The Structure of Inter-Individual Differences in Visual Ability: Evidence from the General Population and Synaesthesia

Jamie Ward[1,2], Nicolas Rothen[3,4], Acer Chang[1,2], & Ryota Kanai[1,2]

[1]School of Psychology, University of Sussex, Brighton, UK

[2]Sackler Centre for Consciousness Science, University of Sussex, Brighton, UK

[3]Institute of Psychology, University of Bern, Bern, Switzerland

[4]Center for Cognition, Learning and Memory, Bern, Switzerland

Manuscript Submitted to: Vision Research

Running Head: individual differences

Address for Contact:

Prof. Jamie Ward,

School of Psychology,

University of Sussex,

Falmer, Brighton,

BN1 9QH, U.K.

Tel. : +44 (0)1273 876598

Fax. : +44 (0)1273 678058

E-mail : jamiew@sussex.ac.uk

ABSTRACT

This study considers how inter-individual differences in visual ability are structured. Visual ability could be a single entity (along the lines of general intelligence, or 'g'), or could be structured according to major anatomical or physiological pathways (dorsal v. ventral streams; magno- v. parvo-cellular systems); or may be a finer-grained mosaic of abilities. To test this, we employed seven visual psychophysical tests (generating 16 measures) on a large (100+) sample of neurotypical participants. A Varimax-rotated PCA (Principal Component Analysis) revealed a two-factor solution that broadly corresponds to a high and low spatial frequency division (consistent with a magno/parvo distinction). Over and above this, two measures (temporal order judgments; gain in contrast sensitivity) correlated with most others, and loaded on both factors, suggesting that they tap broad visual processing demands. These analyses open up further possibilities for exploring the genetic and neuroscientific foundations of differences in visual ability. The tests were also run on a group of individuals with different types of visually-based synaesthesia, given that previous research have suggested they possess a distinct profile of visual abilities. Synaesthesia was linked to enhanced processing of colour and shape/curvature information (amongst others), that may relate to differences in V4 in this group. In conclusion, individual differences in vision are both striking and meaningful, despite our difficulty to imagine seeing the world any differently.

Keywords: individual differences; contrast sensitivity; temporal order judgments; synaesthesia/synesthesia; visual ability; shape; colour/color.

INTRODUCTION

Aside from disorders of vision, normal individual differences in visual perception have been relatively neglected in comparison to other cognitive domains such as attention and memory (e.g. Engle, Tuholski, Laughlin, & Conway, 1999). This may reflect, at least in part, the fact that we have little or no first-person insight into our visual abilities. Whilst we are able to reflect on our tendencies to mind-wander or forget, we are unable to reflect on our relative abilities to perceive motion or detect patterns in dots. In theory, it could be the case that normal visual abilities do not vary in the same way as they do for other cognitive domains. In practice, this is not so. Halpern, Andrews and Purves (1999) reported a two-fold difference between highest and lowest performing participants (N=20) in tests such as wavelength discrimination and contrast sensitivity and a ten-fold difference on an acuity measure. There are two-fold differences in the size of vision-related neuroanatomical regions such as primary visual cortex, V1 (Andrews, Halpern, & Purves, 1997; Song, Schwarzkopf, Kanai, & Rees, 2015), and these differences predict susceptibility to certain perceptual illusions (de Haas, Kanai, Jalkanen, & Rees, 2012; Schwarzkopf, Song, & Rees, 2011). As such individual differences in vision are both striking and meaningful, despite our difficulty to imagine seeing the world any differently.

How might individual differences in vision be structured? Here we shall consider three broad possibilities. Firstly, visual ability may be a single monolithic entity analogous to, or equivalent to, general intelligence or 'g' (e.g. Deary, Bell, Bell, Campbell, & Fazal, 2004). Halpern et al. (1999) conducted a Principal Component Analysis over their set of seven tests of visual ability and found a single 'visual performance factor' explained inter-individual variation across almost all of their tasks (accounting for 30% of total variance). This may reflect differences in the total amount of visually dedicated circuitry or it may be

due to the major source of variation lying within a central hub that contributes to most aspects of vision (e.g. V1 at a cortical level, or photoreceptor density at a more basic level). Earlier research, using a wider range of measures, failed to find support for the notion of a visual 'g' (Guilford, 1967; Thurstone, 1944, 1950). Secondly, visual ability might fractionate according to a small number of anatomical pathways such as dorsal versus ventral stream abilities or magno- versus parvo-cellular abilities. The visual dorsal and ventral stream describes two major cortical pathways arising after V1 that are specialised for colour, object recognition and memory (ventral) versus motion, spatial attention, and vision-for-action (dorsal) (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982). The magno- and parvocellular pathways describe two major sub-cortical pathways: one specialised for motion, low spatial frequency (LSF) and low contrast (magnocellular) and one specialised for colour, high spatial frequency (HSF) and high contrast (parvocellular) (Maunsell, 1987).[1] Evidence for the claim that visual ability is structured according to these divisions has come from, amongst others, visual-evoked potentials in EEG (e.g. Strasburger, Murray, & Remky, 1993) and developmental neuropsychology (Braddick, Atkinson, & Wattam-Bell, 2003). The latter leading to the claim that many (non-opthalmological) developmental disorder are characterized in terms of 'dorsal stream vulnerability'. . However, some recent evidence from normal individual differences in vision failed to support the idea that visual ability fractionates in this way. Goodbourn et al. (2012) used four tests of magnocellular function and found that they tended not to correlate strongly with each other and the correlations were no larger than a test not relying on this system (based on colour). Finally, a third alternative scenario is that there is a multiplicity of visual abilities that are not closely related to each

[1] It has been suggested that there is a direct relationship between these cortical and sub-cortical systems (such that parvocellular system is more important for ventral stream, and magnocellular for dorsal stream) although this division is not absolute and parvo- and magno-systems feed in to both dorsal and ventral streams to at least some degree (Merigan & Maunsell, 1993).

(e.g. Peterzell, Werner, & Kaplan, 1995; Webster & Macleod, 1988). Cappe, Clarke, Mohr and Herzog (2014) argued for this based on low correlations between performance on different visual tests in their study. This may reflect the quasi-modular functionality of visual cortex or the diversity of retinal and ganglion cell types. The latter was the interpretation favoured by Goodbourn et al. (2012). Of course, these three different explanations are not mutually exclusive as shown in other domains such as intelligence (Deary, 2012; Mackintosh, 2011).

There are several reasons why elucidating the structure of inter-individual differences in vision is important. Wilmer (2008) highlights three reasons that we consider in turn: functional organisation, genetics/environment, and utility. The dominant approach to exploring functional organisation is based on dissociations in performance (e.g. in neuropsychology) or neural specialisation (e.g. in fMRI). A complementary approach is latent variable techniques that isolate psychological mechanisms by identifying a limited number of categories that summarize individual differences in terms of associations of tests or measurements (e.g. as in the study of Halpern et al., (1999). Importantly, these techniques provide the foundation for behavioural genetic studies of individual differences. Methods such as GWAS (genome-wide association studies) are 'phenotype first' approaches that link a known individual difference (e.g. in visual ability) to genetic differences. Finally, an understanding of individual differences may have utility both in terms of predicting real world function (e.g. vision for action; orienting attention; face recognition) and also dysfunction. This includes not only visual disorders but also other developmental or acquired conditions that are not defined by visual disturbances but, for whom, individual differences in vision acts as an endophenotype (perhaps pre-symptomatically). This includes autism spectrum disorder (Simmons et al., 2009) and Parkinson's disease (Uc et al., 2005).

The approach taken in the present study is twofold. Firstly, we administered a diverse set of seven tests of visual perception to a group of ~100 participants and explored the relationship between the tests and measures using a latent variable technique. The tests are summarised in Table 1 and were selected on the basis of their putative weighting towards magno/ventral or parvo/dorsal function (and, hence, is a confirmatory rather than exploratory approach). Secondly, we also ran the identical set of tests on a group of participants with developmental synaesthesia who are hypothesised, based on previous research, to differ in certain visual abilities. Synaesthetes have conscious, reliable visual-like experiences that are evoked by stimuli such as words, letters and numbers (often whether written down, heard in speech, or imagined). Grapheme-colour synaesthetes (GCS) experience colours for letters and numbers. Not only do they have atypical visual-like experiences they also appear to have atypical (non-synaesthetic) visual functioning: they perform better at tests of colour discrimination (Banissy et al., 2013); show increased visual evoked potentials, in EEG, to high-frequency but not low-frequency Gabor gratings (Barnett et al., 2008); have lower phosphene thresholds to occipital lobe stimulation (Terhune, Tai, Cowey, Popescu, & Kadosh, 2011); and have been shown to have worse motion coherence (Banissy et al., 2013). This pattern led to the suggestion that they have enhanced ventral/parvocellular function and normal-to-reduced function of the dorsal/magno stream (Rothen, Meier, & Ward, 2012). However, no previous research has compared a wide range of tests on the same participants and nor have they contrasted distinct forms of synaesthesia. The present study also examines sequence-space synaesthesia (SSS) for whom sequences (e.g. months, numbers) are visualised as spatial configurations (e.g. a twisting line in 3D space). The use of this group enables us to explore whether the differences in perceptual ability are specifically related to the presence of synaesthetic colour in the GCS group. One possibility is that whereas GCS reflects ventral stream ability, SSS reflects differences within the dorsal stream given the

dorsal stream specialisation for spatial and numerical cognition (Ramachandran & Hubbard, 2001). We also have a third group of synaesthetes who have both GCS and SSS. This creates a 2x2 between subject design contrasting presence/absence of GCS and presence/absence of SSS (where non-synasthetic controls have an absence of both).

