Individual differences in human eye movements: An oculomotor signature?

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ABSTRACT

Human eye movements are stereotyped and repeatable, but how specific to a normal individual are the quantitative properties of his or her eye movements? We recorded saccades, anti-saccades and smooth-pursuit eye movements in a sample of over 1000 healthy young adults. A randomly selected subsample (10%) of participants were re-tested on a second occasion after a median interval of 18.8 days, allowing us to estimate reliabilities. Each of several derived measures, including latencies, accuracies, velocities, and left-right asymmetries, proved to be very reliable. We give normative means and distributions for each measure and describe the pattern of correlations amongst them. We identify several measures that exhibit significant sex differences. The profile of our oculomotor measures for an individual constitutes a personal oculomotor signature that distinguishes that individual from most other members of the sample of 1000.

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1. Introduction

Eye movements are the most common of all human actions: every second of our waking life we make approximately three of the rapid, stereotyped movements that are saccades (Carpenter, 2004). It is known, however, that there are reliable individual differences in the characteristics of both saccades and smooth-pursuit eye movements (Ettinger et al., 2003; Katsanis, Taylor, Iacono, & Hammer, 2000; Klein & Fischer, 2005; Meyhofer, Bertsch, Esser, & Ettinger, 2016; Smyrnis, 2008; Vikesdal & Langaas, 2016; Wostmann et al., 2013); and it has sometimes been suggested that oculomotor measures are specific enough to be used for biometric identification (e.g. Kasprowski & Ober, 2004; Komogortsev, Karpov, & Holland, 2016; Komogortsev, Karpov, Price, & Aragon, 2012; Poynter, Barber, Inman, & Wiggins, 2013; Zhang, Laurikkala, & Juhola, 2015). We have obtained a comprehensive set of oculomotor measures for over 1000 healthy young adults and have established the reliabilities of the measures by re-testing 10% of the participants after a median interval of 18.8 days. Each measure in itself proves highly reliable; and the *profile* of these parameters does constitute a motor signature that distinguishes an individual from most other members of the cohort.

We included in our battery three types of oculomotor task. In the pro-saccade task, the observer fixates centrally, a peripheral visual target appears suddenly, and he or she is required to fixate the target as quickly as possible (Leigh & Kennard, 2004). In the anti-saccade task, the participant is required to fixate in the exact

opposite direction from that of the target (Evdokimidis et al., 2002; Hallett, 1978). In the smooth-pursuit task the participant is asked to maintain fixation on a moving visual target.

Abnormalities of these three tasks have been reported in many psychiatric and neurological pathologies (Klein & Ettinger, 2008; Leigh & Zee, 2015) and have sometimes been proposed as endophenotypes (Gottesman & Gould, 2003); this is a further reason to know the range of variation of oculomotor measures in the normal population and their test-retest reliabilities. In the anti-saccade task, for example, schizophrenic patients make more direction errors, i.e. make more erroneous pro-saccades, than do controls (e.g. Fukushima et al., 1988) and their anti-saccades have longer latencies (Fukushima, Fukushima, Morita, & Yamashita, 1990); for a review, see Hutton and Ettinger (2006). In ocular tracking ('smooth pursuit') tasks, schizophrenics show an increased number of intrusive saccades and a reduced pursuit gain – defined as the ratio of eye velocity to target velocity (see e.g. Damilou, Apostolakis, Thrapsanioti, Theleritis, & Smyrnis, 2016; Diefendorf & Dodge, 1908; Leigh & Zee, 2015; Levy, Holzman, Matthysse, & Mendell, 1993; O'Driscoll & Callahan, 2008). The latencies of pro-saccades, and the distributions of latencies, are also known to be abnormal in, for example, Parkinson's disease (Perneczky et al., 2011) and in Huntington's disease (Lasker & Zee, 1997).

In the case of normal subjects, only a few studies have examined how variation in one eye-movement task relates to that in another. To what extent do different measures depend on a single underlying mechanism or are the several oculomotor measures completely independent? To address such questions, one can examine the correlations between various eye-movement measures for a large number of individuals: both the absence and the presence of correlations will then give insights into the underlying mechanisms (see Wilmer (2008) for a recent review). Typically, a latent variable analysis (Loehlin, 2004), such as factor analysis, is used to examine the relationship between different variables. One study that has analysed eye movements in this way was that by Fischer, Biscaldi, and Gezeck (1997), who applied factor analysis to six measures derived from pro- and anti-saccade tasks: they found two factors, one relating to anti-saccade performance and one relating to pro-saccade performance. We here extend such an analysis to a wider range of eye-movement measures.

To allow comparisons between eye-movement studies and to disentangle whether the variation between studies arises from the different populations studied or from the idiosyncratic tasks used, it is desirable to standardise the tasks. Smyrnis (2008), in a comprehensive review of the methodology of saccadic and smooth-pursuit paradigms, sets out recommendations for experimental design, target parameters, sampling frequency and data analysis. The present study has been guided by these recommendations. For a group of over 1000 adults, we report the range, distribution and reliability of a large number of oculomotor measures. Correlations were carried out to establish the relationship between each pair of measures. We used factor analysis to investigate whether the observed covariation could be explained by a smaller number of hypothetical factors. We also report correlations with sex and with personality measures. Finally, we examine the extent these standard eye-movement measures constitute a unique signature for a particular individual.

2. Methods

2.1. Participants

There were 1058 participants (413 male and 645 female; age range 16–40, mean = 22.14, SD = 4.09). They were recruited to take part in the PERGENIC test battery, which consisted of a number of optometric, perceptual and oculomotor tests (Goodbourn et al., 2012). All participants were of European ancestry. A large proportion were students from Cambridge University.

In order to establish the test–retest reliability of our measures, a randomly selected 10% of the sample (105 participants; 42 male and 63 female; age range 16–39, mean = 21.66, SD = 4.01) completed the PERGENIC test battery twice. In all but three cases, the two testing sessions were at least one week apart: the range was 2–105 days, with a mean of 26.4 days and a standard deviation of 23.3 days. The median was 18.8 days.

The oculomotor tests occupied approximately 25 min of the total 2.5-h testing duration. Before completing the psychophysical and oculomotor tests, participants underwent an optometric assessment.

The study received approval from the Cambridge Psychology Research Ethics Committee and was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). All participants gave written consent after having been given information about the experiment. They were paid a fee of £25 for their participation.

2.2. Apparatus

Stimuli were presented in a darkened room on a Sony GDM-F520 CRT monitor using a Cambridge Research Systems VSG 2/5 graphics card. The refresh rate of the monitor was 100 Hz. The target for each task was a white disk with a diameter of 0.3° of visual angle presented on a grey background; the target and background had luminances of 75 cd/m^2 and 25 cd/m^2 respectively. The background was continuously present during inter-stimulus intervals. A chin-rest was used to minimise head movements and maintain a viewing distance of 60 cm.

Eye movements were recorded using the head-mounted JAZZ-novo multisensory system (Ober Consulting, Poznan, Poland). The JAZZ-novo measures horizontal and vertical eye rotations using infrared oculography. It is also equipped with two uni-axial gyroscopes that measure the velocity of horizontal and vertical head rotations. All signals are sampled at 1 kHz. The measurable ranges for horizontal and vertical eye rotations are ±35° and ±25°, respectively. The noise level (along the horizontal axis) is equivalent to 6 min of visual angle. Each measurement of eye rotation is an average of the two eyes; this cycloptic measure is intrinsic to the JAZZ-novo sensor system. The signals from the JAZZ-novo were synchronised with the CRT by means of the Windows-independent timer present on the Cambridge Research Systems VSG 2/5 graphics card. The synchronization was accurate to 1 ms (tested empirically).

