

Genes contribute to the switching dynamics of bistable perception

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Ordinarily, the visual system provides an unambiguous representation of the world. However, at times alternative plausible interpretations of a given stimulus arise, resulting in a dynamic perceptual alternation of the differing interpretations, commonly referred to as bistable or rivalrous perception. Recent research suggests that common neural mechanisms may be involved in the dynamics of very different types of bistable phenomena. Further, evidence has emerged that genetic factors may be involved in determining the rate of switch for at least one form of bistable perception, known as binocular rivalry. The current study evaluated whether genetic factors contribute to the switching dynamics for distinctly different variants of bistable perception in the same participant sample. Switching rates were recorded for MZ and DZ twin participants in two different bistable perception tasks, binocular rivalry and the Necker Cube. Strong concordance in switching rates across both tasks was evident for MZ but not DZ twins, indicating that genetic factors indeed contribute to the dynamics of multiple forms of bistable perception.

Keywords: binocular vision, perceptual organization, visual development

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Introduction

Human vision is efficient and often provides unambiguous representations of the environment. However, under certain circumstances, the same visual input can lead to multiple interpretations. Well-known examples of this phenomenon include Rubin's Vase/Face Illusion, Boring's Old Woman/Young Woman Illusion, and the Necker Cube. Though all of these examples fall under the general heading of bistable images, it is clear that each example is unique in what makes the image bistable. In the case of Rubin's Vase/Face Illusion, bistability in the image results from ambiguity in the parsing of background from foreground or border-ownership assignment. In the case of Boring's Old Woman/Young Woman Illusion, ambiguity arises at the level of grouping and face recognition, and in the case of the Necker Cube, surface depth ambiguity is the cause of bistable perception of the cube. Even more unique is the case of binocular rivalry, in which bistability arises

from conflicting information processed by each of the two eyes at corresponding retinal locations; the result is a stochastic alternation in percept between the two inputs.

A key property of bistable perception is the spontaneous nature of the perceptual alternations. The two percepts will alternate even if an observer attempts to maintain one percept. In addition, different bistable images seem to switch at different rates. In the case of binocular rivalry, the rate of percept alternation is also strongly dependent on the image properties (e.g., contrast, location in the visual field, context of stimuli, etc.; Blake & Logothetis, 2002) and, less clearly understood, on factors intrinsic to observers, such as attention (Meng & Tong, 2004; Paffen, Alais, & Verstraten, 2006) and serotonin levels in the brain (Carter, Pettigrew et al., 2005; Nagamine, Yoshino, Miyazaki, Takahashi, & Nomura, 2008). The finding that meditation can have a dramatic effect on rivalry switch rate (Carter, Presti et al., 2005) is also relevant.

Interestingly, even for the same bistable stimulus, switching rate can be very different across individuals,

though reasonably stable in the same individual. Why would different observers experience bistable perceptual switching at different rates? The goal of this study was to investigate whether there are genetic factors that influence the rate of perceptual alternations.

Although the exact neural mechanism behind binocular rivalry remains unknown, it has been proposed that rivalry is the result of a combination of inhibitory cortical circuitry and self-adaptation of the dominant stimulus that gives rise to the stochastic alternation (Kang & Blake, 2010). Given that switch rate is relatively stable for an individual when extrinsic conditions are held constant but still varies across individuals (Aafjes, Huetting, & Visser, 1966), it is possible that individual differences in rivalry rate are the result of individual differences in adaptation or inhibitory circuitry. In the case of binocular rivalry, a recent study by Miller et al. (2010) provides evidence of a heritable basis for individual differences in perceptual switch rate. Specifically, these investigators measured binocular rivalry switch rates in a large sample of monozygotic (MZ) and dizygotic (DZ) twins aged 14 to 16 years of age and found evidence of both additive and non-additive genetic contributions to switch rate in binocular rivalry.