INSERT TABLE 1 ABOUT HERE

METHOD

Participants

The present study recruited a total of 135 participants made up of 101 non-synaesthetes (mean age = 23.7 years; range = 18-63; 31 males) and 34 confirmed synaesthetes (mean age = 30.8 years; range = 18-63; 4 males). A subset of the controls (N=34) were used as a matched group to the synaesthetes (mean age = 30.1 years; range = 18-63; 11 males). All participants had normal or corrected-to-normal vision and did not self-report colour-blindness.

The presence of grapheme-colour synaesthesia was confirmed using an online test of colour test-retest consistency (Eagleman, Kagan, Nelson, Sagaram & Sarma, 2007). This approach is extensively used but obviously presupposes that the associations are consistent (Simner, 2012). Grapheme-colour synaesthetes had an average consistency score of 0.78 (range=0.46-1.47) where the score of 1.43 provides optimal diagnostic sensitivity and specificity between GCS and controls (Rothen, Seth, Witzel & Ward, 2013). There were 12 people with GCS and not SSS, 11 with SSS and not GCS, and 11 with both.

The study was approved by the University of Sussex Cross-Schools Sciences and Technology Research Ethics Committee. Participants were either offered course credit or money (up to £8). The research was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki) and that informed consent was obtained.

Procedure

All tasks were presented on a 39x29 cm CRT monitor with a resolution of 1024 x 768, a refresh rate of 85Hz (screen refresh every 11.8ms) and colour depth of 24 Bit. They sat at a viewing distance of 1.00m, in a blacked-out room, with their head on a chin rest. Tasks were run using MATLAB R2011b and created using the Cogent Toolbox (http://www.vislab.ucl.ac.uk/cogent.php) for MATLAB (The MathWorks, Natick, MA) and Psychtoolbox (Brainard, 1997). The order of the 7 tasks was randomised. A subset of non-synaesthetes (N=20) retook the battery after one week using a different randomised order of the tasks in order to assess retest reliability.

For the four tasks that relied on a staircased threshold procedure (temporal order judgment, glass patterns, radial frequency shape discrimination, motion coherence), the parameter of interest was made more difficult after three successively correct trials and made easier after every incorrect trial. This staircase procedure minimizes bias (Klein, 2001). Each change in parameter represented a reversal, and ten reversals were required before the termination of the task. Figure 1 contains examples trials from the tasks.

INSERT FIGURE 1 ABOUT HERE

Visual search colour task

The visual search colour task required participants to discriminate colours which varied in hue. A version of this task, using different colours, has been used on grapheme-colour synaesthetes (Banissy et al., 2013). Four colour pairs (reflecting the red-green and blue-yellow cone-opponent pathways) and two grey pairs (which acted as control trials) were used (see Supplementary Methods). Each trial began with a white cross-fixation against a grey background, followed by clocklike arrangement (diameter = 6.31^{o}) of 12 coloured circles (diameter = 1.72^{o}) which flash briefly (150ms) on the screen. A small gap separated the circles down the middle, resulting in two hemispheres consisting of six circles each. Each circle was identical except for one which deviated slightly in colour. Participants were required to indicate which side they perceived the different coloured circle to appear in by using a button press using the left and right arrow keys in which both speed and accuracy were emphasised. The task contained 20 practice trials (with no feedback), followed by 192 test trials presented randomly.

Radial Frequency Shape task

The shape sensitivity task presented participants with two shapes: a perfect circle and a polygon which deviated from perfect circularity (a 'non-circle'). The participants were required to detect whether the non-circle appeared first or second by pressing 'Q' or 'P'. Each shape (mean radius, r = 38 pixels) was presented for 0.5 seconds with an inter-stimulus interval of 0.5 seconds in which the screen was blank. The formula for the circle and non-circle are taken from Wilkinson, Wilson and Habak (1998) and reproduced below. The contrast value, C, was 0.8 and the background luminance was 0.5. The non-circle (D4) was created by using a radial frequency (ω) of 4 which makes the circle deform towards a square. The initial radial modulation amplitude intensity (A) was set to 0.008, adjusted in a staircase procedure in steps of 0.0005. The threshold was calculated, after ten reversals, as the mean of the last ten scores.

a.

$$\mathrm{D4}(r) = C\left(1 - 4\left(\frac{r - r_o}{\sigma}\right)^2 + \frac{4}{3}\left(\frac{r - r_o}{\sigma}\right)^4\right) \times \exp\left(-\left(\frac{r - r_o}{\sigma}\right)^2\right)$$

b.

$$r(\theta) = r_o(1 + A\ \sin(\omega\theta + \phi\ ))$$

Glass pattern shape task

Participants were presented with a two interval forced choice: one dot arrangement was presented in a random fashion whilst the other was presented in global circle-like pattern. Participants were required to indicate which dot arrangement contained the 'circle-like' pattern, pressing 'Q' or 'P' according to whether they believed it was presented first or second, respectively. The dots were presented in a central area of 500 x 500 pixels (10.9 °). The stimuli contained 200 dipoles (pairs of dots) with a distance of seven pixels (0.2 °) between each pair and a diameter of three pixels (0.07 °) per dot. The dots were white against a black background. Each screen of dots was presented for 145ms with an inter-stimulus duration of 0.5 seconds. The staircase procedure was set to a coherence level of 50% and adjusted in steps of 2%. The threshold was calculated, after ten reversals, as the mean of the last ten scores.

Motion coherence task

The motion coherence test involved the presentation of random-dot-kinematograms, in which a directional motion signal is present amid a set of moving dots. Some of the dots move in the same, coherent direction, whilst the others move in a random fashion. Participants were required to indicate which direction they perceived the majority of the dots to be moving in, using 'Q' or 'P' according to whether they perceived the dots to move left or

right, respectively. Performance was assessed by recording the threshold by which the participant was still able to perceive an overall motion direction, calculating the minimal signal required to perceive the motion. Each trial contained 1320 white dots against a grey background, in a central 30° x 30°region of the screen. Each dot was 4x4 pixels (approximately 0.12° x 0.12°). Both coherent dots and random dots moved at a speed of 1.5° per second. The stimulus presentation duration was 0.4 seconds with a fade in and out duration of 0.1 seconds either side. The staircase procedure was set to an initial intensity in which 50% of the dots were coherent, decreasing in coherence by 1-dB for each correct judgement and increasing in coherence by 3-dB for each incorrect judgement. The detection threshold was determined, after ten reversals, by the mean of the last three scores.

Temporal order judgement (TOJ) task

The TOJ task required participants to make a judgement about which stimulus was presented first. Two white circles (stimulus radius = 0.3 °) are presented side-by-side (stimulus-to-centre distance = 4.4 °) in rapid succession against a black screen. Participants were required to type ‘Q’ or ‘P’ according to whether they believed the left or right hand circle appeared first, respectively. The circles remained on the screen until participant made a judgement, after which the task moves onto the next trial. The inter-stimulus duration between each trial was 0.5 seconds. The staircase procedure was set to an initial difference of 35.29ms, adjusted in steps of 11.76ms. The threshold was calculated as the mean of the last ten scores.

Quick contrast sensitivity function (qCSF) task

The qCSF task tested participants’ sensitivity to spatial-frequency and contrast (Hou et al., 2010; Lesmes, Lu, Baek, & Albright, 2010). Participants were required to identify a Gabor patch (70 pixel radius) using a two interval forced choice paradigm. A Gabor patch is defined as a sinusoidal wave in a Gaussian envelope, where the sinusoid can vary in spatial-

frequency and contrast. A fixation was presented for 250 msec followed by a Gabor or blank for 120 msec. This was followed by a fixation for 500 msec and a Gabor or blank for 120 msec. Participants were required to type 'Q' or 'P' according to whether they believed the Gabor patch appeared after the first or second fixation, respectively, and to respond within two seconds from the end of stimuli presentation. The initial parameters (priors) for the model were set as peak gain (γ_{max}) of 100, peak spatial frequency (f_{max}) of 2 cycles per degree, width (β) of 3 octaves, and reduced gain at low spatial frequency (δ) of 0.5 log units. The formulae for adjusting parameters on the basis of performance are given by Huo et al. (2010) and Lesmes et al. (2010). The task contained a fixed number of 100 test trials and the estimated parameters after the final trial are analysed.

