for detecting the crowding of texture are both at play. Disentangling the two will be an interesting challenge. One promising line, as Durgin [8] suggests, will be to look for dissociations between number and texture perception. Manuela Piazza, Stanislas Dehaene and Marco Zorzi (personal communication) have shown that dyscalculic individuals have higher Weber fraction for number discrimination than do controls. It would be interesting to study whether discrimination of texture is also affected in these individuals; and to test adaptation to both attributes.

We suspect that the investigation of numerosity as a visual primitive will open a rich vein of connections between visual perception and mathematical intuition. Mathematicians often 'see' their solutions first and verify them later, as many testified to Hadamard [15].

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Horizontal gene transfer and the evolution of cnidarian stinging cells

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Genes are regularly transmitted vertically, within one lineage, from one generation to the next, but they can also be exchanged between lineages by horizontal gene transfer (HGT). HGTs are frequent in prokaryotes and have been shown to play important roles in unicellular eukaryotes, whereas only a few instances are known in animals [1,2]. Here, we provide evidence that a subunit of bacterial poly-γ-glutamate (PGA) synthase was transferred to an animal ancestor by HGT. We suggest that this gene acquisition had important consequences on the evolution of the stinging cells (nematocytes) that cnidarians (sea anemones, jellyfish, corals etc.) essentially use to capture prey.

We were alerted to the possibility of a significant HGT from bacteria to metazoans by the unusual phylogenetic distribution of the polyanionic polymer PGA, which has been only detected extracellularly in some prokaryotes [3], and intracellularly in the capsule of cnidarian nematocytes [4–6]. By attracting cations within the capsule, PGA is critical for the nematocyte discharge, which involves rapid changes in intracapsular osmotic pressure [4]. In bacteria, three *pgs* genes, *AA*, *B*, *C*, have been identified as essential for PGA synthesis [3]. We could detect clear orthologues of *pgsAA* in all available cnidarian genomes (Supplemental Data). In the *Clytia hemisphaerica* medusa (Hydrozoa), *pgsAA* is expressed in the nematogenic area of the tentacle bulb, in the same territory as the nematogenesis marker *minicollagen3-4a* [7] (Figure 1A,B). In the same region, we detected a high quantity of intracellular glutamate, the monomer for PGA synthesis (Figure 1C) and strong expression for two glutamate high affinity transporters (Figure 1D,E). These results are consistent with an involvement of pgsAA in PGA production in nematoblasts.

To investigate the evolutionary origin of the cnidarian *pgsAA* gene, we searched for homologues of *pgs* genes in all available complete genomes from Bacteria, Archaea and Eukaryota (Supplemental data). The vast majority of eukaryotes lacked any *pgs* genes, with only the *pgsAA* subunit detected in a few species belonging to various distantly related eukaryote taxa (Figure 2). The patchy distribution of these eukaryote *pgsAA* homologues within the *pgsAA* tree suggests that they were acquired through several independent HGT events. Furthermore, the clear polyphyly of the major prokaryotic *pgsAA* groups suggests that this gene is highly mobile. Consistent with this, *PgsAA* was detected in no less than five naturally occurring plasmids, providing a possible explanation for HGT over large taxonomic distances. The presence of introns with stop codons in several of the eukaryote *pgsAA* genes, including all but one cnidarian *pgsAA* sequences, might provide a directionality to the HGT from bacteria to these eukaryotes; it is highly unlikely that a gene with intronic stop codons could be successfully transferred from Eukaryotes to Bacteria, in which transcription and translation are directly coupled. All but one of the cnidarian *pgsAA* sequences were grouped in our analyses in a single clade (Clade 1), together with a sequence from the sponge *Amphimedon queenslandica* (Figure 2), while most remaining eukaryote sequences were grouped with a subset of bacterial and archaeal *pgsAA* sequences (Clade 2). An AU test rejected the grouping of Clade 1 sequences with any other eukaryote sequence, indicating that the HGT event occurred in an exclusive ancestor of sponges and cnidarians (Supplemental data). Assuming the classical phylogenetic position of the sponges as the sister group of all other metazoans, we can conclude that this HGT dates back to the root of metazoans, and that the bilaterian animals have secondarily lost the gene. Additional independent transfers of *pgsAA* gene from Bacteria to eukaryotes are inferred within Clade 2 (Supplemental data). In particular, the sea anemone *Nematostella vectensis* harbours a Clade 2 *pgsAA* gene branching with sequences

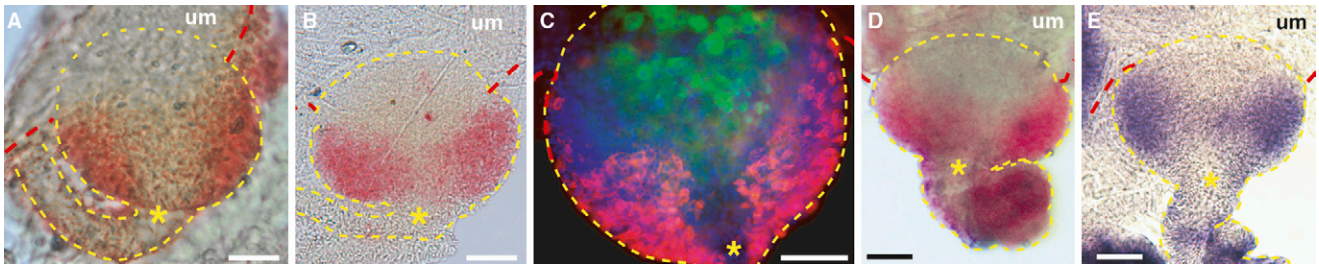

Figure 1. *Che-pgsAA* expression associated with nematogenesis in the tentacle bulb of the medusa of *Clytia hemisphaerica*.

