forelimb and in a closed state in emu forelimb. Mutation of an Ets site within the *Sall1* enhancer ablated its activity during early chicken forelimb development, though activity was recovered later in development. In addition, when placed in the emu wing bud, the wild-type chick enhancer failed to drive limb expression. These results support a model where both Fgf signaling and intact Ets binding sites are required for the activation of key enhancers during early limb development.

While previous studies have investigated the basis of wing size reduction in emus, Young and coworkers provide multiple converging lines of evidence that tell a remarkably consistent story — a reduction in Fgf signaling in early forelimb progenitor cells leads to a delay in cellular proliferation and wing bud outgrowth. As the authors point out, this does not necessarily mean that changes in Fgf signaling caused the initial evolution of flight loss. It is likely, however, that changes in Fgf signaling are one of the primary developmental mechanisms responsible for the subsequent evolution of diminutive wings in the emu. A recent investigation of wing size reduction in the flightless Galapagos cormorant implicated a preponderance of coding mutations in cilia-related genes as contributing factors in the small winged phenotype of this species [5]. Thus, different wing-reduced birds may have convergently evolved undersized forelimbs through different genetic mechanisms. Though it remains to be discovered what genetic mutations are triggering shifts in emu gene expression and enhancer activity, this study significantly expands our understanding of what sets emu wings apart from the wings of flighted birds.

REFERENCES

1. Colosimo, P.F., Hosemann, K.E., Balabhadra, S., Villarreal, G., Dickson, M., Grimwood, J., Schmutz, J., Myers, R.M., Schluter, D., and Kingsley, D.M. (2005). Widespread parallel evolution in sticklebacks by repeated fixation of Ectodysplasin alleles. Science *307*, 1928–1933.

2. McGaugh, S.E., Gross, J.B., Aken, B., Blin, M., Borowsky, R., Chalopin, D., Hinaux, H., Jeffery, W.R., Keene, A., Ma, L., *et al*. (2014). The cavefish genome reveals candidate genes for eye loss. Nat. Commun. *5*, 5307.

3. Harshman, J., Braun, E.L., Braun, M.J., Huddleston, C.J., Bowie, R.C.K., Chojnowski, J.L., Hackett, S.J., Han, K.L., Kimball, R.T., *et al*. (2008). Phylogenomic evidence for multiple losses of flight in ratite birds. Proc. Natl. Acad. Sci. USA *105*, 13462–13467.

4. Hume, J.P., and Martill, D. (2019). Repeated evolution of flightlessness in Dryolimnas rails (Aves: Rallidae) after extinction and recolonization on Aldabra. Zool. J. Linn. Soc. *186*, 666–672.

5. Burga, A., Wang, W., Ben-David, E., Wolf, P.C., Ramey, A.M., Verdugo, C., Lyons, K., Parker, P.G., and Kruglyak, L. (2017). A genetic signature of the evolution of loss of flight in the Galapagos cormorant. Science *356*, eaal3345.

6. Phillips, M.J., Gibb, G.C., Crimp, E.A., and Penny, D. (2009). Tinamous and moa flock together: mitochondrial genome sequence analysis reveals independent losses of flight among ratites. Syst. Biol. *59*, 90–107.

7. Sackton, T.B., Grayson, P., Cloutier, A., Hu, Z., Liu, J.S., Wheeler, N.E., Gardner, P.P., Clarke, J.A., Baker, A.J., Clamp, M., and Edwards, S.V. (2019). Convergent regulatory evolution and loss of flight in paleognathous birds. Science *364*, 74–78.

8. Young, J.J., Grayson, P., Edwards, S.V., and Tabin, C.J. (2019). Attenuated Fgf signaling underlies the forelimb heterochrony in the emu Dromaius novahollandiaea. Curr. Biol. *29*, 3681–3691.

9. Faux, C., and Field, D.J. (2017). Distinct developmental pathways underlie independent losses of flight in ratites. Biol. Lett. *13*, 20170234–4.

10. Bickley, S.R.B., and Logan, M.P.O. (2014). Regulatory modulation of the T-box gene Tbx5 links development, evolution, and adaptation of the sternum. Proc. Natl. Acad. Sci. USA *111*, 17917–17922.

11. Farlie, P.G., Davidson, N.M., Baker, N.L., Raabus, M., Roeszler, K.N., Hirst, C., Major, A., Mariette, M.M., Lambert, D.M., Oshlack, A., and Smith, C.A. (2017). Co-option of the cardiac transcription factor Nkx2.5 during development of the emu wing. Nat. Commun. *8*, 1–11.