Gabor Detection Task

Stimuli consisted of centrally presented, vertical Gabor patches subtending a visual angle of 7.2°, with SF of 0.49 (i.e., low spatial frequency) or 14 c/° (i.e., high spatial frequency), depending on the experimental condition. Considering the gamma of the monitor, these Gabor patches were presented at 0.05 (low), 0.1 (medium), and 0.5 (high) contrast levels (Michelson contrast) on a mid-grey monitor background (23 cd/m^2). Participants were asked to press the space key on the keyboard as soon as they detected a visual stimulus (Gabor patch) at the centre of the monitor. The task consisted of a short practice block of 8 trials which helped to explain the task. Practice trials additionally included feedback about the correctness of the response after each trial. The practice block was followed by 5 experimental blocks which did not include feedback on performance. Each experimental block consisted of 42 stimuli. That is, 5 high frequency / high contrast, 8 high frequency / medium contrast, and 10 high frequency / low contrast trials. Each low frequency condition consisted of 5 trials per block. The higher numbers of trials in the high frequency condition were included to adjust for the relative difficulty of these conditions (in order to obtain

enough hits for reliable reaction times). Each block consisted of an additional 4 trials where no visual stimulus was present. The beginning of each trial was indicated by a central fixation cross which was presented for a variable duration (randomly chosen from 500 ms to 1500 ms). The target stimulus was presented for 340 ms overlaid on the fixation cross. After a response deadline of 1500 ms, the fixation cross disappeared and a 500-ms delay led to the beginning of the next trial. In case a key press was registered before the response deadline, the fixation cross disappeared and the 500-ms delay started.

Quality assurance and exclusion of data

In general, our approach to quality assurance is to only exclude data that is likely to reflect non-compliance with the task instructions. For the Gabor detection task, a high false alarm rate suggests indiscriminate responding. Overall the false alarm rate for non-synaesthetes was low (4.90%, SD=9.23). There were 6 non-synaesthetes and 0 synaesthetes in the 25%+ range (>2SDs) and their data was excluded entirely from this task. For motion coherence and glass patterns, a very high coherence value (>.9) lead to exclusion on these tasks (this leads to removal of N=16 non-synaesthetes and 3 synaesthetes from motion coherence and 4 non-synaesthetes from the glass pattern task). In the colour visual search task, there are 4 control participants with an unusually fast response time (<400 msec on average) who are also at or near chance (mean of 53% correct). This suggests they emphasised speed over accuracy (against the task instructions). There is no general speed-accuracy trade-off in this task (r=-.078 for the remaining 97 non-synaesthetes). Two synaesthetes get excluded using this same criteria and one further synaesthete was excluded because they scored significantly below chance (35% and 17% correct for colour and grey) suggesting they were responding to the side that did not contain the target. For the qCSF task, there was a group of participants (N= 15 controls, and N= 6 synaesthetes) with very low peak gain ($\gamma_{max} < 0.3$) that was indistinguishable from chance. These participants were

excluded. The remaining participants all had a peak gain greater than 1. Three participants were excluded from the radial frequency task (> 2SDs), and none from the temporal order judgment task. Participants who had been excluded from more than 3 tasks were excluded entirely (this applied to three non-synaesthetes).

Test-retest reliability

Twenty control participants (mean age = 19.85 years, range 18-23; male = 5) were selected based on consecutive sampling and retested approximately a week after their initial test session in order to assess the reliabilities of the different tasks. After applying the data exclusion criterion, we calculated the correlations between Session 1 and 2 for each condition of each task. For N=20 a correlation greater than .38 is significant at $p<.05$. For the Gabor Detection task (accuracy), r=.94 averaging across contrasts and spatial frequencies (all component correlations were significant except for low frequency and high contrast in which participants were near ceiling). For the chromatic and achromatic versions of the visual search task the correlations were .80 and .83 (accuracy). For glass patterns, radial frequency shape discrimination, and temporal order judgments the correlations were .68, .39 and .43 respectively. For the qCSF parameters, only γ_{max} (r=.48) and β (r=.67) were reliable across sessions (correlations for f_{max} and δ being .19 and .07 respectively). The motion coherence test had low reliability (r=.19) but this reflects a relatively high proportion of participants who consistently met the exclusion criteria across sessions.

RESULTS

The descriptive statistics for the non-synaesthetic sample are presented in Table 2. Cronbach's alpha is 0.75 based on all measures reported in Table 2. Dropping a measure

does not improve this figure appreciably (a maximum increase of .02) so all measures are retained. The simple correlations between the measures are presented in the Supplementary Results. All of the statistically significant correlations reflect a positive association between abilities: that is, there is no evidence of a trade-off off between some visual abilities at the expense of others. Large effect sizes (r>.5) were only found for correlations between comparable measures within the same task (e.g. stimuli of different contrasts in the Gabor detection task; chromatic and achromatic versions of the visual search). There were eleven medium effect sizes (r>.3) found between tasks. These reflect three broad trends in the data. Firstly, there was an association between the visual search task (chromatic and achromatic stimuli) and the ability to detect low spatial frequency (LSF) Gabors. Secondly, the estimate of peak gain (γ_{max}) from the qCSF predicted performance across a wide range of measures on other tasks (5 medium effect sizes, and 3 small but significant effect sizes). Thirdly and similarly, the temporal order task predicted performance on a wide range of other measures (3 medium effect sizes, and 7 small but significant effect sizes).

INSERT TABLE 2 ABOUT HERE

Rotated Component Analyses

In order to assess the latent variable structure of the data, we conducted a Rotated Component Analysis (i.e., a Principal Component Analysis with Varimax rotation) on the data of the non-synaesthete controls. This is appropriate because the variables are on different scales and our theoretical model assumed a high degree of independence between parvo/ventral and magno/dorsal measures. On the basis of a Parallel Analysis, Revelle and Rocklin (1979) very simple structure, and Velicer's (1976) Minimum Average Partial test

(MAP), each showed that the number of factors to extract was restricted to two. These techniques provide more objective measures to determine the number of factors in comparison to other methods such as taking Eigenvalues greater than one or visual inspection of the scree plot (Courtney & Ray, 2013). Pairwise deletion of missing data was used. The component loading of the different conditions of each task can be found in Table 2. Excluding the data of the qCSF task would not alter the component structure (i.e., the same task conditions would still load on the same components), but the cumulative explained variance would increase from 37% to 45%. Figure 2 shows the relationship between the tasks in terms of their factor loadings.

In summary, the results do not support the notion of a single 'visual performance factor' (cf., Halpern et al., 1999), although some measures (TOJ and peak gain) do have a tendency to correlate across almost all measures. The results instead support fractionation of visual ability. In some respects this resembles a magno/parvo distinction (e.g. the separation of LSF and HSF) whereas in other respects it does not (e.g. the loading of the colour-based task). These issues are returned to in more detail in the discussion.

INSERT FIGURE 2 ABOUT HERE

Effects of synaesthesia on visual perception

The Gabor Detection task and the qCSF were analysed as separate tasks as each gives a more complex set of measures. The remaining five tasks all generate a single threshold measure with the exception of the visual search task which generates two accuracy measures (for chromatic and achromatic targets). The six measures for these 5 tasks were converted to z-scores (based on the control mean and SD) such that a higher z is linked to enhanced performance. This rescaling enabled a 2x2x6 ANOVA contrasting group (as a 2x2 design of

presence/absence of grapheme-colour synaesthesia GCS and presence/absence of sequence-space synaesthesia SSS) and measure (6 levels) that avoids problems of multiple comparisons. The results show a significant GCS x SSS x task interaction ($F(5,265)=2.478$, $p=.032$, $\eta_p^2 = .045$) showing that some groups perform significantly differently on some tasks. There was no main effect of having either GCS ($F(1,53)=2.700$, $p=.106$, $\eta_p^2 = .048$) or SSS ($F(1,53)=0.960$, $p=.332$, $\eta_p^2 = .018$) suggesting that the presence of synaesthesia per se is not linked to globally better or worse performance. There was a main effect of task ($F(5,265)=3.009$, $p=.012$, $\eta_p^2 = .054$) but other interactions were all non-significant (all *p*s >. 10). In order to explore the nature of the interaction a series of planned contrasts were conducted on each task. These consisted of: contrasting synaesthetes (3 groups) against non-synaesthetes (1 group); contrasting grapheme-colour synaesthesia (2 groups) against absence of grapheme -colour synaesthesia (2 groups); and contrasting sequence-space synaesthesia (2 groups) against the absence of sequence-space synaesthesia (2 groups). The results are summarised in Figure 3. There were three significant findings: synaesthetes outperformed non-synaesthetes on colour perception ($t(63)=2.548$, $p=.013$) and the radial frequency shape task ($t(66)=2.617$, $p=.011$). The presence of SSS was linked to enhanced motion coherence discrimination ($t(56)=2.191$, $p=.033$).

INSERT FIGURE 3 ABOUT HERE

The results of the Gabor Detection Task are summarised in Figure 4. The accuracy data can be analysed as a (2x2)x(3x2) ANOVA contrasting groups between subjects (the same 2x2 design as before), and contrast (3 levels) and spatial frequency (2 levels) within subjects. Considering the within-subject effects, there were main effects of spatial frequency ($F(1,61)=116.15$, $p<.001$, $\eta_p^2 = .656$) and contrast ($F(2,60)=71.22$, $p<.001$, $\eta_p^2 = .704$) and a

significant interaction between them ($F(2,60)=55.89$, $p<.001$, $\eta_p^2 = .651$): that is, performance was better when the spatial frequency was low and the contrast was high and the effect of contrast was more pronounced at the high spatial frequency. In terms of group effects, performance on this task was related to the presence of SSS but not GCS. There was a main effect of SSS ($F(1,61)=15.94$, $p<.001$, $\eta_p^2 = .215$), and the presence of SSS interacted with spatial frequency ($F(1,61)=16.94$, $p<.001$, $\eta_p^2 = .207$), contrast ($F(2,60)=3.49$, $p=.037$, $\eta_p^2 = .104$), and a 3-way interaction between SSS, spatial frequency and contrast ($F(2,60)=3.31$, $p=.043$, $\eta_p^2 = .099$). Thus, the SSS group perform better overall, but perform particularly well in the HSF condition and at the lower contrasts. There was no main effect of GCS and this did not interact with any other variable (all ps > .10). The enhanced ability of the SSS group doesn't reflect a general response bias: a 2x2 between subjects ANOVA on the false alarms revealed no main effects of group (SSS: $F(1,61)=.561$, $p=.457$, $\eta_p^2 = .009$; GCS $F(1,61)=.330$, $p=.568$, $\eta_p^2 = .005$) and no interaction ($F(1,61)=1.40$, $p=.241$, $\eta_p^2 = .022$).

