shelf life and reduced susceptibility to disease are specific to anthocyanin hyper-accumulation, as there were no observed differences between control and *Del/Ros1* fruits in firmness, cuticle thickness or cell wall composition at the full ripe stage. During over-ripening, *Del/Ros1* fruits expressed significantly lower levels of multiple genes known to function in cell wall disassembly, such as polygalacturonase.

B. cinerea is an important fruit pathogen and cell wall disassembly is integrally tied to its entry into the fruit [9]. The *Del/Ros1* fruits have the double advantage of remaining firm for a longer period and accumulating substantially higher levels of water-soluble antioxidants. The oxidative burst is an important aspect of infection by necrotrophic pathogens that feed on dead tissue [10,11]. Clearly, the reduced susceptibility of fruits to postharvest diseases complements the reduction in fruit softening to enhance shelf life.

The success of this strategy of increasing antioxidant capacity raises the possibility of extending the

shelf life of other fruits. Much effort has gone into reducing losses of fruits to spoilage and the current work provides another avenue to that end. In summary, this biotechnological approach has the potential to increase the supply of a more nutritious food.

References

- Klee, H.J., and Giovannoni, J.J. (2011). Genetics and control of tomato fruit ripening and quality attributes. Annu. Rev. Genet. 45, 41–59.
- 2. Food and Agriculture Organization of the United Nations, Rome, 2011. Global Food Losses and Food Waste Extent, Causes and Prevention.
- Khush, G., Lee, S., Cho, J.I., and Jeon, J.S. (2012). Biofortification of crops for reducing malnutrition. Plant Biotechnol. Rep. 6, 195–202.
- Martin, C., Butelli, E., Petroni, K., and Tonelli, C. (2011). How can research on plants contribute to promoting human health? Plant Cell 23, 1685–1699.
- Davis, D.R., Epp, M.D., and Riordan, H.D. (2004). Changes in USDA food composition data for 43 garden crops, 1950 to 1999. J. Am. Coll. Nutr. 23, 669–682.
- Butelli, E., Titta, L., Giorgio, M., Mock, H.P., Matros, A., Peterek, S., Schijlen, E.G., Hall, R.D., Bovy, A.G., Luo, J., et al. (2008). Enrichment of tomato fruit with health-promoting anthocyanins by expression of select transcription factors. Nat. Biotechnol 26, 1301–1308.

- Zhang, Y., Butelli, E., De Stefano, R., Schoonbeek, H., Magusin, A., Pagliarani, C., Wellner, N., Hill, L., Orzaez, D., Granell, A., *et al.* (2013). Anthocyanins double the shelf life of tomatoes by delaying overripening and reducing susceptibility to gray mold. Curr. Biol. 23, 1094–1100.
- Jimenez, A., Creissen, G., Kular, B., Firmin, J., Robinson, S., Verhoeyen, M., and Mullineaux, P. (2002). Changes in oxidative processes and components of the antioxidant system during tomato fruit ripening. Planta 214, 751–758.
- Cantu, D., Vicente, A.R., Greve, L.C., Dewey, F.M., Bennett, A.B., Labavitch, J.M., and Powell, A.L.T. (2008). The intersection between cell wall disassembly, ripening, and fruit susceptibility to Botrytis cinerea. Proc. Natl. Acad. Sci. USA 105, 859–864.
- Glazebrook, J. (2005). Contrasting mechanisms of defense against biotrophic and necrotrophic pathogens. Annu. Rev. Phytopathol. 43, 205–227.
- Segmuller, N., Kokkelink, L., Giesbert, S., Odinius, D., van Kan, J., and Tudzynski, P. (2008). NADPH oxidases are involved in differentiation and pathogenicity in *Botrytis cinerea*. Mol. Plant Microbe Interact. 21, 808–819.

Horticultural Sciences, P.O. Box 110690, University of Florida, Gainesville FL 32611-0690, USA. E-mail: hjklee@ufl.edu

http://dx.doi.org/10.1016/j.cub.2013.05.010

Neuronal Coding: The Value in Having an Average Voice

Voices or faces that fall outside of the norm are the memorable ones. Recent human neuroimaging work, however, indicates that the average voice holds considerable currency for neuronal coding. The study also forges a bridge with the face recognition literature.

