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**Sexual conflict and the emergence of sexual  
equality and monogamy  
Transcript**

Date: Thursday, 7 November 2002 - 12:00AM

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by

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# Sexual conflict and the emergence of sexual equality and monogamy

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In the previous lecture we saw how male and female mammals promote their own genes through their patterns of sexual attraction and behaviour. However appearances can, of course, be very deceiving, and while a chosen sexual partner may have all the superficial hallmarks of good genetic quality these may be a façade, hiding defects that are not detectable by the senses. The battlegrounds for conflict between the sexes in promoting their genes therefore extend beyond what the senses can interpret to a level of additional biological warfare where no prisoners are taken. This lecture will examine the different strategies used by the sexes to use this biological battleground to further their interests. It will then consider how and why monogamy has been developed in some mammals, including man, and whether it has led to a reduction in sexual conflict and increased sexual equality. Arising from this it will then finally consider the extent to which monogamy in either man or other mammals is under genetic control.

To do this answers to the following questions will be considered:

Q: How do males and female mammals use biological warfare to promote their own genes?

Q: What species practice monogamy and does it promote female equality?

Q: What controls formation and maintenance of exclusive bonds between partners?

Q: Is there a monogamy gene?

## Q: How do males and female mammals use biological warfare to promote their own genes?

In males the strategy of developing increased body size, weaponry and aggression to compete with other males to gain exclusive access to females has made them the physically dominant sex. Under these circumstances the females have a reduced ability to choose who they mate with because they can effectively enforce compliance.

However, things are far more complex than they might seem and both sexes have arsenals of biological weapons that are constantly ranged against one another in seemingly endless battle.

These battles are fought on a number of different fronts including:

- The male reproductive organs
- The female reproductive organs
- Male and female genomes

So let battle commence by considering how the male can use his equipment to gain an advantage:

Why do male mammals have a penis and is size and complexity important?

'It is very remarkable, considering that the organs have the same rather limited functions to perform, how varied the male genitalia are in their morphology.'

Hill (1972)

So what is it really for?

The obvious answer would seem to be to route sperm more efficiently through the reproductive tract to fertilise an egg and/or facilitate transport of sperm through stimulating female orgasm.

However many species, such as birds, get along fine without significant appendages suggesting that a large and or complex design of penis may not be an absolute requirement for internal fertilisation.

Apart from making them very useful to taxonomists in distinguishing species what could be the purpose of the male penis having such a huge variety of sizes and designs?

One of the first theories to be proposed was that of a "lock and key" scenario. According to this the penis is designed to specially fit optimally only into the vagina of a female of the same species - a kind of species-specific chastity belt strategy with the male holding the key! While there are some good examples of species where this does seem to be the case (i.e. the stumptail macaque), they are by far the exception rather than the rule. In any event there has not been the same degree of co-evolutionary change in the female's genitalia that would have been predicted to occur if this theory were correct.

It has been suggested that the male uses his penis primarily as a tool to remove competitor's sperm from a female's reproductive tract before replacing it with his own. Birds have less need for this since they are mainly monogamous. By this theory tool use as a defining characteristic of species with the highest intelligence might need a slight adjustment! There is certainly some support for this idea in species using multiple intromission techniques (which should be good for removing previous sperm plugs). Some extreme specialists, sharks, have a two-channel penis - one for ejaculating sperm and another for first pumping water into the vagina to clean out any competitor's prior offerings.

The penis may also have developed as an adjunct to powerful forelimbs that grasp the female during sex to assist males in imposing their attentions. Birds have wings rather than forelimbs and so can't do this. This theory also explains why male birds have adapted such elaborate "courtship rituals" compared with male mammals since they cannot force their attentions on females but can only woo them. The authors of this hypothesis use the terms "Don Juan birds" and "Macho mammals" (Caizergues and Lambrechts, 1999).

The most persuasive general hypothesis that has been proposed considers the size and design complexity of this organ to be inversely related to the number of males competing to inseminate females (Eberhard, 1985). Simply put, it can be regarded as a male adaptive response to females exerting their control over which sperm they allow to fertilise their eggs. This makes a clear prediction that both monogamous and polygynous mating strategies (where females would normally be expected to mate with one or very few males) should be less impressive in terms of their size and complexity statistics.