INSERT FIGURE 4 ABOUT HERE

As the LSF stimuli were performed close to ceiling, response times may be more informative for these stimuli. Unfortunately, the low accuracy for HSF trials meant that there were often too few trials to calculate a reliable mean response time across each level of contrast. Collapsing across contrast results in a 2x(2x2) ANOVA comparing spatial frequency and group. There was a main effect of spatial frequency ($F(1,61)=121.87$, $p<.001$, $\eta_p^2 = .666$) consistent with HSF stimuli being harder and, crucially, there was an interaction between the presence of SSS and spatial frequency ($F(1,61)=6.95$, $p=.011$, $\eta_p^2 = .102$). As with detection rates there was a greater advantage for HSF stimuli, relative to LSF, in the SSS group (for HSF $t(63)=1.99$, $p=.05$, and for LSF $t(63)=.15$, $p=.88$ contrasting SSS and non-

SSS groups). There were significant main effects of SSS (they tended to be faster; $F(1,61)=5.15$, $p=.027$, $\eta_p^2 = .078$) and a significant main effect of GCS (they tended to be slower; $F(1,61)=4.32$, $p=.042$, $\eta_p^2 = .066$). No other interactions were significant.

For the qCSF task, each parameter was analysed separately as a between subjects 2x2 ANOVA. There were no group differences or interactions between groups (all *p*s>.10).

DISCUSSION

The present study shows that normal visual abilities vary greatly: some tasks show a 4 or 5 fold difference between best and worst performing participant (e.g. Glass patterns, temporal order judgments). As noted by Wilmer (2008): "Perhaps we have downplayed and failed to make full scientific use of the myriad visual differences that exist between us partially because it is so difficult to imagine a visual world different from the one we personally perceive" (p.575). Indeed, this is strikingly true of synaesthesia: it is just as hard for synaesthetes to imagine perceiving the world without synaesthesia, as it is for other people to imagine what synaesthesia is like (Dittmar, 2009).

We have shown that there is a structure to these differences in visual ability. The results point to different levels of granularity in terms of individual differences in visual ability. Overall, our latent variable analysis showed that there is no evidence of a single 'visual performance factor', contrary to the conclusion drawn by Halpern et al. (1999) using different tests and a much smaller sample (N=20). Having said that, some specific measures (TOJ and peak gain in qCSF) are predictive of performance on a wide range of tests. Evidence from normal variation supports a two-component solution: this is partially consistent with magno/parvo division (e.g. HSF and LSF patterns fall in different components), but not fully so (e.g. the placement of the colour task with LSF Gabor detection

is unexpected). Evidence from synaesthesia suggests the existence of dissociations at a finer level of granularity. That is, there are specific influences occurring in synaesthesia over and above those that give rise to natural variations in visual ability. These observations are considered in more detail below.

The fact that peak gain in contrast sensitivity and temporal order discrimination predict a wide range of visual abilities is noteworthy. It does not appear to be the case that these tests are, in themselves, the most reliable ones because the test-retest reliability is only of a medium effect size (gamma: r =.48; TOJ r=.43) and were, by no means, the most stable of the tests employed. The fact that these measures can predict performance on a range of other measures of visual ability (often with medium effect sizes) suggests that they reflect a very general measure of visual ability[2]. Indeed, these measures loaded on both factors in the Principal Component Analysis. The predictive validity is striking given the dissimilarity between the γ_{max} and the TOJ measure: the qCSF involves central presentation, whereas the TOJ involves peripheral presentation; the gamma measure is a measure of gain in the visual system, whereas the TOJ is a measure of processing of temporal information. It is also striking insofar as the high predictive validity of the gamma measure was not borne out by the other parameters from the qCSF suggesting that it is related to specific ability (γ_{max}) rather than task demands (of the qCSF) in some broader sense. Temporal order judgments have been linked to a specialised dorsal stream "when" pathway (Battelli, Pascual-Leone, & Cavanagh, 2007). Whilst our data do not disprove the existence of such a pathway, it suggests that individual differences in visual TOJ tasks are primarily determined by broad differences within the visual system that are common to a large number of tasks and are not specifically dependent on time perception per se.

[2] If TOJ and γ_{max} were identical constructs then the estimated correlation between these measures, given their reliability over time, is $\sqrt{(.43 \times .48)} = .45$. The observed correlation is close to this at .36.

Our results offer the first empirical support, across a range of tasks, that normal individual differences in visual ability can be described (minimally) in terms of two factors. This has been hypothesised before based on the known neuroanatomical divisions between ventral and dorsal streams and/or magnocellular and parvocellular systems. Other studies that have applied a PCA specifically to spatial frequency channels in contrast sensitivity have identified two (Peterzell & Teller, 1996) or three (Simpson & McFadden, 2005) factors. Although our findings support a two-factor solution it does not map unequivocally on to this distinction. One factor contained detection of low spatial frequency Gabor stimuli, motion coherence, and the delta parameter of the CSF (reduced contrast sensitivity at LSF) which is broadly consistent with a magnocellular/dorsal factor. The other factor contained HSF Gabor detection and the two shape processing tasks, but the test involving colour (the visual search test) did not load on this factor as predicted. The parvocellular system is sensitive to both colour and high spatial frequency information so one might predict an association in abilities to occur here. Instead there was an the association between the visual search task and detection of LSF Gabors both in terms of simple correlations and in terms of factor structure. However, the specific colour-based task used here involved comparing low resolution information across a large region of visual field which may place the bottleneck in processing ability within the dorsal parietal network. The fact that the association was found for both chromatic and achromatic stimuli is consistent with this interpretation.

The synaesthetes did not differ on tasks such as the TOJ and gamma that were shown, in non-synaesthetes, to be good general predictors of visual ability. This result, however, is not problematic because – across the range of tasks employed – the synaesthetes were <u>not</u> performing better in a global sense (i.e. the main effects of synaesthesia tended to be not significant). Instead, the benefits of synaesthesia were found in specific tests or on specific measures (i.e. the effects of synaesthesia was revealed by group x task/measure interactions).

This suggests a more specific influence of synaesthesia on the visual system over and above more global visual ability.

Previous research on people with grapheme-colour synaesthesia has revealed an increased ability to discriminate colours (Banissy et al., 2013; Banissy, Walsh, & Ward, 2009; Yaro & Ward, 2007). This finding is replicated here but extended in several important ways: specifically, we establish for the first time that the enhancement extends to another group of synaesthetes (sequence-space synaesthesia), and that it is not found for achromatic stimuli in the same task. We also establish the novel finding that both types of synaesthesia are linked to enhanced shape/curvature perception in the radial frequency pattern task. Neurons in primate V4, which is important for colour perception, are known to be tuned to curvature coding and radial symmetry (Gallant, Connor, Rakshit, Lewis, & VanEssen, 1996). As such the synaesthetic profile can be regarded as a common core of visual ability across these different, but co-occurring, types of synaesthesia. It is noteworthy that synaesthetes did not perform better on Glass patterns, as this requires shape discrimination too. However, psychophysical studies show that Glass patterns (global coherence) and radial frequency (curvature coding) rely on separable mechanisms (Badcock, Almeida, & Dickinson, 2013) and functional imaging suggests that Glass patterns are linked to activity in a network of regions including those in the dorsal stream (Braddick, O'Brien, Wattam-Bell, Atkinson, & Turner, 2000). It was further hypothesised that grapheme-colour synaesthesia may be linked to an advantage in HSF perception given enhanced visual-evoked potentials to these stimuli (Barnett et al., 2008) but, unexpectedly, these were linked only to sequence space synaesthesia. This raises the possibility that some previous research in this area on 'grapheme-colour synaesthesia' may have been driven by the coincidental presence of this other sub-type. Finally, there was no evidence of a motion coherence disadvantage (contrary to Banissy et al., 2013) but it is to be noted that a faster speed was used in the present study

which is less demanding. The precise explanation for this pattern of visual abilities in synaesthesia remains to be determined, but the general hypothesis is that genetic differences linked to synaesthesia (e.g. Asher et al., 2009) affect the functioning of the visual system leading to both relatively-specific performance enhancements and also to atypical perceptual experiences themselves. These differences may be additional to, or interacting with, normal individual differences in visual ability in non-synaesthetes.

It is important to acknowledge the limitations of the present research too. The sample of synaesthetes was relatively small and we were unable to explore other potentially relevant dimensions of the synaesthetic experience such as the spatial location of the colours (Rogowska, 2011).

