

diversity increases with distance from *MAT*, the ratio of within-tetrad mating to haplo-selfing could be estimated. And from the frequency of heterozygotes it was then possible to estimate the within-tetrad mating rate as 94%, the haplo-selfing mating rate as 5%, and the between-tetrad mating rate as 1% — the first estimates of these important life cycle parameters from wild populations.

These estimates of the frequencies of different modes of mating are population averages. Like the different potential responses to nutrient depletion, their different adaptive functions are not clear but it seems likely that they could be modulated according to environmental or ecological cues. For example, the tetrad ascus may normally promote automixis to preserve locally adapted gene complexes. But ascii eaten by *Drosophila* are digested, freeing the digestion-resistant spores to mate with those from other tetrads, potentially increasing genetic variation in response to dispersal to new habitats.

Whilst oak-associated *S. paradoxus* strains are homothallic homozygous diploids, *S. cerevisiae* isolates are often heterothallic — with a non-functional *HO* allele, unable to switch haploid mating type — heterozygous, and polyploid. These differences may reflect the environments that were sampled rather than any intrinsic differences between the species. The genetic redundancy produced by whole genome duplication might confer benefits such as increased resistance to deleterious mutations and greater adaptive potential, so it may be favoured in harsh or novel environments. In laboratory experiments, polyploid or aneuploid cells were often observed when yeast adapt to stressful conditions, suggesting that yeast cells can benefit from gross changes in their genome contents. The fact that the *Saccharomyces sensu stricto* yeasts have evolved from an ancient tetraploid underscores the potential importance of major chromosomal changes in yeast.

What next?

Yeast technology began when mankind learned how to brew a

pleasant drink, and it has since developed unprecedented scientific power. This power is now being applied to ecology and evolution, with several impressive initial successes. This is not merely a good application of yeast technology to a new field, it is also a way to increase the power of that technology further. We cannot properly interpret the enormous data being produced from model laboratory yeast without knowledge about the environment that yeast evolved in. Determining the natural history of yeast is a daunting challenge but metagenomics, the analysis of environmental DNA without laboratory culturing, offers the possibility of unbiased sampling of the microbial communities in which yeast live. With sufficient knowledge of the abundance of yeast in space and time, combined with further population genetic and experimental methods, we can perhaps start to see the world from a yeast's point of view.

Further reading

- Gore, J., Youk, H., van Oudenaarden, A. (2009). Snowdrift game dynamics and facultative cheating in yeast. *Nature* 459, 253–256.
- Greig, D. (2008). Reproductive isolation in *Saccharomyces*. *Heredity* 102, 39–44.
- Kuehne H.A., Murphy H.A., Francis C.A., Sniegowski P.D. (2007). Allopatric divergence, secondary contact and genetic isolation in wild yeast populations. *Curr. Biol.* 17, 407–411.
- Lee, H.Y., Chou, J.Y., Cheong, L., Chang, N.H., Yang, S.Y., and Leu, J.Y. (2008). Incompatibility of nuclear and mitochondrial genomes causes hybrid sterility between two yeast species. *Cell* 135, 1065–1073.
- Liti, G., Carter, D.M., Moses, A.M., Warringer, J., Parts, L., James, S.A., Davey, R.P., Roberts, I.N., Burt, A., Koufopanou, V. *et al.* (2009). Population genomics of domestic and wild yeasts. *Nature* 458, 337–341.
- Mortimer, R.K. (2000). Evolution and variation in the yeast (*Saccharomyces*) genome. *Genome Res.* 10, 403–409.
- Page, M. (1993). Honest signaling among gametes. *Nature* 363, 539–541.
- Replansky, T., Koufopanou, V., Greig, D., and Bell, G. (2008). *Saccharomyces sensu stricto* as a model system for evolution and ecology. *Trends Ecol. Evol.* 23, 494–450.
- Ruderfer, D.M., Pratt, S.C., Seidel, H.S., and Kruglyak, L. (2006). Population genomic analysis of outcrossing and recombination in yeast. *Nat. Genet.* 38, 1077–1081.
- Tsai, I.J., Bensasson, D., Burt, A., Koufopanou, V. (2008). Population genomics of the wild yeast *Saccharomyces paradoxus*: quantifying the life cycle. *Proc. Natl. Acad. Sci. USA* 105, 4957–4962.
- Tsong, A.E., Tuch, B.B., Li, H., and Johnson, A.D. (2006). Evolution of alternative transcriptional circuits with identical logic. *Nature* 443, 415–420.