This prediction by Eberhard is supported by Dixson (1987) who has analysed different aspects of penile morphology in primate species and found that size and complexity are indeed related inversely to the number of males that typically mate with each female. Thus for monogamous and polygynous males the penis is smaller and simple in design whereas in multimale/multifemale, or dispersed species, it is larger and more complex. Many species of birds are of course also monogamous which would further support this theory.

So one can synthesise these three tenable hypotheses of penile function by saying that from the male point of view it is indeed an effective tool for imposing his sexual attentions on a female, so that his sperm is the most likely to fertilise her eggs. It also comes in handy for disposing of sperm from competitors. However, the ultimate driver for its size and complexity comes down to how many different males a particular female mammal is prepared to have sex with - not how many female partners a male is prepared to have sex with!

So what about sperm design and production?

The penis may be important for introducing sperm into the female's reproductive tract but from then on it is a question of whether the sperm are successful in both gaining access to the female's egg and fertilising it.

One intriguing hypothesis is that males may produce two types of sperm. These have been termed "egg-getters" and "kamikazes". The idea is that the "kamikaze" sperm function to assist the progress of the "egg-getters" by inhibiting the progress of any other "egg-getter" sperm ejaculated into the female's reproductive tract by another male. While in some male primates, notably man, up to a quarter of sperm ejaculated are abnormal and may be "kamikaze" candidates, there is no clear relation between this proportion and the level of male competition.

In the Virginia opossum an amazing feat of co-operation has occurred where sperm fuse together in pairs to swim towards the egg since this apparently gives them an advantage.

In terms of the number of sperm produced there is a clear relationship with male mating strategies. As with penis length and complexity there is also a very strong positive correlation between testis size, and the number of sperm produced per ejaculation, and the number of female partners a male mammal would expect to have sex with in competition with other males.

So at the top end of the scale are mammals that live in polygynous multimale/multifemale groups and at the bottom are the monogamous species.

In terms of the number of sperm produced in a single ejaculate then given that around 50 million are required as a minimum for fertilisation although monogamous males (such as humans), might normally produce 4-5 times this amount those of polygynous ones (such as boars or rams) might produce 100-150 times more than required.

Sperm length also shows some relationship with the amount of competition between males. In this case the more competition a male has the longer are his sperm. The clear record holders in this respect must be a fruit fly species (*Drosophila bifurca*) with an amazing sperm length of 58.3mm, which is some 20 times larger than body-length.

Thus overall the bottom line here for males is that the more females you are likely to have sex with, and the more males you are competing with, the bigger and more sophisticated your penis will be and the larger your testes and size of sperm and the amount ejaculated during sex. Monogamy definitely reduces male competitiveness in these respects.

Can females use their reproductive organs to exert control over which sperm reach their eggs?

So apart from having some influence on the male's penis and sperm what else can the female do? Whichever way you look at it the female mammal's reproductive tract is a pretty hostile environment for the male's sperm and this in itself ensures that only the most healthy and vigorous sperm reach their target - the egg. Indeed, in most cases the male's sperm may spend a day or more trying to do their best impersonation of salmon fighting upstream in their native rivers to their spawning grounds.

While there does not seem to be any general correlation between vaginal length and the mating strategies employed by female mammals it is interesting that primate species where there are marked sex skin swellings at mid-cycle have elongated vaginas at this time. Such species are normally in multimale/multifemale groups where the highest levels of sperm competition would be expected.

One might have predicted that the first male to mate with a female when she is fertile will get his sperm through to her egg first. This does not seem to be the case and there is a distinct last male advantage! Thus the early bird does not necessarily catch the worm when it comes to the sperm and egg story. In some species females can actually store up sperm contributed by the same or different males in compartments within the reproductive tract (spermatheca). In most mammals, including man, sperm are filtered at the uterotubal junction to restrict movement from the uterus into the fallopian tubes. However, whether this sphincter type arrangement actively sorts sperm is unknown.

Whatever arrangements are actually employed to achieve it, the female reproductive tract does seem to give an advantage to the last male who deposits his sperm and can stimulate the female to allow it to access her egg. This is a very good reason for males to worry more about who has had sex with their partner after rather than before them!