In summary, visual ability differs strongly between individuals and is structured into two broad factors, although some measures may load on both factors and finer-grained distinctions may also be found in certain sub-populations (such as developmental synaesthesia).

Acknowledgements

NR is supported by the Swiss National Science Foundation (Grant Number: PZ00P1_154954). JW is supported by the ESRC. We thank Sara Souissi, Lucy Snelson and Kristin Jüneman for their assistance with data collection.

Table 1. A summary of the seven visual psychophysics tasks used

Test	Measure(s)	Notes	Taken or adapted from:
Gabor detection	Accuracy (primary measure), response time (secondary measure)	Simple stimulus detection test at three different contrasts and two spatial frequencies	Murray & Plainis (2003); Perez-Bellido, Soto-Faraco, & Lopez-Moliner, (2013)
qCSF (quick contrast sensitivity function)	Four parameters corresponding to its maximum sensitivity (peak gain γ_{max}), the spatial frequency at the maxima (f_{max}), the attenuation in sensitivity at low spatial frequencies (δ) (primary measures), and the width (β) (secondary measure).	Uses a wide variety of contrasts and spatial frequencies of Gabor stimuli to estimate the shape of the CSF	Lesmes et al., (2010)
Glass Patterns	Threshold (proportion coherent)	An array of pairs of static dots, some of which can be perceived as forming a	Wilson & Wilkinson (1998)

		coherent global shape. Sometimes used as a measure of ventral stream function (Braddick et al., 2003)	
Motion Coherence	Threshold (proportion coherent)	An array of moving dots, some of which can be perceived as moving in a coherent direction. Sometimes used as a measure of dorsal stream function (Braddick et al., 2003)	Banissy et al., (2013); Snowden & Kavanagh, (2006)
Chromatic and achromatic visual search	Accuracy (primary measure), response time (secondary measure)	Detection of a briefly presented oddball stimuli that differed either in hue or luminance (the latter being achromatic)	Gilbert, Regier, Kay, & Ivry, (2006), Banissy et al., (2013)
Radial Frequency Patterns	Threshold (curvature modulation)	A shape discrimination task based on perception of curvature. Neurons in primate V4 respond preferentially to curvature and radial symmetry (Gallant, Braun, & Vanessen, 1993; Gallant et al., 1996); hence a putative ventral stream	Wilkinson et al., (1998)

		measure	
Temporal Order Judgments (TOJ)	Threshold (msec)	Detecting which of two visual flashes occurred first. Linked to dorsal stream functioning (Battelli et al., 2007)	Hirsh & Sherrick Jr., (1961)

Table 2: Descriptive statistics for the 16 measures and the two-factor structure based on a Varimax Rotated Component Analysis. Factor loadings <.20 are not shown, and the highest factor loading is highlighted. For measures in which a lower score reflects better performance (e.g. threshold measures), the sign of the factor loadings is reversed for ease of comparison with other measures. Thus, positive loadings always indicate positive associations with ability.

	N	Mean	SD	Min	Max	Skew	Kurtosis	PC1	PC2
Gabor: HSF / high C	92	0.81	0.31	0.04	1	-1.63	1.08	**0.77**	
Gabor: HSF / med C	92	0.47	0.34	0	1	0.1	-1.38	**0.9**	
Gabor: HSF / low C	92	0.23	0.26	0	0.98	1.44	1.09	**0.78**	
Gabor: LSF / high C	92	0.99	0.02	0.9	1	-2.18	3.97	0.27	**0.52**
Gabor: LSF / med C	92	0.98	0.03	0.84	1	-2.34	6.32	0.22	**0.56**
Gabor: LSF / low C	92	0.96	0.08	0.6	1	-2.54	7.17	0.42	**0.6**
Motion: threshold	84	0.41	0.17	0.14	0.90	0.8	0.15		**0.38**
Visual search: Chromatic	96	0.73	0.1	0.48	0.91	-0.47	-0.29		**0.75**
Visual search: Achromatic	96	0.84	0.09	0.5	0.97	-1.31	2.02		**0.71**
qCSF: peak gain, γmax	86	1.57	0.18	1.03	1.89	-0.85	0.59	0.41	**0.44**
qCSF: fmax	86	0.39	0.17	-0.05	1.01	0.09	1.52	0.29	
qCSF: beta, β	86	0.47	0.13	0.05	0.78	-0.34	0.8		
qCSF: delta, δ	86	0.46	0.19	-0.1	0.87	-0.75	1.06		**0.46**
Glass pattern	97	0.56	0.13	0.27	0.84	0.04	-0.45	**0.39**	0.28
Radial frequency pattern	93	.0060	.0016	.0031	.0100	0.55	-0.43	**0.24**	
TOJ (msec)	96	50	20	19	111	0.55	-0.24	0.42	**0.46**
Proportion Variance								**0.19**	**0.18**
Cumulative Variance								**0.19**	**0.37**

Figure 1: Examples of the trial sequence for the seven tasks used. The red highlighted squares denote correct responses for those tasks in which participants discriminated between two different stimuli.

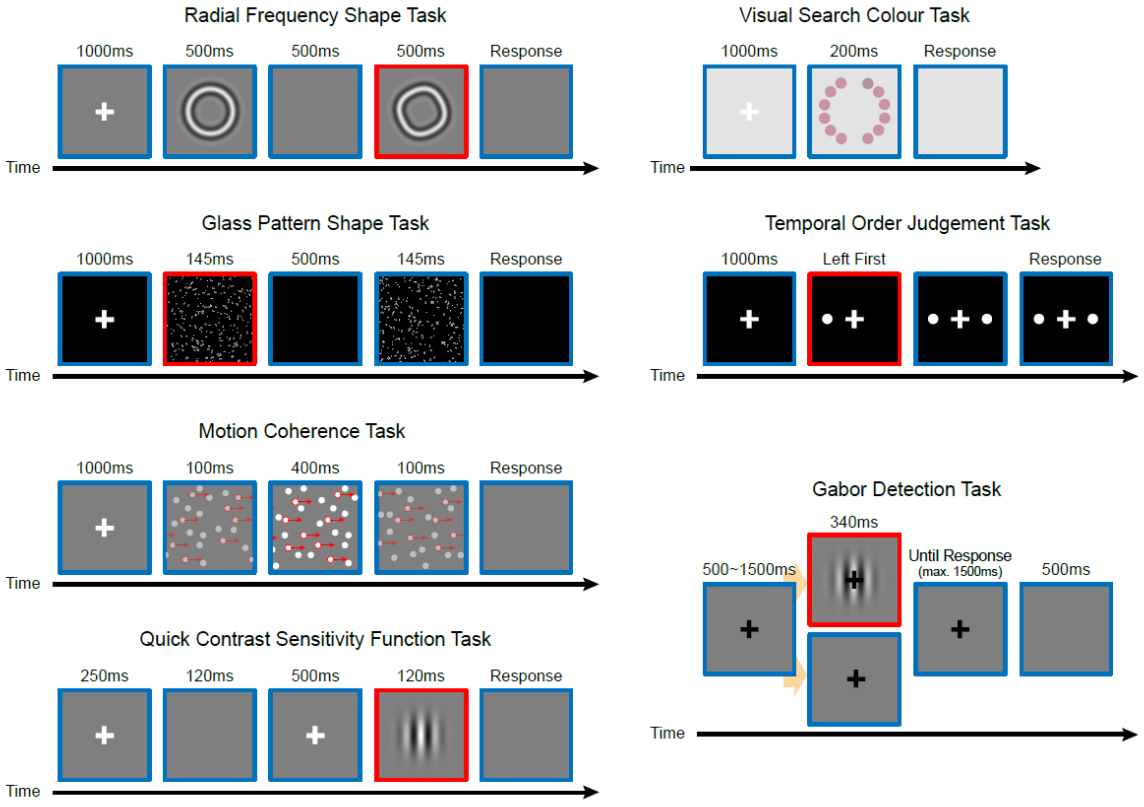


Figure 2: Results of the varimax rotated component analysis showing the component loadings for the 16 measures on the two principal components (PC1 and PC2). Triangles represent measures that load more on PC2 than PC1, and circles represent measures that load more on PC1 than PC2. Positive loadings always indicate positive associations with ability.