However, a question that remains to be addressed is whether genetic factors contribute to switch rates across different bistable phenomena. As mentioned earlier, distinctive mechanisms contribute at least in part to perceptual switching in different types of bistable perception. Among them, binocular rivalry is particularly unique in that the competition originates from an inconsistency between the two eyes. However, despite the apparent distinctiveness of different bistable phenomena, some research (e.g., Carter & Pettigrew, 2003) suggests the existence of common factors that influence the dynamics of diverse types of bistable perception.

In the current study, we sought to investigate this possibility further by examining concordance of switch rates across two different types of bistable perception—binocular rivalry and the Necker Cube—in MZ and DZ twin participants. This enabled us to test the generalizability of a prior study demonstrating the heritability of individual variations in switch rates for binocular rivalry (Miller et al., 2010) and, additionally, to expand the search for the presence of a genetic factor that contributes to individual variations in the switch rate of multiple forms of bistable phenomena. We also measured autonomic activity in the form of heart rate during viewing of the bistable images. This allowed us to evaluate whether individual variations in switching rates of bistable perception might reflect a more general heritable characteristic related to physiological arousal or metabolic activity, as opposed to processes that are more specifically related to sensory neural mechanisms (e.g., inhibitory input and adaptation). For example, it has been shown that caffeine increases both binocular

rivalry rate and heart rate (George, 1936), whereas ethanol decreases binocular rivalry rate and heart rate (Donnelly & Miller, 1995).

Methods

Participants

Subjects consisted of 122 same-sex twin pairs (244 individuals overall) recruited from the Minnesota Twin and Family Study database as part of a larger test protocol. In 18 cases, only one twin participated in the study. Twins with no paired twin data were removed from further analysis, leaving 56 pairs of MZ twins (22 female pairs) and 48 pairs of DZ twins (15 female pairs), ages 23–38, included in Experiment 1. A subset of these subjects, consisting of 26 MZ twin pairs (9 female pairs) and 20 DZ twin pairs (4 female pairs), participated in Experiment 2. Subjects were screened for any significant visual impairments including acuity and color blindness. All subjects received informed consent and were compensated for their participation as approved by the Institutional Review Board at the University of Minnesota. All subjects were naive as to the aims of the study.

Equipment

Stimuli were presented on a 17" CRT monitor with a resolution of 1024×768 pixels and a refresh rate of 85 Hz. Subjects were seated 100 cm from the screen, yielding a viewing angle of 2 degrees for stimuli. Binocular rivalry was established by having participants view overlapping color-filtered images on the monitor screen through red–green anaglyph glasses. Stimulus presentations and trial timing were controlled using the Matlab software package with the PsychToolbox (Brainard, 1997; Pelli, 1997).

Heart rate (HR) data were collected using bipolar electrodes attached to each forearm at the level of the elbow and connected to a Neuroscan Synamps II amplifier. Recordings were made using Neuroscan software and processed offline using Matlab.

Procedures

Participants viewed bistable stimuli through red–green anaglyph glasses while HR data were continuously recorded. In the binocular rivalry condition (Experiment 1), the left eye was presented with a green radial grating and the right eye with a red circular grating (see Figure 1a). To ensure clarity of the task, a practice screen (also depicted in Figure 1) was shown to the participant while initial