Christopher I. Petkov and Quoc C. Vuong

Being accused of having an average voice is not much of a compliment. Simon Cowell, who was a judge on the television show American Idol. has been known to tell contestants, "You look nice, but your voice is distinctly average, I'm afraid". Cowell might not appreciate how difficult it would be for him to identify, let alone judge, an extraordinary voice without a reference to the average or prototypical voice. A new human neuroimaging study [1], reported in this issue of Current Biology, provides strong evidence that a voice-sensitive region in the human brain relies on a representation

of an average male and an average female voice.

Neuronal Coding of Voice Identity The brains of humans [2] and other social animals [3] contain temporal lobe regions called 'temporal voice areas' (TVAs), which are particularly sensitive to sound acoustics associated with voices. It has been unclear, however, how these brain regions code for voice identity.

An earlier notion of the neural coding of identity is that of a 'grandmother cell' [4]. In the extreme, single neurons encode single identities, which could ruin a family reunion if a grandmother's cell became injured. Apart from interesting examples, such as a 'Jenifer Aniston neuron' in the brain of a patient who was familiar with the actress [5], even the researchers who identified these neurons conclude that there is little support for the notion of a one-to-one mapping of neuron-to-identity [6]. Sorry, grandma.

Another prominent view is that 'objects', including faces or voices, are represented as points in a high-dimensional space (Figure 1A) [1,7–10]. For voices, the axes of this space represent acoustic features. The distinctiveness between any two voices can be represented by their geometric distance in this space. That is, the more distinctive that two voices are, the further that they are from each other in this space. These distances have been shown to influence how people judge voice [10,11]. Thus, they could also influence how the brain encodes individual voices.

If the brain has a representation of an acoustic feature space, what is the reference point within this space? That is, how are voices related to each other? One possibility is to compute







(A) Stimuli can be represented as points in a multi-dimensional space: the axes are defined by the relevant stimulus features. Norm-based coding predicts that neural responses increase with distance between the probe stimulus (green circle) and prototype (red triangle). Exemplar-based coding predicts that neural responses relate to the distance between the probe and a nearby exemplar (red circle). (B) Three dimensions of a voice parameter space including female (red) and male (blue) prototypes (triangles). See text for details; adapted and modified from [1].

the distance between individual voices to other voices (exemplar-based coding). Another possibility is to compute the distance between individual voices and the average voice that is at the center of the parameter space (norm-based coding; see Figure 1A). Put another way, do neurons in Simon Cowell's brain evaluate the distinctive features between an individual voice and an extraordinary exemplar, or are individual voices compared to an average, prototypical voice? Latinus et al. [1] obtained evidence that, for the human TVA, the critical comparison is the distance of a voice to its sex-specific prototype.

To demonstrate this, the researchers relied on a recently developed voice parameter space [11]. Although many different acoustical features can be used to distinguish between voices, the authors focused on three in particular: first, the dispersion of the formant frequencies (FD, Figure 1B), associated with how a person's individual vocal tract filters the voiced sound; second, the harmonicity versus noisiness of his or her voice (HNR); and third, the position of the fundamental frequency (f0), associated with voice pitch. Latinus et al. [1] then used sound morphing software to average dozens of male voices to create a male voice prototype [1].

Similarly, they averaged many female voices to create a female voice prototype. Interestingly, and contrary to Cowell's view, averaging voices together to create a voice prototype increases its attractiveness [11]. The authors obtained evidence that listeners rated voices as more distinctive if they were further from their sex-specific prototype in the voice parameter space [1].

Armed with the voices, Latinus et al. [1] used functional magnetic resonance imaging (fMRI) to scan the brain response of human participants as they listened to the voice stimuli. The critical question was whether the hemodynamic brain response to a particular voice would correlate more strongly with its distance to the sex-specific prototype or with its distance to other voices. In the TVA, the researchers found that the response increased with increasing distance from the sex-specific voice prototype. This correlation was significantly weaker when other reference points were used, such as the distance to the preceding voice or the distance to an androgynous prototype voice (an average of all the male and female voices). Interestingly, the primary auditory cortex did not show a relationship between its hemodynamic response and the distance to the sex-specific prototypes.