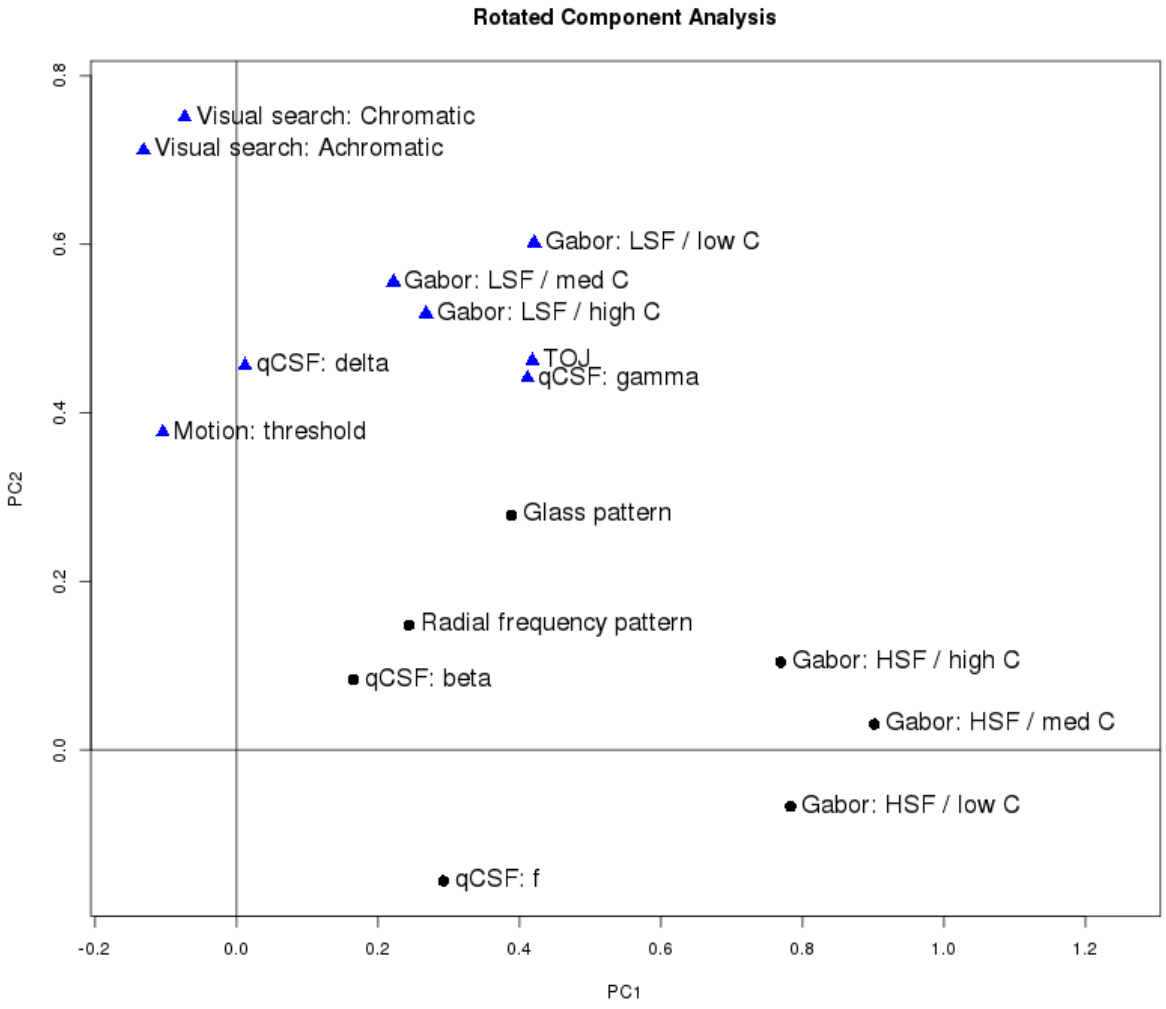


Figure 3: Visual ability of different groups of synaesthetes (GCS = grapheme-colour synaesthesia; SSS = sequence-space synaesthesia) and controls. The arrows indicate better performance. NS = not significant. The 'colour' and 'grey' measures are proportion correct, the 'radial frequency' measure is the curvature modulation amplitude threshold ($x10^2$), the 'motion' and 'glass patterns' are coherence thresholds, and the 'temporal order' measure is msec discrimination threshold. Error bars indicate 1 S.E.M.

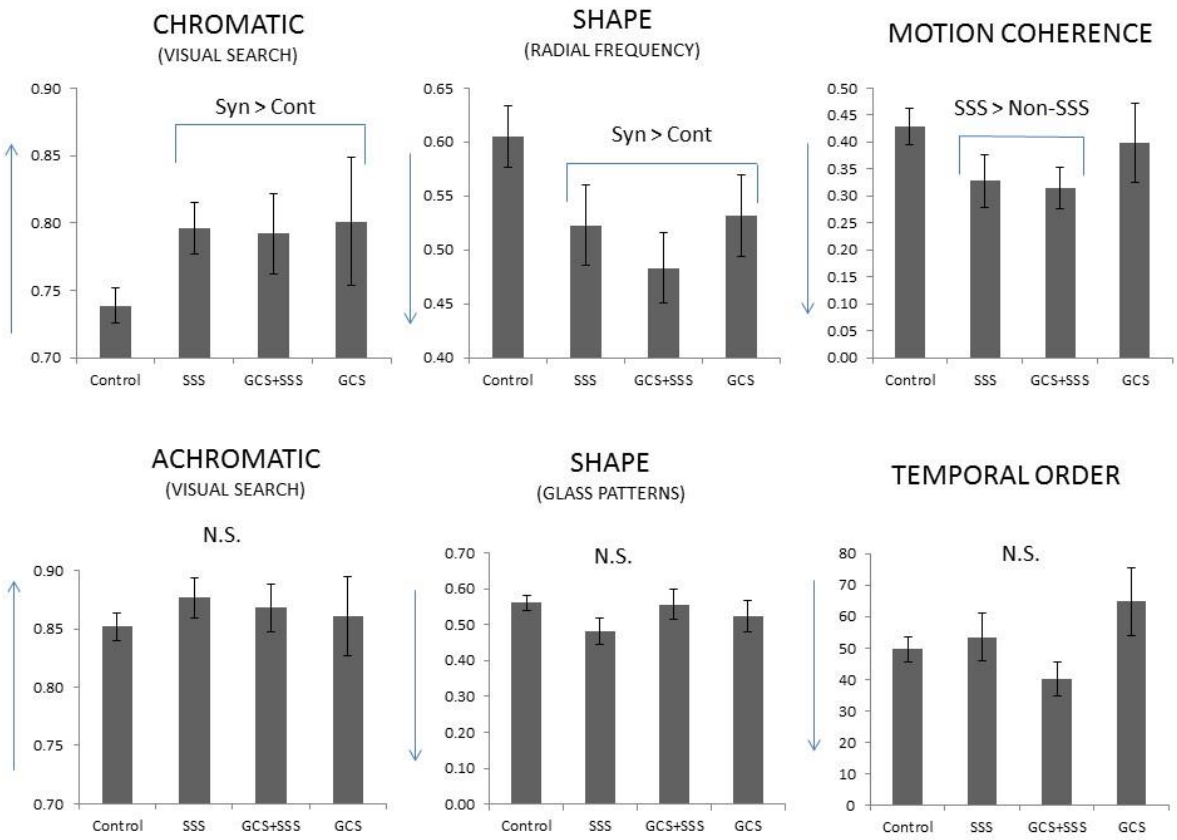
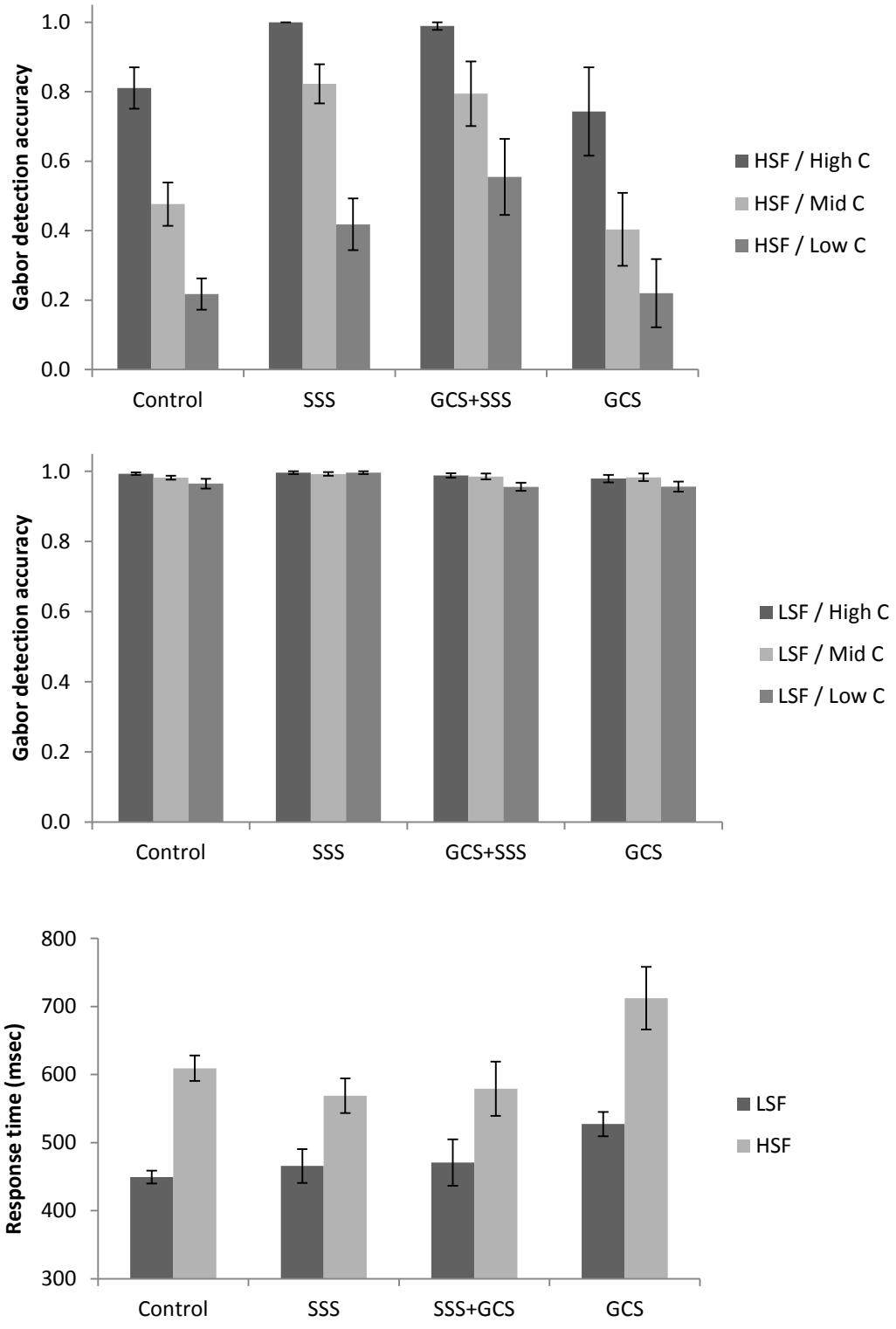


Figure 4: Results for the Gabor detection task for high spatial frequency stimuli (top), low spatial frequency stimuli (middle), and for response times for each spatial frequency collapsed across contrast (bottom). Error bars indicate 1 S.E.M.