2.3. Analysis of oculomotor data

All oculomotor data were processed and analysed using purpose-built programs written in MATLAB (MathWorks, UK). The raw output from the JAZZ-novo system is a digital 12-bit signal. The JAZZ-novo has an in-built mechanism to centre the signal if it approaches the limit of the 12-bit range (0–4096); correction was made for this effect before data processing.

Nine calibrations were performed in the course of testing each participant (see below, §2.4). The gain and the offset for each calibration were calculated using linear regression of the eye signal against the target amplitudes. These factors were applied to the eye-movement data following the calibration. On rare occasions, a particular calibration did not yield an adequate calibration factor (as assessed with goodness of fit statistics) and the closest calibration in time (of the nine) was used in its place.

The eye-movement signal was processed following Bahill, Kallman, and Lieberman (1982). The raw amplitude signal (horizontal and vertical) was filtered with a 300 Hz low-pass filter. A

two-point central difference algorithm (±3 ms spread) was applied to the filtered amplitude data to obtain eye velocity, resulting in a velocity record with a 3 dB bandwidth of 74 Hz. The acceleration of the eye was obtained by applying another two-point central difference algorithm (±4 ms spread) to the velocity record, resulting in an acceleration record with a 3 dB bandwidth of 45 Hz. This sequence of steps, a low-pass filter followed by a two-point central difference algorithm, approximates an ideal differentiator (Bahill et al., 1982). The raw horizontal and vertical head velocity signals were filtered with a 300-Hz low-pass filter. Trials with excessive head movements were removed from further analysis: the algorithm used the standard deviation of the head velocity signal for a given portion of a trial (0–500 ms for the saccadic tasks and the complete trial for smooth-pursuit tasks) as an index of head movement. A trial was excluded if the head-movement index was more than four standard deviations above the mean index for all trials; this resulted in an average of 3.5% of trials excluded per participant.

All saccades in each of the tasks were detected with the same purpose-built saccade algorithm. This algorithm used both eye acceleration and eye velocity criteria to detect and profile a saccade. The presence of a saccade was detected if the eye acceleration exceeded a relative threshold value (six times the median value of the standard deviation of the acceleration signal during the first 80 ms of all trials for a particular person), or if the eye velocity exceeded an absolute threshold of 50°/s (the latter criterion was used very rarely). After detection, the saccade was profiled using the eye velocity record: borders of the saccade were defined as the regions where the eye velocity dropped below three times the median value of the standard deviation of the eye velocity record during the first 80 ms of all trials for a particular person.

2.4. Oculomotor tasks

There were four tasks presented in separate blocks. Block 1 contained a pro-saccade task and Block 2 an anti-saccade task. Blocks 3 and 4 contained smooth-pursuit tasks: a standard smooth-pursuit task and a task designed to capture the initial stages of smooth pursuit. There was a break every 2–3 min; some breaks coincided with block intervals. A seven-point horizontal calibration task was presented at the start of the experiment and after every break: in each calibration, targets were presented at 15°, 10°, 5°, 0°, −5°, −10°, −15° relative to the central fixation point; target duration was 1000 ms. The first calibration also contained a five-point vertical calibration (10°, 5°, 0°, −5°, −10°).

2.4.1. Pro-saccade task

A pro-saccade trial began with the presentation of the target in a central location for a random duration of 500–1500 ms. The target then moved abruptly (next refresh of the monitor) to one of ten peripheral horizontal locations (±3°, ±6°, ±9°, ±12° and ±15°), where it remained for 600 ms. Each peripheral location was presented 20 times in random order, resulting in a total of 200 trials. The participant was instructed to look at the target as quickly and as accurately as possible. There was an inter-trial interval of 1000 ms.

2.4.2. Anti-saccade task

The anti-saccade task was identical to the pro-saccade task except for three features: the number of trials (50 instead of 200; five presentations at each of the ten peripheral locations), the target duration (1000 ms instead of 600 ms) and the instructions (the participants were instructed to look in the exact opposite direction and location to the target as quickly and as accurately as possible).

2.4.3. Smooth-pursuit tasks

A smooth-pursuit trial began with the target located centrally for a random duration of 500–1500 ms. The target then began to move horizontally (in a random direction) at a constant speed (10°/s, 20°/s and 30°/s) until it reached 15° eccentricity where it abruptly changed direction and continued to the opposite side. Each trial contained 5.5 cycles across the screen. There were 8 trials for each speed (four beginning with leftward motion, four with rightward), resulting in a total of 24 trials. The instructions were to remain fixated on the target at all times. The second smooth-pursuit task was identical except that the number of trials was 60 instead of 24 (20 presentations of each target speed) and the stimulus contained only the first half-cycle of the smooth-pursuit waveform.

2.4.4. Exclusions

Owing to equipment failure, 13 people had to be excluded from all four eye-movement tasks; a further 4 had to be removed from both smooth-pursuit tasks; and one further person had to be removed from the second smooth-pursuit task. This gave a total of 1045 participants in the pro- and anti-saccade tasks, 1041 in the standard smooth-pursuit and 1040 in the short trial smooth-pursuit. In the re-test group (105 participants), owing again to equipment failure, one person had to be removed from the saccadic tasks and two from both smooth-pursuit tasks.

2.5. Measures derived from the oculomotor data

2.5.1. Pro-saccade measures

A pro-saccade was characterised as the first saccade in a trial (without any preceding blink) greater than 1.5° and in the same direction as the target. Pro-saccades with latencies below 50 ms or above 500 ms were excluded from analysis. Saccades with latencies that deviated by 2.5 standard deviations from the mean for each participant were also excluded (these comprised 2% of all saccades.)

The primary pro-saccade measures extracted were the latency of a saccade and the relationship between the amplitude and the peak velocity of a saccade, dubbed 'the main sequence' (Bahill, Clark, & Stark, 1975). To allow comparison with other studies, the latency was defined as the median latency. As a measure of the variability of latency we used the standard deviation of the reciprocal latency, instead of the more common standard deviation of latency, since the former is typically found to be more normally distributed. We also give measures derived from the LATER model of Carpenter (1981). Express saccades were defined as pro-saccades that occurred before 125 ms. The mean reciprocal latencies of left and right saccades varied within individuals and the ratio of the two values was taken as a measure of this asymmetry.

The relationship between the peak velocity and amplitude of a saccade was characterised by applying a square root fit, where the peak velocity equals the square root of the amplitude multiplied by a constant (Lebedev, Van Gelder, & Tsui, 1996). The constant represents the predicted peak velocity of a one-degree saccade. This particular fit has the advantage that the main-sequence relationship is characterised by only one parameter. Also, in comparison to other common main-sequence models (inverse linear and power models) it has been shown to be the most accurate and robust fit for saccades with amplitudes between 1.5° and 30° (amplitudes where the peak velocity has yet to saturate) (Lebedev et al., 1996).

In calculating the main sequence, prior to applying the square root fit, saccades with abnormal velocity profiles were excluded from the analysis. To assess abnormality, we took the ratio of the velocity in the first half of the saccade (before peak velocity) to that in the second half of the saccade (after peak velocity): if this measure was outside 2.5 times its standard deviation for an individual, it was

excluded (these exclusions comprised an average of 1.6% of saccades.)

Secondary pro-saccade measures extracted were the proportion of dynamic overshoots and the number of corrective saccades (also called static overshoots or undershoots) (Bahill & Stark, 1975). The former are overshoots that directly follow the saccade with no period of fixation or reduction of the eye velocity; they had to be at least 5 ms in duration. Corrective saccades or two-step saccades are saccades that occur following a brief fixation after the initial saccade. The second saccade can be in the same direction as the initial saccade (referred to as a static undershoot) or in the opposite direction (static overshoot). The criteria for a corrective saccade were that it occurred between 50 and 300 ms following a pro-saccade and that it was in the direction of the target.

