

of cleavage, in which Ago3 sense piRNAs direct cleavage of antisense transcripts producing the 5' monophosphate end of Aub and Piwi antisense piRNAs. A 3'-to-5' exonuclease could then trim the 3' end of piRNA transcripts, perhaps acting together with the Hen1 methyltransferase, which might terminate the trimming process by adding a 2'-O-methyl group to the 3' terminus of the mature piRNA.

Further reading

- Allen, E., Xie, Z., Gustafson, A.M., and Carrington, J.C. (2005). microRNA-directed phasing during trans-acting siRNA biogenesis in plants. *Cell* 121, 207–221.
- Aravin, A.A., Naumova, N.M., Tulin, A.V., Vagin, V.V., Rozovsky, Y.M., and Gvozdev, V.A. (2001). Double-stranded RNA-mediated silencing of genomic tandem repeats and transposable elements in the *D. melanogaster* germline. *Curr. Biol.* 11, 1017–1027.
- Bartel, D.P. (2004). MicroRNAs: genomics, biogenesis, mechanism, and function. *Cell* 116, 281–297.
- Brennecke, J., Aravin, A.A., Stark, A., Dus, M., Kellis, M., Sachidanandam, R., and Hannon, G.J. (2007). Discrete small RNA-generating loci as master regulators of transposon activity in *Drosophila*. *Cell* 128, 1089–1103.
- Brodersen, P., and Voinnet, O. (2006). The diversity of RNA silencing pathways in plants. *Trends Genet.* 22, 268–280.
- Fire, A., Xu, S., Montgomery, M.K., Kostas, S.A., Driver, S.E., and Mello, C.C. (1998). Potent and specific genetic interference by double-stranded RNA in *Caenorhabditis elegans*. *Nature* 391, 806–811.
- Hamilton, A.J., and Baulcombe, D.C. (1999). A species of small antisense RNA in posttranscriptional gene silencing in plants. *Science* 286, 950–952.
- Lee, R.C., Feinbaum, R.L., and Ambros, V. (1993). The *C. elegans* heterochronic gene *lin-4* encodes small RNAs with antisense complementarity to *lin-14*. *Cell* 75, 843–854.
- Napoli, C., Lemieux, C., and Jorgensen, R. (1990). Introduction of a chimeric chalcone synthase gene into *Petunia* results in reversible co-suppression of homologous genes in trans. *Plant Cell* 2, 279–289.
- Parker, J.S., and Barford, D. (2006). Argonaute: A scaffold for the function of short regulatory RNAs. *Trends Biochem. Sci.* 31, 622–630.
- Seto, A.G., Kingston, R.E., and Lau, N.C. (2007). The coming of age for piwi proteins. *Mol. Cell.* 26, 603–609.
- Valencia-Sanchez, M.A., Liu, J., Hannon, G.J., and Parker, R. (2006). Control of translation and mRNA degradation by miRNAs and siRNAs. *Genes Dev.* 20, 515–524.
- Zamore, P.D., and Haley, B. (2005). Ribo-gnome: the big world of small RNAs. *Science* 309, 1519–1524.

Department of Biochemistry and Molecular Pharmacology, University of Massachusetts Medical School, 364 Plantation Street, Worcester, Massachusetts 01605-2324, USA.
E-mail: phillip.zamore@umassmed.edu

Correspondences

Declining left-handedness in Victorian England seen in the films of Mitchell and Kenyon

I.C. McManus and Alex Hartigan

Although left-handers currently form about 11% of the population, only about 3% of those born in 1900 were left-handed, a more than three-fold difference which requires explanation. Whether the difference results from social pressure for left-handers to become right-handed, artefacts resulting from response biases that can occur when questionnaires are used, or perhaps a greater mortality of left-handers is still controversial [1–3]. Left-sided arm-waving, as observed in documentary films made between 1900 and 1906, and which correlates with left-handedness, occurs less often in 391 individuals born in the Victorian period, than in a modern control group. Left arm waving was also more frequent in the older individuals in the Victorian sample, an age effect that excludes any explanation in terms of increased mortality of left-handers. Since Victorian social pressure to wave with the right arm also seems highly unlikely, and there can be no response bias, the most likely interpretation is of a falling rate of left-handedness in the nineteenth century, with a true increase in left handedness during the twentieth century.