References

Andrews, T. J., Halpern, S. D., & Purves, D. (1997). Correlated size variations in human visual cortex, lateral geniculate nucleus, and optic tract. *Journal of Neuroscience, 17*(8), 2859-2868.

Asher, J. E., Lamb, J. A., Brocklebank, D., Cazier, J. B., Maestrini, E., Addis, L., . . . Monaco, A. P. (2009). A Whole-Genome Scan and Fine-Mapping Linkage Study of Auditory-Visual Synesthesia Reveals Evidence of Linkage to Chromosomes 2q24, 5q33, 6p12, and 12p12. *American Journal of Human Genetics, 84*(2), 279-285. doi: 10.1016/j.ajhg.2009.01.012

Badcock, D. R., Almeida, R. A., & Dickinson, J. E. (2013). Detecting global form: separate processes required for Glass and radial frequency patterns. *Frontiers in Computational Neuroscience, 7*. doi: 10.3389/fncom.2013.00053

Banissy, M. J., Muggleton, N., Tester, V., Janik, A. B., Davenport, A., Franklin, A., . . . Ward, J. (2013). Synaesthesia for color is linked to improved color perception, but reduced motion perception. *Psychological Science, 24*(12), 2390-2397

Banissy, M. J., Walsh, V., & Ward, J. (2009). Enhanced sensory perception in synaesthesia. *Experimental Brain Research, 196*(4), 565-571. doi: 10.1007/s00221-009-1888-0

Barnett, K. J., Finucane, C., Asher, J. E., Bargary, G., Corvin, A. P., Newell, F. N., & Mitchell, K. J. (2008). Familial patterns and the origins of individual differences in synaesthesia. *Cognition, 106*, 871-893.

Barnett, K. J., Foxe, J. J., Malholm, S., Kelly, S. P., Shalgi, S., Mitchell, K. J., & Newell, F. N. (2008). Differences in early sensory-perceptual processing in synesthesia: A visual evoked potential study. *NeuroImage, 15*, 605-613.

Battelli, L., Pascual-Leone, A., & Cavanagh, P. (2007). The 'when' pathway of the right parietal lobe. *Trends in Cognitive Sciences, 11*(5), 204-210. doi: 10.1016/j.tics.2007.03.001

Braddick, O., Atkinson, J., & Wattam-Bell, J. (2003). Normal and anomalous development of visual motion processing: motion coherence and 'dorsal-stream vulnerability'. *Neuropsychologia, 41*(13), 1769-1784. doi: 10.1016/s0028-3932(03)00178-7

Braddick, O. J., O'Brien, J. M. D., Wattam-Bell, J., Atkinson, J., & Turner, R. (2000). Form and motion coherence activate independent, but not dorsal/ventral segregated, networks in the human brain. *Current Biology, 10*(12), 731-734. doi: 10.1016/s0960-9822(00)00540-6

Cappe, C., Clarke, A., Mohr, C., & Herzog, M. H. (2014). Is there a common factor for vision? *Journal of Vision, 14*(8). doi: 10.1167/14.8.4

de Haas, B., Kanai, R., Jalkanen, L., & Rees, G. (2012). Grey matter volume in early human visual cortex predicts proneness to the sound-induced flash illusion. *Proceedings of the Royal Society B-Biological Sciences, 279*(1749), 4955-4961. doi: 10.1098/rspb.2012.2132

Deary, I. J. (2012). 125 Years of Intelligence in The American Journal of Psychology. *American Journal of Psychology, 125*(2), 145-154.

Deary, L. J., Bell, P. J., Bell, A. J., Campbell, M. L., & Fazal, N. D. (2004). Sensory discrimination and intelligence: Testing Spearman's other hypothesis. *American Journal of Psychology, 117*(1), 1-18.

Dittmar, A. (2009). *Synaesthesia: A "golden Thread" Through Life?* Essen, Germany: Verlag Die Blaue Eule.

Engle, R. W., Tuholski, S. W., Laughlin, J. E., & Conway, A. R. A. (1999). Working memory, short-term memory, and general fluid intelligence: A latent-variable

approach. *Journal of Experimental Psychology-General*, *128*(3), 309-331. doi: 10.1037/0096-3445.128.3.309

Gallant, J. L., Braun, J., & Vanessen, D. C. (1993). Selectivity for polar, hyperbolic, and cartesian gratings in macaque visual-cortex. *Science*, *259*(5091), 100-103. doi: 10.1126/science.8418487

Gallant, J. L., Connor, C. E., Rakshit, S., Lewis, J. W., & VanEssen, D. C. (1996). Neural responses to polar, hyperbolic, and Cartesian gratings in area V4 of the macaque monkey. *Journal of Neurophysiology*, *76*(4), 2718-2739.

Gilbert, A. L., Regier, T., Kay, P., & Ivry, R. B. (2006). Whorf hypothesis is supported in the right visual field but not the left. *Proceedings Of The National Academy Of Sciences Of The United States Of America*, *103*(2), 489-494. doi: 10.1073/pnas.0509868103

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, *15*, 20-25.

Goodbourn, P. T., Bosten, J. M., Hogg, R. E., Bargary, G., Lawrance-Owen, A. J., & Mollon, J. D. (2012). Do different 'magnocellular tasks' probe the same neural substrate? *Proceedings of the Royal Society B-Biological Sciences*, *279*(1745), 4263-4271. doi: 10.1098/rspb.2012.1430

Guilford, J. P. (1967). *The Nature of Human Intelligence*. New York: McGraw-Hill.

Halpern, S. D., Andrews, T. J., & Purves, D. (1999). Interindividual variation in human visual performance. *Journal of Cognitive Neuroscience*, *11*(5), 521-534. doi: 10.1162/089892999563580

Hirsh, I. J., & Sherrick Jr., C. E. (1961). Perceived order in different sense modalities. *Journal of Experimental Psychology*, *62*(5), 423–432. doi: http://doi.org/10.1037/h0045283

Hou, F., Huang, C.-B., Lesmes, L., Feng, L.-X., Tao, L., Zhou, Y.-F., & Lu, Z.-L. (2010). qCSF in Clinical Application: Efficient Characterization and Classification of Contrast Sensitivity Functions in Amblyopia. *Investigative Ophthalmology & Visual Science, 51*(10), 5365-5377. doi: 10.1167/iovs.10-5468

Klein, S. A. (2001). Measuring, estimating, and understanding the psychometric function: A commentary. *Perception & Psychophysics, 63*(8), 1421-1455. doi: 10.3758/bf03194552

Lesmes, L. A., Lu, Z.-L., Baek, J., & Albright, T. D. (2010). Bayesian adaptive estimation of the contrast sensitivity function: The quick CSF method. *Journal of Vision, 10*(3). doi: 10.1167/10.3.17

Mackintosh, N. J. (2011). *IQ and Human Intelligence (2nd Edition)*. Oxford: OUP.

Maunsell, J. H. R. (1987). Physiological evidence for two visual subsystems. In L. M. Vaina (Ed.), *Matters of Intelligence*. Dordrecht: Reidel.

Merigan, W. H., & Maunsell, J. H. R. (1993). How parallel are the primate visual pathways. *Annual Review of Neuroscience, 16*, 369-402. doi: 10.1146/annurev.ne.16.030193.002101

Perez-Bellido, A., Soto-Faraco, S., & Lopez-Moliner, J. (2013). Sound-driven enhancement of vision: disentangling detection-level from decision-level contributions. *Journal of Neurophysiology, 109*(4), 1065-1077. doi: 10.1152/jn.00226.2012

Peterzell, D. H., & Teller, D. Y. (1996). Individual differences in contrast sensitivity functions: The lowest spatial frequency channels. *Vision Research, 36*(19), 3077-3085. doi: 10.1016/0042-6989(96)00061-2

Peterzell, D. H., Werner, J. S., & Kaplan, P. S. (1995). Individual-differences in contrast sensitivity functions - longitudinal-study of 4-month-old, 6-month-old and 8-month-

old human infants. *Vision Research, 35*(7), 961-979. doi: 10.1016/0042-6989(94)00117-5

Ramachandran, V. S., & Hubbard, E. M. (2001). Synaesthesia - A window into perception, thought and language. *Journal of Consciousness Studies, 8*, 3-34.

