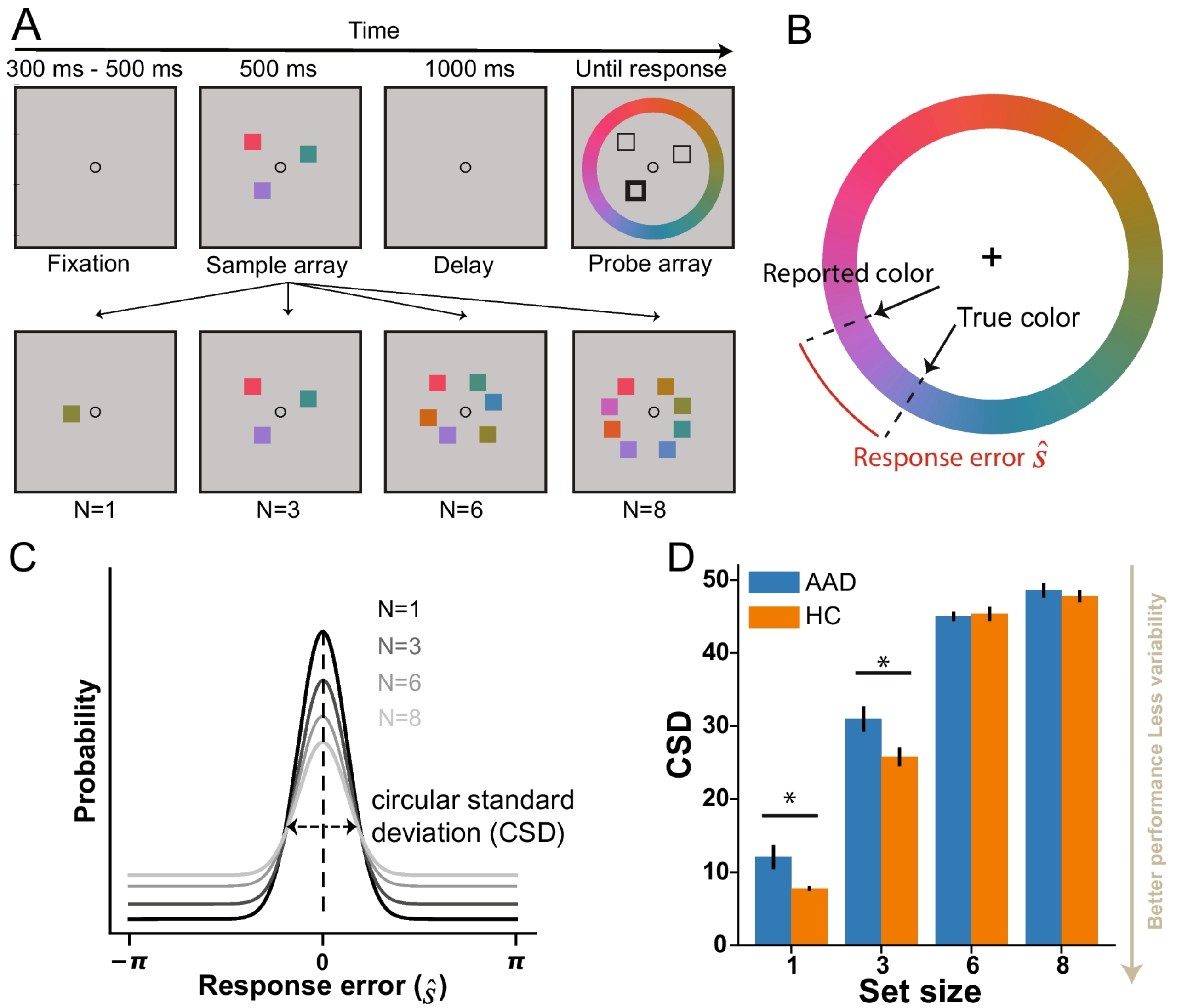

Fig. 1 Trial schematic and the poor VWM performance in the AAD group. **A** A trial begins with a fixation cross at the center of the screen. An array of colored squares appears on the screen (set size = 3 in this example). After a 900 ms delay, the subject is asked to click on the location corresponding to the memorized color of the cued item (the one in the lower left corner in this example). The bottom row illustrates the different set size (*N*) levels of the sample array. Task difficulty increases as the set size level increases. **B** All colors on the color circle are coded as angles within (0, 360º). The absolute angular difference between the true color and the reported color is defined as the response error. **C** Response errors typically follow a von Mises distribution ranging from -π to π. The width (circular standard distribution) of the von Mises distribution indicates the behavioral performance. The distributions become wider as the task difficulty (i.e., set size) increases, since more responses deviate from the true target. **D** CSD of the response errors of the two groups in each set size condition. The AAD group had larger CSD of response errors for set sizes 1 and 3, indicating poorer performance. Error bars represent standard errors across subjects. Significance convention is: *, $p < 0.05$