Norm-based Coding of Identity: A General Principle?

Building on earlier studies (e.g., [10]), Latinus et al. [1] provide strong support for a norm-based coding of voice identity by the human TVA. These results parallel those obtained in a number of visual studies. For example, analogous to the voice-sensitive TVA, the primate brain has face-sensitive regions in the occipital-temporal lobe. One such region in humans is often dubbed the fusiform face area (FFA) because of its apparent selectivity for faces over other visual categories [12]. Loffler et al. [8] showed that the FFA responds stronger to faces further from a prototype face, relative to those closer to the norm. In another study [9], neurons sensitive to faces in the monkey inferior temporal lobe were shown to be tuned around a human face prototype, revealing how norm-based coding could operate at the level of individual neurons. Moreover, there is evidence that norm-based coding strategies could apply to objects [13] and bodies [14]. Together these studies suggest that norm-based coding is a general brain coding principle. However, can alternative coding strategies be excluded?

Proponents of exemplar-based coding note that memories for exemplars can influence how people judge stimuli [15,16]. There is also the concern that brain adaptation effects can be mistaken for norm-based effects. It is known that regions in the brain reduce their response (adapt) when the same or a similar stimulus is repeated [17]. Voices close to the prototype are more similar to each other by virtue of the prototype being at the center of the parameter space. Thus, the voices closer to the prototype would be expected to be responded to less, simply because their similarity would lead to large adaptation. By contrast, distinctive voices that are far away from the prototype are more dissimilar from each other and would elicit less adaptation. Thus, the correlation between TVA response and distance to the prototype can be confounded with adaptation for similar voices within a prototype's vicinity [18].

Aware of this issue, Latinus *et al.* [1] tested whether different adaptation conditions could equally explain the results [1]. Their results show that the correlation between TVA response and the distance to the sex-specific

Dispatch R523

prototype is significantly larger than the one based on voice adaptation. Moreover, this relationship was stronger than the relationship between TVA response and the distance to the androgynous prototype. These additional results strengthen the case for the norm-based coding of voice identity in the TVA.

Nonetheless, it is unlikely that norm-based coding and exemplar-based coding accounts are mutually exclusive. For instance, exemplar-based coding might predominate in certain brain regions, or when a prototype has not been formed or is difficult to form. Also if many 'prototypes' exist, norm-based coding is difficult to distinguish from exemplar-based coding.

Glimpse ahead and the 'Mysterious' Prototype

A psychological curiosity is that the brain apparently can form a prototype without ever experiencing it. In a classic study, Posner and Keele [19] presented participants with many dot patterns, which were synthesized by distorting a prototype pattern. Although participants never saw the prototype during an exposure phase, their responses to it afterwards suggested that they had abstracted it, merely by being exposed to the distorted dot patterns.

If the brain does rely on prototypical face or voice representations, even if it has never experienced them, a number of questions arise: How does the brain form and maintain prototypes? In this regard it is important to consider the form of learning; for instance, Andics and colleagues [10] suggest that the brain flexibly shifts the reference point as we become familiar with other people's voices. Also, what is the fidelity with which prototypes represent certain features, and which features, or life experiences, have a greater influence on the formation of prototypes?

No doubt, studying these issues will continue to provide insights into how we so effortlessly identity others and how this process comes to a grinding halt for people with face or voice recognition deficits. We will possibly also better understand how judges like Simon Cowell evaluate exceptional voices/faces, in relation to those that we as a society might not find as mesmerizing as the neurons in our brains.