¹Department of Biology, University College London, London, UK. ²Institute of Molecular Biology, Academia Sinica, Taipei, Taiwan. E-mail: d.greig@ucl.ac.uk; jleu@imb.sinica.edu.tw

Correspondences

Developmental dyslexia is characterized by the co-existence of visuospatial and phonological disorders in Chinese children

Wai Ting Siok^{1,2}, John A. Spinks^{1,3}, Zhen Jin⁴, and Li Hai Tan^{1,2}

Developmental dyslexia is a neurological condition that is characterized by severe impairment in reading skill acquisition in people with adequate intelligence and typical schooling [1–3]. For English readers, reading impairment is critically associated with a phonological processing disorder [3–5], which may co-occur with an orthographic (visual word form) processing deficit [6], but not with a general visual processing dysfunction in most dyslexics [7]. The pathophysiology of dyslexia varies across languages [8]: for instance, unlike English, written Chinese maps visually intricate graphic forms (characters) onto meanings; pronunciation of Chinese characters must be rote memorized. This suggests that, in Chinese, a fine-grained visuospatial analysis must be performed to activate characters' phonology and meaning; consequently, disordered phonological processing may commonly co-exist with abnormal visuospatial processing in Chinese dyslexia. To test this hypothesis, we conducted an fMRI experiment in which 12 Chinese dyslexics, shown previously [9] to exhibit a phonological disorder, performed a physical size judgment measuring visuospatial dimensions. Compared with 12 control subjects, the dyslexics showed weaker activations in left intraparietal sulcus (IPS) mediating visuospatial processing. Analyses of individual dyslexics' performances further suggest that developmental dyslexia in Chinese is commonly associated with the co-existence of a visuospatial deficit and a phonological disorder.

We previously found that, relative to typically developing reading, dyslexic reading in Chinese is manifested by a phonological disorder, as indexed by weak activity of left middle frontal gyrus (LMFG) in a rhyme-judgment task, in contrast to a physical size decision baseline [9]. We have now used data from that previous study in a novel analysis that focuses on brain activations for physical size decisions (Figure 1A), contrasted with a fixation baseline in order to elucidate whether the phonological disorder co-exists with a visuospatial disorder.

We first calculated activation maps by contrasting brain activity during the physical size judgment and the fixation conditions (Figure 1B,C; see Supplemental data for experimental details). We then directly compared brain activities between normal and dyslexic readers ($p < 0.05$ FDR corrected). Stronger activation was seen in two regions for normal controls (Figure 1D): the left IPS, crucial for the goal-directed detection of the physical sizes of visual stimuli [10], and the lingual gyrus subserving visual analysis of objects. The dyslexics, however, exhibited greater activation than normal subjects in right IPS relevant to non-goal-directed, bottom-up, visuospatial processing [10] (Figure 1E), presumably to compensate the weak and sluggish processing networks in the left homologues. These group results suggest that neural processing of visually-guided spatial properties is disrupted in Chinese dyslexia.

To determine whether visuospatial and phonological disorders co-exist in each of our individual subjects, we computed each dyslexic reader's activations in left IPS and LMFG (Figure 1F). In both regions, ten of the twelve dyslexics exhibited weaker activations than average activity levels of normals. Two dyslexics showed a dissociation pattern: weaker activation in the phonological task but stronger activation in the visuospatial task. This individual variability analysis shows that visuospatial and phonological disorders co-exist in the majority (83.33%) of Chinese dyslexics.