different set size level induce varying encoding precision in VWM, as well as a fixed capacity. Slot-plus-averaging (SA) model assumes discrete memory chunks (Zhang & Luck, 2008), and a recent variant—cosine slots-plus-averaging (cosSA) model—further incorporates stimulus-specific precision (Pratte et al., 2017). The equal-precision (EP) model assumes that continuous memory resources, with resources equally distributed across all items and all trials. In contrast, the variable-precision (VP) model also assumes continuous memory resources but proposes that the resources distributed stochastically across items and trials. The variable-precision-with capacity (VPcap) model further included a fixed capacity to the VP model. Additionally, we incorporated the mechanisms of SE into these seven models, indicated by the SE postfix. For example, SASE refers to the model that combines the SA assumption and the SE mechanism. In Table 2, we categorize these 14 models based whether the SE mechanism is included, whether discrete or continuous memory resources are assumed, and whether an integer capacity is posited.

Table 2 Model families of three factors

Factors	Swap error		Resources		Capacity	
Model families	No SE	SE	Discrete	Continuous	Fix	Infinite
					IL	
				MIX	MIX	
	IL	ILSE	IL	EP	cosSA	
	MIX	MIXSE	cosSA	VP	SA	EP
	cosSA	cosSASE	SA	VPcap	VPcap	VP
Models	SA	SASE	ILSE	MIXSE	ILSE	EPSE
	EP	EPSE	cosSASE	EPSE	MIXSE	VPSE
	VP	VPSE	SASE	VPSE	cosSASE	
	VPcap	VPcapSE		VPcapSE	SASE	
					VPcapSE	

SE: swap errors; *IL*: item-limit; *EP*: equal precision; *SA*: slot average; *VP*: variable precision; *VPcap*: variable precision + capacity limit

All 14 models were separately fitted to the behavioral data of each subject using the method of maximum likelihood estimation. Optimization was performed using the BADS toolbox (Acerbi & Ma, 2017). For each model fitted to each subject's data, we randomly initialized its parameters 20 times and obtained the set of parameters that achieved the maximum log-likelihood. We also computed Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) for model comparisons at the individual level (Fig. 2A). To further assess the model robustness at the group level, we approximated the log model evidence (LME) of each model in each participant using the equation as follows:

$$\log(p\,(D|M)) = \log(p\left(D|\widehat{\theta}, M\right)) - \frac{d}{2}\log N \tag{1}$$

where M indicates a model, D indicates a subject's data, d is the number of free parameters in the model M, and N is the number of trials in the data. We thus obtained the LME of all 14 models for all 84 participants. We then performed group-level Bayesian model selection using *spm_BMS.m* function in the SPM software (Rigoux et al., 2014). The protected exceedance probabilities of all models are shown in Fig. 2B. To further reveal the potential influences of swap errors and to avoid the model dilution problem in model comparisons, we also calculated the log posterior family probability (LPFP) of each family as follows:

$$T_i = \sum\nolimits_{m\in f_i} e^{LME} \cdot p\,(m) \tag{2a}$$

$$LPFP_i = \log\frac{T_i}{\sum_{\mathrm{n}=1}^{k} T_n} \tag{2b}$$

where LME is a 1 ×j vector representing the log model evidence of models in family i, and j is the number of models in this family. $p\,(m)$ is the model prior probability. If we have k families and there are j models in family i, then the prior probability of models in these families is $1/(k \times j)$. We classified model families based on three factors (see Table 2 for more details). For each factor, all 14 models were divided into two model families, and we calculated the LPFP for each participant from the two model families, then we compared the LPFP between two model families for the two groups separately. The results of the comparison are shown in Fig. 2C-E.

Statistical analysis

All ANOVAs and t-tests were performed in the open-source statistical software JASP 0.16.2 (https://jasp-stats.org/). All t-tests were two-tailed except for those on the circular standard deviation (CSD) of response errors in the two groups (Fig. 1B). All multiple comparisons were Holm-corrected using JASP. We performed a mixed ANOVA with the CSD of response errors as the dependent variable, group as the between-subject variable, and set size as the within-subject variable. We also performed several two-sample t-test to examine the group difference in the fitted parameters of the VP model.

Results

Impaired visual working memory in AAD

39 adolescents who have been clinically diagnosed with anxiety disorder (AAD) according to the International Classification of Diseases-10 and 41 demographically matched healthy control (HC) adolescents completed this study.