In some species the female also seems to be able to exert some degree of selection as to whether a male's Y or X-chromosome bearing sperm fertilise her eggs. How this happens is not known but in some ungulate species it is well established that females have higher proportions of male offspring when their own condition, and the availability of resources, is good. When things are not so good they invest in females.

The general theory (The Trivers-Willard model) is that producing male offspring is more energy consuming for females and they need to be fit and well resourced to risk having sons. A number of studies in humans have concluded that where male partners were ten years, or more, older than the female then females were twice as likely to produce sons rather than daughters. Where the male partner was at least 5 years younger than the female, she was twice as likely to produce daughters. It could be argued that older males are likely to be able to offer better resource provision and perhaps stability than younger ones.

In humans it is well known that timing of sex during the menstrual cycle and the relative acidity or alkalinity of the vagina can influence the sex of offspring. While it is possible that the latter may be regulated in other animals there is no evidence that other animals actually alter the times that they have sex during the female's cycle.

Trying to selectively impede or promote the progress of sperm through the reproductive tract, or change its relative acidity, are clearly not foolproof strategies. There is therefore one final level of selection within the egg itself. Both sperm (on the sperm head) and egg (the zona pellucida) contain specific recognition proteins that must bind together in order for the sperm to be allowed to penetrate the zona pellucida and fertilise the egg. This provides a guarantee that sperm from the male of another

species will fail to fertilise the egg. However, it may also be a way whereby the female can determine which type of sperm from a male of her own species is successful.

For the female therefore the bottom line is that whatever type of mating arrangements they have with males they still make it difficult for the male's sperm to get through to their eggs. Hostilities therefore are probably relatively unaffected by monogamy.

Battles fought between male and female genomes

Just when we thought that the battles between the sexes were mainly concluded at the point where the chosen sperm got through to fertilise the female's egg a new battleground has opened up with the discovery of "imprinted" genes in mammals.

Research by Azim Surani and others in the 1980s first uncovered the phenomenon of genomic imprinting. Nuclear transplantation techniques in mice were used to create embryos that had only one of two sets of parental chromosomes (uniparental embryos) or that inherited specific chromosomes from one parent (uniparental disomy).

Such uniparental embryos were not viable beyond around 7 days and it became clear that the father and the mother were therefore contributing differentially to the genomes of their offspring - this effectively kicks into touch any idea that the human race can evolve quickly to become unisex!

It has subsequently been shown that whereas the majority of genes are biallelically expressed (i.e. the offspring inherit and express one copy from the father and one from the mother) there a small number of so-called "imprinted" genes where the gene from one parent carries a mark that identifies its origin. This allows either the paternal or maternal copies of these genes in the cells of a particular tissue to be effectively "silenced" by a process called demethylation. In this way, offspring only functionally express copies of such genes from one parent or the other (see Reik and Walter, 2001).

This form of monoallelic inheritance as opposed to the standard biallelic one has far reaching implications and is a further way the two sexes may compete with one another to influence what kind of offspring are produced.

Possibly as few as 100 of the 30,000 or so genes in the mammalian genome are imprinted in this way although it is already becoming clear that they play very important roles in foetal development as well as in control of social and cognitive functioning in adults. Also, because only one copy of the gene from a particular parent is expressed this increases the potential risk of mutagenic interference with normal expression. Such disruptions in this gene family are implicated in a number of human neurological and mental disorders (Prader-Willi, Angelman and Tourette Syndromes, Autism, Bipolar affective disorder, Epilepsy and Schizophrenia).

To understand how this family of genes can be utilised by the different sexes to compete with one another one has to understand that they are used to promote the interests of one sex by switching off (silencing) the imprinted genes that would promote the interests of the other. This happens because each sex can effectively halve the overall level of expression of a gene in their offspring.

The classic example of this is the growth of a foetus. The paternal imprinted genes act to promote maximum in utero growth of a foetus to maximise chances of survival by influencing the placenta and switching off their genes that inhibit growth. The cost to the mother of producing big babies is high and may threaten her survival so she uses her imprinted genes to reduce the effectiveness of growth factor promoting genes. Thus it has been shown in mice that deletion of the paternally expressed imprinted growth-factor gene *Igf2* results in smaller placentas and subsequent offspring size (Constancia et al., 2002) whereas deletion of maternally expressed *Igf2r* gene (which acts as a scavenger for *Igf2*) results in foetal overgrowth (Wang et al., 1994)

Paternally expressed imprinted genes (such as *PEG3*) also seem to act to promote maternal and nurturing behaviour (Li et al., 1999). This again would seem to be an important way for males who do not participate in parental care to help guarantee survival of their offspring.

