Attentional Processing in Bistable Perception is Influenced by Genetic Effects Associated with Sinistrality.

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Abstract

Binocular rivalry displays and ambiguous figures such as the Necker cube elicit a perceptual reversal effect mediated by attentional and perceptual processes. Perceptual dominance times are highly variable between individuals and may be partially influenced by genetic factors. This study examined the role of putative genetic effects associated with familial sinistrality, derived from a novel pedigree-based genetic model. In a continuous Necker viewing task, dominance times were significantly correlated ($R^2 = .36$) with a multifactorial estimate of genetic effects associated with non right-handedness. No association with genetic estimates was found in an intermittent viewing condition. These results suggest that genetic factors associated with functional asymmetries may also affect noise-based perceptual alternation, but not short term visual memory.

Keywords: Bistable Perception; Attention; Individual Differences; Familial Sinistrality

Introduction

Functional cerebral lateralization has been proposed to arise from a combination of constraints on interhemispheric connectivity (Ringo, Doty, Demeter, & Simard, 1994) and the properties, such as excitability, of neural assemblies within each hemisphere (Levitan & Reggia, 2000). Cerebral lateralization, particularly for language, is often associated with individual hand preference as well as the handedness of close relatives (Tzourio-Mazoyer et al., 2010), suggesting a genetic contribution to functional asymmetry. Genetic effects associated with familial handedness may in turn be linked to subtle neurobiological differences, including the distribution of neurotransmitters involved in regulating neural excitability, noise or interhemispheric connectivity. We adopt a simple behavioral paradigm, the Necker cube viewing task, that may be sensitive to these factors at multiple time scales to identify possible associations between neural function and familial handedness.

A variety of ambiguous visual displays can induce bistable (or multistable) perception in observers, a state in which the subjective interpretation of the display alternates between perspectives. This can be induced through ambiguous figures (e.g. the Necker cube and Rubin's face/vase illusion), ambiguous motion or binocular rivalry displays in which different images are shown to each eye. Binocular rivalry displays allow more control over stimulus presentation and are more widely studied than ambiguous displays, but similar processes are assumed to drive alternation in both types of displays. Dominance times–the duration for which a particular interpretation is perceived–are highly variable between individuals (Aafjes, Hueting, & Visser, 1966) and may be partially influenced by genetic factors in both binocular rivalry

and Necker cube displays (Shannon, Patrick, Jiang, Bernat, & He, 2011). Several factors, including the visual properties of the stimuli (e.g. intensity (Levelt, 1967)), eye movements and attention, have been proposed to affect perceptual reversals.

Eye movements are related to perceptual reversals, but it is not clear that eye movements directly cause reversals. Fixating on one face of the Necker cube biases perception, but does not eliminate perceptual alternation, suggesting that reversals are not merely the result of scanning different areas of the visual field (Toppino, 2003). Scotto, Oliva, and Tuccio (1990) showed Necker cube images that were partially corrected for eye-movements which resulted in an increased reversal rate over normal viewing conditions, further suggesting that bistable perception is not merely a product of scanning eye movements across the visual field. van Dam and van Ee (2005) examined the relation between perceptual reversals and eye movements and found no correlation between reported reversals and involuntary micro-saccades, however saccades and eye blinks were suppressed prior to button presses. This suppression occurred both when subjects reported perceptual flips and experimentally controlled stimulus flips. The number of blinks and saccades did not decrease prior to random button presses that were unrelated to the stimulus. Thus, bistable perception appears to be related to a cognitive process that then directs visual attention, rather than the direct result of visual field changes.

The present study investigates individual variability in Necker cube dominance times as a function of putative genetic effects associated with hand preference. Handedness and familial sinistrality are known to affect lateralization of other brain functions, notably language (Tzourio-Mazoyer et al., 2010). Familial sinistrality has also been found to influence spatial processing (e.g. Mckeever (1986)) and resting brain states (Hancock, 2012), but has not been widely studied with respect to the cognitive processes involved in bistable perception. Although Necker cube viewing is typically not a lateralized task, fMRI and EEG studies suggest that the reversal phenomenon is right-lateralized, at least initially (Pitts, Martínez, Stalmaster, Nerger, & Hillyard, 2009; Britz & Pitts, 2011) and dominance time is associated with grey matter volume in the right, but not left, superior parietal lobe (Kleinschmidt, Sterzer, & Rees, 2012). Unilateral transcranial magnetic stimulation and caloric stimulation can disrupt binocular rivalry and Necker cube reversals (Miller et al., 2000), supporting bilateral contributions to bistable perception. While interhemispheric transfer across the corpus

may play some part in normal switching, it is unlikely to have a critical effect on dominance cycles (Miller et al., 2000; Pettigrew, 2001). Instead, Pettigrew suggests that a subcortical oscillatory mechanism, perhaps in the ventral tegmental area, may drive rivalry. A model of interhemispheric switching between two percepts is also difficult to reconcile with the similar dynamics found in multistable perception, including tristability (Wallis & Ringelhan, 2013).