We used the classical delay-estimation VWM task (Fig. 1A) to measure the performance of the two groups (Zhang & Luck, 2008). The absolute difference between the reported color and the true color of the target is defined as the *response error* for that trial (Fig. 1B). Across trials,

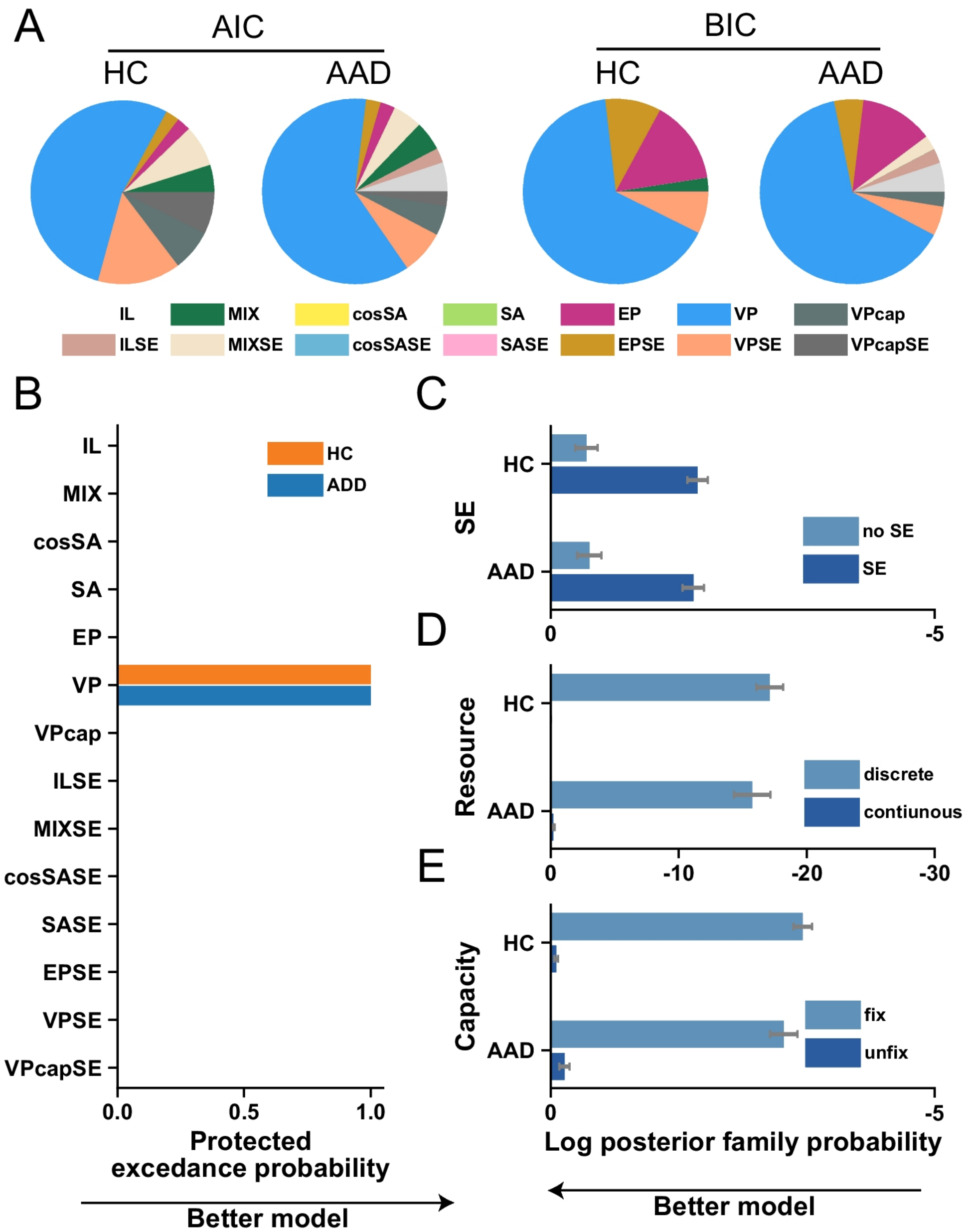

Fig. 2 Model and model family comparisons. **A** The proportion of participants for whom a model is the best-fitting model by AIC and BIC. For both AIC and BIC, and for both groups, the variable precision (VP) model is the best model for the majority of participants. The model names with and without the postfix "SE" indicate whether a model includes swap error in the model or not. **B** Protected exceedance probability of the 14 models. A model with a higher protected exceedance probability is a better model. The VP model is the best model (other models' are minimal and barely seen). **C**-**E** Log posterior family probabilities of three factors: with (SE) or without (no SE) swap errors, discrete or continuous memory resources, and fixed or infinite memory capacity. The results here indicate that the models assuming no swap errors, continuous memory resources, and infinite capacity outperform their counterparts