At the level of the brain one of the most fascinating findings is that maternal genes preferentially contribute to the cortical "primarily cognitive and thinking parts" whereas paternal ones contribute mainly to the limbic and hypothalamic areas "the emotional and motivational parts" (Allen et al., 1995). Perhaps in a real sense mothers contribute to our intelligence and fathers to our baser instincts!

However in one important sense females may have the upper hand in being able to selectively influence males through imprinted genes located on the X-chromosome. While female offspring inherit an X chromosome from both father and mother,

males only inherit their X from the mother. X-linked imprinted genes in males therefore only reflect what females want in their male offspring.

The "what women want" story can to some extent be deduced from investigating the effects of X-monosomy seen in Turner's syndrome in human females and which has also been generated experimentally in mice. In this condition only one X chromosome is present instead of two (i.e. 39XO instead of 40XX) and this may either be from the father or the mother. When the X comes from the mother the offspring have higher visuospatial abilities (good for hunting and map-reading in the car!). When the X comes from the father then offspring have greater social skills, verbal IQ and ability to inhibit responses (see Isles and Wilkinson, 2000)

Since fathers are unable to contribute their X-chromosomes to their sons this may help explain why males are less social, verbally sophisticated and restrained, but are highly focussed and good at finding their way around. Presumably females want to keep it this way otherwise they could have used their imprinted genes to assist in improving, or reducing, these skills in their sons!

So in a very real sense both sexes are capable of manipulating the genomes of their offspring to promote both social and cognitive skills that are ultimately important for the survival

If imprinted genes really are an important part of the battle between the sexes to promote their own interests then, as with the other aspects of biological competition between the sexes, one might predict that monogamous or polygynous reproductive strategies would weaken their influence. This has yet to be confirmed, although there are differences in these genes between species and they have yet to be found in birds, which are largely monogamous.

What we do know is that the distribution of these genes in terms of paternal or maternal expression is still roughly 50:50 in humans. So whereas monogamy may have reduced male conflict at the level of the penis and sperm, but the female has maintained her defences, on this genome battleground males and females seem still be watching their backs equally.

### **Q: What species practice monogamy and does it promote female equality?**

The figures you get to answer this question depend very much on your definition of monogamy. If total exclusivity in terms of mating is used then current evidence would suggest that very few species completely qualify - although obviously variable proportions of individual pairings within a number of species do.

Even if one defines a monogamous species as being one where individuals from the two sexes form long-term exclusive partnerships that can have some flexibility in terms of either social or sexual exclusivity, only around 12% of primates and 3% of the total 4000 or so species of mammal have signed up even to this.

The best studied examples are dik-dik, prairie voles and pine voles, the Californian mouse, marmosets and tamarins,

Of 238 human societies surveyed by LeBarre only 43 (18%) have enforced monogamy - the remainder have mainly adopted polygamy. However, monogamy has become more prevalent in current larger human societies at advanced stages of political evolution (40-50%).

The superstars of monogamy are birds where as many as 90% of species qualify although the advent of DNA testing has made it clear that sexual exclusivity is not as extensive as once thought.

So what makes a species adopt monogamy?

The simple answer to this is that it probably only happens where it is beneficial for both sexes to make what is an obvious compromise to maximum reproductive flexibility and potential. For it to become a species trait then presumably mutual convenience ultimately selects for behavioural aspects that support monogamy to come under some degree of genetic control.

The following would seem to be the main candidates for driving adoption of monogamy by members of a species, although probably none are absolutely essential in isolation:

In more solitary species where females are dispersed over wide distances it may pay males to simply stick with one female - this may be true of some species but there are many monogamous species where members are not dispersed.

From a male point of view it can also mean that more individuals get to reproduce in comparison with all other mating systems where it is mainly the most dominant males that have reproductive success. It also reduces the necessity for inter-male aggression and competition for access to females - It has been argued strongly that this was the main reason why some human cultures have switched from polygamy to monogamy. It is pretty difficult to get males to act co-operatively either in terms of fighting battles or providing community resources if they are denied access to females by a small number of dominant, polygynous leaders. Monogamy also improves reproduction rates compared with polygamy and so can also be viewed as important for survival of species, like man, where few offspring are produced at a time and are dependent for long periods on intensive parental care.

