plankton, is easier to see than they are. We now know from the new work by Bagge *et al.* [2] that they add antireflection coatings to this transparency, making them non-reflective as well. In the case of *Cystisoma*, the legs, and occasionally the carapace itself, are covered with evenly spaced, tapered microprotuberances. When these were carefully measured and then modeled using a variety of theoretical approaches, they were found to reduce surface reflections by some two orders of magnitude (varying with wavelength and angle of incidence). The modeling required estimations of the refractive indices of seawater and chitin, but since these are widely measured elsewhere the outcomes are quite convincing. Having antireflection surfaces on the appendages is particularly useful because these have elevated surface area:volume ratios and move constantly, giving them potentially prominent visibility. Besides *Cystisoma*'s nanoprotuberances, its cuticle and that of six other hyperiid species (including the fearsome *Phronima*) were found to be covered with monolayers of small spherical particles. Optical modeling shows that these surface coatings play a similar antireflective role. While the particles have not yet been conclusively identified, indications are that they are nanoplanktonic bacteria that have entered an exosymbiotic relationship with the amphipods, yet another example of the many roles that bacteria have been found to play in the lives of eukaryotes.

At this point, measurements of actual reflections from living hyperiids and estimates of their visibility in the sea are lacking. Further, the role of scattering from internal surfaces and structures was not included in the modeled results. Many of these animals occupy forbidding habitats, accessible only by blue-water scuba diving or the use of autonomous or manned submersibles, and anyone who has searched for them in the ocean knows from experience that they are notoriously difficult to see and capture. Specimens captured in deep plankton tows and brought to the surface are usually damaged and often killed, making it difficult to obtain reliable measurements of their visibility. However, the required work will assuredly be done by this team or other future biological oceanographers. Meanwhile, it will be fascinating to learn how common it is for transparent marine animals to employ antireflection coatings and (in the case of the bacterial symbionts) who exactly it is that coats them.

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Microbial Evolution: Xenology (Apparently) Trumps Paralogy

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Within-genome gene duplication is generally considered the source of extra copies when higher dosage is required and a starting point for evolution of new function. A new study suggests that horizontal gene transfer can appear to play both roles.

New genes are generally thought to arise from old genes by the 'duplication and divergence' model famously explicated by Susumu Ohno almost fifty years ago [1]. In this model, one of the duplicates continues to carry out the original function while the other, relieved of that responsibility, is free to mutate and

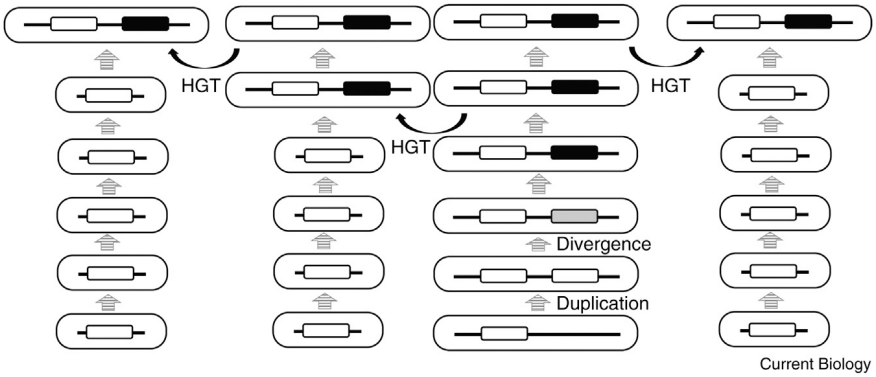

Figure 1. How xenology trumps paralogy.
New gene function (increased shading) arises through divergence after duplication (paralogy), but then spreads to the majority of lineages (within or between species) by horizontal gene transfer (HGT).

be selected for a new function, though this may be achieved only rarely. For prokaryotes, holding on to such within-lineage duplications (paralogs) long enough to evolve a new function, let alone establish sizeable, functionally differentiated gene families, may be problematic. Whether (as with some large populations) there is selection *for* genomic streamlining or (as with small isolated ones) not enough selection *against* it, a general prokaryotic mutational bias favoring deletions over insertions is expected to limit the lifespan of temporarily useless extra copies [2,3]. Thus, acquisition of *novel* functions in prokaryotes is likely to be driven by horizontal gene transfer (HGT) rather than duplication and divergence [4]. Gene amplification producing immediately useful extra copies is another matter, and when there is continuing selection for overproduction of encoded proteins (as in the face of certain environmental stressors or antibiotics) long arrays of tandemly duplicated isofunctional gene copies can be maintained — a gene dosage effect [5]. Thus, what is surprising in a new report by Hehemann *et al.* [6], published recently in *Nature Communications*, is not that HGT between vibrio lineages seems to be responsible for a mix-and-match assembly of functionally differentiated genes for polysaccharide degradation, but that this process also drives increases of copy numbers within these families. The extra copies are xenologs, not paralogs.

Hehemann *et al.* compare the genomes of 84 members of the Vibrionaceae, documenting changes in types and numbers of copies of genes involved in the stepwise degradation of the brown algal glycan alginate. Alginate lyases (Aly) of gene families PL6 and PL7 initiate degradation of the polysaccharide, while oligoalginate lyases (Oal) of families PL15 and PL17 complete its conversion to catabolizable sugar monomers. The authors use the program AnGST [7] to infer evolutionary events that have affected the history of individual Aly and Oal genes in each genome. AnGst is a phylogenomic method that 'reconciles' observed differences between a given gene tree and the species tree by inferring the number of evolutionary events, such as HGT, gene duplication and loss, speciation and gene birth. Each type of event is assigned a cost *a priori*, and the reconciliation scenario minimizing the sum of associated costs is favored, satisfying a generalized parsimony criterion. One of the advantages of AnGST over less sophisticated approaches is that it accounts for the uncertainty in gene trees, as well as for the topology of the gene family tree (rather than just its presence or absence across genomes), while inferring the direction of gene transfers.