2.5.2. Anti-saccade measures

The primary measures from the anti-saccade task were the proportion of anti-saccade errors (trials on which the participant made an erroneous pro-saccade) and the latency of correct anti-saccades (saccades in the opposite direction to the target). Secondary measures included the median latency of erroneous pro-saccades and the amplitude gain of correct anti-saccades (anti-saccade amplitude divided by target amplitude).

2.5.3. Smooth-pursuit measures

The primary measure for smooth pursuit was the pursuit gain: eye velocity divided by the target velocity. Blinks and saccades were removed. Also, the regions in the periphery where the target changed direction were excluded, i.e. regions where the target had an absolute eccentricity greater than 10°. The pursuit segments for each target speed were combined and the absolute median velocity determined for each of the three speeds. The gain for each speed was calculated by dividing the median eye velocity by the target velocity for that speed. The mean of the three values is the pursuit gain reported.

As a global measure of pursuit performance, we also calculated the root mean square error of the eye position versus the target position. The complete pursuit signal was used excluding blinks. The frequency of intruding saccades and the type of saccades (catch-up saccades, anticipatory saccades or square wave jerks) were also quantified. A catch-up saccade (CUS) was defined as a saccade in the direction of pursuit that decreased positional error. An anticipatory saccade (AS) was defined as a saccade in the direction of pursuit that increased positional error and was greater than 1.5° in amplitude (Smyrnis, 2008). Square-wave jerks occurred infrequently and were excluded from further analysis. The numbers of CUS and AS were divided by the total pursuit time to give the number per second of each.

Two measures were obtained from the second smooth-pursuit task: the median latency to the first saccade in the direction of the target, and the pre-saccadic acceleration – a slight acceleration in eye position just prior to a saccade and in the same direction (Carl & Gellman, 1987; Wilmer & Nakayama, 2007). The constant acceleration was quantified by fitting a regression line to the eye-velocity signal from the onset of acceleration to saccadic onset; the mean slope of all trials was obtained representing the mean constant acceleration. Acceleration onset was detected by examining the amplitude signal immediately preceding saccadic onset: onset occurred when this amplitude signal went within the confidence intervals (three times the error of the fit) of a regression line fitted to the first 80 ms of the amplitude signal for each trial.

2.6. Statistical analysis

To establish the test–retest reliability of each of the 21 oculomotor measures, the scores from the two independent sessions were correlated for the subset of re-tested participants. To allow comparisons with other studies, we calculated three different correlation coefficients: Pearson's, Spearman's and intra-class correlation (ICC) coefficients. Spearman rank correlation is not typically reported in the oculomotor literature but it is a useful metric in that deviations from normality (particularly in the tails of the distribution) do not affect it, whereas small deviations from normality can result in an over- or under-estimation of the correlation when Pearson's or ICC are used.

Internal consistency for each measure was established by dividing the data from the complete first session sample into two portions and then carrying out a Spearman rank correlation between these two portions. In the odd-even method a score for each measure was determined separately for odd- and even-numbered trials; in the split-half method a score for each measure was determined separately for the first and the second half of the trials.

In carrying out the factor analysis a Box–Cox transformation (Box & Cox, 1964) was performed on each measure to achieve distributions that were close to Gaussian, since many of the measures had skewed distributions. The factor analysis used principal component analysis with oblique promax rotation to determine the factors (Jolliffe, 2002).

2.7. Questionnaire measures

Prior to attending the testing session in the laboratory, participants completed a 75-item online questionnaire. Included in the questionnaire were items to gather demographic information (age, sex, ancestry, level of education), two items to establish preferred hand (for throwing and for writing), and items about visual and auditory attributes (Bosten et al., 2015). The questionnaire also incorporated a 20-item self-report personality scale, the Mini-IPIP (International Personality Item Pool; Donnellan, Oswald, Baird, & Lucas, 2006), which assesses the 'Big Five' personality factors: Openness, Conscientiousness, Extraversion, Agreeableness and Neuroticism (Costa & McCrae, 1992). Each response was on a five-point Likert scale and there were four items per factor. To obtain an individual's factor score, responses to the four items were summed and normalised to the interval $[-1, 1]$.

In a follow-up study (see Verhallen et al., 2017) we obtained scores on the Autism-Spectrum Quotient (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001). These scores were available for 521 of the participants from our original laboratory study (333 female) and were obtained via a 50-item on-line questionnaire. The mean AQ score was 17.32 (SD = 7.58, range 3–39). Twenty-five participants scored at or above 32: scores in this range are suggestive of autism-spectrum disorder.

2.8. Sighting dominance

The optometric testing included a variant of the Miles test to estimate sighting dominance (Miles, 1929): the participant, seated in front of an acuity chart, was asked to outstretch both arms and to overlay the hands to create a small aperture between the thumbs and index fingers. The experimenter then asked the participant to position the aperture so that it revealed on designated letter on the chart. The participant was then asked to slowly draw the hands towards the face, keeping both eyes open, and keeping the letter visually centred within the aperture. The participant invariably drew the hands towards one or other eye, which was recorded as preferred.

Table 1
Reliability and descriptive statistics of eye-movement measures.