The political, economic, social and reproductive consequences of monogamy as opposed to polygyny have recently been summarised by Price (1999). His summary statistics for 156 contemporary nation states are as follows:

Parameter Monogamous (84 states) Polygynous (72 states)

Mean population size 52.15 million 19.93 million

Abolished death penalty 7 times more likely

Democracy 64% 25%

Low levels of corruption 42% 5%

Per capita gross domestic product (GDP) \$10,000 \$2000

Military strength High Low

From the female point of view monogamy may be the best strategy for getting a male to help with parental care - you only have to look at birds to confirm this point. However, in some monogamous species like the dik-dik the male still does not look after the offspring but simply follows the female and her calf around. However one possible advantage of paternal behaviour in the context of monogamy is that it allows females to become reproductively active more quickly since they are not so tied up with long-term childcare.

Monogamy also gives females a real opportunity to fully exercise choice as regards which male to reproduce with. Ostensibly this is because monogamy is associated with a considerable downgrading of male coercive weaponry, particularly in terms of body size, and levels of aggression (i.e. if you don't need to spend so much time fighting off male rivals you don't need to be so big and aggressive!).

This might seem on the face of it to be escaping from one kind of enslavement to another. However, it is by looking at what females actually do in supposed monogamous pair relationships that reveals how they can exert greater control over their choice of male partner by exercising a clear duality of purpose in their reproductive priorities.

The study of extra-pair copulations (EPCs for short) by female birds and mammals has shown that:

- (a) Somewhere between 10 and 25% of offspring produced by females in stable monogamous relationships are not fathered by their male partners.
- (b) Females are much more likely to play away at the time of their maximum fertility.
- (c) By doing this females can effectively maximise their potential for producing offspring best suited for survival by utilising sperm-competition between their partner and another male or males.

It seems that females may be covering all the options by making sure that they reproduce with the fittest male while making sure they keep a resource provider and child-carer in tow!

This is elegantly demonstrated in women by studies on facial attractiveness by David Perrett's group at the University of St Andrews. They found that whereas women found more feminised types of male face more attractive for the majority of their menstrual cycle they switched to preferring more masculine versions of the same faces at the time of ovulation. The theory is that men more in touch with their feminine side are more socially adept and make better parents whereas the more masculine "macho" males may have the best genes for immune protection and survival (Penton-Voak et al., 1999).

It has also been proposed that females may benefit from monogamy through reduced risk of infanticide that can occur in both primates and other mammals that adopt polygynous mating strategies.

Finally, it has been argued that the choice of monogamy as a reproductive strategy reduces the risk of sexually-transmitted

diseases - a highly topical observation in terms of current priorities for advocating protected sex in humans.

So do monogamous animals get divorced and why?

While in some species of birds, like kittiwakes, pairs may split up for reproductive incompatibility reasons - i.e. during a breeding season they fail to produce offspring - it would seem that for the most part divorce in other animals, as in humans, is not so directly linked to fertility problems.

Divorce in humans, and other animals, is highly associated with the incidence of playing away. Interestingly, a divorce outcome can sometimes occur irrespective of whether such playing away is real or imagined. Thus in one much quoted experiment in the monogamous Mountain Bluebird a researcher (David Barash) placed a stuffed male bird near to a nest while the female was sitting on it. When the real male that was paired with her returned he first attacked the stuffed male and proceeded to attack his female partner, ousted her from the nest and subsequently pair up with another female.

"Open marriages" do not seem to be on the agenda for other monogamous species any more than they are for humans. Thus adultery is mainly only carried on in secret and at high speed, although males are far less careful than females in this respect. In most instances of course females will have most to lose from the break up of any relationship so it does pay to be more discreet.

Clandestine adulterous behaviour in macaques has been described where a female has temporarily strayed from her normal male consort to go behind and rock and have a "quicky" with another male. The female then re-emerges and behaves as if nothing untoward has happened and the other male even tries to hide his erection!

