Cognitive-perceptual traits influence use of physics laws to enhance visual motion tracking

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Abstract

Schizophrenia and Autism Spectrum Disorder (ASD) can disrupt cognition and consequently behaviour. Traits of ASD and the subclinical manifestation of schizophrenia, schizotypy, have been studied in healthy populations with overlap found in trait profiles linking ASD social deficits to negative schizotypy, and ASD attention to detail to positive schizotypy. Here, we probed the relationship between sub-trait profiles, cognition and behaviour, using a predictive tracking task to measure individual eye movements under three gravity conditions. 48 healthy participants tracked an on-screen bouncing ball under familiar gravity, inverted antigravity and horizontal gravity control conditions while eye movements were recorded and dynamic performance quantified. Participants completed ASD and Schizotypy inventories generating highly correlated scores, r = 0.73. All tracked best under the gravity condition, producing anticipatory downward responses from stimulus onset under gravity which were delayed upwards under antigravity. Tracking performance was not associated with overall ASD or schizotypy trait levels. Combining measures using Principal Components Analysis (PCA), we decomposed the inventories into sub-traits unveiling interesting patterns. Positive Schizotypy was associated with ASD dimensions of rigidity, odd behaviour and face processing, and which all linked to anticipatory tracking responses under atypical antigravity. In contrast, negative schizotypy was associated with ASD dimensions of social interactions and rigidity, and to early stimulus-driven tracking under gravity. There was also substantial nonspecific overlap between ASD and Schizotypy dissociated from tracking. Our work links positive-odd traits with anticipatory tracking when physics rules are violated, and negative-social traits with the application of expected physics.

Cognitive-perceptual traits influence use of physics laws to enhance visual motion tracking

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Abbreviations

SATQ – Subthreshold Autism Trait Questionnaire, SPQ – Schizotypal Personality Questionnaire, RMSE – Root Mean Square (position tracking) Error, PCA – Principal Component Analysis, FEF – Frontal Eye Fields

Abstract

Schizophrenia and Autism Spectrum Disorder (ASD) can disrupt cognition and consequently behaviour. Traits of ASD and the subclinical manifestation of schizophrenia, schizotypy, have been studied in healthy populations with overlap found in trait profiles linking ASD social deficits to negative schizotypy, and ASD attention to detail to positive schizotypy. Here, we probed the relationship between sub-trait profiles, cognition and behaviour, using a predictive tracking task to measure individual eve movements under three gravity conditions. 48 healthy participants tracked an on-screen bouncing ball under familiar gravity, inverted antigravity and horizontal gravity control conditions while eye movements were recorded and dynamic performance quantified. Participants completed ASD and Schizotypy inventories generating highly correlated scores, r = 0.73. All tracked best under the gravity condition, producing anticipatory downward responses from stimulus onset under gravity which were delayed upwards under antigravity. Tracking performance was not associated with overall ASD or schizotypy trait levels. Combining measures using Principal Components Analysis (PCA), we decomposed the inventories into sub-traits unveiling interesting patterns. Positive Schizotypy was associated with ASD dimensions of rigidity, odd behaviour and face processing, and which all linked to anticipatory tracking responses under atypical antigravity. In contrast, negative schizotypy was associated with ASD dimensions of social interactions and rigidity, and to early stimulus-driven tracking under gravity. There was also substantial nonspecific overlap between ASD and Schizotypy dissociated from tracking. Our work links positive-odd traits with anticipatory tracking when physics rules are violated, and negative-social traits with the application of expected physics.

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Introduction

Schizophrenia and Autism Spectrum Disorders (ASD) are common heterogenous conditions that have historically been considered distinct. Recently, cognitive and behavioural overlap between them has been suggested, following observations that they share similarities in psychosocial and pathophysiological features and phenotypes that may be signatures of underlying comorbidity (Chisholm, Lin, Abu-Akel & Wood, 2015). Clinically-motivated research has focused on practical rigid diagnostic clarification with limited consideration of variation within specific symptoms (Ford, Apputhurai, Meyer, & Crewther, 2018). Improving the mechanistic understanding of variable cognition and behaviour, and the underlying genetic and neural correlates is a crucial step towards better characterisation, which could ultimately enhance diagnostic and treatment practices (De Giorgi et al., 2019; Klopper et al., 2017). We pursue a mechanistic approach here by probing phenotype variability within a healthy population.

Schizotypy refers to a set of personality traits mirroring symptoms of schizophrenia at a subclinical level, characterised by dimensions (positive, negative and disorganised) that run on a continuum from healthy to psychosis (Nelson, Seal, Pantelis, & Phillips, 2013; Raine, 1991). In a large healthy sample (N=1678), Ford et al. (2018) used latent profile analysis to identify eight clusters encompassing dimensions of schizotypy and ASD. Subgroups involving psychosocial difficulties represented a shared social autism-negative schizotypy domain (Abu-Akel et al., 2017), an autism-schizotypy subgroup reflected a non-specific overlap of ASD and schizotypal traits, while psychosis and a moderate aspect of schizotypy appeared to be independent. Further research identified consistent overlapping and diametrically opposed facets of phenotypes. With a sample of N=640, Nenadić et al. (2021) used Principal Components Analysis (PCA) to study multiple psychometric measures of schizotypy and ASD in a German and separate Swiss/French population. They identified loss

of function and communication deficits as phenotypes of ASD traits showing convergence with negative and disorganized features of schizotypy. However, attention to detail in ASD was diametrically opposed to positive schizotypal trait dimensions.