Factors known to influence asymmetric brain function—such as familial sinistrality—may have effects on bistable perception, but these likely reflect neural differences within hemispheres that could contribute to lateralization during development (Levitan & Reggia, 2000). Specifically, we hypothesize that familial sinistrality may partially account for individual differences in neural excitability or noise, two critical parameters that determine dominance times in many models of bistable perception (e.g. Moreno-Bote, Rinzel, & Rubin, 2007). In addition, bistable perception offers an interesting test case for identifying such effects at multiple levels of processing. The two Necker cube viewing tasks used here—a continuous viewing and intermittent viewing condition—are likely to differentially recruit perceptual processes. Bistable perception recruits a fronto-parietal network of brain regions, presumed to reflect contributions of both frontal, higher-level attention processes and lower-level perceptual processes (Sterzer, Kleinschmidt, & Rees, 2009). Intermittent viewing conditions extend dominance times (Leopold, Wilke, Maier, & Logothetis, 2002), likely reflecting in increased role for visual memory processes in posterior brain regions. Functional studies suggest that brain asymmetries are multifactorial with partially independent factors controlling lateralization in brain regions associated with language, attention and vision (Liu, Stufflebeam, Sepulcre, Hedden, & Buckner, 2009). Genetic effects associated with familial sinistrality are proposed to influence one or more of these functions, which may be observed as individual variability in the continuous Necker cube task (reflecting contributions of attention and visual processing, modulated by short-term dynamics) or in the intermittent viewing task (reflecting primarily visual working memory or slow neural processes).

Genetic Models of Handedness

Most studies of familial handedness effects treat familial handedness as a categorical variable, broadly classifying subjects as those reporting only right-handed relatives (FS-) or reporting at least one non right-handed relative (FS+). Considering the low heritability of handedness (20-30%, Medland et al. (2009)), problems introduced by considering variable family sizes and family envelopes of interest (Bishop, 1990), and placing subjects who may have vastly different susceptibilities into the same group, categorical classification is likely to be an underpowered approach to studying genetic effects associated with handedness. Power can be increased substantially with the use of non-categorical measures of familial sinistrality, such as the proportion of left-handed relatives (Corey & Foundas, 2005), but these are not widely used. Even when more genetically informed familial handedness measures are used, these are sometimes based on a particular theory of genetic transmission and expression, thus confounding familial handedness effects with a specific, and likely incorrect, genetic model (e.g. McManus (1995)). Applying these theories to calculate the likelihood of individual genotypes (which might then be used a covariate) also requires assumptions regarding allele frequencies to be made. Recently, Karev (2011) proposed a quantitive measure of familial handedness based on weighting left-handed relatives by relatedness, finding that this measure correlates with hand preference measures.

In an effort to increase power and more robustly associate familial sinistrality effects with putative genetic effects, a standard multifactorial threshold model was used to estimate genetic load for left handedness in individual subjects. This model treats the phenotype as function of multiple genetic loci, each probably associated with small genetic effect, and multiple environmental effects. Unlike single gene models (Annett, 1985; McManus, 1991; see McManus, Davison and Armour (in press) for a multi-locus variant of the dextral chance model), this approach does not assume that the genetic component of the phenotype is controlled largely or entirely by posited genes with a given transmission probability and penetrance, however it can account for such effects when alleles make additive contributions to the phenotype (as is this case in McManus's model). This approach extends Karev (2011) by considering not only the relatedness of left-handed relatives but also their expected genetic effects. This is similar to McManus (1995), but relies only a standard multifactorial model, as opposed to a particular major gene model. The basic assumption of the multifactorial genetic model is that multiple loci additively contribute to a continuous phenotype and interact with environmental effects. For example, a multifactorial model of height would assume a set of loci with alleles at each loci adding or subtracting a small amount from the phenotype. The summed contribution of these alleles is the *additive genetic effect* or *genetic load*. The genetic effect interacts with environment, for example hormones or nutrient levels, to produce the expressed phenotype. Formally, we can consider the contribution of genes to a phenotype as being described by the linear model