| Measure	Units	Descriptive statistics				Test–retest reliability			Internal consistency	
		Mean	Median	sd	Range	P	r	ICC	Odd-even	Split-half
Pro-saccade measures										
Main sequence	$°\,s^{-1}$	114.5	114.1	13.6	69.9–164.2	0.86	0.88	0.88	0.99	0.94
Median latency	m s	177.2	174	18.52	142–322	0.83	0.84	0.84	0.93	0.85
Latency standard deviation	$s\,d^{-1}$	0.001	0.001	0.0002	0.0005–0.0021	0.78	0.75	0.74	0.82	0.70
Express saccades	Proportion	0.044	0.026	0.0573	0–0.420	0.70	0.82	0.81	0.74	0.67
LATER median	$m\,s^{-1}$	0.006	0.006	0.0006	0.0037–0.0076	0.80	0.83	0.83	0.95	0.86
LATER slope	$z\,ms^{-2}$	1009	976.5	222.7	389–1861	0.80	0.79	0.76	0.78	0.66
LATER intercept	z	−5.714	−5.464	1.401	−11.43–(−2.63)	0.77	0.77	0.74	0.80	0.66
Left-right latency ratio	Ratio	0.985	0.983	0.078	0.608–1.37	0.77	0.83	0.83	0.72	0.62
Dynamic overshoots	Proportion	0.813	0.845	0.145	0.265–1	0.82	0.83	0.82	0.92	0.84
Static overshoots	Proportion	0.08	0.065	0.06	0–0.374	0.71	0.71	0.71	0.76	0.68
Static undershoots	Proportion	0.49	0.497	0.163	0.032–0.898	0.79	0.83	0.83	0.91	0.81
Anti-saccade measures										
Error rate	Proportion	0.377	0.35	0.215	0–1	0.82	0.84	0.84	0.83	0.74
anti-saccade latency	ms	305.5	301	43.06	113–539	0.73	0.73	0.73	0.76	0.65
Error saccade latency	ms	187.7	182	31.272	128–518	0.77	0.72	0.72	0.61	0.59
anti-saccade gain	Amplitude ratio	0.93	0.897	0.253	0.256–3.05	0.78	0.77	0.74	0.56	0.54
Smooth pursuit measures										
Gain	Velocity ratio	0.795	0.814	0.138	0.307–1.076	0.88	0.86	0.86	0.96	0.89
RMSE	°	3.095	2.5	1.834	0.874–13.54	0.79	0.81	0.80	0.91	0.86
Catch-up saccades	Hz	0.641	0.607	0.298	0.067–1.979	0.78	0.74	0.72	0.93	0.87
Anticipatory saccades	Hz	0.234	0.197	0.167	0–0.837	0.83	0.83	0.83	0.93	0.89
Median latency	ms	197.4	196	20.02	152–282	0.85	0.84	0.84	0.85	0.82
Pre-saccadic acceleration	$°\,s^{-2}$	36.65	33.93	18.75	−15.07–153.2	0.72	0.78	0.76	0.73	0.70
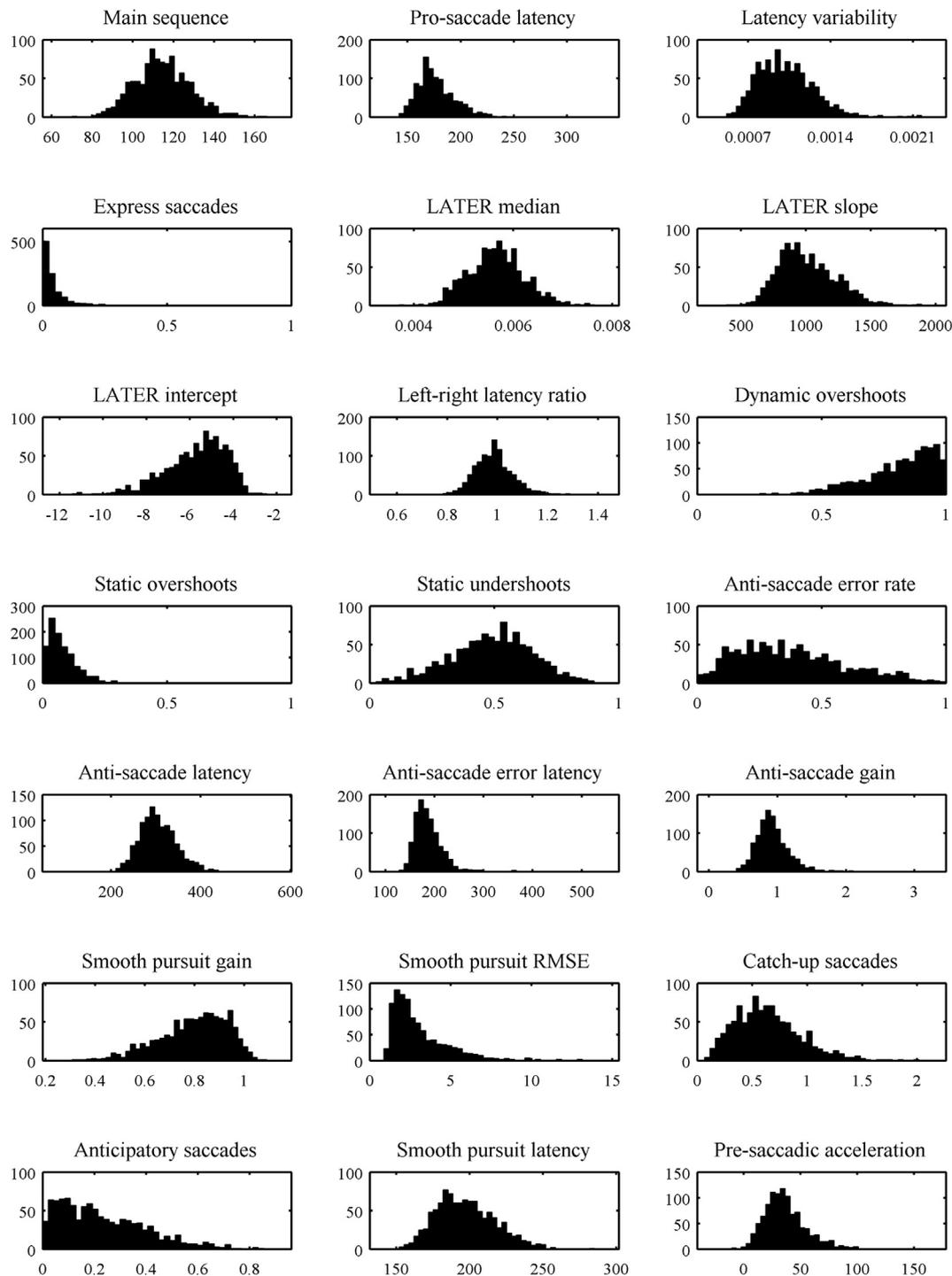
Fig. 1. Distribution of each eye-movement measure. The units for each distribution are given in Table 1.

3. Results

3.1. Distributions and reliabilities

Table 1 shows the mean, standard deviation and range of each of the 21 eye-movement measures for the full cohort of participants who took part in the first session. The corresponding distributions are shown graphically in Fig. 1. The Lilliefors test showed that most of the distributions deviated significantly from normality ($0.0236 \geq D_n \leq 0.22$; $0 \geq p \leq 0.184$; $\alpha = 0.0025$), the three exceptions being: main sequence, LATER median and static undershoots.

All measures show individual differences: most exhibit 2- to 3-fold differences between participants, while some show greater than 10-fold differences. These ranges are consistent with ranges previously reported (Smyrnis, 2008). However, variance in measurements made on a single occasion can never be taken as evidence for individual differences, since the variance may be instrumental or may be within-subject in its origin. It was critical to our purposes to estimate the reliability over time of individual

Table 2
Sex differences within eye-movement measures.

Measures	Male mean	Female mean	t-stat	p-value	df
Main sequence	114.24	114.66	0.469	0.63936	1038
Pro-saccade latency	174.98	178.54	3.052	0.00233	1038
Latency variability	0.00104	0.00100	−2.237	0.02549	1038
Express saccades	0.053	0.0387	−3.944	0.00009	1038
LATER median	0.0058	0.0056	−4.711	0.00000	1038
LATER slope	991.32	1020.1	2.038	0.04182	1038
LATER intercept	−5.7167	−5.7112	0.053	0.95748	1038
Left–right latency ratio	0.9894	0.9827	−1.368	0.17162	1038
Dynamic overshoots	0.7583	0.8478	10.201	0.00000	1038
Static overshoots	0.0846	0.0773	−1.953	0.05114	1038
Static undershoots	0.5011	0.4823	−1.826	0.06818	1038
Anti-saccade error rate	0.3507	0.3946	3.238	0.00124	1038
Anti-saccade latency	297.44	310.6	4.892	0.00000	1037
Anti-saccade error latency	183	190.67	3.909	0.00010	1036
Anti-saccade gain	0.9114	0.9415	1.881	0.06027	1037
Smooth pursuit gain	0.8139	0.7819	−3.681	0.00024	1038
Smooth pursuit RMSE	2.7841	3.2968	4.444	0.00001	1038
Catch-up saccades	0.7458	0.5732	−9.495	0.00000	1038
Anticipatory saccades	0.2112	0.2493	3.625	0.00030	1038
Smooth pursuit latency	193.63	199.84	4.950	0.00000	1038
Pre-saccadic acceleration	36.487	36.752	0.222	0.82399	1038

variation; and to this end, 10% of participants completed the measurements a second time, after a mean interval of 26 days.