Between 1897 and 1913, Sagar Mitchell and James Kenyon made a series of documentary cinematographic films in northern England, of which 826 cellulose nitrate film negatives were found in June 1994 (see en.wikipedia.org/wiki/Mitchell_%26_Kenyon). Two selections of these films

have subsequently been released on DVD, *The lost world of Mitchell and Kenyon* (2004) (LW), and *Electric Edwardians: The films of Mitchell and Kenyon* (2005) (EE). We examined these films for lateralised behaviours, using a PC-based program to watch the films in slow motion and grab individual frames as a record. A pilot study of LW showed arm waving to be the most frequent lateralised behaviour, and the main analysis looked at all episodes of arm waving in EE. A modern control group of equal size to EE was obtained by entering 'waving' into Google Image (see the Supplemental data available on-line with this issue for technical details).

Most of the 391 arm waves in EE were carried out by males (N = 360, 92.1%). In EE the left arm was used in 61 (15.6%) cases, compared with 95/391 left-arm waves (24.3%) in the modern controls ($\chi^2 = 9.23$, 1 df, $p = .0023$). In the Victorian subjects, arm waving correlated strongly with age (Table 1: χ^2 (Overall) = 18.56, 4 df, $p = .00096$; χ^2 (linear) = 15.04, 1 df, $p = .00011$). Sensitivity analysis showed the age effect was robust against possible mis-classification of age (see Supplemental Results).

Figure 1 compares the arm-waving data with the extensive hand-writing data of Gilbert and Wysocki [4]. In modern data there are more left-wavers than left-writers (just as left-footedness, left-eyedness and left-earedness are more common than left-hand writing [5]). Knowing the modern relationship of handedness and waving (see Supplemental Results), estimated rates of left-handedness can be calculated from the arm-waving data for those born in the Victorian era (see Figure 1, in which estimated rates of left-handedness are shown as open circles and the dashed line). Earlier Victorian rates of left-handedness are broadly equivalent to modern rates, whereas rates then decline, with

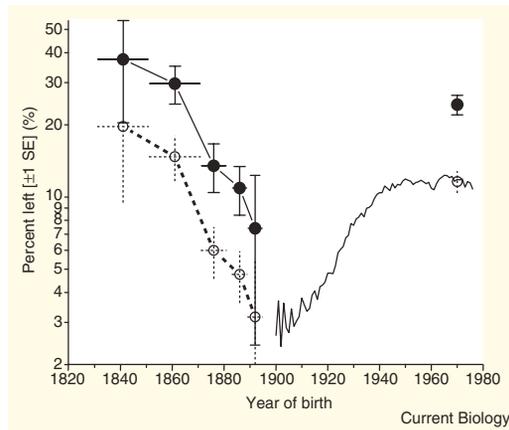


Figure 1. Change in the proportion of left-handers since 1820.

The abscissa shows the year of birth of subjects, and the ordinate shows the percentage of left sided use on a logarithmic scale, so that equal proportional changes are represented by lines that are approximately parallel. The wiggly, solid black line at bottom right shows the proportion of the population in the extremely large Gilbert and Wysocki [4] study who reported using the left hand for writing. Solid black circles connected by solid black lines and with solid error bars show the percentage of subjects waving with their left arm (\pm one standard error). The open circles connected with dashed lines, and with dashed error bars show the same data as the solid circles, except that they show estimated rates of left-handed writing on the basis of the association between handedness and waving (see Supplemental Results). Vertical error bars are conventional standard errors, whereas horizontal error bars indicate the age range indicated in the leftmost column of Table 1.

Vertical error bars are conventional standard errors, whereas horizontal error bars indicate the age range indicated in the leftmost column of Table 1.

the lowest values for those born between about 1890 and 1910.

