

atoms that reside in particular environments (arrangements of nearby atoms). This in turn causes the surface atoms in different facets to have distinct catalytic activities. This fundamental insight dates back to the classic discovery that {111} surfaces on single crystals of platinum are typically much more catalytically active than {100} surfaces in reactions that form aromatic compounds.

Indeed, Huang and colleagues' cuprous oxide nanocrystals clearly exhibit very different catalytic properties depending on the facets displayed. The authors found that cubic nanocrystals that are bound exclusively by {100} faces are essentially inactive in the photodegradation reaction of methyl orange, whereas octahedra bound by {111} surfaces are moderately active catalysts. Rhombic dodecahedra bound by {110} surfaces, however, caused much faster photodegradation of methyl orange than the other nanocrystal shapes. The authors speculate that the observed catalytic activities correlate with the surface density of copper sites on the different facets, although they report no direct evidence for this. It is also unclear whether many of the atoms on nanocrystal surfaces undergo rearrangements during the reactions, or how ligand molecules that are bound to the different surfaces — either during crystal formation or in the photodegradation reactions — affect catalytic activity.

The new findings¹ form part of a growing body of literature documenting surface-dependent catalytic activities, perhaps most notably for metals. For example, key studies performed on the surfaces of samples of macroscopic single crystals under ultra-high-vacuum conditions have shown that some reactions are sensitive to surface structure⁴. A quintessential case is the platinum-catalysed reaction of benzene with hydrogen: the {100} platinum surface yields only cyclohexane (a saturated hydrocarbon) as a product, whereas the {111} surface also yields cyclohexene (an unsaturated analogue of cyclohexane)⁴.

This dependence of catalytic activity on surface structure extends to metal nanocrystals, particularly in the case of platinum, palladium and rhodium. For instance, in the hydrogenation of benzene, platinum nanocrystals that expose well-defined {100} and {111} surfaces behave⁵ in much the same way as larger crystals. In another example, faceted palladium nanocrystals that have high-index surfaces — {730} and {221} surfaces, which contain a high density of atomic steps and ledges — were found⁶ to be much more active catalysts in 'Suzuki' carbon-carbon bond-formation reactions than nanoparticles that have typical {100} surfaces. Such high-index faceted nanoparticles are also better catalysts for some electrochemical reactions^{7,8}. And returning to cuprous oxide, highly faceted polyhedral microcrystals that display high-index {311} surfaces are especially good catalysts for the oxidation of carbon monoxide⁹.

Although it is clear that the reactivity and selectivity of nanoparticle catalysts depend on the shape (and hence the exposed surfaces) of the particles, in many cases it is unclear whether these effects are truly surface-dependent. This is especially true for reactions in solution or in the gas phase, where there is evidence that changes to particle surfaces and shapes may occur during the reactions¹⁰. Methods for the direct *in situ* surface analysis of molecules adsorbed to nanocrystals in solution, analogous to the techniques commonly used to study larger single crystals, need to be developed to address this issue. Nevertheless, as Huang *et al.*¹ have shown, sculpting the shape of nanocrystals is a promising approach for developing catalysts that produce only one desired reaction product out of many other possible products at high reaction rates — an essential requirement for a wide variety of industrially important reactions. ■

PLANT BIOLOGY

Equal-parenting policy

During early embryo development in animals, maternal genes are expressed in preference to those of the zygote — the newly fertilized egg. But in plants it seems that zygote genomes switch on within hours of fertilization. [SEE LETTER P.94](#)

CHRISTOPHER J. HALE
& STEVEN E. JACOBSEN

Fertilization occurs when two gametes merge to form a zygote. The zygote's genome comprises two sets of chromosomes — one maternal, the other paternal. In animals, the stages of development immediately after fertilization are disproportionately controlled by maternally inherited factors, with the zygotic genome being switched on gradually in waves of activation¹. Whether plants undergo a similar maternal-to-zygotic transition in genomic activity has been a long-standing question. In contrast to previous work², Nodine and Bartel³ show (page 94 of this issue) that a plant zygote's protein-coding transcriptome — its total complement of protein-coding RNA transcripts — contains relatively equal maternal and paternal contributions. It seems, therefore, that plants and animals have evolved distinct strategies for managing the early steps in the transition from two gametes to an organism with maternal and paternal copies of the genome*.