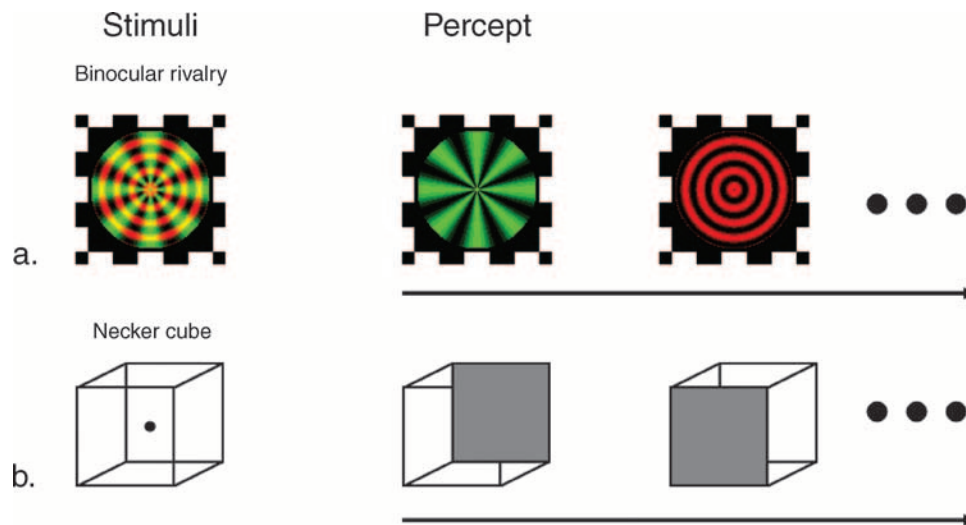


Figure 1. Experimental design and stimuli. (a) Following a brief practice session, subjects viewed red–green circular and radial gratings through red–green filtered anaglyph glasses resulting in a stochastic alternation in visual perception between the two images (binocular rivalry). Stimuli were presented for two 30-s blocks with a 10-s rest block in between. (b) Experimental design was repeated using a Necker Cube stimulus.

instructions were given. Participants were instructed to view the test image and press one button when the image appeared like the green radial grating and another button when the image appeared like the red circular grating. Subjects were instructed to press the appropriate button once each time their perception switched. Following the practice session, participants viewed the dichoptic stimulus for two 30-s trials, separated by a 10-s break in which a blank screen appeared. A subset of participants (20 DZ twin pairs [4 female pairs] and 26 MZ twin pairs [9 female pairs]) also viewed a bistable Necker Cube stimulus under experimental conditions (Experiment 2; see Figure 1b) that were the same except that the anaglyph glasses were not worn.

Data analyses

Since we were interested in the extent to which rate of switch is attributable to genetic influence, subjects who did not indicate any switch in the rivalrous stimulus over the length of one full (30 s) experimental block (i.e., 2 MZ pairs and 1 DZ pair in Experiment 1, 4 MZ pairs and 3 DZ pairs in Experiment 2) were deemed ineligible and omitted from further analyses.

We first examined the consistency of switching rate within individuals when extrinsic factors were held constant. We then used intraclass correlational analyses to compare switching rates between MZ and DZ twins for each of the two tasks to establish general heritability across differing bistable phenomena. Next, we tested for evidence of common dynamics in differing bistable phenomena by comparing switching rates for individuals across tasks and for members of twin pairs across tasks using cross-twin,

cross-task correlations. For correlations of this latter type, each twin with data for both the Necker Cube and binocular rivalry tasks was included twice in the analysis, once for each task. A positive correlation between tasks would suggest the existence of genetic factors that contribute to more global factors involved in determining switching dynamics. Finally, we tested the specificity of these possible global factors by examining the relationship between heart rates and switching rates in both tasks.

Results

For both MZ and DZ participants in each of the task procedures, correlational analyses revealed that switch rates during blocks 1 and 2 were highly correlated: $r_s = 0.72$ and 0.78 , respectively, $p_s < 0.0005$, for binocular rivalry; $r_s = 0.83$ and 0.70 , respectively, $p_s < 0.0005$, for the Necker Cube (Figure 2). This result indicates high within-subject reliability for switching rate for both binocular rivalry and the Necker Cube perception. Next, using intraclass correlations to index similarity between twin pairs, we found that the perceptual switch rates in binocular rivalry were strongly correlated for MZ twins ($r = 0.54$, $F[1, 53] = 3.36$, $p < 0.0005$) but not for DZ twins ($r = 0.017$, $F[1, 46] = 1.04$, $p > 0.45$; see Figure 3a). Similarly, we found that the perceptual switch rates for the Necker Cube were strongly correlated for MZ ($r = 0.57$, $F[1, 21] = 3.61$, $p < 0.002$) but not DZ twins ($r = 0.057$, $F[1, 16] = 1.12$, $p > 0.41$; Figure 3b). Differences in the magnitude of correlation coefficients for MZ and DZ twins were then evaluated