How might the two disorders co-occur in dyslexic reading? One possibility is that they correlate with each other, with the visuospatial disorder being a marker of more fundamental perceptual problems that may mediate the phonological

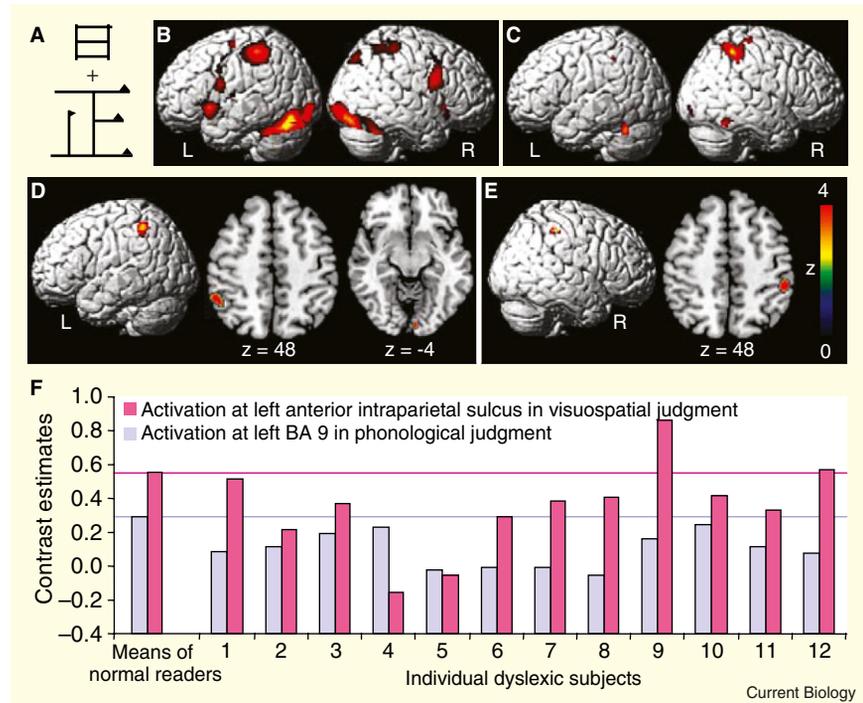


Figure 1. Examples of experimental materials and brain regions with significant activation during physical size judgment.

(A) Examples of stimuli. Subjects decided whether two characters viewed simultaneously had the same physical size. (B,C) Cortical activation associated with physical size judgment contrasted with fixation baseline in normal and dyslexic Chinese readers, respectively. (D) Regions more significantly activated in normal readers in comparison with dyslexic readers. Activation was seen in the left anterior intraparietal sulcus crucial for visuospatial analysis ($x = -51, y = -44, z = 48$; Z-score = 4.16) and the right lingual gyrus responsible for visual processing of objects ($x = 4, y = -88, z = -4$; Z-score = 4.20). (E) The right anterior intraparietal sulcus was more significantly activated in dyslexic readers than normal readers ($x = 51, y = -33, z = 48$; Z-score = 4.71), which might reflect use of a less efficient strategy during physical size judgments. (F) Brain activations in the left middle frontal gyrus and the left intraparietal sulcus for individual dyslexic children. The left middle frontal gyrus critically mediates phonological processing in Chinese reading, while the left intraparietal sulcus contributes to visuospatial processing. Means of normal subjects are an average brain activation level pooled across all the 12 normal readers. All the statistical analyses reported in (B–E) use a significance threshold of $P < 0.05$ FDR-corrected. Behavioural measures indicate lower accuracy and longer latency in the dyslexic group than in normal readers (see Supplemental data), which is a perennial problem in fMRI studies. However, we found lower activation in some regions of interest and higher activation in others, revealing that performance differences are not simply driving the activation differences. L, left hemisphere; R, right hemisphere. Planes in axial sections in (D,E) are labeled with the height (mm) relative to the bicommissural line.

problem. A second possibility is that Chinese dyslexics are neither good in phonological nor visuospatial judgments, but the two disorders are independent rather than being causally or otherwise dependent on each other. Further analyses on the entire sample of subjects ($n = 24$) indicated no correlation between activations of left IPS and LMFG ($r = 0.110, p = 0.312$). There was also no correlation between behavioral measures in the two tasks ($r = 0.359, p = 0.101$ for latency; $r = 0.040, p = 0.858$ for accuracy). In the dyslexic group, no correlation was significant at either the behavioral or the brain

level. Our results suggest that the visuospatial and phonological disorders occur independently.