For the plant species *Arabidopsis thaliana*, a wealth of whole-genome sequence data exists for closely related yet genetically distinct lines known as ecotypes⁴. To directly measure the respective contributions of the maternal

*This article and the paper³ under discussion were published online on 22 January 2012.

Peidong Yang is in the Department of Chemistry, University of California, Berkeley, Berkeley, California 94720, USA, and at King Abdulaziz University, Jeddah, Saudi Arabia. e-mail: p_yang@berkeley.edu

- Huang, W.-C., Lyu, L.-M., Yang, Y.-C. & Huang, M. H. *J. Am. Chem. Soc.* **134**, 1261–1267 (2012).
- Paracchino, A., Laporte, V., Sivula, K., Grätzel, M. & Thimsen, E. *Nature Mater.* **10**, 456–461 (2011).
- Siegfried, M. J. & Choi, K.-S. *Adv. Mater.* **16**, 1743–1746 (2004).
- Somorjai, G. A. & Li, Y. *Introduction to Surface Chemistry and Catalysis* 2nd edn, Ch. 9 (Wiley, 1994).
- Bratlie, K. M., Lee, H., Komvopoulos, K., Yang, P. & Somorjai, G. A. *Nano Lett.* **7**, 3097–3101 (2007).
- Wang, F. *et al. J. Am. Chem. Soc.* **133**, 1106–1111 (2011).
- Chen, Q.-S. *et al. J. Am. Chem. Soc.* **133**, 12930–12933 (2011).
- Habas, S. E., Lee, H., Radmilovic, V., Somorjai, G. A. & Yan, P. *Nature Mater.* **6**, 692–697 (2007).
- Leng, M. *et al. J. Am. Chem. Soc.* **132**, 17084–17087 (2010).
- Joo, S. *et al. Nature Mater.* **8**, 126–131 (2009).

and paternal genomes to the zygotic transcriptome, Nodine and Bartel crossed two of these ecotypes and sequenced the RNA content of the resulting zygote. Using the genetic differences between the parents, they then matched these RNAs to either the maternal or the paternal genome.

The authors observed a near-equal abundance of RNA sequences derived from each parental genome in the plant embryos as early as the one- to two-cell stage. Only a small number of genes showed biased expression. They also performed reciprocal crosses — switching which ecotype provided the male and female gamete. It emerged that most of these cases of bias were probably due to genetic or epigenetic differences (chemical modifications that alter gene expression without affecting the DNA sequence) between the two ecotypes used, rather than being a result of which ecotype was used as the male or the female parent. These findings imply that the plant zygotic genome is essentially switched on only hours after fertilization.

Nodine and Bartel's results are in contrast to other reports^{2,5} suggesting that the maternal-to-zygotic transition in plants is gradual, as is the case for animals. The most comprehensive of these reports², published last year, used a genomics approach similar to that of the current study, and found that more than 80% of the *Arabidopsis* transcriptome in early