Poor Smooth Pursuit Eye Movements (SPEM) are an established endophenotype of schizophrenia and schizotypy. Deficits in motion processing and target prediction in schizophrenia contribute to SPEM abnormalities (Barnes, 2008) with findings replicated in schizotypy (Koychev et al., 2016). Often thought of as two separate systems, SPEM and saccadic movements form part of a single sensorimotor repertoire, served by continuous estimates of future eve positions and velocity-related error signals (Goettker & Gegenfurtner, 2021). Along the pathway driving the oculomotor response, there are dynamic interactions between input, predictions and errors enabling tracking whilst maintaining perceptual stability (Goettker, Braun, & Gegenfurtner, 2019). We previously showed that motion tracking under gravity may present a means of studying individual differences in incorporating predicted gravity into cognitive processing (Meso, De Vai, Mahabeer & Hills, 2020). Predictions of future positions of moving objects exploit gravity and participants' eye movements are guided by prediction to different extents (Jörges & López-Moliner, 2019). Observers are generally capable of distinguishing different settings of gravitational acceleration of parabolic trajectories with poor precision (Jörges, Hagenfeld, & López-Moliner, 2018). ASD has also been shown to drive deficits in ocular motor function with a recent review identifying saccade accuracy, inhibitory control and impaired tracking as common issues (Johnson, Lum, Rinehard & Fielding, 2016). However, the initiation of eye movements and disengaging from targets did not seem impaired in ASD groups.

The functioning of the ocular motor system is underpinned by a network of brain areas within cortex and beyond (Masson and Perrinet, 2012). The cerebellum is integral to problem-solving in spatial orientation due to its role in vestibular processing and representations of gravity needed for behaviour rely on it (MacNeilage & Glasauer, 2018). Cerebellar lesion patients exhibited deficits in perception of gravitational direction in a perceived tilt task (Dakin, Peters, Giunti & Day, 2018). Activity in the Frontal Eye Fields (FEF), an area that serves target prediction with an internal representation, has been found to be reduced during SPEM in schizophrenic patients (Faiola et al., 2020). Corresponding reductions have not been observed in schizotypy (Meyhöfer et al., 2015). Furthermore, using functional Magnetic Resonance Imaging and connectivity analyses, patients with recent-onset psychosis and low-schizotypy controls were indistinguishable based on brain activity during SPEM performance. However, using machine-learning, participant group classifications were made using a right FEF seed region, based on its connectivity within subcortical and cortical structures, frontal cortex, cerebellum and hypothalamus (Schröder et al., 2022). As interconnected cortical areas MT (Middle Temporal) and MST (Medial Superior Temporal) process visual motion signals producing commands for smooth pursuit, FEF may regulate this output with real-time gain control (Ono & Mustari, 2012; Ono, 2015). These findings, which highlight a potential predictive role for FEF within a wider network, suggest that individual variation in SPEM ability is subtler than previously thought and demands a fine-grained exploration of prediction, representation and information integration mechanisms.

In a recent study, high schizotypy participants had worse performance during predictive pursuit than a control low schizotypy group, but SPEM in a sinusoidal tracking task showed no differences (Faiola, Meyhöfer & Ettinger, 2020). In the prediction task, participants tracked a stimulus that moved at a constant velocity and was pseudorandomly blanked in half the trials, with instructions given to continue eye movements during the blank. These findings imply the prediction deficit is separate from general SPEM performance even along a sinusoidal path, consistent with findings of Meso et al., (2020), who manipulated prediction using two gravity conditions. The current work will address three questions. First, can we conceptually replicate the previous work on tracking under gravity (Meso et al., 2020) with additional controls and the inclusion of an ASD inventory? Second, can we unveil differences in tracking performance dynamics and organise them in terms of anticipation (pre-sensory response), early open-loop and later closed-loop responses? Finally, can we characterise the multidimensional relationship between schizotypy and ASD subtraits, and link these to eye-tracking measures for a meaningful interpretation of clusters? We take a combined experimental and theoretical approach and answer each one of these questions in turn.

Materials and Methods

Participants We tested 48 participants (29 Female, 19 Male, Age M=22.1, SD= 3.9, IQR = $\{19,23\}$) recruited by opportunity sampling at Bournemouth University. Participants received £5 for their time. The study was approved by the Research Ethics Committee of Bournemouth University and was carried out in accordance with the principles of the Declaration of Helsinki. Participant numbers could not be determined by standard power calculation. Similar eye-tracking tasks require 6 to 10 participants (e.g. Meso, Montagnini, Bell, & Masson, 2016; Meso, Gekas, Mamassian, & Masson, 2022), so trait inventory requirements determined numbers. Previous power estimates suggested 45 participants (Meso, De Vai, Mahabeer, & Hills, 2020), as did a recent reliability and replicability study on SPEM and traits (Schröder, Baumert, & Ettinger, 2021).

Stimulus and Materials

Stimuli were generated on a Windows 7 PC running bespoke Matlab (Mathworks) routines in Psychoolbox (Brainard, 1997; Pelli, 1997). Presentation was on a Cambridge Research Systems 32' Display++ Monitor with 1920 x 1080-pixel resolution and 100Hz refresh rate. The monitor was placed 80cm from participants. Eye movements were recorded from the right eye using an SR Eyelink Video eye tracker operating at 1000Hz with movement restricted by a head/chinrest. The stimulus was based on Meso et al., (2020), with sizes scaled to an on-screen virtual square with sides of 900pix containing the stimulus presentation area of 23.4 degrees of visual angle (°). The black ball had 0.21° diameter with motion characterised by Equations (1) to (4).

$$\mathbf{V_x}(t\)=d\ [?]\mathbf{S_x}\ (1)$$

$$P_{x}(t) = X_{0} + d [?]S_{x}t (2)$$

 V_x in Equation (1) is the constant horizontal component of the speed with S_x set from {4, 16} deg/s for fast/slow and direction d set from {-1,1} for left/right. The time-varying horizontal position P_x in Equation (2) depended on S_x starting at the centre of the screen, X_0 .

$$\mathbf{V_v}(t) = \mathbf{S_v} + \mathbf{\epsilon} + g \ [?]t \ (3)$$

 $P_{v}(t) = Y_{0} + (S_{v} + \varepsilon)t + (g [?]t^{2})/2 (4)$

 V_y in Equation (3) is the vertical speed component initiated as $S_y = 2^{\circ}/s$ and ε is a number from a flat continuous distribution of $\pm \{0 \text{ to } 0.5\}^{\circ}/s$ away from the direction of acceleration g, which is $\pm 9.81^{\circ}/s^2$ for the gravity (+) and antigravity (-) conditions. The position P_y in Equation (4) incorporates the initial position at the centre of the screen Y_0 and the integration of Equation (3) for position. The resulting motion is that expected for a ball just smaller than a professional soccer ball.