$$y = X\beta + Aa + e. \tag{1}$$

where y is the measured phenotype, X is a matrix of observations for fixed effects (sex and founder status, in this case), β is the vector of fixed effects, a is the vector of additive genetic effects and e is a vector of environmental effects. A is an $n \times n$ matrix describing how n individuals are related in terms of their expected allele sharing. For example, $A_{i,j} = .5$ indicates that individuals i and j share (theoretically) 50% of their genes, i.e. i and j are siblings or a parent/offspring pair. For simplicity, we consider only autosomal effects.

We employ the Bayesian formulation of (1)

$$y|\beta,a,\sigma_e^2 \sim N(X\beta+Aa,I\sigma_e^2) \tag{2}$$

with

$$a|A,\sigma_a^2 \sim N(0,A\sigma_a^2) \tag{3}$$

and an uninformative prior for fixed effects β, e.g.

$$\beta \sim N(0,10^6) \tag{4}$$

For binary phenotypes, we assume that the observed phenotype is obtained by thresholding a latent continuous variable (the *liability*) (Falconer, 1965). If the liability, ℓ, exceeds a threshold value t_0 (say $t_0 = 0$, since the liability distribution can be shifted arbitrarily), then the binary phenotype (e.g. disease or left-handedness) is expressed. The liability is distributed as in (2)

$$\ell|\beta,a,\sigma_e^2 \sim N(X\beta+Aa,I\sigma_e^2). \tag{5}$$

where ℓ is mapped to a categorical phenotype $c = 1,2,\ldots,k$ by the partition

$$t_0 < t_1 < t_2 < \ldots < t_{k-1} < t_k. \tag{6}$$

so that

$$\Pr(y_i = c|l_i,t_{c-1},t_c) = \begin{cases} 1 & t_{c-1} < l_i \le t_c \\ 0 & \text{otherwise.} \end{cases} \tag{7}$$

Fitting this model to family pedigrees provides a posterior distribution of additive effects for each individual in the pedigree that can be then be used as a covariate.

Pedigrees

Data for fitting the model were obtained from a survey of hand preferences for blood relatives distributed to 4561 students in introductory psychology courses at the University of Arizona. Respondents were asked to report hand preferences (left, right, ambidextrous or unknown) for each parent and grandparent. For brothers, sisters, aunts and uncles, respondents were asked to provide the number of relatives in each relation with left, right, ambidextrous or unknown hand preference from the options 0, 1, 2 and "3 or more" (coded as 3 relatives). Respondents also reported their sex, hand preferences for writing, drawing and throwing a ball (on a five point scale from 'strong left' to 'strong right') and foot preference for kicking a ball. Respondents were considered right-handed if they reported a 'moderate right' or 'strong right' preference for writing hand, ambidextrous if they reported 'no preference' and left-handed if they reported a 'strong left' or 'moderate left' hand preference. Respondents were not given any criteria for determining relatives' handedness. A similar questionnaire was administered to each experimental participant.

Since the observed liability for right-handed individuals is always below threshold, purely right-handed families are uninformative with respect to random effect estimates, i.e.

the posterior distribution of additive genetic effects is fixed by the prior distribution. To improve the mixing properties of the model, effects were estimated only for individuals in FS+ families and individuals with missing data who did not form an ancestral link in a given pedigree were removed from the pedigree. For example, avuncular relatives and grandparents of unknown handedness were removed, but a parent of unknown handedness who had multiple children of known handedness would be retained. Families with fewer than three phenotype individuals were also removed. Pedigrees were pruned using the `prunePed` function in the R `MCMCglmm` package (Hadfield, 2010). Phenotypes of the remaining unknown individuals were replaced at random, conditional on known family members. Convergent logit models were estimated with MCMCglmm using a slice sampling Monte Carlo Markov chain (MCMC) algorithm with block updating (Sorensen & Gianola, 2002; Hadfield, 2010) for 2,500,000 iterations with a burn in period of 500,000 iterations and thinning interval of 100.