The right-hand columns of Table 1 show reliabilities and internal consistencies for each oculomotor measure. All the correlations are highly significant, ($p < 0.0001$; $\alpha = 0.001$ with Bonferroni correction for 48 tests). The test–retest reliabilities ranged from 0.685 to 0.884. For each measure, Pearson's, Spearman's and ICC correlations were similar (with means of 0.8, 0.789 and 0.793, respectively). In the internal consistency measures, the odd-even method resulted in higher consistency for the two measures than did the split-half method: Odd-even results ranged from 0.558 to 0.989 (mean = 0.827), whereas the split-half results ranged from 0.542 to 0.937 (mean = 0.755). In sum, the oculomotor measures extracted are stable not only within a single session but also across sessions that are separated by a median interval of 18.8 days. All measures exhibit substantial individual differences.

Table 3
Correlation matrix. Spearman rank correlations between each pair of oculomotor measures. Nominally significant correlations ($\alpha = 0.05$, uncorrected) are shown in light grey. Significant correlations following a Bonferroni correction for 210 tests ($\alpha = 0.000238$) are shown in dark grey.

	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1. Main sequence	-0.182	-0.073	0.071	0.166	0.060	-0.123	0.034	0.437	0.301	-0.081	-0.023	-0.079	-0.112	0.160	0.070	-0.079	-0.049	0.020	-0.124	0.113
2. Pro-saccade latency		0.141	-0.470	-0.945	-0.051	0.422	-0.044	-0.109	-0.085	-0.280	-0.171	0.328	0.691	0.070	-0.250	0.265	-0.119	0.155	0.530	-0.100
3. Latency variability			0.529	-0.083	-0.975	0.920	-0.011	-0.068	0.098	-0.065	0.229	0.185	-0.127	0.056	-0.262	0.272	-0.091	0.181	0.170	-0.147
4. Express saccades				0.592	-0.576	0.285	0.076	0.012	0.166	0.191	0.326	-0.120	-0.474	0.038	-0.044	0.056	0.009	0.054	-0.193	-0.014
5. LATER median					0.004	-0.395	0.059	0.095	0.112	0.300	0.177	-0.357	-0.682	-0.031	0.247	-0.253	0.143	-0.150	-0.525	0.115
6. LATER slope						-0.905	0.010	0.064	-0.100	0.032	-0.249	-0.158	0.191	-0.047	0.252	-0.259	0.078	-0.184	-0.126	0.153
7. LATER intercept							-0.026	-0.102	0.041	-0.159	0.151	0.289	0.091	0.057	-0.321	0.337	-0.135	0.228	0.321	-0.186
8. Left-right latency ratio								-0.014	0.031	0.028	0.008	-0.031	-0.041	-0.033	0.041	-0.036	-0.002	0.001	-0.075	-0.014
9. Dynamic shoots									0.138	-0.084	0.002	-0.034	-0.045	0.099	-0.009	-0.062	-0.217	0.062	-0.095	0.060
10. Static Overshoots										-0.369	0.011	-0.121	-0.068	0.200	-0.051	0.032	-0.072	0.061	-0.051	0.005
11. Static Undershoots											0.186	-0.060	-0.187	-0.178	0.024	-0.066	0.303	-0.012	-0.174	-0.032
12. Anti-saccade error rate												0.083	-0.304	0.117	-0.297	0.341	-0.131	0.254	0.067	-0.190
13. Anti-saccade latency													0.300	-0.167	-0.132	0.136	-0.091	0.042	0.330	-0.128
14. Anti-saccade error latency														-0.014	-0.088	0.099	-0.039	0.031	0.315	-0.014
15. Anti-saccade gain															-0.179	0.167	-0.207	0.198	0.111	0.014
16. Smooth pursuit gain																-0.748	0.280	-0.756	-0.429	0.435
17. Smooth pursuit RMSE																	-0.414	0.707	0.435	-0.268
18. Catch-up saccades																		-0.438	-0.215	0.030
19. Anticipatory saccades																			0.278	-0.263
20. Smooth pursuit latency																				-0.250
21. Pre-saccadic acceleration																				

Legend: p < 0.000238, significant; p < 0.05

3.2. Relationship to sex and personality

Table 2 shows the mean values and *t*-test statistics for males and females for each oculomotor measure. Significant sex differences (after Bonferroni correction; $\alpha = 0.0024$) are observed in over half of the measures. Substantial, and highly significant, differences between men and women occur in the proportion of dynamic overshoots in pro-saccades and in the frequency of catch-up saccades in smooth pursuit, with greater than 10% differences between sexes. Other significant sex differences have more modest effect sizes, but are systematic in direction: regardless of the task, men tend to be faster than women at initiating saccades; and men tend to have better smooth pursuit (judged by their smooth-pursuit gain and RMSE values) and better anti-saccade performance than do women. The significantly higher anti-saccadic error rate shown by women is consistent with an earlier report by Crawford et al. (1998), who studied a combined group of schizophrenic and healthy subjects.

Removing the effects of sex, we calculated partial correlations between oculomotor measures and five dimensions of personality derived from a short, self-report questionnaire (Donnellan et al., 2006). We selected ten eye-movement measures, choosing ones that were reasonably uncorrelated or were ones that are used regularly in the literature. One correlation was very highly significant following Bonferroni correction for 45 tests ($\alpha = 0.0011$): extraversion was positively correlated with smooth-pursuit RMSE (Spearman's $\rho = 0.150$). In other words, higher levels of extraversion are associated with poorer accuracy in tracking a moving target. Extraversion also correlated significantly with the variability of saccadic latencies (Spearman's $\rho = 0.103$).

None of our eye-movement variables showed a Spearman correlation with Autism-Spectrum Quotient greater than 0.06 when sex was used as a covariate; and none of these correlations was significant after Bonferroni correction.

3.3. Handedness and sighting dominance

Table 1 shows that there are highly reliable individual differences in the asymmetry of pro-saccadic latencies, the Spearman test-retest correlation being 0.83. When such asymmetries have previously been reported they have sometimes been found to be associated with handedness (e.g. Pirozzolo & Rayner, 1980) or with eye dominance (e.g. Kolesnikova, Tereshchenko, Latanov, & Shulgovskii, 2010), although in a large sample Constantinidis et al. (2003) found no relationship between a composite measure of lateral preference and asymmetry of prosaccadic latency (see also Vergilino-Perez et al. (2012). We therefore record here that in our own large sample we observed little relationship between asymmetry of pro-saccadic latency and either preferred hand (composite of preference for throwing and writing; Spearman's $\rho = 0.00$, $p = 0.99$) or sighting dominance (Spearman's $\rho = 0.06$, $p = 0.047$ before Bonferroni correction).

3.4. Correlations between eye-movement measures

The wide range of variation among the population coupled with the high intra-individual reliability (Table 1 and Fig. 1) shows that people vary systematically in their oculomotor control. To understand the underlying sources of this variance, it is instructive to determine how each eye-movement parameter varies with each other.

Table 3 shows the Spearman rank correlations between each possible pair of eye-movement measures. Nominally significant correlations ($\alpha = 0.05$, uncorrected) are shown in light grey. Significant correlations following a Bonferroni correction for 210 tests ($\alpha = 0.000238$) are shown in dark grey; these comprise more than half (111 of 210) of the correlations. However, the majority of the significant correlations (91 of 111) had a Spearman $\rho < 0.3$; the large sample size allows us to detect quite modest relationships between the measures. Many of the higher correlations, with a Spearman $\rho \geq 0.3$ (20 of 210), are between measures that fall within the same subset. For example, many latency measures correlate highly, independently of the task. Similarly, smooth-pursuit measures correlate with each other more than they do with measures from other tasks. As would be expected from the model of Friedman, Jesberger, and Meltzer (1991), and in agreement with Radant and Hommer (1992), we found a large negative correlation (-0.756) between smooth-pursuit gain and the frequency of anticipatory saccades. In agreement with Zanelli et al. (2005), who studied a mixed group of normal and schizophrenic subjects, we find a significant negative correlation (of ~ 0.3) between smooth-pursuit gain and error rate in the anti-saccade task – a correlation that may reflect a general trait of distractibility.

