narrative, yet will have to take into account that at the end of the day, the computational machine itself may present even better experiments and conduct them with our help. The Renaissance creature of the 21st century is not necessarily only a biological being. As a brain scientist, I see it as an exciting evolutionary development.

What do you think are the big challenges facing your discipline? As far as memory research is concerned, I think that in the absence of dictionaries that translate spatiotemporal patterns of brain activity to distinct mental and behavioral tokens, we are bound to remain confined to the analysis of mechanisms but not specific mental content, and memory is ultimately about content. Further, without these translation rules, we will not be able to tell decisively whether changes that we detect in brain structure and function, be they at the molecular, cellular or circuit level, are indeed relevant to the internal representation that embodies a specific token in memory, or are only conditions for memory to be established, or reflection of auxiliary processes such as homeostasis.

As far as neuroscience at large is concerned, on top of the information revolution, noted above, our scientific discipline is in the process of shifting from the vantage point of the passive observer to that of the active player capable of altering the brain, either by biology or by brain–machine interfaces or both. Bionics is around the corner. We have to be prepared, not only by teaching our students the right mix of scientific disciplines, but also by alerting them to the social responsibility that this revolution entails.

Having said all that, the deepest challenges are yet unknown. I actually envy my students because they have more of the unknown ahead of them. I just read this morning a report that our galaxy is crammed with earth-like stars. Can you imagine the challenge posed by encountering a new creature light years away, let alone discussing the brain with an alien neurobiologist?

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Quick guides

Polyandry

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What is polyandry? Polyandry is when a female mates with two or more different males (the male equivalent, one male mating with multiple females, being called ‘polygyny’). Monandry on the other hand is when a female only mates with a single male. True monandry, therefore, requires that a female becomes completely unreceptive after an initial copulation, or remains receptive to only one individual. Until recently, monandry was viewed as the most typical form of female sexual behaviour.

Why is that? Part of the reason might have been that the predominantly male scientists of the past had various preconceptions about how females, human or otherwise, should behave.

Little did they know... Indeed. The breakthrough came with DNA fingerprinting. Fingerprinting studies revealed that the patterns of mating that biologists had viewed through their binoculars did not match the actual patterns of paternity among offspring. Instead, females across a very broad range of species were found to be mating with multiple males (Figure 1). This was most startling in birds previously thought to be monogamous. An example is the dunnock, which the Reverend Frederick Morris urged his Victorian parishioners to imitate for its “humble and homely… deportment and habits”. The resulting ‘polyandry revolution’ has led to a paradigm shift in the study of reproductive behaviour. Polyandry is now a common trait that evolutionary biologists must try and explain.

Why would females mate more than once? Historically females have been assumed to gain everything they need from mating once, fertilising all their eggs with one donation of sperm from a single male. Moreover, we have usually

Figure 1. Polyandry is extremely widespread across animals.
Top left: little did the Rev. Frederick Morris know that female dunnocks (*Prunella modularis*) solicit copulations from multiple males, which peck at the cloaca to stimulate her to eject the sperm of previous partners. (Photo: Arend Vermazaren.) Top right: the grey foam nest tree frog (*Chiromantis xerampelina*) shows extreme simultaneous polyandry. (Photo: Daran Kandasamy.) Bottom left: female Sulawesi crested macaques (*Macaca nigra*) show extreme sexual swellings around the time of ovulation. These swellings are highly attractive to males, and are thought to partially conceal ovulation. (Photo: Brian Valentine.) Bottom right: in *Drosophila pseudoobscura*, polyandry protects populations against extinction caused by a selfish sex-ratio distorter (which results in all-female broods). Males which carry this selfish genetic element are poorer sperm competitors, so polyandry increases the chances of mating with distorter-free males. (Photo: Martin Whiting.)

assumed that female reproductive success is limited mainly by available resources, such as food, while male reproductive success is limited by the number of females they can inseminate. While this remains generally true, it did mean that the possible benefits of multiple mating to females were neglected.