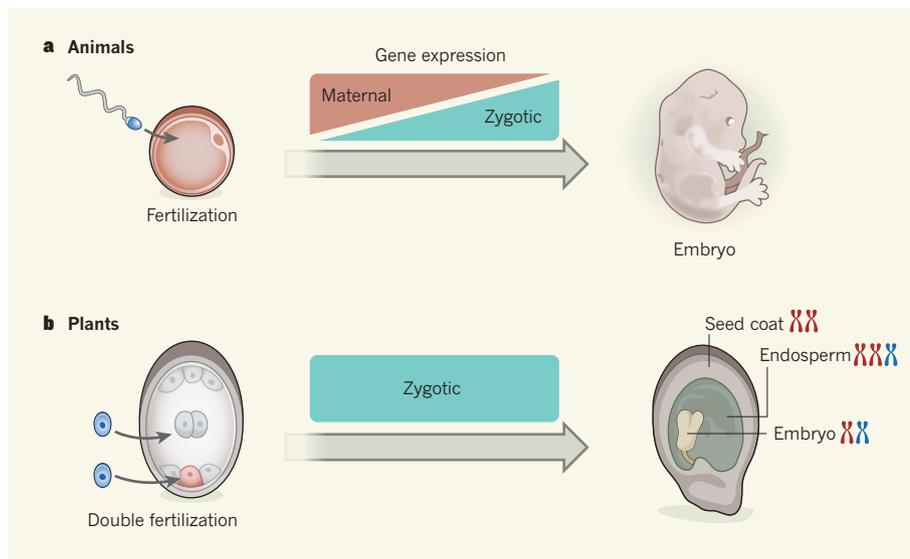


Figure 1 | Maternal-to-zygotic genomic transition in plants and animals. **a**, In animals, a single fertilization event between maternal and paternal gametes forms the zygote (not shown). Initially, the animal embryo is under predominant control of the maternal genome, and the zygotic genome is only gradually activated over the course of embryogenesis. **b**, In plants, a double fertilization process generates the zygote and the endosperm tissue. Both the endosperm and the embryo are encased in maternal tissue that generates the seed coat. Chromosome symbols represent maternal (red) and paternal (blue) genomes. Nodine and Bartel³ show that, in contrast to the case for animals, the plant zygotic genome is activated almost immediately after fertilization.

embryos is derived from the maternal genome.

What might explain such different results between the two studies? Nodine and Bartel³ suggest that the most likely answer is that the embryo samples of the earlier study were contaminated by maternal tissue. This is because, in *Arabidopsis* as in other flowering plants, the embryo is surrounded by a seed coat and other maternally derived tissue (Fig. 1), making the isolation of high-purity embryonic tissue difficult — a problem for the extremely sensitive genome-sequencing techniques used in both studies. After observing this maternal-contamination effect in pilot studies, Nodine and Bartel³ overcame the problem by extensively washing the isolated embryo cells.

One question arising from Nodine and Bartel's study is why activation of the zygotic genome is so different between plants and animals. Because the two kinds of organisms evolved multicellularity independently⁶, and have very different life histories, it is perhaps not surprising that the maternal-to-zygotic transition also differs between them. In plants, gametes are generated from cells derived from a pool of undifferentiated cells that are also responsible for generating structures such as leaves^{7,8}, rather than from a distinct germ-cell lineage as occurs in animals. In addition, fertilization itself is radically different in flowering plants compared with animals, with each seed being the product of two fertilization events (Fig. 1b). In this process, one fertilization event forms the endosperm, a tissue that is functionally similar to the mammalian placenta, and which contains two sets of maternal

chromosomes and one set of paternal chromosomes. A second fertilization event results in the formation of the embryo. It is noteworthy that, although Nodine and Bartel show that the embryo experiences equal transcriptome contributions from both parental genomes, gene expression in the embryo-nourishing endosperm shows extensive parental influence³; these effects are due to uneven nuclear 'dosage' as well as to epigenetic imprinting effects.

Another question is how the early plant embryo coordinates rapid integration of two genomes and the concomitant activation of a resulting zygotic genome. In animals, a suite of mechanisms acts to clear maternal factors, such as proteins and RNAs, from the developing zygote and to activate the zygotic genome^{1,10}. It is unclear whether similar mechanisms operate in plants. Tantalizingly, epigenetic processes such as DNA methylation and demethylation, as well as regulatory small RNA molecules, have recently been implicated⁹ in the control of both gamete and endosperm development. Future studies of these pathways may reveal mechanisms for the regulation of gene expression in embryonic plants.

Understanding how a functional plant genome so quickly emerges from two progenitor genomes is vital for understanding plant development, and for informing approaches to plant breeding and plant biotechnology. In many crop species, combining two different parental genomes can generate regular and predictable hybrid vigour, known as heterosis. In some species this vigour is obvious very early in development¹¹. Consistent with these observations, Nodine and Bartel's work³ suggests that



50 Years Ago

In a Cantor Lecture ... Dr. Tom A. Margerison described how science could be presented on television not only to the specialist audience but especially to the layman. In spite of the absolute necessity of science and technology, the 10–15 per cent of the population who guide the destiny of Britain, the professional men, the majority of teachers, the industrialists, the politicians, are almost completely ignorant about science. The bridging of this gap in this most influential part of the population is of great urgency. There are many ways in which television can help to close the gap.
From Nature 3 February 1962