One of our measures, the left–right ratio of latencies, had no significant correlates and thus appears to vary independently of all the other measures. An asymmetry in latency has previously been attributed to an asymmetry in the number of express saccades (Weber & Fischer, 1995). This was not found here: in our sample only 13% of the variance is shared between these two measures of asymmetry.
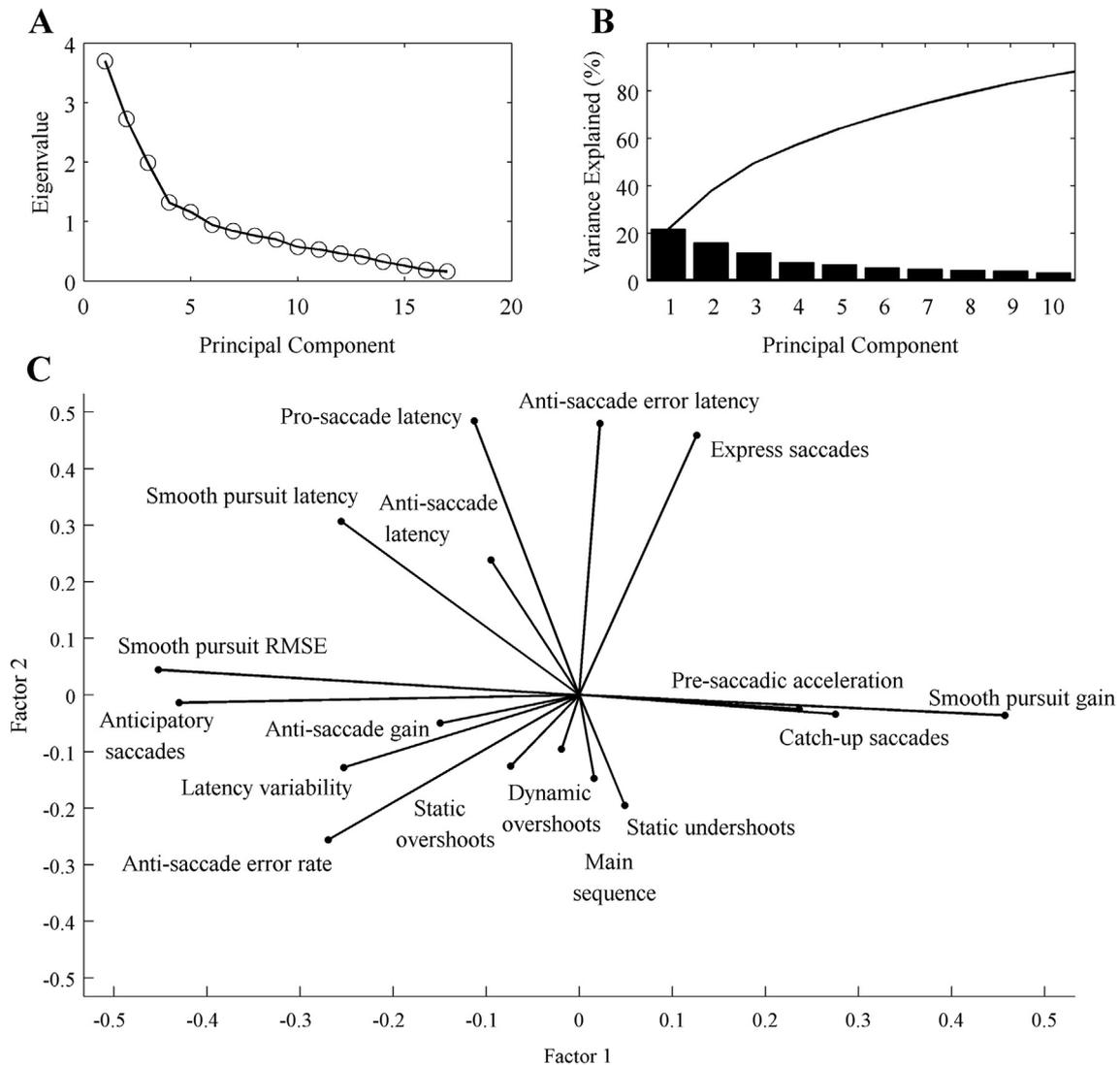
3.5. Factor analysis

To determine whether the dimensionality of the data set could be reduced, a factor analysis was carried out. We excluded the LATER variables from the analysis as these are closely related to, and very highly correlated with, pro-saccade latency or latency variability. Also omitted was left–right latency ratio, as it correlated with no other measure. In order that slower reaction times gave higher scores on all latency measures, the proportion of express saccades was transformed to 1 – proportion of express saccades.

Fig. 2 shows a scree plot (A) and a pareto plot (B) of the principal component analysis. The first two factors account for 38% of the variance, and the loadings for a two-factor solution are shown in Fig. 2C. The first factor represents a dimension of ocular-tracking performance: there are positive loadings for smooth-pursuit gain, catch-up saccades and pre-saccadic acceleration, and negative loadings for smooth-pursuit RMSE and anticipatory saccades. Thus, as would be expected, a greater number of anticipatory saccades are associated with a drop in smooth-pursuit gain and an increase in smooth-pursuit RMSE. The second factor has high positive loadings from latency measures, irrespective of task, and it has negative loadings from anti-saccade error and static-undershoots. This factor may represent a speed-accuracy dimension: people who have shorter latencies make more anti-saccade errors and make more saccadic eye movements before final fixation.

3.5. The oculomotor signature

In the previous section we were concerned with the correlations between measures. However, Fig. 2A and B show that the proportion of explained variance increases only gradually as larger numbers of components are included in the analysis: so it is not possible to completely categorise an individual by his or her loadings on a small number of factors. Although our own purpose is not to offer a biometric procedure, the reliability of our measures illustrate the biometric potential of oculomotor measures, and here we ask how specifically an individual person can be characterised if a large number of measures (or derived components) are taken into account.

Fig. 2. Factor analysis. (A) Scree plot: eigenvalues for each principal component ordered by the most significant eigenvalue. (B) Pareto plot illustrating the percentage variance explained by the 10 most significant components (bar graph) and cumulatively (line). (C) Loadings for the two-factor solution illustrated as vectors originating from the origin. Measures from the ocular tracking task load strongly on Factor 1, whereas latency measures load strongly on Factor 2.

To examine to what extent a given person has a characteristic eye-movement signature we carried out a simple classification procedure. Eighteen of the twenty-one eye-movement measures (the LATER measures were excluded) were treated as dimensions of a multidimensional space. Each person was represented by a point in this 18-dimensional space, corresponding to his or her scores on the 18 measures. If each person had a unique eye-movement signature it would be possible to identify this person on a subsequent testing session by his or her location in the multidimensional space. A critical feature of our study is that a randomly selected subset of individuals, comprising 10% of the sample, returned for a second, independent, test session. These participants were used in the present analysis. Prior to the classification procedure, each eye-movement measure for the separate sessions was normalised by transformation to z-scores. The Euclidean distance in 18-dimensional space between each second-session participant (n = 103) and every first-session participant (n = 1040) was calculated. These distances were ranked and we counted how many participants separated the second-session participant from his or her position in the first session. The results are shown in Fig. 3.