response errors should follow a von Mises distribution (Fig. 1C). Clearly, task difficulty increases as the number of to-be-remembered squares (i.e., set size) increases. Furthermore, as task difficulty increases, the overall distributions of response errors become wider. We therefore calculated the circular standard deviation (CSD) of response errors as a measure of memory quality for each trial, as color errors in this experiment is a circular continuous variable. It is important to note that we used the CSD rather than the average response error, because the mean reflects bias rather than the magnitude of error (i.e., the spread or width of the response error distribution) in color estimation. This approach is consistent with the commonly used metric in delay-estimation tasks (Zhang & Luck, 2008). Unsurprisingly, we found a significant main effect of set size ($F(3, 234) = 744.864$, $p < 0.001$, $\eta_p^2 = 0.905$), indicating that the subjects' CSD of response errors increased as set size increased. We also observed the main effect of group ($F(1, 78) = 4.821$, $p = 0.031$, $\eta_p^2 = 0.058$), indicating the overall poorer performance of the AAD group as compared to the HC group. Importantly, there was a significant interaction between group and set size ($F(3, 234) = 4.21$, $p = 0.006$, $\eta_p^2 = 0.051$). Post-hoc analyses showed that, as compared to HC, the AAD group had higher CSD of response errors when set sizes were low (set size 1, $t(78) = 2.694$, $p = 0.049$, Cohen's $d = 0.603$, Holm corrected; set size 3, $t(78) = 3.243$, $p = 0.011$, Cohen's $d = 0.725$, Holm corrected). The two group's performance were comparable when set sizes were high (set size =6, t(78) =0.2, p= 1.00, Cohen's d= 0.045, Holm corrected; set size 8, t(78) =0. 514, p= 1.00, Cohen's d= 0.115, Holm corrected).

Computational modeling of VWM performance

Although the above analyses have firmly established the poorer VWM performance of the AAD group, the underlying computational factors that cause such differences remain unclear. To gain further mechanistic insight into the aberrant behavior, we used the computational models that commonly used in basic VWM research. The overall analysis consists of two steps. First, we identify the best-fitting model that best describes the behavior of both groups. We then compare the fitted parameters between the groups in this best-fitting model to reveal the group differences. Notably, in the first step, we did not assume the appropriate model a priori, but instead took an unbiased approach to systematically fit and compare a total of 14 computational models in the VWM basic research. The intuitions of all models are summarized in the Method sections. All mathematical details of the models are documented in Supplementary Information Note 1.

We developed models that incorporate the various combinations of mechanisms assumed in previous studies, including whether a model includes swapping errors, whether a model assumes discrete or continuous memory resources, and whether a model assumes a fixed capacity. This modeling approach resulted in different assumptions and model structures. This approach is also known as factorial model comparison (Oberauer, 2023; van den Berg et al., 2014). This is critical because we do not make strong prior assumptions about what the mechanism must be but instead search exhaustively from a large pool of possible mechanisms. Theoretically, the apparent behavioral differences between the two groups could result from either qualitatively different observer models or quantitatively different parameters of the same model. Factorial model comparisons and parameter analyses allow us to distinguish between these two scenarios.

We fit all 14 models to each participant's data and quantified the model performance using Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC). As shown in Fig. 2A, the variable precision (VP) model outperformed other candidate models when evaluated under both AIC and BIC. In addition, we also performed random-effects Bayesian model selection at the group level (Rigoux et al., 2014), and the VP model exhibited the highest protected exceedance probability over all other competing models (Fig. 2B). The model comparisons at both the individual and the group levels strongly suggest that the variable precision model is the best-fitting model to explain the VWM performance of both groups.

Family-wise model comparisons reveal similar memory components in both groups

As mentioned above, the 14 models incorporate different combinations of theoretical assumptions. For example, the VP model has three basic assumptions: (1) continuous memory resources; (2) infinite memory capacity; (3) no swap error. When evaluating each individual factor (e.g., continuous vs. discrete memory resources), we need to combine the models within each family and perform family-wise model comparisons to avoid possible model dilution. Here, we further evaluated three theoretical factors here: (1) whether memory resources are continuous or discrete; (2) whether memory capacity is a fixed number or infinite; (3) whether swap errors exist. To do this, we calculated the log family evidence of the model families for each question (Penny et al., 2010). For example, the models IL, SA, cosSA and their variants ILSE, SASE, cosSASE form a model family that assumes discrete memory resources. The models MIX, EP, VP, VPcap and their variants MIXSE, EPSE, VPSE, and VPcapSE are the counterpart that assumes continuous memory resources. When evaluating discrete vs. continuous memory resources, we should compare the two model families rather than two individual models. All model families are summarized in Table 2.

The results show that the model family assuming continuous rather than discrete memory resources can better explain the data (Fig. 2D). Similarly, the model families assuming infinite memory capacity (Fig. 2E) or no swap errors (Fig. 2C) outperformed the other families (see detailed model family comparisons in Methods). Most importantly, these results held for both groups, indicating that the two groups shared the qualitatively same observer model in this VWM task.