Our task used real characters as stimuli, which might entail implicit reading processes that involve unconscious phonological activation mediated by left inferior parietal cortex [2]. This interpretation is less tenable, however, because parietal regions representing phonology in reading, as demonstrated in our [9] and others' studies [2], are more ventral relative to the parietal area serving the present visuospatial analysis.

Our study therefore demonstrates that developmental dyslexia in

Chinese is typically characterized by the co-existence of visuospatial and phonological disorders in a dyslexic child. This pattern of behavioral and pathophysiological profiles is different from that in English dyslexia, which is generally associated with a core phonological deficit in the absence of abnormal visual processing [7].

Supplemental Data

Supplemental data are available at [http://www.cell.com/current-biology/supplemental/S0960-9822\(09\)01549-8](http://www.cell.com/current-biology/supplemental/S0960-9822(09)01549-8)

Acknowledgments

This work was supported by grants from the Ministry of Science and Technology of China (2005CB522802), National Natural Science Foundation of China (30621004), Research Grants Council of Hong Kong (775709M), and National Institutes of Health (1R01HD056107-01A). We thank A. Chan, D. Dong, Y. Ha, J. Kwok, and J. Yang for assistance.

References

1. Goswami, U. (2006). Neuroscience and education: from research to practice? *Nat. Rev. Neurosci.* 7, 406–413.
2. Turkeltaub, P.E., Gareau, L., Flowers, D.L., Zeffiro, T., and Eden, G. (2003). Development of neural mechanisms for reading. *Nat. Neurosci.* 6, 767–773.
3. Hoefft, F., Meyler, A., Hernandez, A., Juel, C., Taylor-Hill, H., Martindale, J.L., McMillon, G., Kolchugina, G., Black, J.M., Faizi, A., et al. (2007). Functional and morphometric brain dissociation between dyslexia and reading ability. *Proc. Natl. Acad. Sci. USA* 104, 4234–4239.
4. Horwitz, B., Rumsey, J.M., and Donohue, B. C. (1998). Functional connectivity of the angular gyrus in normal reading and dyslexia. *Proc. Natl. Acad. Sci. USA* 95, 8939–8944.
5. Schlaggar, B.L., and McCandliss, B.D. (2007). Development of neural systems for reading. *Annu. Rev. Neurosci.* 30, 475–503.
6. Temple, E., Poldrack, R.A., Salidis, J., Deutsch, G.K., Tallal, P., Merzenich, M.M., and Gabrieli, J.D.E. (2001). Disrupted neural responses to phonological and orthographic processing in dyslexic children: an fMRI study. *NeuroReport* 12, 299–307.
7. Ramus, F., Rosen, S., Dakin, S.C., Day, B.L., Castellote, J.M., White, S., and Frith, U. (2003). Theories of developmental dyslexia: insights from a multiple case study of dyslexic adults. *Brain* 126, 841–865.
8. Siok, W.T., Perfetti, C.A., Jin, Z., and Tan, L.H. (2004). Biological abnormality of impaired reading is constrained by culture. *Nature* 431, 71–76.
9. Siok, W.T., Niu, Z.D., Jin, Z., Perfetti, C.A., and Tan, L.H. (2008). A structural-functional basis for dyslexia in the cortex of Chinese readers. *Proc. Natl. Acad. Sci. USA* 105, 5561–5566.
10. Corbetta, M., Kincade, J.M., Ollinger, J.M., McAvoy, M.P., and Shulman, G.L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nat. Neurosci.* 3, 292–297.