Procedure Participants were screened for normal or corrected-to-normal vision with a visual acuity letter chart. Bespoke Matlab programs were used for trait inventories with mouse clicks to record responses. The 74item Schizotypal Personality Questionnaire – SPQ (Raine, 1991) and 24-item, 5-point Subthreshold Autism Trait Questionnaire – SATQ (Kanne, Wang, & Christ, 2012) were used. The tracking task was separated into three blocks of Gravity, Antigravity and Control. In the control condition, stimulus orientation was rotated by 90 degrees from the gravity condition so that vertical motion was defined by Equations (1) and (2) and horizontal by (3) and (4) and gravity acted rightwards. Each block had 160 trials of 1.25s duration with participant-initiated button presses to proceed. Trials started with a 500ms central dark grey fixation circle which disappeared at trial onset and the stimulus was followed by a grey screen. Participants were instructed to fixate on the central spot and track the ball as well as they could. Blocks contained 80 fast and 80 slow trials and lasted approximately 10 minutes. The task interleaved the inventories with the conditions fixed in the same order i.e. SPQ, gravity, SATQ, antigravity and control, with breaks in between so that it lasted about 40 minutes. Changes from the procedure of Meso et al., (2020), were that participants always started on the gravity condition, trials were shorter (1.25s not 2s), tasks included the control condition and we used a higher precision psychophysics screen, the CRS Display++.

Design and data analysis

We used a multivariate within-participants design. The Independent Variables were Gravity direction with three levels: Gravity (G) – downwards acceleration, Antigravity (AG) – upwards and Control (C) - rightwards; ball Speed with two levels: Slow $(4^{\circ}/s)$ and Fast $(16^{\circ}/s)$. The key measures were the two inventories: the SPQ and SATQ, RMSE (Root Mean Square Error between dynamic eye position and ball position), and Saccades (rates and sizes). We also recorded participant age and sex. Data pre-processing to extract the RMSE and Saccades is detailed in Meso et al., (2020). We reduced the RMSE responses to 25 samples, each covering a 20ms window from onset at 0ms to 500ms, RMSE was measured for the x-direction capturing responses to the motion component at a constant speed for conditions G and AG, and for the y-direction capturing responses subject to acceleration due to simulated rightward gravity. We quantified learning as performance improvement during a block of 80 trials, by subtracting averaged RMSE value for the last 20 trials from that of the first 20 trials under the same speed condition. Learning was positive if there was improvement. We analysed the trait responses and a restricted subset of eye movement measures focusing on (i) the relationship between SPQ and SATQ, (ii) the relationship between the inventories and RMSE measures, (iii) the relationship between the inventories and the saccades, and (iv) dynamic changes in the relationships between both RMSE and saccades under the G and AG conditions. For each of the four, we ran correlations with alpha adjusted for the number of comparisons undertaken. (v) We also ran mean comparisons between gravity conditions for RMSE, Saccades and RMSE-learning. These were done using a Wilcoxon signed rank test because of the deviations from normality. Finally, we ran a correlation type Principal Components Analysis (Joliffe, 2002) to unpack the relationship between a restricted set of 21 measures. These variables were selected to cover sub-traits of the SPQ and SATQ, Saccade rates and amplitudes and RMSE measures. both at stimulus onset (0ms) and during the open loop of response (~160ms). Meaningful components were identified using parallels analysis of the variance (Joliffe and Cadima, 2016). For simplicity, we focused analysis on the slow speed condition which showed similar patterns to the faster condition but was an easier tracking task.

Results

Tracking performance across gravity conditions

We measured the dynamic RMSE value (difference between onscreen ball and eye position) every 20ms over the first 500ms, separately for horizontal and vertical components. In the horizontal direction, with ball motion at a constant speed (4 or $16^{\circ}/s$), average performance, RMSE-x gradually worsened between 0 and 200ms. This was because horizontal direction was unpredictable in each trial and the stimulus response. which started around 85-95ms, required a catch-up saccade and so only improved after 200ms (Figure 1A and C, darker grey traces). For RMSE-y in the vertical direction where acceleration acted, the gravity condition was the same within each block of trials so motion could be predicted and anticipated by the participant after some trials. The average response was therefore about 0.5° from onset for the full 500ms (Figure 1B and D darkest grey trace). In contrast, for the antigravity condition, average tracking was worse at $\sim 0.8^{\circ}$ from onset gradually improving until 300ms, implying there was an anticipatory antigravity response that was less effective than under gravity (Figure 1B, D mid grey trace). This result is consistent with the previous study (Meso et al., 2020), with worse performance and slower dynamics under AG. The differences are statistically evaluated in the next section. Importantly, the control condition with horizontal gravity was similar to the gravity condition, but with a baseline averaged initial performance of 0.6° , 0.1° worse than the gravity condition (Figure 1A and C lightest grey trace). This suggests there is a performance advantage for the downwards gravity condition that is reduced by 0.1° in the horizontal rightward gravity control condition.