Reduced memory resources in AAD

If the two groups shared the same observer model, their performance differences could therefore be attributed to parameter differences. We further examined the fitted parameters of the VP model in both groups. The VP model has four free parameters (Fig. 3). The initial resources ($\overline{J}_1$) indicates the total amount of memory resources, as a continuous value, that a subject possesses. The initial resource is also the key parameter of interest here. The power decay exponent α indicates how fast the averaged resources ($\overline{J}$) received by each item decrease as the set size (N) increases. The actual memory resources each item receives vary from trial to trial, which is reflected by the resource allocation variability

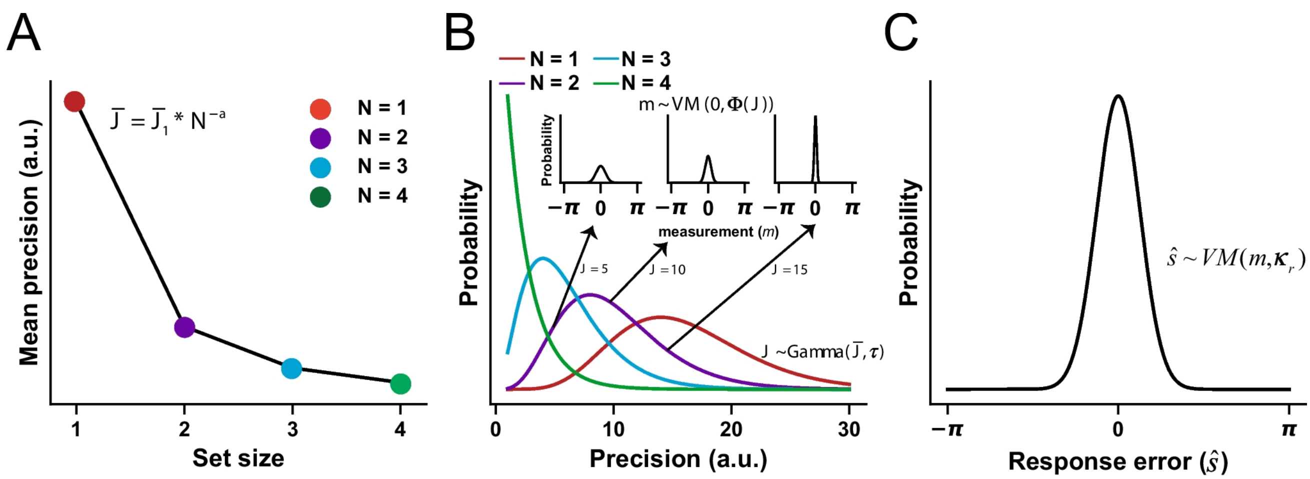

Fig. 3 The variable precision model. Please see the mathematical details of all 14 models in Supplementary Note 1. **A** Given a fixed amount of total the average resources ($\overline{J}_1$) allocated to an item ($\overline{J}$) decrease as a power function (decay parameter as α) of the number (N) of total items. **B** The actual resources allocated to an item (J) follow a Gamma distribution ($Gamma(\overline{J}, \tau)$) with the mean ($\overline{J}$) derived in Panel A and the variance τ. The resources determine the width of the von Mises distribution ($VW(0, \Phi(J))$) of the sensory measurement m given the input stimulus s. Here, Φ is a transformation function that converts the resource variable J into the precision parameter of the von Mises function. **C** Given the sensory measurement m, the output choice is $\widehat{s}$. The variability is determined by the choice variability κ_r . The variable precision model assumes continuous memory sources and an infinite number of items that can be held in memory

parameter (τ). There is also decision variability (κ_r), which indicates the variability of responses when an individual makes a motor response.

We found a significant group difference in initial resources (two-sample t-test, t(78) =2.321, p= 0.023, Cohen's d= 0.519). Such average memory resources allocated to an item inevitably decrease as set size increases. Lower initial resources lead to significantly lower amounts of resources when set size is low (Fig. 4). There were no statistical differences in decay exponent (t(78) =0.751, p= 0.455, Cohen's d= 0.168), resource allocation variability (t(78) =0.332, p= 0.741, Cohen's d= 0.074). We also observed a significant group difference in choice variability (t(78) =2.401, p= 0.018, Cohen's d= 0.537). The higher choice variability may reveal more lapses or compulsivity in making motor responses in the AAD group. The analysis of the fitted parameters of the VP model suggests that the lower amount of resources and the higher variability in choice execution are the main determinants accounting for the worse VWM performance in the AAD group.

Estimated memory resources associated with anxiety severity

Next, we seek to understand the functional role of estimated initial resource and choice variability. It remains unclear whether the computational modeling can capture the group-level differences or individual differences in anxiety symptoms. We found that the initial resource estimates (Pearson's r= −0.463, p= 0.0098) rather than choice variability (Pearson's r= 0.092 p= 0.629) can predict the individual anxiety severity in the AAD group. Such an association with anxiety severity was not found for either initial resource estimates (Pearson's r= 0.055, p= 0.734) or choice variability (Pearson's r= 0.011, p= 0.945) in the HC group (see Fig. 4F-I). These results further support the initial memory resources as a putative behavioral marker of anxiety in adolescents.

Discussion

In this study, we focus on the behavioral signatures and computational substrates of the well-established impaired working memory performance in AAD. We assessed the VWM performance of a clinically diagnosed AAD group and a HC group using the classic delay-estimation task. To unbiasedly disentangle the potential factors contributing to the behavior, we fitted 14 mainstream computational models, and performed systematic model comparisons and parameter analyses. Results showed that the two groups shared the same observer model—the variable precision model, but the AAD group generally had a lower amount of initial memory resources. Importantly, estimated memory resources served as a predictor of self-reported anxiety symptom severity.

