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studies suggest that the cytoskeletal architecture of actively dividing cells is incompatible with that required for morphogenesis. Mutations in two genes in *C. elegans*, *gad-1* and *emb-5*, lead to premature division of the endoderm cells and their failure to invaginate [18,19]. Concomitant with a heterochrony in cell fate specification, a delay in the lengthening of the cell cycle, required for the reorganization of the cytoskeleton of gastrulating cells, might also contribute to the distinct morphology of the *T. diversipapillatus* ‘gastrula’.

Gastrulation was among the key innovations of metazoan evolution. It seems likely that, once it was invented, the basic mechanics were preserved while many unique properties were allocated to the various phyla of animals. The radically different appearance of gastrulation in *C. elegans* and other metazoans may have arisen from relatively modest changes in the location and timing of specification. Secondarily simplified animals like *C. elegans* have become exceedingly parsimonious with their cells: for example, the function of the kidney in *C. elegans* has been relegated to a single cell [20]. Similarly, it may be appropriate to regard the two endoderm cells that initiate gastrulation in this animal as an invaginating sheet, albeit a very small one. It is conceivable that the cellular mechanisms involved in mobilizing germ layer progenitors into the embryo interior may be virtually identical, whether this movement involves a large sheet of cells or only two cells. Though embryos appear very different on the surface, inwardly they may be closely similar.

**References**

1. Beetschen, J.C. (2001). Amphibian gastrulation: history and evolution of a 125 year-old concept. Int. J. Dev. Biol. *45*, 771–795.
2. Schierenberg, E. (2005). Unusual cleavage and gastrulation in a freshwater nematode: developmental and phylogenetic implications. Dev. Genes Evol. *215*, 103–108.
3. Aguinaldo, A.M., Turbeville, J.M., Linford, L.S., Rivera, M.C., Garey, J.R., Raff, R.A., and Lake, J.A. (1997). Evidence for a clade of nematodes, arthropods and other moulting animals. Nature *387*, 489–493.
4. Martin, V.J., Littlefield, C.L., Archer, W.E., and Bode, H.R. (1997). Embryogenesis in hydra. Biol. Bull. *192*, 345–363.
5. Arendt, D., and Nubler-Jung, K. (1999). Rearranging gastrulation in the name of yolk: evolution of gastrulation in yolk-rich amniote eggs. Mech. Dev. *81*, 3–22.
6. Technau, U., and Scholz, C.B. (2003). Origin and evolution of endoderm and mesoderm. Int. J. Dev. Biol. *47*, 531–539.
7. Wiegner, O., and Schierenberg, E. (1999). Regulative development in a nematode embryo: a hierarchy of cell fate transformations. Dev. Biol. *215*, 1–12.
8. Voronov, D.A., and Panchin, Y.V. (1998). Cell lineage in marine nematode *Enoplus brevis.* Development *125*, 143–150.
9. Leptin, M. (2005). Gastrulation movements: the logic and the nuts and bolts. Dev. Cell *8*, 305–320.
10. Putzke, A.P., and Rothman, J.H. (2003). Gastrulation: PARtaking of the bottle. Curr. Biol. *13*, R223–R225.
11. Hall, B.K. (1999). In Evolutionary Developmental Biology, Second Edition Edition. (Kluwer Academic Publishers).
12. Blaxter, M.L., De Ley, P., Garey, J.R., Liu, L.X., Scheldeman, P., Vierstraete, A., Vanfleteren, J.R., Mackey, L.Y., Dorris, M., Frisse, L.M., et al. (1998). A molecular evolutionary framework for the phylum Nematoda. Nature *392*, 71–75.
13. Voronov, D.A., Panchin, Y.V., and Spiridonov, S.E. (1998). Nematode phylogeny and embryology. Nature *395*, 28.
14. Gould, S.J. (1992). Ontogeny and phylogeny–revisited and reunited. Bioessays *14*, 275–279.
15. Smith, K.K. (2003). Time’s arrow: heterochrony and the evolution of development. Int. J. Dev. Biol. *47*, 613–621.
16. Nance, J., and Priess, J.R. (2002). Cell polarity and gastrulation in *C. elegans.* Development *129*, 387–397.
17. Duncan, T., and Su, T.T. (2004). Embryogenesis: coordinating cell division with gastrulation. Curr. Biol. *14*, R305–R307.
18. Nishiwaki, K., and Miwa, J. (1998). Mutations in genes encoding extracellular matrix proteins suppress the *emb-5* gastrulation defect in *Caenorhabditis elegans.* Mol. Gen. Genet. *259*, 2–12.
19. Knight, J.K., and Wood, W.B. (1998). Gastrulation initiation in *Caenorhabditis elegans* requires the function of *gad-1*, which encodes a protein with WD repeats. Dev. Biol. *198*, 253–265.
20. Nelson, F.K., and Riddle, D.L. (1984). Functional study of the *Caenorhabditis elegans* secretory-excretory system using laser microsurgery. J. Exp. Zool. *231*, 45–56.