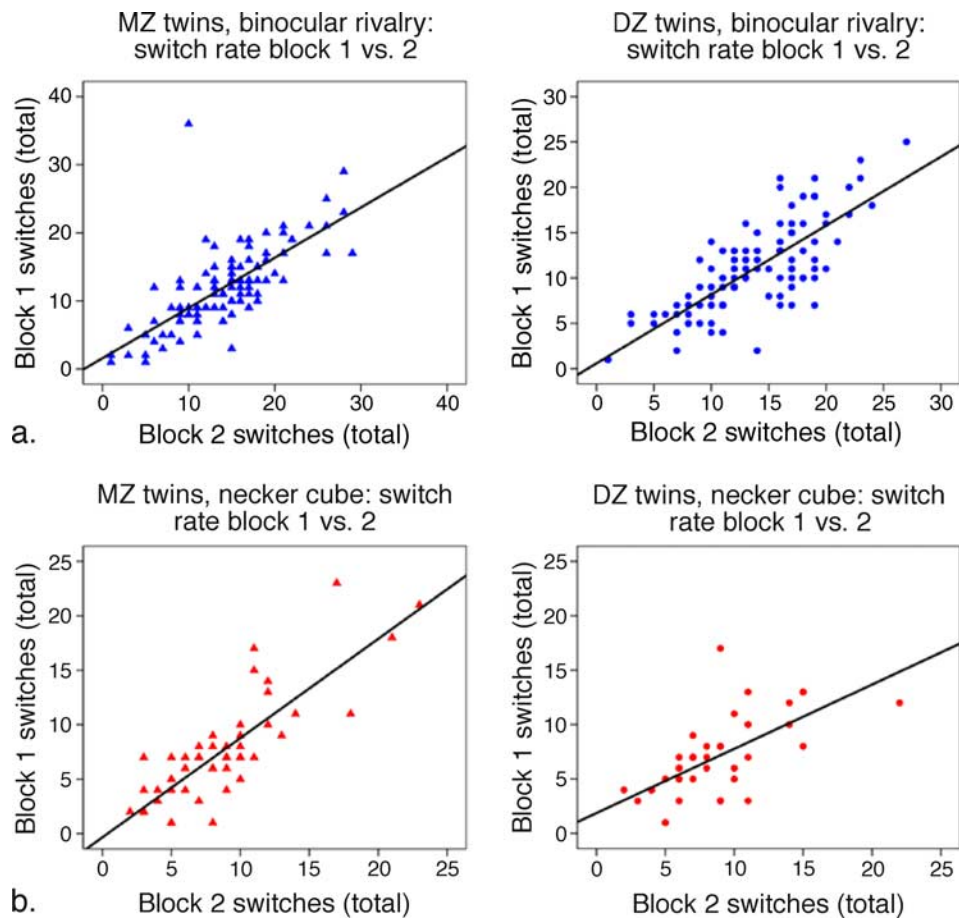


Figure 2. Interblock switch rate reliability. Switch rates for block 1 and block 2 were highly correlated for MZ and DZ twins (a) for binocular rivalry ($r_s = 0.72$ and 0.78 , respectively, $p_s < 0.0005$) and (b) for the Necker Cube task ($r_s = 0.83$ and 0.70 , respectively, $p_s < 0.0005$).

for significance by transforming raw intraclass correlation coefficients to Fisher's Z metric and performing an F -test of the one-tailed null hypothesis that $r_{MZ} = r_{DZ}$. These follow-up analyses demonstrated that r_{MZ} indeed exceeded r_{DZ} for both the binocular rivalry ($p < 0.01$) and the Necker Cube ($p < 0.05$) tasks. These results provide further support for previous claims that binocular rivalry switching rate is partly heritable (Miller et al., 2010).