Changing concepts of visual working memory

Our results are of particular interest to both computational cognitive scientists and clinical neuroscientists. Following the spirit of emerging interdisciplinary field—computational psychiatry, we use the existing computational theories from basic research to understand the atypical

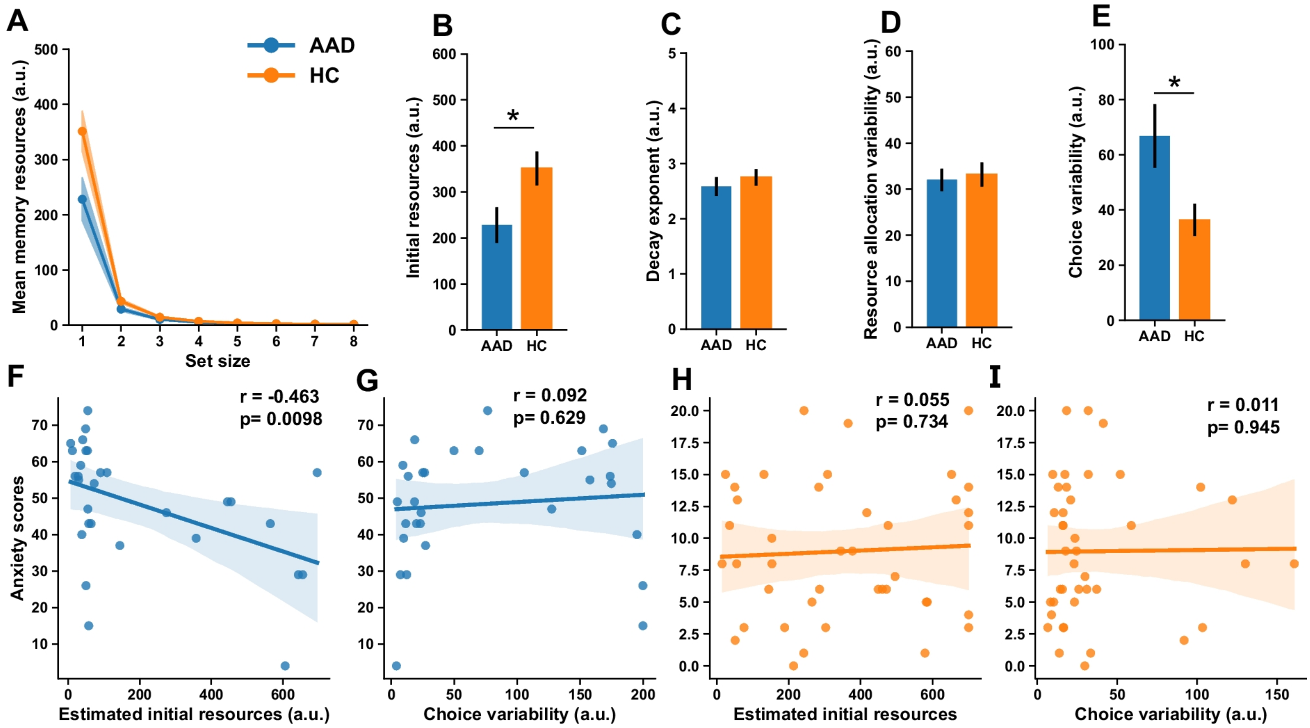

Fig. 4 Parameter analyses of the modeling results and symptomology correlations. **A-E** Parameter analyses of the modeling results. The memory resource functions reveal that both groups use less average memory resources as the set size increases. However, the AAD group exhibits fewer initial resources (Panel B). No group differences are observed in the decay exponent (Panel C), resource allocation variability (Panel D). The AAD group shows a higher choice variability (Panel E). The shaded area in panel A, and the error bars in panels B-E represent the standard errors across subjects. **F-I** Symptomology correlations. Individual anxiety scores in the AAD group are correlated with estimated initial resources (panel ***F***) but not with choice variability (panel ***G***) from the VP model in. There are no significant correlations between initial resources (panel ***H***) and choice variability (panel ***I***) with anxiety scores in the HC group. The shaded areas represent the 95% confidence intervals of the correlation lines