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# Social Cognition: Imitation, Imitation, Imitation

**Monkeys recognize when they are being imitated, but they seem unable to learn by imitation. These facts make sense if imitation is seen as two different capacities: social mirroring, when actions are matched and have social benefits; and learning by copying, when new behavioural routines are acquired by observation.**

**Richard W. Byrne**

Imitation gets a bad press: we know it is the sincerest form of flattery, and of course for effective education the learner must be able to copy the teacher, but on the whole, ‘imitation’ is linked to shallow, cheap and even fraudulent behaviour. It comes as a shock to discover that, as far as we know, most non-human animals are unable to imitate [1]: is imitation, after all, rather clever?

In everyday human life, imitation is remarkably prevalent: babies imitate the facial movements of adults within minutes of birth [2]; lovers find themselves unconsciously mirroring the other’s posture, and sycophants do the same with the stance and mannerisms of the powerful [3]; when you copy a friend’s wave in a dense crowd it shows them immediately you’ve seen them; and even the most inarticulate mechanic can show us what to do to fix our car’s engine. Imitation certainly comes naturally to humans.

The idea that imitation is a special faculty, critical in child development and perhaps a central aspect of human uniqueness, has gained ground in psychology over recent years [4,5]. The discovery of ‘mirror neurons’ [6,7] — cells in the premotor area of the brain that are activated by a hand performing a simple goal-directed action and respond equally whether the hand is one’s own or another person’s

— offers hope of understanding the neural basis of this important ability. Confusingly, though, these neurons were discovered in the brains of monkeys — and monkeys are thought unable to imitate [8]. What is going on?

To find out, it is useful to distinguish two kinds of imitation, *social mirroring*, and *learning by copying*, each of which seems to function for a different purpose [9]. To improve our car maintenance, we need to augment our skill repertoire by assembling new programmes of behaviour — the function is skill acquisition. For imitation to help this process, our brain must be able to decode the behaviour of the expert mechanic and then re-synthesize it for ourselves, using as building blocks simpler components that we can perform already [10].

Learning by copying therefore requires powerful perceptual-cognitive processes to decompose complex behaviour, along with the ability to build up new skills from simpler components. But social mirroring may in principle be achieved by much simpler cognitive processes, because it does not require anything new to be learnt [11]. (Smiling or tongue-protrusion may be ‘new’ in a technical sense, for a baby so young that it has had little time to explore its small behavioural repertoire, but no learning is involved. Those actions come naturally, as they are in the baby’s latent repertoire.)

Several forms of imitation seem best understood as social mirroring, those cases in which the function seems to be some form of empathy or mutual identification. In each, imitation shows the other that one is ‘in tune’ with them, whether the other is the mother of a new-born baby, a lover or boss, or just a friend out of shouting range. Social mirroring is based on matching the current behaviour of another with similar-looking actions of one’s own: and mutual identification requires synchrony, not creativity. The starting point for mirroring is therefore to be able to recognize when another is doing something that the self can also do. This sort of generalization, of course, is just what mirror neurons achieve; so, a monkey should surely be able to recognize when another’s behaviour is like its own. Until now, it has been a puzzle that the scarcity of monkey imitation suggested otherwise.

Annika Paukner and her colleagues [12] have now resolved this anomaly by empirically separating imitation recognition from imitation itself, and found that monkeys can indeed recognize when another’s behaviour matches their own. In their experiment, two humans performed actions in synchrony with a monkey’s own. Both humans and monkey manipulated similar small cubes with hands and mouth. However, one person copied the precise actions the monkey was doing at the time, whereas the other performed other actions — just as monkey-like behaviour, but not the precise actions the subject was using at that time. Monkeys consistently preferred to look at the person who was imitating them, except when they were mouthing the cube — perhaps because they were then unable to see clearly what the humans were doing.