In all images, the tentacle bulb is viewed from the external side. The yellow dotted line encircles tentacle bulb and tentacle, the yellow asterisk indicates the site of tentacle insertion on the apical pole of the bulb, and the red dotted line delimits the border of the umbrella. (A) *In situ* hybridization showing *Che-pgsAA* expression (in red) in the apical part of the bulb, on each side of the tentacle insertion site. (B) *In situ* hybridization showing *minicollagen3* expression (in red) in the same territories. (C) Anti-glutamate immunostaining (red) and DAPI nuclear staining (blue) in a tentacle bulb. Natural fluorescence of endodermal cells appears in green. (D) *In situ* hybridization revealing *Che-GluT1* expression (in red). (E) *In situ* hybridization revealing *Che-GluT2* expression (in purple) in the same territory. Scale bars: A: 2.5mm; B–E: 25 μm.

from the annelid *Capitella capitata* and the archaeon *Methanosarcina acetivorans*, clearly resulting from an additional HGT. This grouping makes no phylogenetic sense, but can perhaps be explained by ecology, as all three species live in the same costal brackish waters with anoxic sediments rich in organic compounds and Bacteria [5,8,9].

We suggest that a *pgsAA* gene transferred from a prokaryote to a metazoan ancestor was exploited in the cnidarian lineage for PGA synthesis during nematocyte formation. PgsAA might have improved nematocyst function, and thus could be a good candidate for the first example of a HGT with significant impact on the evolution of an entire animal phylum. Indeed, nematocytes are vital for cnidarians and constitute the major shared derived feature of the phylum.

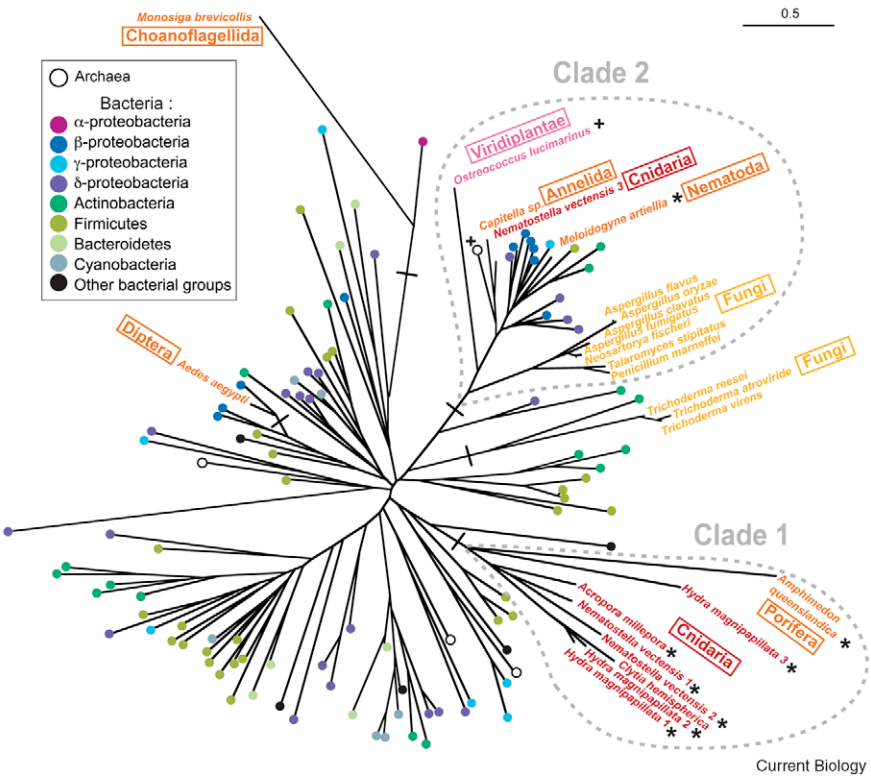

Figure 2. Phylogenetic analysis of *pgsAA* sequences and the phylogenetic distribution of *pgsAA*.

Best unrooted tree following AU test (Supplemental data) of pgsAA amino-acid sequences from selected Bacteria (taxonomic positions are indicated by a color code) and including all available sequences from Archaea and Eukaryota. The asterisk indicates species with stop codons in the introns of their *pgsAA* gene. '+': Species with a genomic context suggesting that genes neighbouring *pgsAA* are also of bacterial origin. Branches crossed by a bar indicate statistically supported clades (Bootstrap value > 90% and/or significant *p*-values in the AU test in the case of Clade 2) that include eukaryotes.

Supplemental data

Supplemental data are available at http://www.current-biology.com/cgi/content/full/18/18/R858/DC1

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