These Victorian data on arm-waving resolve several problems concerning the historical data on handedness and lateralisation, studying a behaviour that is unlikely to be subject to strong social coercion, and excluding response bias by examining actual behaviours rather than potentially biased questionnaire responses. Left-sided usage is not only lower in the Victorian sample, but in strong contrast to modern data, left-arm usage in the Victorian subjects increases with age, thereby excluding increased mortality of left-handers as an explanation. It can therefore be concluded not only that left-handedness was truly less frequent at the end of the Victorian period, but that the

rate of left-handedness had been falling during the nineteenth century (and that is compatible with data suggesting that long-term historic and prehistoric rates of left-handedness were similar to modern rates [6,7]).

The reasons for the Victorian decline in left-handedness are far from clear, although some children were undoubtedly discouraged from writing with their left hand. Ireland [8], writing in *Brain* in 1880, described how, “[Left-handed children] were not allowed to use their left hands in writing for ciphering. Great trouble had, in fact, been taken to make them desist from using their left hands”. Increasing literacy rates [9], coupled with universal schooling and ever-increasing industrialisation and machine tool use in the

nineteenth century, may have made left-handers more visible and hence more subject to the stigmatisation of which modern left-handers still complain [10]. Such explanations might be testable using cross-national comparisons of countries with early or late industrialisation and universal literacy. Because handedness, cerebral lateralisation and atypical laterality are associated with a range of conditions such as dyslexia, stuttering, autism and psychosis, the data also raise the tantalising possibility that their rates may also have changed concomitantly.

Supplemental data

Supplemental data are available at <http://www.current-biology.com/cgi/content/full/17/18/R793/DC1>

Acknowledgments

We are very grateful to Michael Peters for providing us with re-analyses of data from his 1992 paper.

References

1. Coren, S., and Halpern, D.F. (1991). Left-handedness: A marker for decreased survival fitness. *Psychol. Bull.* 109, 90-106.
2. Harris, L.J. (1993). Do left-handers die sooner than right-handers? Commentary on Coren and Halpern's (1991) "Left-handedness: A marker for decreased survival fitness". *Psychol. Bull.* 114, 203-234.
3. Hugdahl, K. (1996). Left-handedness and age: Comparing writing/drawing and other manual activities. *Laterality* 1, 177-183.
4. Gilbert, A.N., and Wysocki, C.J. (1992). Hand preference and age in the United States. *Neuropsychologia* 30, 601-608.
5. Porac, C., and Coren, S. (1981). *Lateral Preferences and Human Behaviour*. (New York: Springer Verlag).
6. Coren, S., and Porac, C. (1977). Fifty centuries of right-handedness: The historical record. *Science* 198, 631-632.
7. Faurie, C., and Raymond, M. (2005). Handedness frequency over more than 10,000 years. *Proc. R. Soc. Lond. B* 271, S43-S45.
8. Ireland, W.W. (1880). Notes on left-handedness. *Brain* 3, 207-214.
9. Stone, L. (1969). Literacy and education in England 1640-1900. *Past Present* 42, 69-139.
10. McManus, I.C. (2002). *Right Hand, Left Hand: The Origins of Asymmetry in Brains, Bodies, Atoms and Cultures*. (London, UK/Cambridge, MA: Weidenfeld and Nicolson/Harvard University Press).

Table 1: Arm waving in relation to estimated date of birth in the EE sample and the modern control group.

Estimated age (birth cohort)	Arm used for waving			% left waving	Standard error
	Right	Left	Total		
6-12 (1892)	25	2	27	7.4%	5.0%
13-19 (1886)	139	17	156	10.9%	2.5%
20-29 (1876)	109	17	126	13.5%	3.0%
30-49 (1861)	52	22	74	29.7%	5.3%
50-69 (1841)	5	3	8	37.5%	17.1%
Total EE sample	330	61	391	15.6%	1.8%
Modern sample	296	95	391	24.3%	2.2%