What are these benefits? The benefits of polyandry can be categorised into those that increase a female's fitness directly and those that do so indirectly. The most obvious direct benefit is the acquisition of sufficient sperm to fertilise all of a female's ova. Other material benefits gained during copulation include various kinds of nuptial gifts — from food items through to nutritious spermatophores, which males transfer during copulation and females can utilise to increase their fecundity. Such gifts can substantially increase fecundity and in many insect species multiply mated females on average produce more offspring than singly mated females. Polyandry can also increase the extent of male parental care of offspring, as in birds such as the superb fairy-wren (*Malurus cyaneus*), or access to resource rich-territories controlled by males.

What else? In addition, mating with multiple males may prevent harm coming to your offspring. For instance, polyandry may be a strategy which females adopt to reduce the risk of infanticide. Males of many primates and other mammal species will not hesitate to kill an unrelated infant, bringing the mother back into oestrus in order to sire her subsequent offspring. However, by mating with several males, a female may 'hide' the paternity of her offspring (*e.g.* in the macaque; Figure 1). If there is even a small chance that a male could be the sire, then infanticide would not be a worthwhile risk for a male.

What about indirect benefits? Indirect benefits occur when mating multiply increases offspring fitness through genetic mechanisms. Such mechanisms might include increasing the access to 'good genes' or 'compatible genes' from one or more male partners. Alternatively, having several males fertilise your eggs could result in a more genetically diverse set of offspring which might increase the probability of offspring survival in changing environments. Indirect benefits are involved in increasing female fitness in various species, such as the grey foam nest tree frog (Figure 1); clutches from multiple fathers in this species have higher survival than clutches sired by a single male. However, apart from some well-established examples (Figure 1), our understanding of the importance of indirect genetic benefits to polyandry remains limited.

How does polyandry affect males? The effects depend largely on timing. When females mate with multiple males in reasonably quick succession, sperm from those males will compete for fertilisations. Polyandry, therefore, adds an extra level to male–male competition. This leads to selection on males to secure their paternity. Males can adopt various strategies to prevent sperm competition, for instance by guarding the females or by inserting mating plugs into females after copulation. Some males also strategically vary the size of their ejaculate based on the threat of sperm competition, and these ejaculates might contain seminal proteins that alter female receptivity or that speed up egg laying. Males may even harm females during insemination.

Wait, doesn't that make polyandry costly for females? Yes, it can do so indeed. Multiple mating may be costly in terms of reduced foraging efficiency, as well as increased predation or disease transmission. Polyandry can also reduce the amount of paternal care males invest if they are unsure of paternity. In birds, males were found to invest less in offspring feeding when the frequency of extra-pair copulations was high. Furthermore, males often transfer substances to females which actually reduce their lifetime fitness. Sometimes, however, the cost of refusing an additional mating is greater than accepting it, leading to a strategy of cost minimisation known as 'convenience polyandry'. Whether or not polyandry is adaptive for females will depend on the balance of costs and benefits. And these costs and benefits will vary across environments and potentially across individual females. This makes studying the economics of polyandry very challenging.

What about sexual selection? Clearly polyandry will have far reaching effects for sexual selection, but the exact nature of this interaction is yet to be fully elucidated. First of course, polyandry can be associated with stronger sexual selection in females, as is the case with so-called 'sex-role reversed' species in which females compete for access to males (who typically provide vital resources or parental care, limiting female reproductive success). More generally though, polyandry certainly creates the potential for sexual selection before and after copulation by influencing mating success and paternity. Furthermore, females may exhibit cryptic choice after copulation to bias paternity towards one or more males. However, polyandry can also reduce sexual selection by reducing the variance in male mating success. In red jungle fowl (*Gallus gallus*), for instance, polyandry weakens pre-copulatory sexual selection on social status. Post-copulatory sexual selection on the other hand increased in intensity in high-polyandry groups. To fully understand the effect polyandry has on sexual selection, we will need to study how polyandry influences the many different ways individuals compete for mates and their gametes across their lifetimes.

Where can I find out more?

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