Revelle, W., & Rocklin, T. (1979). Very Simple Structure - Alternative procedure for estimating the optimal number of interpretable factors. *Multivariate Behavioral Research, 14*(4), 403-414. doi: 10.1207/s15327906mbr1404_2

Rogowska, A. (2011). Categorization of synaesthesia. *Review of General Psychology, 15*, 213-227.

Rothen, N., Meier, B., & Ward, J. (2012). Enhanced memory: Insights from Synaesthesia. *Neuroscience and Biobehavioral Review, 36*(8), 1952-1963.

Schwarzkopf, D. S., Song, C., & Rees, G. (2011). The surface area of human V1 predicts the subjective experience of object size. *Nature Neuroscience, 14*(1), 28-30. doi: 10.1038/nn.2706

Simmons, D. R., Robertson, A. E., McKay, L. S., Toal, E., McAleer, P., & Pollick, F. E. (2009). Vision in autism spectrum disorders. *Vision Research, 49*(22), 2705-2739. doi: 10.1016/j.visres.2009.08.005

Simner, J. (2012). Defining synaesthesia. *British Journal of Psychology, 103*, 1-15.

Simpson, W. A., & McFadden, S. M. (2005). Spatial frequency channels derived from individual differences. *Vision Research, 45*(21), 2723-2727. doi: 10.1016/j.visres.2005.01.015

Snowden, R. J., & Kavanagh, E. (2006). Motion perception in the ageing visual system: Minimum motion, motion coherence, and speed discrimination thresholds. *Perception, 35*(1), 9-24. doi: 10.1068/p5399

Song, C., Schwarzkopf, D. S., Kanai, R., & Rees, G. (2015). Neural Population Tuning Links Visual Cortical Anatomy to Human Visual Perception. *Neuron, 85*(3), 641-656. doi: 10.1016/j.neuron.2014.12.041

Strasburger, H., Murray, I. J., & Remky, A. (1993). Sustained and transient mechanisms in the steady-state visual-evoked potential - onset presentation compared to pattern-reversal. *Clinical Vision Sciences, 8*(3), 211-234.

Terhune, D. B., Tai, S., Cowey, A., Popescu, T., & Kadosh, R. C. (2011). Enhanced Cortical Excitability in Grapheme-Color Synesthesia and Its Modulation. *Current Biology, 21*(23), 2006-2009. doi: 10.1016/j.cub.2011.10.032

Thurstone, L. L. (1944). *A Factorial Study of Perception*. Chicago, IL: University of Chicago Press.

Thurstone, L. L. (1950). Some primary abilities in visual thinking. *Proceedings of the American Philosophical Society, 94*(6), 517-521.

Uc, E. Y., Rizzo, M., Anderson, S. W., Qian, S., Rodnitzky, R. L., & Dawson, J. D. (2005). Visual dysfunction in Parkinson disease without dementia. *Neurology, 65*(12), 1907-1913. doi: 10.1212/01.wnl.0000191565.11065.11

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical systems. In D. J. Ingle, M. A. Goodale & R. J. W. Mansfield (Eds.), *Analysis of Visual Behaviour*. Cambridge, MA: MIT Press.

Velicer, W. F. (1976). Determining number of components from matrix of partial correlations. *Psychometrika, 41*(3), 321-327. doi: 10.1007/bf02293557

Webster, M. A., & Macleod, D. I. A. (1988). Factors underlying individual-differences in the color matches of normal observers. *Journal of the Optical Society of America a-Optics Image Science and Vision, 5*(10), 1722-1735. doi: 10.1364/josaa.5.001722

Wilkinson, F., Wilson, H. R., & Habak, C. (1998). Detection and recognition of radial frequency patterns. *Vision Research, 38*(22), 3555-3568. doi: 10.1016/s0042-6989(98)00039-x

Wilmer, J. B. (2008). How to use individual differences to isolate functional organization, biology, and utility of visual functions; with illustrative proposals for stereopsis. *Spatial Vision, 21*(6), 561-579. doi: 10.1163/156856808786451408

Yaro, C., & Ward, J. (2007). Searching for Shereshevskii: What is superior about the memory of synaesthetes? *Quarterly Journal of Experimental Psychology, 60,* 682-696.

Supplementary Method. *Colour stimulus co-ordinates in xyY colour space.*

Colour	X	Y	Y
Red A	0.345	0.299	19.33
Red B	0.363	0.324	19.33
Yellow A	0.373	0.369	19.33
Yellow B	0.363	0.391	19.33
Green A	0.261	0.339	19.33
Green B	0.255	0.311	19.33
Blue A	0.275	0.275	19.33
Blue B	0.296	0.272	19.33
Light Grey A	0.313	0.33	11
Light Grey B	0.313	0.33	13
Dark Grey A	0.313	0.33	19
Dark Grey B	0.313	0.33	21
Background	0.313	0.33	25

Note. Colour stimulus co-ordinates in CIExyY colour space. The white point used for conversion was x=.313, y=.329, Y=50.47cd/m^2.

Supplementary Result. Pearson correlations between the different measures. Red highlights large effect sizes (r>.5) and orange highlights medium effect sizes (r>.3). Pink highlights represent small effect sizes that are, nonetheless, statistically significant. All significant effects reflect a positive association between different visual abilities (some correlations may be negative due to lower threshold measures reflecting better performance). * p<.05, **p<.01. Considering only medium and large effects, these can be explained by four tendencies. (1) a tendency for different measures within the same task to correlate together; (2) a tendency for detection for low SF (Gabor detection) to correlate with visual search; (3) a tendency for the gamma measure of the qCSF to correlate with other measures (4) a tendency for the gamma measure of the qCSF to correlate with other measures.

		Gabor Detection Task							Motion coherence	Visual Search		qCSF				Glass Patterns	Radial Frequency	TOJ
		HSF high C	HSF low C	HSF mid C	LSF high C	LSF low C	LSF mid C	False Alarms		Chromatic	Achromatic	gamma	fmax	beta	delta			
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	r		.399**	.690**	.224*	.384**	.187	.056	.036	.083	.065	.308**	.206	.108	-.096	-.299**	-.242*	-.219*
	p		.000	.000	.031	.000	.073	.593	.752	.433	.540	.005	.066	.339	.393	.004	.022	.037
	N		93	93	93	93	93	93	80	91	91	81	81	81	81	91	89	91
2	r			.789**	.200	.266*	.166	.186	.068	.016	-.033	.175	.046	.154	.130	-.172	.002	-.283**
	p			.000	.055	.010	.112	.075	.550	.879	.759	.119	.687	.171	.246	.104	.988	.007
	N			93	93	93	93	93	80	91	91	81	81	81	81	91	89	91
3	r				.272**	.366**	.237*	.054	.026	.054	.045	.273*	.123	.188	.094	-.226*	-.020	-.383**
	p				.008	.000	.022	.605	.819	.609	.670	.014	.275	.092	.405	.031	.851	.000
	N				93	93	93	93	80	91	91	81	81	81	81	91	89	91
4	r					.363**	.284**	.120	-.046	.343**	.260*	.301**	-.006	.266*	-.251*	-.123	.046	-.250*
	p					.000	.006	.250	.687	.001	.013	.006	.957	.016	.024	.245	.670	.017
	N					93	93	93	80	91	91	81	81	81	81	91	89	91
5	r						.538**	-.044	-.183	.224*	.347**	.316**	.027	-.018	-.292**	-.280**	-.066	-.459**
	p						.000	.678	.105	.033	.001	.004	.811	.871	.008	.007	.540	.000
	N						93	93	80	91	91	81	81	81	81	91	89	91
6	r							.045	-.211	.363**	.288**	.097	.066	.015	-.026	-.205	.079	-.289**
	p							.672	.061	.000	.006	.389	.560	.897	.817	.051	.462	.005
	N							93	80	91	91	81	81	81	81	91	89	91
7	r								.154	-.196	-.169	-.143	-.150	.142	.092	.028	.171	.114
	p								.171	.063	.110	.203	.182	.206	.413	.790	.108	.284
	N								80	91	91	81	81	81	81	91	89	91
8	r									-.182	-.107	-.060	.027	.068	.097	.049	.096	.139
	p									.100	.335	.606	.817	.559	.399	.661	.390	.211
	N									83	83	77	77	77	77	83	82	82
9	r										.612**	.218*	-.072	.041	-.193	-.114	-.208*	-.282**
	p										.000	.046	.516	.712	.079	.273	.045	.006
	N										97	84	84	84	84	95	93	95
10	r											.178	-.246*	-.016	-.067	-.125	-.040	-.194
	p											.106	.024	.884	.545	.228	.704	.060
	N											84	84	84	84	95	93	95
11	r												.073	.086	-.338**	-.336**	-.234*	-.362**
	p												.506	.433	.001	.002	.032	.001
	N												86	86	86	85	84	84
12	r													-.212*	-.060	-.023	-.056	-.139
	p													.050	.583	.838	.613	.208
	N													86	86	85	84	84
13	r														-.268*	.025	-.114	.065
	p														.013	.824	.302	.559
	N														86	85	84	84
14	r															.029	.218*	.238*
	p															.791	.047	.030
	N															85	84	84
15	r																.143	.289**
	p																.167	.005
	N																95	95
16	r																	.132
	p																	.206
	N																	93
17	r																	
	p																	
	N																	