VWM performance in AAD. Working memory deficits are widespread in almost all psychiatric disorders, including schizophrenia (Forbes et al., 2009; Zhao et al., 2021), major depressive disorder (Rose & Ebmeier, 2006), and children with attention-deficit/hyperactivity disorder (Martinussen & Tannock, 2006) etc. Despite the widely documented deficits in working memory, the etiological mechanisms remain elusive. This may be due to the lack of a comprehensive understanding of the processes underlying VWM even in basic science. In recent years, there has been a rapid conceptual shift regarding to the mechanisms of VWM. Early work postulated VWM as discrete memory slots (e.g., magic number 7) (Luck & Vogel, 1997; Zhang & Luck, 2008). Recent findings, however, challenge this view and instead propose that memory resources should be formulated as continuous quantities (Bays & Husain, 2008; Ma et al., 2014). Despite the current debate in basic VWM research, we took an unbiased approach and thoroughly compared several influential computational models representing both the discrete-chunk and the continuous-quantity theories. We can safely conclude that, at least in our data, memory resources appear in a continuous form (see Fig. 2 model comparisons and Fig. 3 the VP model) and the AAD group has apparently fewer resources. In addition, we specifically emphasize that, although superficially similar, memory resources and memory capacity play very different roles in cognitive computation in visual working memory. For example, as set size increases, the average resources allocated to each item decrease (Fig. 4A). Fewer memory resources lead to more imprecise processing of individual items. Instead, memory capacity indicates the maximum number of items that can be encoded in memory. If the set size exceeds the memory capacity, some items will not be encoded at all, and color responses to those items should be completely random. Only through model comparisons and parameter analyses can we distinguish these theoretically differentiable cognitive constructs.

We emphasize that memory resources and capacity, two concepts that are easily intermingled in previous studies, are independent within the framework of the VP model. Suppose an observer has a total of 8 units of memory resources (a continuous quantity) and a fixed capacity of 4 items. When 3 items are presented, each item receives 8/3 units of resources. When 5 items are presented, the resources are distributed among a maximum of 4 items, with each receiving 8/4 =2 units, while the fifth item receives none. If the fifth item is probed, the observer must guess its color randomly. Now, consider another observer with a larger total amount of resources (9, 10, or 20 units, etc.). Regardless of the total amount available, resources can only be allocated to a maximum of 4 items (i.e., defined by capacity), always leaving at least one item without resources. Thus, capacity determines the maximum number of items that can receive memory resources, while memory resources define the amount distributed among them.

In addition to the issues regarding whether memory resources are discrete or continuous, and whether a fixed capacity exists, we also considered the potential influence of SE in VWM. SE refers to the phenomenon in which participants erroneously recall the color of an uncued item rather than the cued target. SE has been suggested as a significant source of error, separate from pure encoding failures (Bays, 2016). However, in our data, we found no significant evidence supporting the presence of SE, nor did it contribute to the behavioral group differences. This result has important implications for constraining future computational models.

An interesting aspect of our findings is that there is no qualitative difference between the groups in terms of the best-fitting model. This suggests that the behavioral differences observed between groups are primarily driven by quantitative differences in certain model parameters, rather than the use of distinct VWM processing models. These results also highlight the challenges in identifying specific cognitive deficits in adolescents with atypical development (AAD).

Unveiling the mechanisms

The conventional view that patients with anxiety disorders have reduced memory capacity is mostly derived from directly measured behavioral results on memory span tasks. For example, the most commonly used digit span task asks subjects to recall a list of digits in the same or reversed order. In this scenario, the memory span is quantified as the average number of items correctly recalled or as the longest list that can be perfectly recalled (Conway et al., 2005). The span task has been widely used in clinical measurement, in part because of its effectiveness and validity. However, the definition of memory span used here is descriptive of performance rather than mechanistic interpretations. A memory span seems to suggest that one can only encode a certain number of digits. However, it is also possible that these digits are encoded into memory, but with fewer resources (i.e., low memory precision). The computational modeling approach developed in basic VWM research can help disentangle these possibilities. Recently, the span tasks have been expanded to include complex span tasks, which impose additional cognitive demands, and dynamic span tasks, which require online updating of working memory content. A meta-analysis of all simple, complex, and dynamic span tasks provides evidence for the working memory deficits in people with anxiety disorders (Moran, 2016).

Here, we advocate a paradigm shift from conventional clinical tests to experimental paradigms whose underlying computational processes have been clearly defined. For example, the delay-estimation task is a classic VWM task for which the process models have been extensively studied. The process models can help to disentangle the underlying components and to provide a more mechanistic understanding of cognitive deficits in psychiatric disorders. Here, we use the process model—variable precision model—to decompose the VWM process into four factors: memory resources, memory capacity, resource allocation variability, and choice variability. Memory resources and memory capacity have long been proposed as the potential factors contributing to anxiety-related VWM decline. Resource allocation variability indicates the extent to which memory resources can be optimally allocated across items and trials. Choice variability indicates the amount of noise in the decision or motor execution phase. Here the finding of reduced memory resources directly supports the long-standing hypothesis that anxiety constrains memory resources. More importantly, our analyses here also quantified and compared other factors. The results show that they are unlikely to be critical factors contributing to VWM decline at least in our paradigm. This is useful because the same framework applies to different forms of psychopathology. For example, we have found that resource allocation variability is the main contributor to VWM deficits in schizophrenia (Zhao et al., 2021). In summary, future computational psychiatric research should consider including more tasks whose underlying processes are relatively well understood.