In addition, our data allowed us for the first time to directly compare heritability across bistable phenomena in the same individuals. Since a smaller number of subjects participated in the Necker Cube task, a supplemental analysis was performed in which binocular rivalry data were examined only for those subjects who also participated in the Necker Cube task (21 DZ twin pairs [4 females] and 26 MZ twin pairs [9 females]). Results of this analysis were consistent with those for the analysis that incorporated all subjects (MZ twins: $r = 0.57$, $F[1, 25] = 3.66$, $p < 0.001$; DZ twins: $r = -.11$, $F[1, 19] = 0.80$, $p > 0.69$; $r_{MZ} > r_{DZ}$, $p < 0.01$).

Further, across participants as a whole (i.e., regardless of twin status), switch rates for binocular rivalry correlated robustly with those for the Necker Cube, $r = 0.47$, $p < 0.0005$ (see Figure 4a). However, cross-twin, cross-task

correlations revealed that switching rates for one twin in the binocular rivalry task significantly predicted switching rates for the other twin in the Necker Cube task among MZ twin pairs only, $r = 0.37$, $p < 0.01$ (for DZ twin pairs, $r = -0.20$, $p > 0.23$; $r_{MZ} > r_{DZ}$, $p < 0.01$; see Figure 4b).

Analyses of the HR data revealed no correlation between switch rate and HR level for either task (binocular rivalry, Necker Cube), either across participants as a whole ($r = -0.081$, $p > 0.25$; $r = 0.035$, $p > 0.74$, respectively) or across co-twins within MZ ($r = 0.061$, $p > 0.53$; $r = 0.075$, $p > 0.62$, respectively) or DZ ($r = -0.14$, $p > 0.20$; $r = 0.23$, $p > 0.17$, respectively) subsamples. This result indicates that the observed concordance in switch rate between MZ twins is not simply a reflection of concordance in overall arousal or activation.

Discussion

Results of the current investigation demonstrate a heritable basis for individual differences in binocular rivalry, consistent with the findings of another recent