100 Years Ago

Mr. Harding's letter ... reminds me of an experience which ... may be of sufficient interest to place upon record in these columns ... It must, I think, have been in 1866 or 1867 ... that I had occasion to go from the West to the East End of London. Starting upon my journey about 10 p.m., it began to rain soon after I left the house in Bayswater, and I opened an umbrella, which, to my surprise, became stiffer and heavier every moment, and was found on examination to be so thickly glazed over with ice that it was impossible to close it. At the same time the pavements and roadway were also becoming uniformly glazed; pedestrian movement was most difficult, and all horse traffic was suspended. Although an experience of some forty-five years ago, the impression left upon my memory is still vivid — the ludicrous sight of people carrying ponderous and rigidly frozen umbrellas which they could not close, the stream of skaters down Oxford Street and Holborn, and the silence due to the absence of vehicles, all came to mind on reading Mr. Harding's letter.
From Nature 1 February 1912

zygotic-genome dynamics in plants, including, perhaps, some aspects of heterosis, are established almost immediately after fertilization. ■

Christopher J. Hale is in the Department of Molecular, Cell and Developmental Biology, and **Steven E. Jacobsen** is at the Howard Hughes Medical Institute, University of California, Los Angeles, Los Angeles, California 90095, USA.
e-mails: cjhale@ucla.edu; jacobsen@ucla.edu

1. Tadros, W. & Lipshitz, H. D. *Development* **136**, 3033–3042 (2009).
2. Autran, D. *et al. Cell* **145**, 707–719 (2011).

3. Nodine, M. D. & Bartel, D. P. *Nature* **482**, 94–97 (2012).
4. Cao, J. *et al. Nature Genet.* **43**, 956–963 (2011).
5. Vielle-Calzada, J.-P., Baskar, R. & Grossniklaus, U. *Nature* **404**, 91–94 (2000).
6. Grosberg, R. K. & Strathmann, R. R. *Annu. Rev. Ecol. Evol. Syst.* **38**, 621–654 (2007).
7. Sundaresan, V. & Alandete-Saez, M. *Development* **137**, 179–189 (2010).
8. Twell, D. *Sex. Plant Reprod.* **24**, 149–160 (2011).
9. Feng, S., Jacobsen, S. E. & Reik, W. *Science* **330**, 622–627 (2010).
10. Walser, C. B. & Lipshitz, H. D. *Curr. Opin. Genet. Dev.* **21**, 431–443 (2011).
11. Meyer, S., Pospisil, H. & Scholten, S. *Plant Mol. Biol.* **63**, 381–391 (2007).

individual heads, both groups used markers that emitted fluorescence of a different colour for each head, a method previously applied^{7,8} to another motor protein, myosin V.

To facilitate the two-colour labelling, both groups generated dynein molecules in which the two subunits had been artificially linked to each other. DeWitt *et al.* attached different fluorescent quantum dots (semiconductor nanocrystals) to modified dynein heads that dimerized in the presence of the small molecule rapamycin. By contrast, Qiu *et al.* attached complementary DNA strands and different fluorescent organic molecules (less stable but smaller than quantum dots) to dynein heads, so that the DNA molecules self-associated to link both heads together. To observe the stepping mechanism, both groups^{1,2} slowed dynein's movement by using an ATP concentration that was much lower than that normally found in the cell's cytoplasm. From computerized image analysis, they were able to track the positions of individual dynein heads in two dimensions with an accuracy of about 3 nm.

The primary finding of both studies is that dynein has a highly variable stepping pattern (Fig. 1). For most steps, the heads moved alternately, but they passed each other only infrequently. After each step, the head-to-head distance varied widely, from less than 5 nm to 50 nm, which is indicative of uncoordinated stepping. By contrast, other motor proteins such as kinesin-1 show strictly coordinated stepping. In kinesin-1, only the lagging head can bind ATP, because of a mechanism that relies on the strain between the two heads. This mechanical coupling forces the heads to step in a strictly alternating pattern, because the hydrolysis of the ATP molecule causes the lagging head to make the next step⁹.