Mirror neurons have sometimes been misleadingly described as ‘monkey see, monkey do’ cells, but the work of Paukner and colleagues [12] strongly supports the interpretation given by the original discoverers of mirror neurons, Giacomo Rizzolatti and collaborators [13]. They argued that the mirror neuron system functions by identifying the current disposition and likely future actions of other individuals. In the experiment of Paukner *et al.* [12], the monkey responds to the special disposition of the imitating human, the fact that ‘we’re in tune’. If the ability to recognize a familiar action being done by another is combined with a tendency to do the same thing, then a simple but powerful mechanism for social mirroring is the result, and this has been called *response facilitation* [11]. We do not, of course, find ourselves copying the actions of everyone we observe: only ‘significant others’ trigger response facilitation. Who we find significant will vary with circumstances: for a new-born, any adult carer; for a toddler, mum or dad, but an adolescent more often identifies with peers; for lovers, loved-ones; for a sycophant, a strong boss, and so on. But in each case when behavioural mirroring is seen, the same simple underlying mechanisms may be in operation.

Response facilitation may also underlie many experimental results in animals that have been interpreted as learning by copying, imitation *sensu* skill acquisition. The procedure most widely used as an experimental test of imitation, the ‘two-action methodology’, does not require any new behaviour to be built up. In the test, a chimpanzee for instance is shown a box opened by means of one of two simple actions, both of which suffice to open it; the behaviours are familiar ones to the subject, but the puzzle box is new [14]. Then the chimpanzee is given a closed box: the data shows that it will be more likely to try first whichever action it recently saw done.

It is possible that this test recruits imitation for skill learning, and that even if the procedure had been a novel one the chimpanzee would have managed to copy it, thus adding to its repertoire of skills. But a simpler explanation is that response facilitation causes mirroring of the recently seen action. (Of course, as the action is effective, the chimpanzee will be likely to use it again under the same circumstances; but that is conventional associative learning.) Interestingly, human-reared chimpanzees and monkeys have given much stronger evidence of imitation in these experiments [15,16] — precisely as would be expected if the mechanism tapped is social mimicry rather than learning by copying, as for human-reared primates people are much more significant others, and humans do the demonstrating in all these experiments.

Two major questions remain for the future, and their answers may be related: is mirroring of familiar actions also involved in learning by copying, and can any non-human animal learn by copying? It is not impossible that the two kinds of imitation, whose differing functions hint at separate evolutionary histories, rely on quite unrelated brain mechanisms. Learning by copying involves hierarchical construction of a behavioural program [9], just as does linguistic syntax, so a common origin is possible, uniquely on the human line of evolution. But it is tempting (and parsimonious) to relate the powerful properties of the mirror neuron system to the perceptual deciphering required in learning by copying.

Some theorists view the imitative learning of a 2 year old child as simply an extension of neonatal imitation [17]: as social mirroring develops, it enables learning by copying. This simple scheme leaves unexplained why macaque monkeys do not follow the same developmental path, and seem unable to learn by imitation. Alternatively, it has been suggested that imitative learning co-opts the perceptual decomposition power of the mirror neuron system, evolved originally in response to social needs, for a new purpose [10]. In animals that are able to construct new behavioural routines by hierarchical planning, then the sequence of actions picked out by the successive firing of mirror neurons becomes far more useful, as the basis for constructing a novel, complex skill.

Monkeys and very young children lack such hierarchical constructional ability, so their imitation is restricted to social mirroring. Although learning by copying has proved difficult to study experimentally in animals, observational evidence implies that great apes learn their elaborate feeding skills by imitation [18]. If so, then the evolutionary origins of syntactical skill may lie earlier than the advent of language itself, in the feeding needs of our ancient ancestors and their flexible co-option of an existing neural system [19].