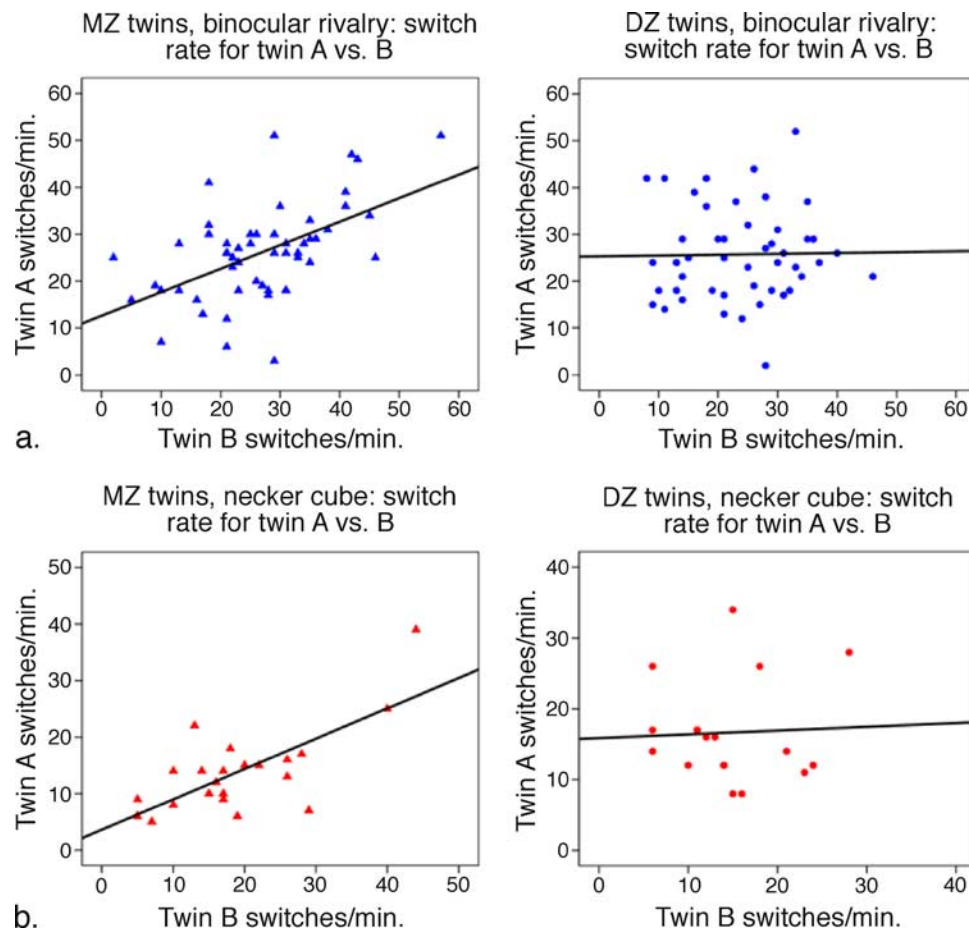


Figure 3. Switch rate correlations for MZ and DZ twins during presentations of (a) binocular rivalry and (b) Necker Cube. Using intra-class correlational analysis, we found moderate-level concordance in switch rates between MZ ($r = 0.54$, $p < 0.0005$) but not DZ ($r = 0.017$, $p > 0.45$) twins for the binocular rivalry procedure (a). Similarly, we found moderate concordance in switch rates between MZ ($r = 0.57$, $p < 0.002$) but not DZ ($r = 0.057$, $p > 0.41$) twins in the bistable figure (Necker Cube) procedure (b). [Note: The correlation for MZ twins in the Necker Cube task remained robust ($r = 0.49$, $F[1,21] = 2.96$, $p < 0.008$) even when scores for the two most extreme twin pairs, evident in the left plot of (b), were Winsorized (reined-in) to a value of 2 SDs from the mean.]

study (Miller et al., 2010). We also extended this prior work by demonstrating significant heritability of switch rates for the Necker Cube procedure in the current twin participant sample. The current study also demonstrated higher concordance for MZ as compared to DZ twins in switch rates *across* the two types of bistable perception. This finding provides support for the idea that similar genes are involved in determining the dynamics of switching for multiple forms of bistable perception, possibly through a shared neural mechanism.

Given these results, our data are consistent with recent theories positing common factors involved in bistable switch (Carter & Pettigrew, 2003) and suggest further that these factors may be heritable. However, it remains unclear what such factors represent in neural terms. One possibility evaluated in the current study was that general physiological or metabolic rate differences across individuals might contribute to variations in switching rates, given evidence that factors that influence physiological arousal as indexed

by heart rate activity can also influence binocular rivalry (George, 1936). Specifically, to test the hypothesis that common heritable factors contribute to perceptual switch rate indirectly, through an impact on cardiovascular activity, we collected heart rate data from participants during the two tasks and evaluated it in relation to switch rates. We found no correlation between heart rate and switching rate for either twin subsample (MZ, DZ) in either bistable perception task, suggesting that switch rate differences in bistable perception across individuals reflect individual differences in relatively specific neural mechanisms.