Methods

Participants

Nineteen participants (10 female) with no reported non right-handed relatives and 26 (14 female) participants with at least one reported left-handed relative, all native English speakers, were recruited from introductory psychology courses at the University of Arizona, Tucson, AZ, USA and received course credit for participation. Participants were screened by self report for history of brain injury, neurological and psychiatric disorders, medication, and normal vision. Research was approved by the University of Arizona Institutional Review Board.

Procedure

A white-on-black Necker cube (Figure 1A) was presented, centered on a 15 inch LCD display at a viewing distance of 15 inches. Stimuli subtended a visual angle of approximately 4 degrees. Stimuli were presented using the MATLAB-based (Mathworks, Natick, MA) Psychtoolbox (Brainard, 1997) on Windows XP. Participants were seated at eye level with the center of the display using a chin rest to minimize movement. Participants were instructed to focus on a small cross in the center of the Necker cube, to avoid deliberately switching perspectives and to report perspective changes by pressing a key corresponding to the new perspective. The left and right arrow keys of a standard keyboard were labeled with images of the "left" (Figure 1B) and "right" (Figure 1C) perspectives, respectively. Participants were instructed to respond with the first and second fingers of their right hand and were familiarized with the two perspectives prior to the experiment. The experiment consisted of a continuous viewing condition, designed to elicit spontaneous perceptual reversals followed by an intermittent viewing condition designed to extend dominance times (Leopold et al., 2002) and recruit memory processes (Pastukhov & Braun, 2008) or slow neural dynamics.
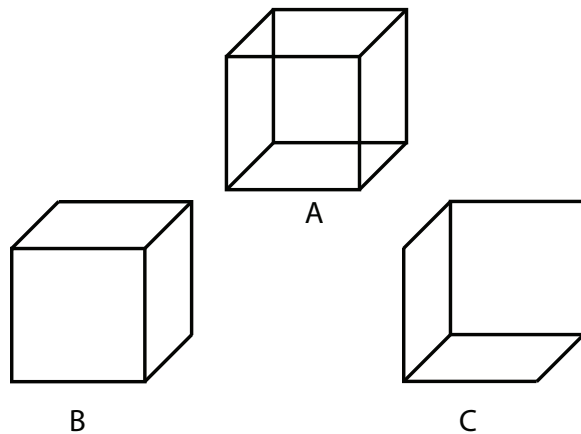
Figure 1: A Necker cube (A) and the perceived left (B) and right (C) perspectives.

In the continuous viewing condition, the Necker cube was continuously presented during four blocks, with self-paced breaks between each block. In each block, the complete Necker cube was shown for 200 seconds. As a check for random responses, one perspective, selected at random, of the complete Necker cube was reduced in intensity over 30 seconds to gradually produce a partially unambiguous cube and a corresponding increase in dominance time. This process began 0-30 seconds (uniformly distributed) after the end of each block, followed by a 30 second presentation of the complete Necker cube. In the intermittent viewing condition, participants saw an alternating sequence of a Necker cube followed by a fixation screen without the cube. On each intermittent trial, the Necker cube was shown for 750, 1225 or 2000 ms followed by a fixation screen for 1000, 2236 or 5000 ms. All combinations of stimulus duration and inter stimulus interval (ISI) were repeated 24 times. Participants reported their perspective at the beginning of each trial and again if a reversal was experienced.

Results

Log-transformed dominance times, defined as the time between alternate-side button presses, were analyzed using linear mixed effects models with random intercepts per subject and sex, block, perspective and genetic load as fixed effects. Likelihood ratio tests were used to select models. Reported p-values were estimated using MCMC as implemented in the `languageR` package (Baayen, 2007).

Continuous Viewing

Dominance time increased for all participants during the partially disambiguated display periods ($M = 11.88$ sec, $SD = 6.94$), indicating their responses were not stimulus-independent. No significant effect of sex or block was found. There was a significant positive association between additive genetic effects and dominance time ($\beta = .68, p = .005$).