12. Ohuchi, H., Nakagawa, T., Yamamoto, A., Araga, A., Ohata, T., Ishimaru, Y., Yoshioka, H., Kuwana, T., Nohno, T., Yamasaki, M., Itoh, N., *et al*. (1997). The mesenchymal factor, FGF10, initiates and maintains the outgrowth of the chick limb bud through interaction with FGF8, an apical ectodermal factor. Development. *124*, 2235–2244.

13. Buenrostro, J.D., Giresi, P.G., Zaba, L.C., Chang, H.Y., and Greenleaf, W.J. (2013). Transposition of native chromatin for fast and sensitive epigenomic profiling of open chromatin, DNA-binding proteins and nucleosome position. Nat. Methods *10*, 1213–1218.

Language: Do Bilinguals Think Differently in Each Language?

Karen Emmorey
School of Speech, Language, and Hearing Sciences, San Diego State University, 6495 Alvarado Road, Suite 200, San Diego, CA 92120, USA
Correspondence: kemmorey@sdsu.edu
https://doi.org/10.1016/j.cub.2019.09.009

Whether the representation of concepts depends on the language used to express them is controversial. A new study with sign–speech bilingual participants has found that neural representations of semantic categories, such as fruit, are shared across languages but individual items, such as apple, are not.

Does the language you speak influence the way you think? What if you know two languages: do you think differently in each language? Human thought generally involves the retrieval of conceptual (semantic) knowledge that is stored in memory, and there is on-going debate about whether language can influence the nature of such conceptual representations [1,2]. Some studies have found that the language you speak influences how you categorize objects [3], how you perceive color [4], and how you remember the spatial location of objects [5]. But others have argued that such effects reflect the on-line use of language in cognitive tasks and do not provide evidence that language shapes the nature of conceptual representations [2]. In a new paper in this issue of *Current Biology*,

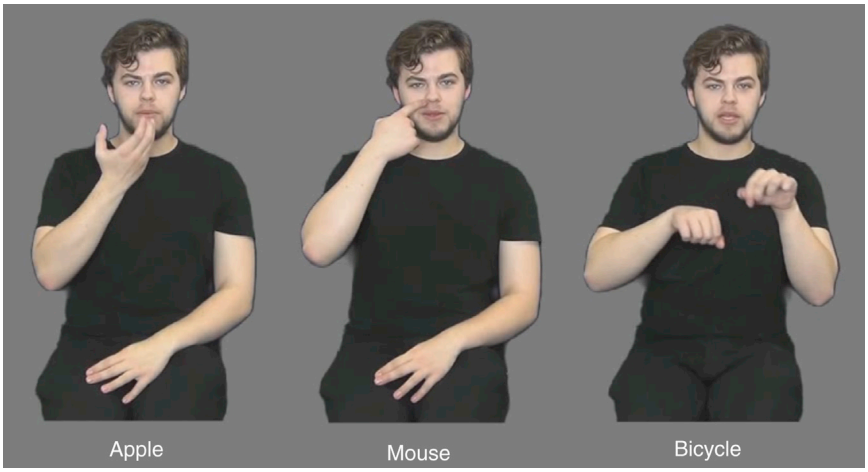

Figure 1. Example signs from British Sign Language (BSL) and their English translations from three semantic categories, fruit, animals and transport.
The dramatic differences between signs and words allows for a strong test of whether the bilingual brain represents semantic concepts similarly in each language. Evans *et al.* [6] found that neural representations of semantic categories are shared across languages (and modalities), but the neural representation of within-category concepts differed for BSL and English. These findings challenge the predominant view that semantic representations are shared across languages [16]. (Photos courtesy of Samuel Evans.)

Evans *et al.* [6] report that semantic categories, such as fruit, animals, transportation, are represented in the brain in a manner that is independent of a given language, in this case British Sign Language (BSL) and English, but the neural representations for individual category items, such as apple, mouse, bicycle, are not shared across languages.