¹State Key Laboratory of Brain and Cognitive Sciences, ²Department of Linguistics, and ³Vice-Chancellor's Office, The University of Hong Kong, Pokfulam Road, Hong Kong, China. ⁴Beijing 306 Hospital, Beijing 100101, China. E-mail: tanlh@hku.hk

Herbivory in a spider through exploitation of an ant–plant mutualism

Christopher J. Meehan^{1,5}, Eric J. Olson², Matthew W. Reudink³, T. Kurt Kyser⁴, and Robert L. Curry¹

Spiders are thought to be strict predators [1]. We describe a novel exception: *Bagheera kiplingi*, a Neotropical jumping spider (Salticidae) that exploits a well-studied ant–plant mutualism, is predominantly herbivorous. From behavioral field observations and stable-isotope analyses, we show that the main diet of this host-specific spider comprises specialized leaf tips (Beltian food bodies; Figure 1A) from *Vachellia* spp. ant-acacias (formerly *Acacia* spp.), structures traded for protection in the plant's coevolved mutualism with *Pseudomyrmex* spp. ants that inhabit its hollow thorns [2]. This is the first report of a spider that feeds primarily and deliberately on plants.

Jumping spiders use advanced color-vision, agility, and cognitive skills to prey upon invertebrates [3]. The Salticidae is the largest family of spiders (>5,000 species), and members of this diverse group employ a broad range of foraging strategies. However, departures from carnivory in salticids — or in any of the 40,000 described spiders — are rare [1]: several cursorial spiders imbibe nectar as an occasional supplement to animal prey [4], and some juvenile orb-weavers incidentally ingest pollen when recycling their webs [5].

We discovered herbivory in *B. kiplingi* during field studies in southeastern Mexico (Quintana Roo, involving *V. collinsii* acacias inhabited by *P. peperii* ants) and northwestern Costa Rica (Guanacaste Province, involving *V. collinsii* and *V. cornigera* inhabited by *P. spinicola*, *P. flavicornis*, or *P. nigrocincta*). Between 2001 and 2008, we systematically observed individual *B. kiplingi* in these two regions to study foraging behavior. We supported direct observations of spiders in Mexico with high-definition videography.

Individuals at both sites fed predominantly on Beltian bodies,

which represented nearly the full diet of spiders in Mexico (91% of items consumed) but relatively less in Costa Rica (60%; $\chi^2 = 14.2$, $df = 3$, $P < 0.05$; Figure 1B). Spiders occasionally supplemented Beltian bodies with extrafloral nectar, another resource central to the ant–acacia mutualism [2]. They also preyed on acacia-ant larvae, small nectar-feeding flies, and (rarely) smaller conspecifics.

We observed focal *B. kiplingi* circumventing the well-known defenses of the acacia's *Pseudomyrmex* ant-inhabitants, which keep the plant free of most herbivores and encroaching vegetation [2]. These spiders occur almost exclusively on ant-occupied acacias, where they breed year-round and generally build their nests at the distal tips of older leaves (86%; $N = 110$) that have low rates of ant patrol (see Supplemental Data available on-line). Foraging *B. kiplingi* actively avoid ant-guards and exhibit situation-specific strategies (for example, changing targets if approached by ants) when harvesting Beltian bodies and when taking nectar or ant larvae (Supplemental Movies S1–S5).

Stable-isotope analyses confirmed *B. kiplingi* herbivory (Figure 1C; see also Supplemental Data). Our results are consistent with other food-web studies: the tissues of herbivores tend to have lower ¹⁵N:¹⁴N ratios (expressed as $\delta^{15}\text{N}$) relative to carnivores, whereas consumers tend to match ¹³C:¹²C ratios ($\delta^{13}\text{C}$) of their food [6]. Mexican *B. kiplingi* specimens had $\delta^{15}\text{N}$ profiles averaging 4.8% lower than those of other jumping spiders from surrounding vegetation, but only 2.1% and 2.9% higher than ant workers and Beltian bodies, respectively. *B. kiplingi* spiders and ant workers at this site had $\delta^{13}\text{C}$ signatures virtually identical to those of Beltian bodies, whereas other spiders exhibited $\delta^{13}\text{C}$ values that did not match those of Beltian bodies.

Using dietary mixing models (see Supplemental Data), we estimate that *B. kiplingi* in Mexico ($N = 50$) derive >95% of assimilated C and N from ant-acacias, including $89 \pm 13.2\%$ (mean \pm SE) directly from plant tissue and $8 \pm 7.9\%$ indirectly from acacia-ant larvae. Individuals of all age-sex classes had similar diets, suggesting that spiders in this population are