Reconciliation methods are powerful, but need to be used cautiously. Depending on the algorithm, they can be very sensitive to the quality of the input gene trees. Most incongruences between gene and species trees can be explained by myriad event combinations, one of which will be favored over the other, depending on the cost (and/or probability) associated with each type of event. But in reality, we have no mechanistic rationale that allows us to precisely estimate these costs *a priori*. Even less might we expect such costs to be universally applicable across the tree of life. Each lineage (and each gene family) has its own idiosyncracies, and there may well be groups in which duplication is the principle route to stably maintained paralogy because the deletion bias is weaker, the agents of horizontal transfer (phages and plasmids) less active and/or the lineages more effectively separated, microecologically and/or microgeographically. This is why the most recent and sophisticated reconciliation methods [8] aim to estimate the relative cost and probability of various events from the data itself instead of being fixed *a priori*.

Caveats notwithstanding, the authors conclude not only that "several different pathways were assembled by an evolutionary Ping Pong of rapid back and forth transfers", but that when a genome carries multiple copies of a given family (say the 11 copies of PL7 in *V. breoganii*) this too is often the result of HGT, not within-lineage duplication. Reassuringly, such a conclusion is based not only on phylogenetic reconciliation but the genes' dispersed chromosomal locations and frequent association with integrase and transposase genes and/or regions of aberrant base composition, hallmarks of HGT. Interestingly, in an earlier survey in which chromosomal dispersal (and sequence divergence) was used to distinguish paralogs from xenologs, Treangen and Rocha [9] concluded that "horizontal transfer, not duplication, drives the expansion of protein families in prokaryotes" (indeed, this was their title).

In keeping with the Polz and Alm labs' long term program correlating fine-scale genomic differentiation with microecology — the study of speciation without foolhardy commitment to any definition of 'species' [10] — Hehemann *et al.* characterize the physiology of their strains and correlate that with the number and type of alginate and oligoalginate genes. (Hehemann, a Max Planck group leader, is the algal polysaccharide expert here; readers will remember his 2010 discovery of transferred genes allowing

digestion of sushi in the gut microbes of Japanese people [11].)

The authors find that alginate and alginate lyase activities mirror gene content and dosage both quantitatively and qualitatively (in terms of useable alginate polymer length) and that some strains (with shorter lag times in growth experiments) more actively excrete ('broadcast') degradative enzymes. Possibly this is a variable property of the gene products themselves (different export and tethering characteristics), indicating acquisition of new (not just more) function through xenology, possibly from outside the vibrio populations studied. In this case, we still might ask whether in the end duplication and divergence are not the creative force (Figure 1). It could be that prokaryotic gene duplicates not under selection for increased gene dosage are just occasionally held onto long enough to differentiate functionally. This being rare — and HGT within and between species being frequent — it will be the case that in most genomes harboring two functionally differentiated copies, these will be xenologs, not paralogs. And if HGT is indeed more frequent than duplication [4], this will be true even without functional differentiation.

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Visual Neuroscience: Seeing Causality with the Motor System?

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Understanding how humans perceive cause and effect in visual events has long intrigued philosophers and scientists. A new study in primates reveals the neural correlates of perceived causality at the single-cell level, but in an unexpected place — the motor system.

Clap your hands: we have all learned how to do this when we were very young, babies in fact, most likely from our parents or siblings. Clapping is a milestone for the developing infant that, beyond motor coordination, involves the perception of causality: two hands, stopping each other in mid-flight, *cause* that unmistakable sound. The inference of causality provides structure to a dynamic visual world, is crucial for successful manipulations of it (Figure 1), and shapes the way we describe it: she pulls the cloth off the table; he kicks the door shut; the waves rock the boat. Indeed, babies as young as 6 or 7 months of age appear to discern causality in abstract visual displays such as the launching stimulus, in which one object is seen to cause another object to move by crashing into it [1,2]. These findings fueled debates started by the father of the field, the Belgian psychologist Albert Michotte [3]. On the basis of spontaneous reports of subjects seeing launching stimuli, Michotte proposed that the detection of causality is an immediate, visual process, rather than a reflective, cognitive one, and that it is innate, rather than acquired through learning [4,5]. In a new study reported in this issue of *Current Biology*, Caggiano *et al.* [6] discovered neurons that appear to encode visual events with specific causal properties, such as spatiotemporal contingencies. Unexpectedly, these neurons are in the motor cortex, giving a new twist to how we think about the mechanisms giving rise to the perception of causality.

Caggiano *et al.* [6] recorded from neurons in area F5 of the primate brain, which contains large numbers of so-called mirror neurons that respond to both performing a certain action as well as seeing the same action performed. Their monkeys viewed short and highly controlled videos of naturalistic actions. One version of the video (the grasping version) begins with a pepper lying on a table, and then a hand moves into the frame, picks up the vegetable, and removes it from view. The second version (the placing version) is the same video played backwards, showing a hand moving into view and putting down the