Figure 1: Dynamic RMSE performance measure in degrees plotted on the ordinate axis, Mean and Standard Error for 48 participants, against time in ms from stimulus onset on the abscissa for gravity (black, G), antigravity (dark grey, AG) and control with horizontally accelerating gravity (light grey and dash/dot lines, CO) conditions. (a) For the horizontal direction in the slow condition. (b) Vertical direction, slow condition showing worse performance for AG from onset to 200ms. (c) Horizontal fast condition with catch up saccades around 100-300ms. (d) Vertical fast condition similar to (b) with better performance for G than AG.

ASD and SPQ traits and links to eye tracking

The Schizotypy Personality Questionnaire (SPQ) produced scores comparable to previous work with Median = 16 and IQR = 18.5. Participant scores were almost evenly distributed below 30 (See Figure 2A). The SATQ produced scores comparable to previous work with Median = 17.5 and IQR = 11.5 and scores were approximately normally distributed (Figure 2B). We ran a Pearson's correlation between the SPQ and SATQ and found a strong relationship with r = 0.735, $p = 2.73 \times 10^{-9}$ (Figure 2C). We did not decompose the SPQ and SATQ sub-clusters, to avoid expansion to the 15 permutations (3 SPQ clusters x 5 SATQ) and therefore used PCA. Instead, we first looked at the relationship between the inventories and the vertical RMSE-y at stimulus onset (0ms), which reflects anticipatory responses. For the four comparisons using a Pearson correlation between the SPQ and RMSE-y with r = -0.026, p = 0.86, and similarly a low correlation between SATQ and RMSE-y at with r = -0.074, p = 0.62. Under the antigravity condition, there was a

low correlation between the SPQ and the RMSE-y with r = 0.065, p = 0.66, and similarly between SATQ and RMSE-y with r = 0.025, p = 0.86. There was therefore no significant relationship between the trait measures and the tracking performance in the gravity direction at onset (Figure 2D, E, G and H). We then analysed the relationship between the traits and the eight saccade measures, adjusting the alpha value for the Pearson correlations to 0.00625. Under the gravity condition, there was a non-significant negative correlation between the SPQ and the Saccade rate, r = -0.169, p = 0.25, and similarly for the SATQ and saccade rate, r = -0.153, p = 0.30. Under the antigravity condition, the correlation was near zero for the SPQ and the saccade rates, r = -0.047, p = 0.75, and the SATQ and the saccade rate, r = -0.039, p = 0.79. The traits showed little relation to the rates (Figure 3A-D). For the saccade amplitudes, under the gravity condition, there was a non-significant negative correlation between the SPQ and the amplitudes, r = -0.12, p = 0.40, and the SATQ and amplitudes, r = -0.12, p = 0.41. For the antigravity condition, these were again near zero for SPQ and amplitude, r = 0.041, p = 0.78, and SATQ and amplitude, r = -0.017, p = 0.91. Traits showed little relationship with the amplitudes (Figure 3E-H).



Figure 2: Summary of 48 participants' data showing SPQ and SATQ trait measures and vertical RMSE for the slow tracking condition. (a) and (b) show the frequency distributions of SPQ and SATQ scores with descriptive statistics. (c) Strong correlation between SPQ and SATQ scores. (d) to (e) Weak correlation

between SPQ and onset, 0ms, RMSE for both gravity and antigravity conditions, and (f) moderate correlation between gravity and antigravity RMSE. (g) to (i) weak correlation between SATQ and onset, 0ms, RMSE for both conditions, G and AG, and then the distributions of the onset y-RMSE values for gravity (darker) and antigravity (lighter) showing separation between condition performance. (j) to (l) show moderate correlation between gravity and antigravity RMSE, increasing strength through 80ms, 160ms and 240ms. (m) to (o) show distributions of y-RMSE distributions for gravity (darker) and antigravity (lighter) which become less distinct over time from 80ms to 240ms.

Eye tracking differences across gravity conditions

Tracking was measured separately across G and AG conditions both for the constant speed component – x and the accelerating component -y. We first considered the relationship between the tracking measures for the accelerating direction RMSE – y and for the G and AG conditions. We carried out four Pearson's correlations to track this relationship dynamically from onset (0ms) through to the closed-loop response at 240ms in four windows. Alpha was adjusted to 0.0125 for four comparisons. There was a significant correlation between individual RMSE – y values across all the time windows: at 0ms, r = 0.422, p = 0.00282; near response onset at 80ms r = 0.472, $p = 7 \ge 10^{-4}$; during the open loop at 160ms r = 0.481, p =5.47 x 10⁻⁴; and during the closed loop r = 0.532, $p = 9.8 \times 10^{-5}$. Interestingly, the correlations increase in strength over time from onset, suggesting that the earliest anticipatory responses have less shared processing between the G and AG stimulus cases than the later closed-loop response (Figure 2F, J-L). We then tested for a difference in the RMSE – y responses between the G and AG conditions for the same sequential time windows. We used a Wilcoxon signed rank test because of the non-parametric distributions (see Figure 2I, M-O). There was a significant difference between the G and AG responses for the earliest two windows, with the values at 0ms for G: Median = 0.41° and for AG: Median = 0.73° , with W = 167, p = 0.0000157, and at 80ms for G: Median = 0.37° and for AG: Median = 0.56° , with W = 265, p = 0.000923. At 160ms and 240ms, there was no significant difference between G and AG responses, with W = 513, p = 0.44, and W = 550, p = 0.70 respectively. Early responses in the gravity direction are consistently best for the G condition and initially poorer for the AG condition (Figure 2I, M-O). Similar differences are found between the G and Control conditions. The pattern of results showing better performance under G and delays under AG replicates previous findings (Meso et al., 2020). We then compared the values of both saccade measures under the two gravity conditions, adjusting alpha for the two tests. For the rates, significantly fewer saccades are produced per second under G: Median = 1.36 than under AG: Median = 1.58, W = 245, p = 0.000735. For the amplitudes, there is no significant difference in the size of saccades produced under the G and AG conditions, W = 448, p = 0.15 (Figure 3I and J). Finally, we looked at the effect of learning across trials for both the constant speed motion with RMSE - x and the motion subject to acceleration RMSE - y and adjusted alpha for two comparisons to 0.025. For the first (x), there is a difference between the conditions with less learning under G: Median = -0.06° than AG: Median = 0.03° , W = 319, p = 0.0058. For the accelerating condition (v), learning is again lower for G: Median = -0.02° than AG: Median = 0.19° , W = 248, p = 0.000488. This result suggests that performance in the gravity condition did not generally improve over the course of trials while that under the antigravity condition generally did, especially under acceleration (Figure 3K-L).