In 61 of the 103 cases the nearest neighbour in multidimensional space between session 2 and session 1 was the same participant. In other words, from their performance on second test, approximately 60% of our participants identify themselves uniquely in the original cohort of 1040. In 84 cases a second-session participant was a distance of fewer than five participants away from his or her first-session location (there were at most four other participants closer to the second-session location); and in 95 cases a second-session participant was fewer than 10 people away from his or her first-session point. Thus, even with only one session and only one estimate of each eye-movement measure, a person's eye movements can be used to identify him or her with moderate success, among more than one thousand people.

We have seen above that there are strong correlations among the individual measures (Table 3). Could a classification of similar accuracy be achieved by using a space of fewer dimensions, either by eliminating some of measures or by using not the raw measures but components drawn from a Principal Component Analysis? Fig. 3B offers an answer to these questions. The solid black line shows the increase in accuracy as more and more of the raw eye-movement measures are used, each measure being introduced
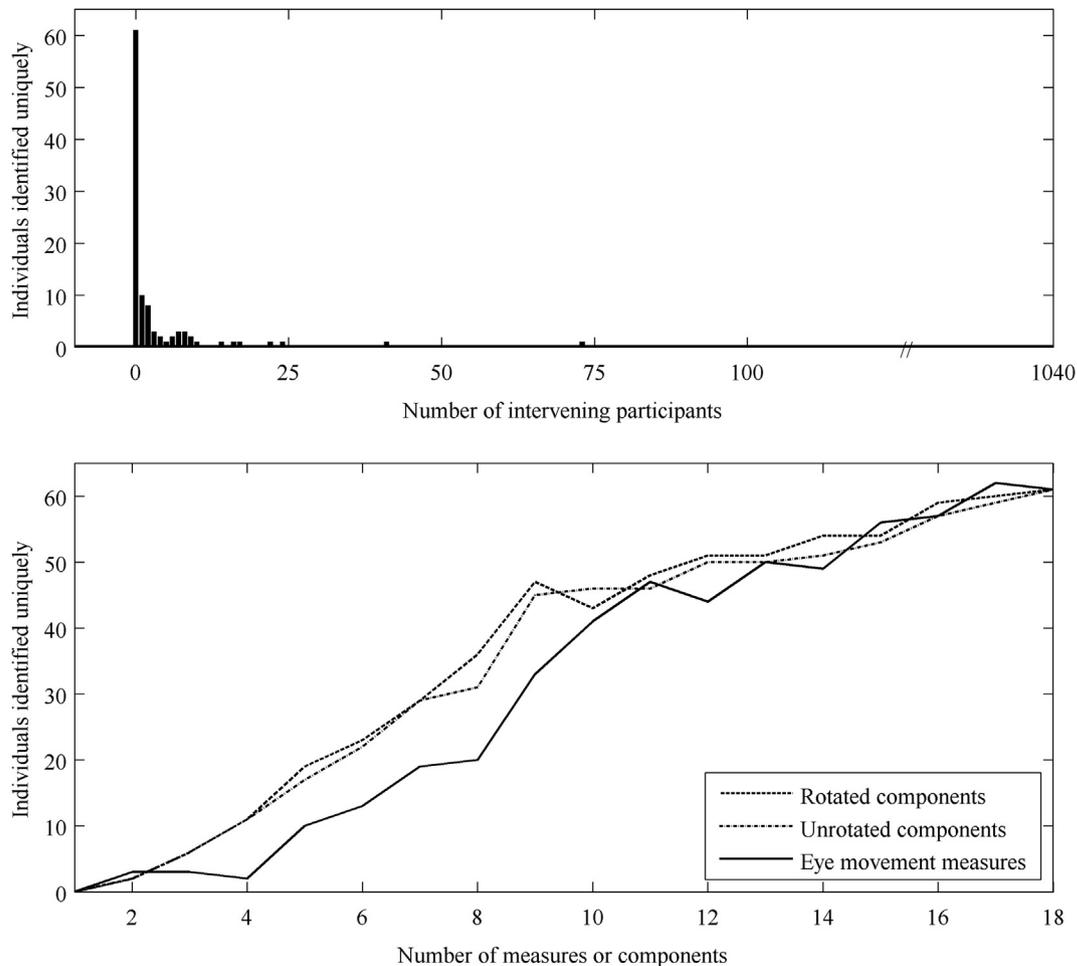
Fig. 3. The uniqueness of a person's eye movements. A. To obtain these results each of the 103 participants who were re-tested on a second session was located in a 18-dimensional space, where the dimensions correspond to each of our oculomotor measures. We then calculated the Euclidean distance of each of these participants to each of the 1040 first-session participants in this same space. These distances were ranked and we counted how many participants separated the second-session participant from his own position in the first session. In the present histogram we plot the absolute number of second-session participants against the number of intervening participants. For more than half of our re-tested participants there was no intervening participant, i.e. the closest neighbour to the second-session participant was his own first-session self. B. Here we show how the number of uniquely identified participants increases with the number of eye-movement measures (black line) or with the number of principal components taken into account (dashed lines).

in order of its reliability (Table 1). When the measures are introduced in this sequence, it does appear that almost all of them are needed to achieve a high level of classification. It is true there are a very large number of alternative permutations that could be used for the sequence of adding measures, but the remaining two curves in Fig. 3B point to a similar conclusion. Here we plot the increase in the number of uniquely identified individuals as we use more and more components derived from a Principal Component Analysis (using either unrotated or rotated components). Here components are being added in order of the variance that they account for. To achieve the same accuracy as achieved in our original 18-dimensional space, the number of components that are needed is similar to the number of raw measures.

4. Discussion

4.1. The range and the reliability of individual differences

Substantial individual variations are apparent for all our oculomotor measures, and in this finding our results are consistent with earlier large population studies of saccades (Constantinidis et al., 2003), of anti-saccades (Evdokimidis et al., 2002) and of smooth pursuit (Lenzenweger & O'Driscoll, 2006). Most of our measures

exhibit a range of two- to three-fold, while some measures, notably RMS error for smooth pursuit, show a more than ten-fold range. Fig. 1 and Table 1 show the means and the distributions that are observed within the healthy population studied here: these normal data need to be taken into consideration when interpreting oculomotor behaviours in clinical groups.

Most importantly both the saccadic and the smooth-pursuit measures were very reliable within testing sessions and were stable between sessions – a stability that is required if oculomotor measures are to be used as endophenotypes. The present results replicate, and in many cases improve on, the high reliability of individual oculomotor measures reported in the literature (Ettinger et al., 2003; Iacono & Lykken, 1981; Klein & Fischer, 2005). Our main-sequence measure (peak velocity versus amplitude) shows the greatest increase in reliability in comparison to previous studies (Boghen, Troost, Daroff, Dell'Osso, & Birkett, 1974; Bollen et al., 1993; Versino, Castelnovo, Bergamaschi, Romani, & Cosi, 1992). The largest of these studies had 58 participants (Bollen et al., 1993), but had a very low test–retest reliability with an ICC of 0.23 for the slope of the log peak velocity versus log amplitude. Our improved reliability may reflect sampling rate (1000 Hz vs 200 Hz) or the fitting procedure (Bahill et al., 1982; Lebedev et al., 1996).

We extracted several measures for which there are no previous estimates of test–retest reliability, such as saccadic overshoots/undershoots, smooth-pursuit pre-saccadic acceleration, left-right asymmetry of latency, and the parameters of Carpenter's LATER model (Carpenter, 1981). These measures also proved to have moderate to high test–retest reliability.

