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A population study of binocular function

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ABSTRACT

As part of a genome-wide association study (GWAS) of perceptual traits in healthy adults, we measured stereo acuity, the duration of alternative percepts in binocular rivalry and the extent of dichoptic masking in 1060 participants. We present the distributions of the measures, the correlations between measures, and their relationships to other psychophysical traits. We report sex differences, and correlations with age, interpupillary distance, eye dominance, phorias, visual acuity and personality. The GWAS, using data from 988 participants, yielded one genetic association that passed a permutation test for significance: The variant rs1022907 in the gene *VTI1A* was associated with self-reported ability to see autostereograms. We list a number of other suggestive genetic associations ($p < 10^{-5}$).

1. Introduction

Human binocular function shows large individual variation. For example, stereopsis – the ability to detect binocular disparities – varies from a "hyper acuity" of few seconds of arc to complete stereo blindness. The characterization of individual differences in binocular function has the potential to yield insights into the underlying biological mechanisms (Wilmer, 2008). With the proliferation of 3D technologies, there is also practical interest in individual differences in binocular function, to ensure that the full range of binocular abilities is catered for.

As part of the PERGENIC study into the genetic basis of individual differences in perception, we measured crossed and uncrossed stereo acuity, dichoptic masking and binocular rivalry in a population of 1060 normal healthy adults. Here we present population distributions for each measure, and the correlations between the measures. We also report correlations between these binocular measures, and demographic and other psychophysical measures. Genome-wide association analysis of our data has yielded a number of "suggestive" associations between the binocular measures and single nucleotide polymorphisms ($p < 10^{-5}$); and one genome-wide significant association with self-reported ability to see autostereograms ($p = 1.7 \times 10^{-8}$). The latter association passes a permutation test.

1.1. Stereo acuity

Stereo acuity is often considered a "hyper acuity", since under optimal conditions some people are able to detect differences in binocular disparity of a few seconds of arc, differences smaller than the diameter of individual photoreceptors (Westheimer, 1975). However, there is a large range of performance across individuals. Population studies have reported estimates of median stereo acuity ranging from 12.4 to 37.2 s of arc (Bohr & Read, 2013; Coutant & Westheimer, 1993; Zaroff, Knutelska, & Frumkes, 2003), but between 1 and 14% of people are stereo blind (Bohr & Read, 2013; Coutant & Westheimer, 1993; Rahi, Cumberland, & Peckham, 2009; Richards, 1970; Zaroff, Knutelska, & Frumkes, 2003). Population estimates of stereo acuity and of the prevalence of deficits may be affected by the method of measurement, by the retinal location, size and duration of the targets, by differences in population sampling and by differences in exclusion criteria between studies (Heron & Lages, 2012).

Poor stereopsis has a variety of known causes including strabismus, anisometropia, convergence insufficiency, early unilateral cataract, and unilateral retinal damage. It may also in some cases be caused by direct disruption of the specialist neural machinery that underlies stereopsis. Relative to other visual functions, stereo

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acuity seems to be disproportionately affected by aging (Wright & Wormald, 1992; Zaroff, Knutelska, & Frumkes, 2003); and poor stereo acuity has been noted in vascular dementia (Mittenberg, Choi, & Apple, 2000).

Electrophysiological results show that binocular visual neurons can be tuned to retinal disparities (Barlow, Blakemore, & Pettigrew, 1967). Different neural populations are tuned to crossed and uncrossed disparities, and the tuning is finest for stimuli falling close to the horopter (e.g. Poggio, 1995). Several authors have suggested that stereo acuity may be heritable, and Richards (1970) proposed an autosomal model on the basis of psychophysical data from parents and offspring.

The evidence suggests that stereopsis develops in infancy between the second and sixth months of life, with crossed stereo acuity developing significantly earlier than uncrossed (Birch, Gwiazda, & Held, 1982). The development of stereopsis requires appropriate stimulation from the environment and can be disrupted by occlusion or misalignment of one eye (Blakemore, 1979; Hubel & Wiesel, 1965). However, there is some evidence to suggest that stereopsis can be acquired in adulthood (Barry, 2012).

1.2. Binocular rivalry

Binocular rivalry arises when incompatible images are presented to the right and left eyes. Observers experience an alternation of percepts between the image presented to the left eye and that presented to the right. There are large individual differences in the rate of alternation, with a range spanning at least an order of magnitude (Pettigrew & Carter, 2004). Test–retest reliabilities for average percept duration are moderate to high, with past studies reporting $r_s = 0.69$ (Whittle, 1963), $r_p = 0.7$ (Miller et al., 2010) and $r_p = 0.8$ (Pettigrew & Miller, 1998, in bipolar patients and controls).