Figure 3: Relationship between trait measures and saccade metrics and visualisations of estimates of learning through performance improvements over conditions (see text for details). Eye movements here are for the slow condition only. (a) to (d) Show weak negative correlation between SPQ/SATQ and saccade rates under both gravity (G) and antigravity (AG) conditions; those for gravity have higher values. (e) to (h) Show weak correlations between SPQ/SATQ and saccade sizes/amplitudes. (i) and (j) saccade rates and sizes show little difference between gravity conditions. (k) and (l) RMSE learning i.e. performance improvement during task shows no difference between gravity and antigravity for the horizontal (x-direction), but more improvement during the task for the vertical direction (y-direction) under the antigravity condition with a median of 0.19° compared with -0.02°.

Principal component analysis

Given the number of variables measured, we could not answer all questions of interest using standard correlations and hypothesis-based statistical tests without an explosion of familywise error. Like others (Nenadić et al., 2021, Meso et al., 2020) we took a data-driven approach and identified variables of interest for a correlation-based PCA. We selected a set of 21 measures from over 200 possible measures in the multivariate experiment including the AGE, the three main clusters of the SPQ, the five sub-traits of the SATQ, and eye tracking with both saccade and RMSE measures for the G and AG condition. Table 1 contains the PCA results with the 21 variables listed and their loadings for the first seven components. These seven components in the table (in descending order of their strength) are selected based on parallels analysis restricting explained data variance to 75%. We use the data loadings to guide our qualitative description of each of the orthogonal components. The first component is dominated by eye movement measures with little contribution from AGE and the inventories. It likely captures individual differences in eye movements which make some participants better at eye-tracking tasks than others. The second component captures general overlap between the SPQ and the SATQ, unrelated to eye movements. The third component is dominated by the positive cluster of the SPQ and the odd, face and rigidity traits of the SATQ. In addition, eye movement for open loop constant speed tracking (160ms) and anticipatory antigravity tracking responses and learning. The fourth captured negative SPQ and social interaction and rigidity of the SATQ. For eye movements, saccade rates/amplitudes and open loop and anticipatory tracking under the gravity condition. The fifth captured social interactions and odd clusters of the SATQ and for eye movements, saccade rates and *learning under the gravity* condition. Both the fourth and fifth components had a contribution from AGE, but this was not considered reliable because of our narrow spread of participant ages. The sixth and seventh components were difficult to characterise, with the former being predominantly driven by eye movements and the latter by traits.

Table 1 : Principal component Analysis results looking at the relationship between variables covering the inventories, saccade metrics and tracking performance in the form of RMSE. The first seven components explaining 75% of the variance are included. Selected variable labels are given in the first column. Numbers represent variable loadings with higher loadings above |0.20| highlighted.

			COMPONENT #	COMPONENT #	COMPONENT #
			1	2	3
		Variance (%)	20.0	17.9	10.2
	Variable Name				
	AGE		-0.02	-0.16	0.03
(Qs)	SPQ - positive		-0.02	0.38	-0.23
	SPQ - negative		-0.11	0.35	0.11
	SPQ - disorganised		-0.10	0.39	-0.16
	SATQ - Social Int.		-0.08	0.31	0.06
	$\mathrm{SATQ}-\mathrm{Odd}$		-0.05	0.23	-0.31
	SATQ - Read Faces		-0.04	0.35	0.24
	SATQ - Language		-0.16	0.30	0.02
	SATQ - Rigidity		-0.07	0.24	-0.23
(G)	Saccades - Amplitude		0.33	-0.02	0.00
	RMSE - y (0ms)		0.32	0.07	-0.10
	Saccades - rate (200ms)		-0.30	-0.06	-0.14
	RMSE - x (160ms)		0.14	0.17	0.52
	RMSE - y (160ms)		0.23	0.17	-0.07
	RMSE - y, learn (0ms)		-0.09	-0.15	-0.15
(AG)	Saccades - Amplitude		0.37	0.05	-0.13
	RMSE - y (0ms)		0.37	0.11	-0.20
	Saccades - rate (200ms)		-0.34	0.02	-0.17
	RMSE - x (160ms)		0.15	0.12	0.45
	RMSE - y (160ms)		0.34	0.11	-0.17
	RMSE - y, learn (0ms)		0.18	-0.10	-0.25

Discussion

In this work, we studied the relationship between both ASD and schizotypy traits, recently demonstrated to have overlapping characteristics (Ford et al., 2018; Abu-Akel et al., 2017; Nenadić et al., 2021), and their association with cognition and behaviour probed through a gravity tracking task (Meso et al., 2020). Both ASD and Schizophrenia have been found to disrupt ocular motor function (Barnes, 2008; Johnson, Lum, Rinehard & Fielding, 2016) and questions remain about the commonality of the specific disruption. In this context, the work involved a conceptual replication and extension of research which introduced the gravity ball tracking task. We found that participants were much better at tracking under the familiar gravity condition than when the direction was inverted in the antigravity condition (Meso et al., 2020). This tracking task was different from more widely used predictive sinusoidal tracking with blanking along the trajectory (Faiola, Meyhöfer & Ettinger, 2020), as participant performance could be improved by the use of knowledge about gravity (Jörges & López-Moliner, 2017). In the current work, we similarly demonstrated an advantage for the downward gravity condition over others and unpack the multitude of results from the multivariate eye movement and inventory measures by answering three broad questions. We first interpret the findings in the context of replicating and extending Meso et al., (2020), with the inclusion of the ASD inventory and controls. Second, we unveil differences in tracking dynamics and discuss their implications. Finally, we characterise the multidimensional relationship between eye movements, ASD traits and Schizotypy.