Dominance times were significantly shorter for the "right" perspective ($\beta = .47, p < .001$).
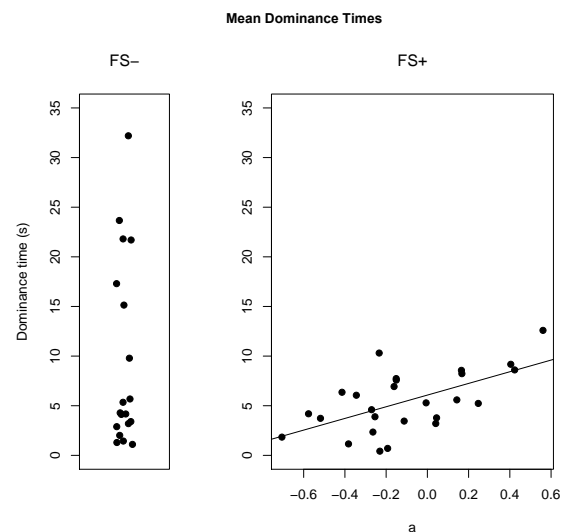

Figure 2: Correlation ($R^2 = .36$) between continuous viewing dominance times and estimated additive genetic effects (a). FS- individuals are shown for comparison only.

Intermittent Viewing

Intermittent viewing times were uncorrelated with continuous viewing times ($r = -.05$, $p = .74$) or estimated genetic effects ($r = .13$, $p = .53$; Figure 3) and were significantly longer ($M = 17.84$ sec, $SD = 17.65$) than continuous dominance times ($t(43) = 6.70, p < .001$).

Discussion

Increasing estimated genetic load for non right-handedness in right-handed subjects was associated with increased dominance times in the continuous viewing condition. Although no control for differences in overall motor response speed as a function of familial sinistrality was included, the increase in dominance time during disambiguated display periods and intermittent viewing suggests that participants' responses were directly related to the perceived orientation of the Necker cube. Current models of bistable perception propose that reversals are the result of an interaction between parietal/occipital perceptual and visual working memory processes and noisy frontal attentional processes (Sterzer et al., 2009). In the context of these models (Gigante, Mattia, Braun, & Del Giudice, 2009; Moreno-Bote et al., 2007), the dissociation between familial sinistrality effects in the continuous and intermittent viewing conditions suggests that the genetic effects of interest selectively act on frontal processes or the interaction between frontal and parietal regions.

No group differences were found when familial sinistrality was considered as a dichotomous variable. Although the FS-
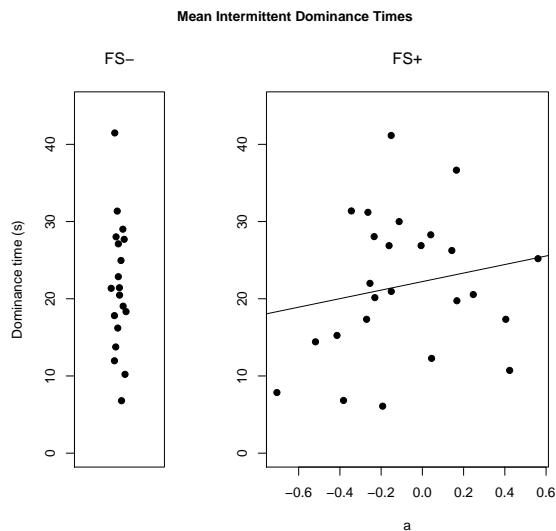
Mean Intermittent Dominance Times

Figure 3: Correlation between intermittent viewing dominance times and estimated additive genetic effects (a). FS-individuals are shown for comparison only.

group might be expected to have fewer genetic effects found in the FS+ group, and therefore show an overall group difference in dominance times, the obtained result is consistent with a gene-gene interaction model for handedness. Under this model, the estimated genetic effects, a, associated with phenotypic handedness may be decomposable into alleles that influence bistable perception and possibly other aspects of cognition and brain organization (a_b) and one or more alleles (a_h) that contribute to hand preference in the presence of a_b effects. Thus the FS- and FS+ groups may have similar distributions of a_b effects and dominance times while the FS- group lack the a_h alleles needed to express non right-handedness in conjunction with a_b alleles. With handedness as a phenotype, the a_b effects of interest can only be estimated in conjunction with a_h effects and not at all in the FS- group.

These findings validate the utility of applying a multifactorial genetic model of handedness to account for individual differences in cognitive behavior and support views of lateralization and related brain function as a complex trait, both in terms of phenotype and genetics. The neural mechanisms of the familial sinistrality-related increase in dominance times are unknown, but likely reflect differences in attentional processing or the coupling of attentional and visual levels of processing. The increases in dominance times could reflect changes at the local circuit or neurotransmitter level leading to decreased levels of neural noise that trigger perceptual reversals (e.g. Moreno-Bote et al., 2007) .

Acknowledgments

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