4.2. Sex differences

More than half of our measures exhibit significant sex differences, some of them substantial (Table 2): thus women show over 10% more dynamic overshoots in the pro-saccade task and show an 18% higher mean RMS error for smooth pursuit. We observed lower rates in women of catch-up saccades in smooth pursuit, a result that is in the opposite direction to the finding of Lenzenweger and O'Driscoll (2006). The discrepancy is likely to arise in part from a difference in the definition of catch-up saccades (Smyrnis, 2008). Lenzenweger and O'Driscoll defined catch-up saccades as any saccade that was preceded and followed by pursuit gain and was <5° in amplitude, whereas our criterion was based on positional error: if the saccade decreased positional error it was defined as a catch-up saccade and if it increased it (and was >1.5°) it was defined as an anticipatory saccade.

Our finding of shorter pro-saccade latency in males is in agreement with earlier studies (Ettinger et al., 2004; Ettinger et al., 2005). It is curious that males also make fewer errors in the anti-saccade task (see Table 2): in competition models, such as that of Cutsuridis, Smyrnis, Evdokmds, and Perantonis (2007), faster pro-saccades should lead to higher error rates. The male superiority in the anti-saccade task does not seem to due to a speed-error trade off, even though within each sex such a trade-off may be present.

We should add one note of caution with regard to sex differences in this and other studies. A study explicitly directed at sex differences in any behavioural trait ought to sample randomly from the total male and female membership of a specific population. Otherwise there is always the possibility that males and females are not equated with respect to some relevant, but unidentified, factor. Such random sampling from the full parent population is rarely achieved, even in studies explicitly designed to examine sex differences. The men and women in the present sample were drawn from a relatively homogeneous Cambridge population, but there is always the possibility that they differ statistically in some factor other than sex.

4.3. Personality

Since there are large individual differences in most oculomotor measures, and since the movements of the eyes are thought to reflect central processes of decision and control, it is plausible to ask whether the individual variations are related to conventional measures of personality. Selecting healthy participants who had either very high or very low scores on the Eysenck extraversion scale, Nguyen, Mattingley, and Abel (2008) found that extraverts made more errors on an anti-saccade task.

In the present study, we found significant relationships of extraversion with the variability of saccadic latencies and with RMSE for smooth pursuit. Although the sizes of the correlations are modest – it is the large size of our sample that allows us to detect them – it is notable that significant relationships emerge between objectively measured eye-movement behaviour and responses to a very brief, self-report questionnaire completed on a separate occasion. To place the results in context, consider that smooth-pursuit RMSE accounts for a fraction of the variance in extraversion that is of a similar order to the fraction of variance accounted for by one of the strongest relationships between a

known gene and a personality measure – that between diplotypes of the gene for neuropeptide Y and measures of neuroticism (Zhou et al., 2008).

Abnormalities of gaze towards social stimuli are unquestionably present in persons with autism (e.g. Klin, Jones, Schultz, Volkmar, & Cohen, 2002), but abnormalities have also been reported on non-social oculomotor tasks, particularly smooth pursuit and anti-saccade tasks (e.g. Johnson, Lum, Rinehart, & Fielding, 2016; Takarae, Minshew, Luna, Krisky, & Sweeney, 2004). It is interesting therefore to record that within our (largely student) population, there were no significant correlations between eye-movement measures and AQ.

4.4. Saccades and smooth pursuit

Saccades and smooth pursuit are the two principal types of visually guided eye movements. Saccades serve to bring objects of interest on to the fovea, whereas pursuit movements maintain targets on the fovea when the stimulus or the observer is moving. The input to the saccadic subsystem is traditionally taken to be a position signal whereas the input to the pursuit subsystem is a motion signal. These two types of signal are likely to be extracted by different sensory processes – position by a ventral system and motion by directionally selective units early in the visual pathway that feed into the Medial Temporal area of the cortex and the dorsal stream (Carpenter, 1988).

This is the first time measures of pro-saccades, of anti-saccades and of ocular tracking have been included in a factor analysis of individual differences in eye movements; and it is instructive that a set of measures from the smooth-pursuit task proved to be strongly correlated with one another and that they were correlated less strongly with other eye-movement measures (anti-saccade error rate is an exception). This result is consistent with classical evidence, from pathology, pharmacology and single-unit electrophysiology (Cogan, 1952; Rashbass, 1959; Rashbass, 1961; Thier & Ilg, 2005), that saccades and ocular tracking depend on separate neural subsystems. Petit and Haxby (1999), in an fMRI study report that different sub-regions of the frontal eye fields are activated by the two types of eye movement.

However, Orban de Xivry and Lefevre (2007) have pointed out that the smooth-pursuit system needs to collaborate with the saccadic system in order to improve tracking of a target that moves in an unpredictable way. Thus, when a target begins to move and before the pursuit motion has started, the oculomotor system generates a saccade to compensate for the increasing position error. Similarly, if the gain of the pursuit is not sufficient to track a rapidly moving target, catch-up saccades are generated. In our own factor analysis, it is not only the gain of the pursuit itself that is heavily weighted on the first factor but also measures of anticipatory and catch-up saccades. And it is not that participants with low gain make more catch-up saccades: rather, those with a gain closer to unity have more catch-up saccades. So our preference is to identify this factor not with a type of eye movement nor with a distinct neural subsystem, but with a type of task, that of tracking a moving target.

The second factor to emerge from our analysis is identified with latency, both saccadic and smooth-pursuit latency. This factor may in part reflect individual differences in central decision mechanisms (Carpenter, 1981).

4.5. An oculomotor signature?

Whereas there were high correlations between certain pairs of eye-movement measures, many correlations between other pairs of measures were low. Since the several measures are individually very reliable and since they are relatively uncorrelated, a set of

eye-movement measures – such as those of the present battery – provide a robust signature for a particular individual. Certainly the oculomotor signature is specific enough that it might serve to detect changes in health of an individual (e.g. Antoniades, Xu, Mason, Carpenter, & Barker, 2010; Cunniffe et al., 2015; Dawson et al., 2011).

In the near future, telephones and personal computing devices are likely to incorporate eye-movement recorders, to allow users to control functions by oculomotor gestures. In these, and other domains, could standard eye-movement measures be used for identification? This question has been actively raised in the biometric literature (e.g. Juhola, Zhang, & Rasku, 2013; Komogortsev et al., 2016). The procedures of the present normative study were not of course designed for routine biometric use: they required a minimum of 20 min of testing and repeated calibration during the testing session. But the biometric potential of oculomotor measures is certainly demonstrated by the high reliabilities we obtained Measures selected from the present set might be usefully combined with other oculomotor measures. For example, the interval between micro-saccades during fixation is an individual characteristic that is stable for at least a year (Filin, 2002; Filin, Sidorov, Ananin, & Zagorodnikova, 1973) and the precision and duration of a person's fixations are correlated across different tasks (Poynter et al., 2013). Individuals may also be characterised by their scan pattern and their predominant direction of eye movement when they freely view a complex static or dynamic scene (Buswell, 1935).

One interesting recent approach in the biometric literature has been to use not the raw properties of a person's saccades but the inferred properties of their oculomotor plant (Komogortsev et al., 2012). In general, however, it is not well understood why there is such rich variation among people in how they move their eyes, and it is curious that the question has not often been systematically explored outside the non-biometric literature. Many stages in the processing hierarchy could contribute to the variation: for example, differences in sensory processing, e.g. in the detection of transients or of motion (Wilmer & Nakayama, 2007); differences in central decision making, as emphasised in the LATER model (Carpenter, Reddi, & Anderson, 2009); differences in the properties or connectivities of motor centres; differences in muscle tissue; and differences in mechanical factors such as the structure of the orbit and the size and shape of the eyeball. Nor is it yet understood how far the individual differences arise from differences in experience, and how far from genetic differences. The rapid advances in genetic technologies and their application to eye movements will shed light on the source and nature of the variability. What is clear is that a very personal signature is embedded in the eye movements that each of us make.

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