Replication of the gravity advantage in tracking

Participants were asked to track a moving ball in repeated trials within blocks of separate gravity conditions. As such, within two or three trials from the start of the block, participants could implicitly or explicitly expect that the vertical component in the gravity and antigravity conditions would have the same acceleration over trials within the block. Under the gravity condition, all participants were good at tracking throughout the half-second duration from motion onset we analysed. Tracking was about 20% better than under the control condition, in which gravity acted in the rightward direction, suggesting that implicit knowledge of the physics-based expectations of gravity enhanced visual tracking (similarly suggested by Jörges & López-Moliner, 2019). The antigravity condition engendered much larger individual differences in responses and poorer tracking. Some participants were able to anticipate the accelerating response in the upward direction before the visual system could produce a stimulus-driven response, and most were able to improve to a point at which tracking performance was best and at a plateau matched across all conditions by about 300ms from onset. In the current work, we sought to better understand these dynamic differences across conditions. Meso et al., (2020) used linear mixed models to control for random effects and identify a relationship between Schizotypy trait levels and both RMSE and saccades which involved an interaction with gravity direction condition. Here, we have extended this previous work, aiming to better understand how the dynamic eye response depended on violations of the physics of gravity and trait characteristics.

Schizotypy and ASD trait relationships

We used two established and quick-to-answer inventories: one for ASD – the SATQ (Kane et al., 2012) and the other for schizotypy - the SPQ (Raine, 1991). Individual scores for the two inventories were found to be highly correlated. Large recent studies have shown that the two conditions are related and suggested that individuals with a clinical ASD diagnosis were about 3.5 times more likely to receive a concurrent diagnosis of schizophrenia (Zheng, Zheng & Zou, 2018). Similarly, overlaps have been identified in traits of both ASD and Schizotypy in healthy undiagnosed participants across multiple cultures (Abu-Akel et al., 2017; Nenadić et al., 2021). The heterogeneity of ASD and Schizotypy traits means that the overlap can also be separated into quite distinct clusters; for example, a first encompassing negative schizotypy and poor social communication (ASD), a second encompassing positive schizotypy and attention to detail (ASD) and a third with less specific overlap (Abu-Akel et al., 2017; Nenadić et al., 2021). Indeed, our two inventories decomposed the trait measures into three broad dimensions (from nine smaller ones) for Schizotypy and five dimensions for ASD (Raine, 1991; Kane et al., 2012). We expected some of these subtrait dimensions to be associated with the specific eye movement metrics. When we measured the correlation between both overall single trait levels and various eye movement measures, there were unsurprisingly no significant relationships. Instead, this motivated the use of a data-driven approach to parcel out the variance into the various contributions in a similar way to what was achieved by the linear mixed models in Meso et al., (2020), to observe more subtle relationships.

Gravity direction performance and dynamics

The gravity condition was generally found to be better performed than the antigravity condition. When the saccades were compared between these conditions, there was a significant difference between rate of saccades produced, with fewer saccades under the gravity conditions when compared to the antigravity conditions. However, the sizes of these saccades were not different. This may have been driven by more catch-up saccades in the antigravity condition. We separated the tracking measure of RMSE into four response epochs from anticipatory at onset, sensory response threshold, open-loop response and finally a closed-loop response. This was done to reduce the complexity of the continuous tracking responses and capture key ocular motor signatures that isolate anticipatory responses, in the absence of the stimulus from the earliest unelaborated sensory responses and later responses which incorporate sensorimotor feedback loops (Masson & Perrinet, 2012; Meso et al., 2022). We first looked at the correlation between the RMSE in the vertical response for both the gravity and antigravity conditions across the four time windows. All four windows showed a significant relationship between performance in both gravity conditions, with the relationship weakest in the anticipatory responses occurring before the sensory response was visible and getting progressively stronger, with a peak in the last closed loop epoch. This finding suggests that the anticipatory response is at least partially driven by separate mechanisms in the gravity and antigravity condition, with downward gravity able to draw on prior knowledge about the physics rules in a fast, preattentive way (Jörges & López-Moliner, 2017). Further, in the antigravity condition, the RMSE responses themselves were also poorest for the anticipatory condition and subsequently less poor at the threshold of stimulus response in the second epoch considered. Although, in both these earlier windows, RMSE was significantly different from the gravity response. In the latter two windows, responses were not different across the gravity and antigravity conditions. Late in the ocular motor response, integrative processes serving motion estimation incorporate visual feedback and therefore error signals (Goettker, Braun, & Gegenfurtner, 2019; Meso et al., 2022). By contrasting these later open-loop and closed-loop responses to the earlier epochs, we therefore expected to be able to separate motion perception deficits previously characterised (Barnes, 2008) from specifically prediction deficits (Koychev et al., 2016). On top of that, in contrasting the gravity and antigravity conditions in the multivariate analysis that followed, we have prediction scenarios involving the overfamiliar case of downward gravity and the rule-contravening case of antigravity, which unpacked some seeming contradicting results on tracking deficits in schizotypy (Koychev et al., 2016; Meyhöfer et al., 2015). We also calculated a measure of learning to quantify improvement of performance over the course of a block and found that learning improved more in the antigravity than gravity condition, with a larger improvement of almost two and a half times in the accelerating vertical direction when compared with the constant speed horizontal direction. Participants were therefore able to get slightly better over the course of the trials, particularly for the antigravity condition in anticipating the upwards direction. This learning could not however extend to a level to match the established prior knowledge about the physics of gravity. The dynamic performance measures, saccade metrics and learning measures were therefore all of interest in the multivariate analysis involving trait measures.