Sign languages are structured quite differently from spoken languages and thus provide an excellent tool to investigate the possible impact of language (and language modality) on conceptual representations. Sign languages are perceived visually, rather than auditorily, are produced by the hands and body, rather than by the vocal tract, and are distinct from the spoken languages used in the same region (for example, BSL and English have different grammatical rules). Sign languages tend to have more simultaneous structure than spoken languages; for example, phonological units — distinctive handshapes, locations, and movements — are often articulated at the same time, rather than produced as a string of segments, as are consonants and vowels [7]. Nonetheless, sign languages are parallel to spoken languages in multiple respects. Firstly, with respect to how children acquire them [8]: for example, children learning sign from birth show the same developmental milestones, including babbling. Secondly, with respect to cross-linguistic variation [9]: for example, languages that are historically unrelated, such as American Sign Language and BSL, are mutually unintelligible. And thirdly, and crucially, with respect to the neural regions involved in language processing [10,11]: sign and speech both engage ‘core’ language regions in the left hemisphere. Evans *et al.* [6] capitalized on these similarities and differences to investigate the influence of both language modality and bilingualism on the neural representation of conceptual knowledge in a group of sign–speech bilinguals: hearing people who were highly proficient in BSL and English.

If conceptual representations are the same for sign and speech, then similar neural patterns should be evoked when either viewing BSL signs or listening to English words. Evans *et al.* [6] used representational similarity analysis (RSA) and functional magnetic resonance imaging (fMRI) to test for shared versus language-specific neural representations of individual concepts (see Figure 1 for examples) and for the semantic categories to which these concepts belong. Rather than measuring the average level of neural activity within experimental conditions, as is done with standard fMRI, RSA compares the pattern similarity of neural activation distributed across voxels (tiny brain ‘cubes’ representing the summed activation of many neurons); these voxel patterns are assumed to reflect neural representations [12]. The RSA results revealed similar neural activation patterns for semantic categories across BSL and English in left posterior middle temporal cortex, a brain region that has long been implicated in semantic processing [13]. Thus, the neural representation of high-level semantic categories is *not* impacted by language or by modality. However, neural patterns differed for individual signs and words that referred to the same concepts (translation equivalents). Within each language, the neural patterns were similar for words or signs that were produced by different models (a male and a female). Thus, the neural pattern for item-level concepts is stable across models and exemplars within a language, but not across languages. Evans *et al.* [6] interpret these findings as suggesting that language acts as a ‘subtle filter’ through which we experience the world.

But how might this ‘subtle filter’ work? Why might the BSL sign APPLE elicit a different neural pattern than the spoken English word ‘apple’ in the same person? One possibility that Evans *et al.* [6] considered was that signs are more likely to resemble what they mean (are more iconic) than words. For example, the BSL sign APPLE resembles how you hold an apple and is produced near the mouth (Figure 1). This explanation is unlikely, however, because the authors found no relationship between the degree of iconicity and semantic feature similarity at the item level (or at the category level). The authors also considered polysemy (multiple meanings) as a possible explanation, citing the observation that signs often have more meanings than words. However, the basic-level names used in this study — orange, apple, grapes, mouse, lion, monkey, train, bus, bicycle — are unlikely to have more meanings in BSL than English. Another, more likely explanation is that semantic representations of individual items are colored by their phonological structure, which differs dramatically for signed and spoken languages. Supporting this hypothesis, Evans *et al.* [6] found that speech-specific regions that encoded item-level information were located in auditory cortex, while sign-specific regions were located in visual cortex.

Thus, the neural encoding of item-level semantic representations of signs and words may not be amodal and appears to retain sensitivity to language modality.

The obvious next step will be to conduct a similar study with bilinguals who know two spoken languages. Previous work [14] with Dutch–English bilinguals listening to animal words in each language (such as 'paard' and 'horse') used brain-based decoding methods to reveal shared item-level semantic representations in the left anterior temporal lobe, another region known to be involved in semantic representation. Another study [15] replicated this result with Dutch–French bilinguals, although the neural overlap was not in the temporal lobe, but failed to find shared semantic representations across modalities: listening to 'maan' ('moon' in Dutch) and reading 'lune' ('moon' in French). Neither study tested for shared semantic category representations across languages. The existing evidence thus suggests that input modality, auditory or visual, shapes semantic representations at the specific item-level, but not at a more general category level. Lexical-level semantic representations are more tightly linked to their input representations, sound, print or sign, and may therefore be impacted by distinct properties of these representations, for example the size of phonological *versus* orthographic neighborhoods or differing semantic co-occurrence frequencies in each modality.