MOLECULAR MOTORS

A staggering giant

The protein dynein 'walks' along filaments to transport various cargoes within the cell. Two studies reveal that, unlike other motor proteins, dynein's steps are not strictly coordinated.

WILHELM J. WALTER & STEFAN DIEZ

When you are walking down the street your feet probably take alternating steps, with one foot passing the other each time. Alternatively, you might walk without letting your feet pass one other, in a limping motion. However, regardless of the stepping pattern, your walking will be highly coordinated. At the molecular scale, the motor protein dynein also 'walks' along filaments to carry vesicles and organelles to specific locations within a cell. But is coordination between dynein's two 'feet' required for walking? Two papers — one by DeWitt *et al.*¹ in *Science* and another by Qiu *et al.*² in *Nature Structural & Molecular Biology* — independently address this question and come to the surprising conclusion that dynein uses both random and coordinated walking.

Cytoplasmic dynein is a giant, multi-subunit protein that uses the chemical energy stored in the molecule ATP to transport cargoes³. It moves along microtubules — long polymeric tubes composed of dimers of the protein tubulin, typically arranged to form 13 parallel tracks. Dynein has two 'head' domains linked by their respective 'tails', whereby the heads act as 'feet' for walking along the microtubules. Each head contains four binding pockets for ATP and a microtubule-binding site. Of the four ATP-binding pockets, one catalyses ATP hydrolysis to generate energy for walking; the other three are thought to be important for the regulation of dynein activity⁴.

Previous work^{5,6} using single dynein motors bound to beads revealed that during processive motility on microtubules —

the process by which a motor takes multiple steps without dissociating from the microtubule — dynein moves by 8-nanometre steps. This distance corresponds to the periodicity of the dimeric tubulin subunits along the microtubule tracks. However, little is known about the coordination of the two dynein heads during motion.

To make the dynein heads visible and study the stepping mechanism during processive motion, DeWitt *et al.*¹ and Qiu *et al.*² attached fluorescent markers to the dynein heads and used fluorescence microscopy. Moreover, to distinguish between the movement of the two

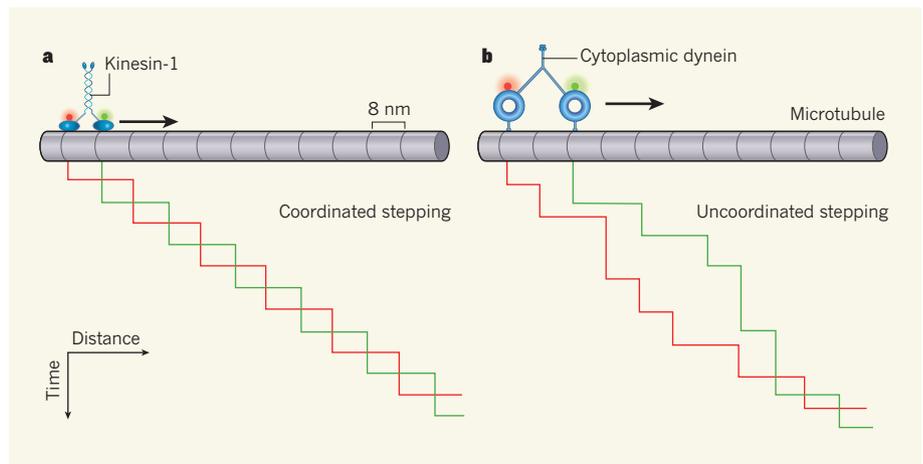


Figure 1 | Stepping patterns in motor proteins. **a**, Some motor proteins, such as kinesin-1, move in a highly coordinated way along microtubules (polymeric protein tubes; grey). The traces show the stepping of individual motor heads (each labelled with a different fluorescent marker, red or green). **b**, DeWitt *et al.*¹ and Qiu *et al.*² show that, by contrast, cytoplasmic dynein moves in a variable stepping pattern. Although the heads often move alternately, they only seldom pass each other, and the spacing between them varies strongly over time.