Multidimensional patterns identified

We used PCA to unpack the relationships between the different variables in this experiment and link the trait measures to the eye movements. PCA has previously been used to study trait measures from healthy populations (Nenadić et al., 2021) and with eye-tracking metrics (Meso et al., 2020). They were ideal in this scenario given the multiple dimensions of the inventories (Raine, 1991; Kane et al., 2012) reflecting the heterogeneity of the constructs of interest – ASD trait and schizotypy. We used a simple correlation form of PCA and parallels analysis to restrict our components of interest to seven (Joliffe and Cadima, 2016). The ordered components become progressively less strong and therefore less dominant in the explanation of the trends in the results. The first two of these components explaining 38% of the variance separately captured all-round eye movement performance at 20% and non-specific overlap between all dimensions of both inventories at about 18%. Interestingly, these dominant components may explain why direct correlations between individual eye movement measures and the inventories might not be expected to identify strong links. Instead, these substantial separated parts of the variance may account for the strong correlation between inventories, which has a non-specific profile overlap previously proposed (Abu-Akel et al., 2017; Zheng, Zheng & Zou, 2018).

The next two components together accounting for just under 20% of the variance were the most interesting in the current work. These separated the negative schizotypy dimension from the positive dimension. In the first of these, the Positive schizotypy was associated with the ASD trait dimensions of oddness and rigidity and related with opposite sign to the ability to read faces. This relationship is consistent with that identified by Nenadić et al. (2021). This component was also linked to tracking performance in the constant speed horizontal direction during the stimulus response, i.e. a tracking eye movement that is more general and not dependent on prediction. In the vertical direction, however, the association was with the antigravity condition in the anticipatory response and antigravity learning metrics. Therefore, these eye movements suggest for the first time that this *positive-odd*cluster of traits may relate to general motion tracking, while also associated with an ability to adapt to motion that contravenes expectations of the physics of gravity. This finding extends that of Meso et al., (2020), as well as previous work using blanking paradigms (Koychev et al., 2016).

The second of these components links the negative dimension of schizotypy with the ASD trait dimensions of social interaction and rigidity, consistent with previous work (Nenadić et al., 2021; Ford et al., 2018). This *negative-social* component is also strongly associated with tracking in the gravity direction, specifically under the gravity condition, both in the anticipatory and the later open loop response. This result is therefore consistent with the possibility that participants' use of long term learned prior information about gravity could be associated specifically with this negative-social dimension. Indeed, it has been hypothesised that Schizophrenia is driven by poor predictive mechanisms that should be based on learned rules (Millard, Bearden, Karlsgodt, & Sharpe, 2022) and gravity could represent such a prior (Jörges & López-Moliner, 2017; Meso et al., 2020).

Each of the three remaining components contributing just under 18% of the total variance were less reliably interpretable, either because of a potentially spurious high age-related correlation, non-specific associations with either eye movements or equally non-specific relationships between inventory responses. The key finding in the current work is therefore in the characteristic eye movements associated with the *positive-odd* and *negative-social* trait dimensions. Interestingly, in both cases, there is an association with predictive tracking. In the case of *negative-social*, this is the application of physics rules associated with gravity. Following on from the work of Faiola et al., (2020) and MacNeilage & Glasauer, (2018), we can make a testable prediction that downward gravity stimuli will specifically drive predictive responses in both the FEF and the cerebellum. On the other hand, the *positive-odd* case is associated with the learning of physics rules that enable prediction but contravene expectations of natural physics. In such a context, we expect that there will still be contributions from the FEF to support the anticipatory aspects of the task, but less of a contribution from the cerebellum in terms of physics rules of gravity (MacNeilage & Glasauer, 2018; Dakin, Peters, Giunti & Day, 2018).

Conclusion

In this work, we showed that the participant tracking of the motion of a ball subjected to downward gravity was faster and better than tracking under the contravention of physics rules introduced by our antigravity condition. Performance, however, revealed large individual differences which we analysed along with inventories of ASD traits and schizotypy, to unveil two key findings which come with testable predictions. The first is that the positive-odd cluster of characteristics is expected to be specifically associated with the use of learnt rules that contravene physics, while the second is that the *negative-social* cluster is expected to be associated with the use of an established potentially pre-attentive prior. We therefore encourage colleagues to consider testing these arising predictions in imaging, behavioural and clinical studies.

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Data Accessibility

We will make data available following any requests. Following publication, we will make anonymised data available online.

References

Abu-Akel, A., Testa, R. R., Jones, H. P., Ross, N., Skafidas, E., Tonge, B., & Pantelis, C. (2018). Attentional set-shifting and social abilities in children with schizotypal and comorbid autism spectrum disorders. Australian & New Zealand Journal of Psychiatry, 52(1), 68-77. Barnes, G. R. (2008). Cognitive processes involved in smooth pursuit eye movements. Brain and cognition, 68(3), 309-326.

Brainard, D. H., & Vision, S. (1997). The psychophysics toolbox. Spatial vision, 10 (4), 433-436.