Variability in rate of rivalry has been found to correlate with patterns of saccadic eye movements (Hancock et al., 2012), with level of dichoptic masking (Baker & Graf, 2009), with retinotopic activity in extrastriate visual cortex triggered by the suppressed image (Yamashiro et al., 2014), and with variability in the structure of parietal cortex (Kanai, Bahrami, & Rees, 2010). Rate of rivalry is faster in children than adults (Hudak et al., 2011; Kovacs & Eisenberg, 2004) and declines with increasing age in adulthood (Jalavisto, 1964; Ukai, Ando, & Kuze, 2003). Rate of rivalry has been found to be reduced in bipolar disorder (Miller et al., 2003; Pettigrew & Miller, 1998; Vierck et al., 2013) and in autism (Robertson et al., 2013).

Recently, Miller et al. (2010) have inferred from twin data that rate of binocular rivalry is heritable, with 52% of the variance in rivalry rate attributable to additive genetic factors. Consistent with a reduced rate of rivalry in bipolar disorder, a candidate gene study by Schmack et al. (2013) suggested that the bipolar risk allele (2R) of the D4 dopamine receptor gene *DRD4* is associated with slow perceptual switching.

1.3. Dichoptic masking

In binocular or dichoptic masking, a stimulus presented to one eye is made harder to detect by a mask presented to the other. Individual differences in dichoptic masking have been noted (Baker & Meese, 2007), though to date no figure for test–retest reliability has been reported.

Baker and Graf (2009) have found that individual difference in dichoptic masking are correlated with individual differences in binocular rivalry: Both within and between individuals, stronger masking is associated with longer percept durations in binocular rivalry. This association suggests the two phenomena may arise from a common suppressive process.

2. Methods

Our measurements of binocular function were made as part of the PERGENIC genome-wide association study of individual differences in perceptual traits (Goodbourn et al., 2012; Lawrance-Owen et al., 2013). The PERGENIC battery consisted of about 80 perceptual measures and took about 2.5 h for participants to complete. In the first forty minutes of the session participants were optometrically assessed, were optically corrected if necessary, and were asked to perform some standard clinical tests of vision, including the TNO test.

2.1. Participants

One thousand and sixty participants (647 female) took part in the PERGENIC study. They were recruited from the Cambridge area, and many were students at the University of Cambridge. They were paid £25 for taking part. A subset of 105 participants, selected at random, returned for testing in a second session at least one week after the first session, allowing us to measure test–retest reliabilities. Participants were corrected to best optical acuity at the beginning of the session, and were given lenses to wear if acuity improved by at least 0.1 logMAR with the correction. Two hundred and thirty-four participants were given lenses for both eyes, and 110 participants were given lenses for one eye only. As a preliminary measure to guard against population stratification, all participants in our sample were of self-reported European origin.

The study was approved by the Cambridge Psychology Research Ethics Committee, and was carried out in accordance with the tenants of the Declaration of Helsinki. All participants gave written informed consent before taking part.

2.2. Visual acuity, sighting dominant eye, pupil size, inter-pupillary distance and phoria

Monocular and binocular logMAR visual acuity was measured using an EDTRS chart before and after a refraction using a standardized protocol.

We measured sighting dominant eye by a variant of the Miles test (Miles, 1929). Participants were seated facing a Snellen chart for measuring acuity, and asked to stretch out both arms, creating a small aperture with the thumbs and index fingers of both hands. They were asked to fixate on a letter on the chart through the aperture and then, keeping both eyes open, to bring their hands slowly toward their face. The experimenter noted the eye that the hands were drawn toward, and assigned this eye as the sighting dominant eye.

Pupil size and interpupillary distance were measured by taking a photograph of participants' eyes using a digital camera (DS126191; Canon, Tokyo, Japan) mounted at a distance of 105 cm. Photographs were flash-illuminated, and were taken while participants were adapted to a blank gray field ($27^\circ \times 31^\circ$ wide) with a luminance of 30 cd/m^2.

We measured near (equivalent to 40 cm) and far (equivalent to 6 m) horizontal and vertical phorias using the Keystone telebinocular (Mast Concepts, Reno, NV). Methods and results have been published elsewhere (Bosten et al., 2014).

2.3. TNO test

We used the sixteenth edition of the TNO test (Laméris Ootech, Nieuwegein, The Netherlands) presented at a distance of 40 cm,