References

- Latinus, M., McAleer, P., Bestelmeyer, P.E.G., and Belin, P. (2013). Norm-based coding of voice identity in human auditory cortex. Curr. Biol. 23, 1075–1080.
- Belin, P., Zatorre, R.J., Lafaille, P., Ahad, P., and Pike, B. (2000). Voice-selective areas in human auditory cortex. Nature 403, 309–312.
- Perrodin, C., Kayser, C., Logothetis, N.K., and Petkov, C.I. (2011). Voice cells in the primate temporal lobe. Curr. Biol. 21, 1408–1415.
- Quiroga, R.Q., Fried, I., and Koch, C. (2013). Brain cells for grandmother. Sci. Am. 308, 30–35.
- Quiroga, R.Q., Reddy, L., Kreiman, G., Koch, C., and Fried, I. (2005). Invariant visual representation by single neurons in the human brain. Nature 435, 1102–1107.
- Quiroga, R.Q., Kreiman, G., Koch, C., and Fried, I. (2008). Sparse but not 'grandmother-cell' coding in the medial temporal lobe. Trends Cogn. Sci. 12, 87–91.
- Cutzu, F., and Edelman, S. (1996). Faithful representation of similarities among three-dimensional shapes in human vision. Proc. Natl. Acad. Sci. USA 93, 12046–12050.
- Loffler, G., Yourganov, G., Wilkinson, F., and Wilson, H.R. (2005). fMRI evidence for the neural representation of faces. Nat. Neurosci. 8, 1386–1390.

- Leopold, D.A., Bondar, I.V., and Giese, M.A. (2006). Norm-based face encoding by single neurons in the monkey inferotemporal cortex. Nature 442, 572–575.
- Andics, A., McQueen, J.M., Petersson, K.M., Gal, V., Rudas, G., and Vidnyanszky, Z. (2010). Neural mechanisms for voice recognition. Neuroimage 52, 1528–1540.
- Bruckert, L., Bestelmeyer, P., Latinus, M., Rouger, J., Charest, I., Rousselet, G.A., Kawahara, H., and Belin, P. (2010). Vocal attractiveness increases by averaging. Curr. Biol. 20, 116–120.
- Kanwisher, N., McDermott, J., and Chun, M.M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. J. Neurosci. 17, 4302–4311.
- Kayaert, G., Biederman, I., Op de Beeck, H.P., and Vogels, R. (2005). Tuning for shape dimensions in macaque inferior temporal cortex. Eur. J. Neurosci. 22, 212–224.
- Bhodes, G., Jeffery, L., Boeing, A., and Calder, A.J. (2013). Visual coding of human bodies: Perceptual aftereffects reveal norm-based, opponent coding of body identity. J. Exp. Psychol. Hum. Percept. Perform 39, 313–317.
- Nosofsky, R.M. (1992). Exemplar-based approach to relating categorization, identification, and recognition. In Multidimensional Models of Perception and Cognition, F.G. Ashby, ed. (Hillsdale, NJ: Erlbaum), pp. 363–393.
- Palmeri, T.J., and Gauthier, I. (2004). Visual object understanding. Nat. Rev. Neurosci. 5, 291–303.
- Grill-Spector, K., and Malach, R. (2001). fMR-adaptation: a tool for studying the functional properties of human cortical neurons. Acta. Psychol. 107, 293–321.
- Kahn, D.A., and Aguirre, G.K. (2012). Confounding of norm-based and adaptation effects in brain responses. Neuroimage 60, 2294–2299.
- Posner, M.I., and Keele, S.W. (1968). On the genesis of abstract ideas. J. Exp. Psychol. 77, 353–363.

Institute of Neuroscience, Newcastle University, Newcastle upon Tyne, UK. E-mail: chris.petkov@newcastle.ac.uk, quoc.vuong@newcastle.ac.uk

http://dx.doi.org/10.1016/j.cub.2013.04.077

Genital Evolution: Cock-a-Doodle-Don't

Losing the penis in species with internal fertilization may seem paradoxical, but birds have managed to do it multiple times. A new study addresses one developmental mechanism responsible for penis reduction in birds, and opens the door to further examination of this little understood evolutionary phenomenon.

Patricia L.R. Brennan

Most amniotes with internal fertilization have a penis, with the exception of most birds [1]. What could have driven the loss of an organ that seems crucial to internal fertilization, and how exactly can a penis be lost? The answer to the first question is still largely unresolved [2,3]. However, in this issue of *Current* *Biology*, we get an answer to the second question in a paper by Herrera *et al.* [4] that describes a developmental mechanism responsible for the loss of intromittent function in the avian penis.

Only three percent of avian species belonging to two main clades have retained the ancestral copulatory organ: the Paleognathes (e.g., ostriches, kiwis and tinamous), and the Galloanseridae (e.g., chickens, turkeys, megapodes, cracids and ducks) [1]. All other birds have completely lost the penis. Avian penis evolution is complex