Chisholm, K., Lin, A., Abu-Akel, A., & Wood, S. J. (2015). The association between autism and schizophrenia spectrum disorders: A review of eight alternate models of co-occurrence. Neuroscience & Biobehavioral Reviews, 55, 173-183.

Dakin, C. J., Peters, A., Giunti, P., & Day, B. L. (2018). Cerebellar degeneration increases visual influence on dynamic estimates of verticality. Current Biology, 28(22), 3589-3598.

De Giorgi, R., De Crescenzo, F., D'Alò, G. L., Rizzo Pesci, N., Di Franco, V., Sandini, C., & Armando, M. (2019). Prevalence of non-affective psychoses in individuals with autism spectrum disorders: a systematic review. *Journal of clinical medicine*, 8 (9).

Faiola, E., Meyhöfer, I., & Ettinger, U. (2020). Mechanisms of smooth pursuit eye movements in schizotypy. Cortex, 125, 190-202.

Ford, T. C., Apputhurai, P., Meyer, D., & Crewther, D. P. (2018). Cluster analysis reveals subclinical subgroups with shared autistic and schizotypal traits. *Psychiatry research*, 265, 111-117.

Goettker, A., Braun, D. I., & Gegenfurtner, K. R. (2019). Dynamic combination of position and motion information when tracking moving targets. *Journal of Vision*, 19 (7), 2-2.

Goettker, A., & Gegenfurtner, K. R. (2021). A change in perspective: The interaction of saccadic and pursuit eye movements in oculomotor control and perception. *Vision Research*, 188, 283-296.

Jörges, B., Hagenfeld, L., & López-Moliner, J. (2018). The use of visual cues in gravity judgements on parabolic motion. Vision research, 149, 47-58.

Jörges, B., & López-Moliner, J. (2017). Gravity as a Strong Prior: Implications for Perception and Action. Frontiers in human neuroscience, 11, 203.

Jörges, B., & López-Moliner, J. (2019). Earth Gravity-Congruent Motion Benefits Pursuit Gain for Parabolic Trajectories. *Journal of Vision*, 19 (10), 302b-302b.

Kanne, S. M., Wang, J., & Christ, S. E. (2012). The Subthreshold Autism Trait Questionnaire (SATQ): development of a brief self-report measure of subthreshold autism traits. *Journal of autism and developmental disorders*, 42(5), 769–780.

Koychev, I., Joyce, D., Barkus, E., Ettinger, U., Schmechtig, A., Dourish, C. T., \ldots & Deakin, J. F. W. (2016). Cognitive and oculomotor performance in subjects with low and high schizotypy: implications for translational drug development studies. *Translational psychiatry*, 6 (5).

MacNeilage, P. R., & Glasauer, S. (2018). Gravity perception: The role of the cerebellum. *Current Biology*, 28 (22).

Masson, G. S., & Perrinet, L. U. (2012). The behavioral receptive field underlying motion integration for primate tracking eye movements. *Neurosci Biobehav Rev*, 36(1), 1-25.

Meso, A. I., De Vai, R. L., Mahabeer, A., & Hills, P. J. (2020). Evidence of inverted gravity-driven variation in predictive sensorimotor function. *European Journal of Neuroscience*, 52 (12), 4803-4823.

Meso, A. I., Gekas, N., Mamassian, P., & Masson, G. S. (2022). Speed estimation for visual tracking emerges dynamically from nonlinear frequency interactions. *Eneuro*, 9 (3).

Meso, A. I., Montagnini, A., Bell, J., & Masson, G. S. (2016). Looking for symmetry: Fixational eye movements are biased by image mirror symmetry. *Journal of Neurophysiology*, 116 (3), 1250-1260.

Meyhofer, I., Steffens, M., Kasparbauer, A., Grant, P., Weber, B., & Ettinger, U. (2015). Neural mechanisms of smooth pursuit eye movements in schizotypy. *Human brain mapping*, 36 (1), 340-353.

Millard, S. J., Bearden, C. E., Karlsgodt, K. H., & Sharpe, M. J. (2022). The prediction-error hypothesis of schizophrenia: new data point to circuit-specific changes in dopamine activity. Neuropsychopharmacology, 47(3), 628–640.

Nelson, M. T., Seal, M. L., Pantelis, C., & Phillips, L. J. (2013). Evidence of a dimensional relationship between schizotypy and schizophrenia: a systematic review. *Neuroscience & Biobehavioral Reviews*, 37 (3), 317-327.

Nenadić, I., Meller, T., Evermann, U., Schmitt, S., Pfarr, J. K., Abu-Akel, A., & Grezellschak, S. (2021). Subclinical schizotypal vs. autistic traits show overlapping and diametrically opposed facets in a non-clinical population. *Schizophrenia research*, 231, 32-41.

Ono, S., & Mustari, M. J. (2012). Role of MSTd extraretinal signals in smooth pursuit adaptation. *Cerebral cortex*, 22 (5), 1139-1147.

Ono, S. (2015). The neuronal basis of on-line visual control in smooth pursuit eye movements. *Vision Research*, 110, 257-264.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spatial vision*.

Raine, A. (1991). The Spq - a Scale for the Assessment of Schizotypal Personality Based on Dsm-Iii-R Criteria. *Schizophrenia Bulletin*, 17(4), 555-564.

Schröder, R., Faiola, E., Fernanda Urquijo, M., Bey, K., Meyhöfer, I., Steffens, M., ... & Ettinger, U. (2022). Neural Correlates of Smooth Pursuit Eye Movements in Schizotypy and Recent Onset Psychosis: A Multivariate Pattern Classification Approach. *Schizophrenia Bulletin Open*, 3 (1).

Zheng, Z., Zheng, P., & Zou, X. (2018). Association between schizophrenia and autism spectrum disorder: A systematic review and meta-analysis. *Autism research*, 11(8), 1110–1119.