New 'brain-decoding' techniques, such as RSA, are beginning to uncover how multiple languages are represented in the brain and the extent to which concepts are shared across languages. The study by Evans *et al.* [6] is the first to investigate this question using different degrees of semantic granularity. For bilinguals, high-level semantic categories are more likely to be represented similarly across languages, but semantic representations for individual words may be shaped by whether they are heard or seen in each language. It remains an open question whether these neural differences in encoding semantic representations have an impact on behavior and thought in bilinguals.

REFERENCES

1. Lucy, J.A. (1997). Linguistic relativity. Annu. Rev. Anthropol. *26*, 291–312.
2. Gleitman, L., and Papafragou, A. (2013). Relations between language and thought. In Handbook of Cognitive Psychology, D. Reisberg, ed. (New York: Oxford University Press), pp. 504–523.
3. Boutonnet, B., Dering, B., Viñas-Guasch, N., and Thierry, G. (2013). Seeing objects through the language glass. J. Cogn. Neurosci. *25*, 1702–1710.
4. Winawer, J., Witthoft, N., Frank, M.C., Wu, L., Wade, A.R., and Boroditsky, L. (2007). Russian blues reveal effects of language on color discrimination. Proc. Natl. Acad. Sci. USA *104*, 7780–7785.
5. Majid, A., Bowerman, M., Kita, S., Haun, D.B., and Levinson, S.C. (2004). Can language restructure cognition? The case for space. Trends Cogn. Sci. *8*, 108–114.
6. Evans, S., Price, C.J., Diedrichsen, J., Gutierrez-Sigut, E., and MacSweeney, M. (2019). Sign and speech share partially overlapping conceptual representations. Curr. Biol. *29*, 3739–3747.
7. Brentari, D. (1998). A Prosodic Model of Sign Language Phonology (Cambridge: MIT Press).
8. Meier, R.P., and Newport, E.L. (1990). Out of the hands of babes: On a possible sign advantage in language acquisition. Language *66*, 1–23.
9. Zeshan, U., and Palfreyman, N. (2017). Sign language typology. In The Cambridge Handbook of Linguistic Typology, A.Y. Aikhenvald, and R.M.W. Dixon, eds. (Cambridge: Cambridge University Press), pp. 178–216.
10. MacSweeney, M., Woll, B., Campbell, R., McGuire, P.K., David, A.S., Williams, S.C., Suckling, J., Calvert, G.A., and Brammer, M.J. (2002). Neural systems underlying British Sign Language and audio-visual English processing in native users. Brain *125*, 1583–1593.
11. Emmorey, K., Mehta, S., and Grabowski, T.J. (2007). The neural correlates of sign versus word production. Neuroimage *36*, 202–208.
12. Haxby, J.V., Gobbini, M.I., Furey, M.L., Ishai, A., Schouten, J.L., and Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. Science *293*, 2425–2430.
13. Binder, J.R., Desai, R.H., Graves, W.W., and Conant, L.L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. Cereb. Cortex *19*, 2767–2796.
14. Correia, J., Formisano, E., Valente, G., Hausfeld, L., Jansma, B., and Bonte, M. (2014). Brain-based translation: fMRI decoding of spoken words in bilinguals reveals language-independent semantic representations in anterior temporal lobe. J. Neurosci. *34*, 332–338.
15. Van de Putte, E., De Baene, W., Price, C.J., and Duyck, W. (2018). Neural overlap of L1 and L2 semantic representations across visual and auditory modalities: a decoding approach. Neuropsychologia *113*, 68–77.
16. Francis, W.S. (2005). Bilingual semantic and conceptual representation. In Handbook of Bilingualism: Psycholinguistic Approaches, J.F. Kroll, and A.M. de Groot, eds. (Oxford: Oxford University Press), pp. 251–267.

Cell Division: Tailoring a Swiftly Scaling Spindle

Kelly E. Hartsough and Claire E. Walczak*
Indiana University School of Medicine-Bloomington, Medical Sciences, Bloomington, IN 47405, USA
*Correspondence: cwalczak@indiana.edu
https://doi.org/10.1016/j.cub.2019.09.055

A new study looks across frog species to identify molecular factors important in meiotic spindle scaling.

Size is a fundamental feature that governs the function of many biological processes. Cell size can differ drastically across organisms, cell types, and developmental stages. In each of these instances, subcellular structures must be scaled in accordance to the size of their respective cell type. *Xenopus* frogs are a powerful model system to understand the scaling mechanisms of the meiotic spindle as it relates to egg and organism size [1]. In a new study published in this