Nonetheless, further systematic research is needed to establish precisely what neural mechanisms determine the dynamics of bistable perception. A recent study by Kang and Blake (2010) posits that binocular rivalry dynamics are determined by a combination of intrinsic noise, inhibitory signaling, and adaptation of the stimulus. If genetic factors do in fact contribute to the rate of switching for rivalrous stimuli, further systematic research is needed

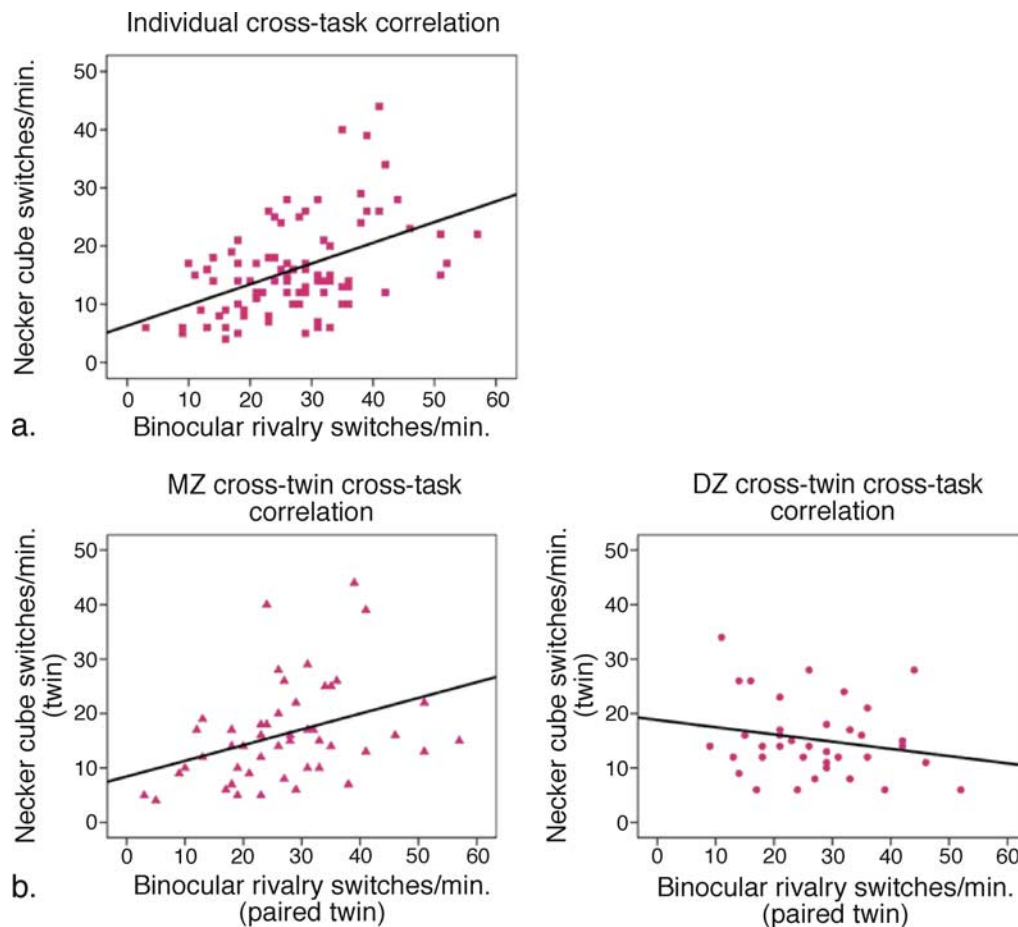


Figure 4. Between-task switch rate correlations. (a) Using simple correlational analysis in the sample as a whole, binocular rivalry switch rates for individuals were found to correlate robustly ($r = 0.47$, $p < 0.0005$) with their bistable figure (Necker Cube) switch rates. (b) Cross-twin, cross-task correlations. Analyses of switch rate concordance for twin pair members across the two tasks revealed significant positive correspondence for MZ twins, $r = 0.37$, $p < 0.01$, but not for DZ twins, $r = -0.20$, $p > 0.23$.

to determine the degree of heritability of each of these components, their respective contributions to switch rates for binocular rivalry and Necker Cube tasks, and whether similar or common mechanisms can account for dynamics in other types of bistable phenomena.

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