**References**

1. Galef, B.G. (1988). Imitation in animals: History, definitions, and interpretation of data from the psychological laboratory. In Social Learning: Psychological and Biological Perspectives. T. Zentall and B.G. Galef, Jnr., Eds. (Erlbaum: Hillsdale, New Jersey.), pp. 3-28.
2. Meltzoff, A.N., and Moore, M.K. (1983). Newborn infants imitate adult facial gestures. Child Dev. *54*, 702–709.
3. Chartrand, T.L., and Bargh, J.A. (1999). The Chameleon effect: The perception-behavior link and social interaction. J. Pers. Soc. Psychol. *76*, 893–910.
4. Meltzoff, A.N., and Prinz, W., eds. (2002). The imitative mind: development, evolution, and brain bases. (Cambridge University Press: Cambridge.)
5. Hurley, S., and Chater, N. (2004). Perspectives on imitation: from mirror neurons to memes. (Cambridge MA: MIT Press.)
6. Rizzolatti, G., Fadiga, L., Fogassi, L., and Gallese, V. (1996). Premotor cortex and the recognition of motor actions. Brain Res. *3*, 131–141.
7. Gallese, V., Fadiga, L., Fogassi, L., and Rizzolatti, G. (1996). Action recognition in the premotor cortex. Brain *119*, 593–609.
8. Visalberghi, E., and Fragaszy, D.M. (1990). Do monkeys ape? In Language and Intelligence in Monkeys and Apes. S.T. Parker and K.R. Gibson, Eds. (Cambridge University Press: Cambridge.), pp. 247-273.
9. Byrne, R.W., and Russon, A.E. (1998). Learning by imitation: a hierarchical approach. Behav. Brain Sci. *21*, 667–721.
10. Byrne, R.W. (2003). Imitation as behaviour parsing. Phil. Trans. Roy. Soc. Lond. (B) *358*, 529–536.
11. Byrne, R.W. (1995). The thinking ape: evolutionary origins of intelligence. (Oxford: Oxford University Press.)
12. Paukner, A., Anderson, J.R., Borelli, E. , Visalberghi, E., and Ferrari, P.F. (2004). Macaques (*Macaca nemestrina*) recognize when they are being imitated. Biology Letters, DOI: 10.1098/rsbl.2004.0291.
13. Rizzolatti, G., Fadiga, L., Fogassi, L., and Gallese, V. (2002). From mirror neurons to imitation: facts and speculations. In The imitative mind: development, evolution, and brain bases. A. Meltzoff and W. Prinz, Eds. (Cambridge University Press: Cambridge.), pp. 247-266.
14. Whiten, A., Custance, D.M., Gomez, J.-C., Teixidor, P., and Bard, K.A. (1996). Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). J. Comp. Psychol. *110,* 3–14.
15. Tomasello, M., Savage-Rumbaugh, E.S., and Kruger, A.C. (1993). Imitative learning of actions on objects by children, chimpanzees, and enculturated chimpanzees. Child Dev. *64*, 1688–1705.
16. Custance, D., Whiten, A., and Fredman, T. (1999). Social learning of an artificial fruit task in capuchin monkeys (*Cebus apella*). J. Comp. Psychol. *113*, 13–23.
17. Meltzoff, A.N. (2002). Elements of a developmental theory of imitation. In The imitative mind. A.N. Meltzoff and W. Prinz, eds. (Cambridge University Press: Cambridge.), pp. 19-41.
18. Byrne, R.W. (2005). Detecting, understanding, and explaining animal imitation. In Perspectives on imitation: from mirror neurons to memes. S. Hurley and N. Chater, eds. (MIT Press: Cambridge, MA.), pp. 255-282.
19. Byrne, R.W. Parsing behaviour. A mundane origin for an extraordinary ability? In The Roots of Human Sociality (in press). S. Levinson and N. Enfield, eds. (Berg: Oxford.)

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# Chromosome Segregation: Seeing Is Believing

**For chromosome segregation in mitosis, each centromere directs assembly of a complex, proteinaceous structure — the kinetochore, which connects the chromosome to microtubules of the mitotic spindle. A recent study has provided important new insights into the mechanism by which kinetochores capture spindle microtubules.**

**Kerry Bloom**

The mechanisms that contribute to accurate chromosome segregation are manifold and complex. The players have been identified from early genetic mapping studies, cytological observations of autoimmune patients and genetic screens in model organisms. Centromeres are responsible for directing the assembly of a complex proteinaceous structure, the kinetochore. The kinetochore provides the linkage between the chromosome and microtubules of the mitotic spindle. How the kinetochore engages the microtubule, promotes the complex oscillatory dance by which replicated chromosomes attain correct attachment, yet maintain the ability to correct errors has been the subject of intensive study.

This is a complex process, but the idea that we might be able to dissect it by genetic and molecular analysis was given a