Group differences when tested multiple targets

In this study we only observed the group difference at low set size levels (i.e., 1/3) rather than high set size levels (i.e., 6/8). The lack of group differences for the high set size conditions may be because of floor performance (i.e., a lower CSD indicates better performance). However, we had to collect the data for floor performance because it is critical for model fitting. It is possible that the group differences emerge when multiple targets rather than a single target are cued for recall. In that scenario, participants are asked to sequentially reproduce the colors of multiple targets. The memory and recall of sequences have recently become a focal contention in both human (Fan et al., 2021, 2024) and monkey studies (Tian et al., 2024; Xie et al., 2022). While this paradigm is intriguing and offers new insights, it also presents challenges in terms of behavioral modeling. Specifically, how to model the interference effects between sequentially presented items and the associated memory retrieval processes remains an open question. Future studies may build formal quantitative models of sequence memory and learning at both behavioral and neural levels.

Clinical implications of reduced memory resources in AAD

Assessing working memory resources is of significant importance in the adjunctive diagnosis of adolescent anxiety disorders. Adolescents are at a critical stage of cognitive and emotional development (Steinberg, 2005), and those with anxiety disorders typically exhibit weaker emotional regulation when faced with stress and emotional challenges (Sackl-Pammer et al., 2019; Schafer et al., 2017). These patients often struggle to cope effectively with emotional fluctuations, manifesting symptoms such as emotional instability or an exaggerated response to threats. The atypical cognitive control abilities may stem from fewer cognitive resources. However, these features are often misconstrued as normal adolescent behavior, thereby interfering with clinical diagnosis (Beesdo-Baum & Knappe, 2012). Our study demonstrates that a reduction in working memory resources is a primary mechanism underlying working memory deficits in adolescents with anxiety disorders, and this reduction can predict the severity of anxiety symptoms. By quantifying working memory resources, clinicians can more accurately diagnose adolescent anxiety and assess symptom severity.

Our evaluation of working memory resources provides a key foundation for individualized therapeutic approaches. Cognitive Behavioral Therapy (CBT) has been shown to be effective for AAD, because it improves emotional regulation and coping strategies by identifying and modifying negative thought patterns (Kendall & Peterman, 2015; Suveg et al., 2009). However, anxiety symptoms are not only related to negative thoughts and emotional reactions, but are also closely tied to limitations in working memory function (Kendall & Peterman, 2015). By assessing the working memory resources of AAD, therapists can identify cognitive bottlenecks and adjust CBT strategies accordingly. For example, for patients with limited working memory resources, working memory training can be integrated into CBT techniques such as emotional exposure or cognitive restructuring, enhancing the patient's emotional coping abilities (Wang et al., 2023).

Limitations and future directions

Our study certainly has several limitations that can be addressed in future research. First, one of the advantages of our work is that we included clinical patients who were strictly diagnosed by experts. However, under the ICD-10 framework, anxiety disorder in adolescents is considered as a unified concept that includes all related subtypes, including social anxiety disorder, generalized anxiety disorder, and so on. It is intriguing to investigate the computational mechanisms underlying working memory dysfunction in different forms of anxiety disorders. Second, in this study, we deliberately recruited the adolescents who had only anxiety but not the comorbidity with depression. Our aim here is to minimize the potential confounding effect of depression. However, this manipulation also makes it difficult to generalize our results to more realistic cases, as the comorbidity of anxiety and depression is common in real life. Investigating the effects of comorbid depression on cognitive deficits in AAD will be a promising future direction. Third, anxiety is typically characterized by two dimensions: worry/apprehension and arousal/emotionality (Nitschke et al., 2001). It remains unclear how these two dimensions are manifested in working memory deficits. Fourth, the ultimate goal of computational psychiatry is to identify unique behavioral or neural markers to aid in therapy. Here, we identify the memory resources for low set size conditions as a key determinant of the memory deficits in AAD. Expanding memory resources through intervention may be a useful way to alleviate anxiety. Finally, due to the difficulty of administering behavioral tests in the hospital setting, we expect future studies to increase the sample size and test more VWM tasks and conditions to further validate the reduced-resource hypothesis of anxiety in adolescents.

Conclusions

In conclusion, this study assessed the VWM performance of a clinically diagnosed AAD group and a HC group using the classic delay-estimation task. The results of the study demonstrate that both groups employed the same observer model—the variable precision model. Nonetheless, the AAD group generally had reduced memory resources. What's more, estimated memory resources served as a predictor of self-reported anxiety symptom severity. Our results provide a parsimonious explanation for the atypical VWM performance in AAD and have strong implications for future treatments, such as cognitive-behavioral therapy, for anxiety disorders.

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Author contributions R-Y.Z. and T.K. conceived and designed the study. R-Y.Z. prepared the computer program for the Behavioral task. C.W., L.S. and H.X. collected the data. R-Y.Z., Y.F., and Z.J.C. analyzed the data. R-Y.Z. and J.J. wrote the paper. R-Y.Z. and Y-Y.G. revised the manuscript. All authors provide feedback to the manuscript.

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Declarations

Conflict of interest The authors declared that they had no conflict of interest with respect to their authorship or the publication of this article.

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