Other evidence from birds has shown that even when adultery does not result in a break-up cuckolded may punish such unfaithfulness in their partners by reducing the quality of their paternal care.

So what drives adoption and maintenance of a monogamous life-style?

Clearly if monogamy is simply a good political strategy for both sexes to deal with economical, environmental, social, and immunological problems then unless there are also adaptive changes at the genome level one would expect considerable variation within a single species depending upon their habitat.

This simple conclusion has fuelled expectation for the discovery of "Monogamy genes"!

There are some remarkable animals that have allowed scientists to search for the physiological bases of monogamy. Both sub-species of mice and voles have representatives that either belong to the monogamy club or do not.

Thus, Prairie and Pine voles are highly social, monogamous and the males show parental care whereas Montane and Meadow voles are asocial, promiscuous and show no paternal care. The same pattern can be seen in the Californian mouse compared with other mouse strains.

As a starting point it is clearly important to decide what it is one would be looking for in such a search for the physiological bases of monogamy. This must effectively come down to two things:

- (1) A mechanism for developing exclusive social bonding between individuals
- (2) A mechanism for maintaining such social bonds in the face of potential threats to them.

### **Q: What controls formation and maintenance of exclusive bonds between partners?**

Many female mammals from non-monogamous species have already developed the necessary equipment to form individual bonds with their offspring. The mechanisms involved in this will be discussed in more detail in my next lecture. However, from a practical point of view this means that many female mammals have the capacity to adopt monogamy with relative ease. Indeed, females have broadly employed the same systems for bonding individually with male partners as they have with their babies. Perhaps females really do treat their male partners as if they are overgrown kids!

The relatively asocial male mammal has needed to change most to embrace monogamy and has evolved a slightly different bonding mechanism to females as a consequence. For this reason alone one could argue that males may have needed



monogamy more than females.

For monogamous mammals the general principle is that bonding follows sex and thus in a very real sense sex must occur before taking marriage vows!

For females the major focus has been on the role of a small peptide hormone in the brain called oxytocin. This peptide, as we shall see in more detail in my next lecture, is released within the brain in response to stimulation of the vagina and cervix during birth and promotes maternal behaviour as well as offspring bonding. However, it is also released in response to similar, although less intense, stimulation provided by the male during sex in humans, rodents and sheep. Direct infusions of this peptide into the brains of voles make females bond with males without having to mate with them.

When oxytocin is released during sex it does three main things. In the first place it helps the female learn to recognise the smell (and perhaps cues from other sensory modalities) of the individual male she had sex with. In the second place it stimulates parts of the brain dealing with reward so that recognition of the male is associated with a pleasurable experience. Lastly the peptide also promotes reductions in female anxiety levels that may have particularly built up through having to face all the perils of life on her own - a problem shared is a problem halved!

While cells and pathways that make up the brain oxytocin system are very similar across mammals, including man, and mainly comprise those parts of the limbic system and hypothalamus dealing with social behaviours and recognition, sex, emotion and stress, there are differences in the distribution patterns of its receptor. Only one oxytocin receptor has so far been identified and a distinguishing feature of its distribution in monogamous mammals is that it is more highly expressed in the nucleus accumbens - a region of the brain particularly associated with reward. It has thus been hypothesised that for females pair-bonds with males may particularly be re-inforced by this link between sex-induced oxytocin release and the stimulation of pleasure centres in the brain. Indeed, the likelihood is that oxytocin acts to produce this pleasurable aspect of bonding through altering dopamine release in the nucleus accumbens since stimulating one of the latter's receptors (the D2 receptor) can also cause pair bond formation.

What has yet to be fully explained is why having sex with another male while in an existing pairing does not make the female also bond with them. My own work on maternal sheep bonding with their lambs may partly explain this since oxytocin is also involved and giving birth to a second lamb does not interfere with the bond that may already have been formed with a first one (Kendrick, 2000). Since bonds with lambs are reinforced and presumably strengthened over time through a mother's interactions with them, so the bond between a female and a long-term sexual partner should be stronger than one formed with a "one-night" stand. Indeed, in voles the strength of partner preference does develop with successive matings. Of course the situation would change if the frequency of sex with a new partner were to increase.

With males the situation is slightly different. Here, although they also have oxytocin pathways and receptors they play less of a role in pair-bonding. Instead, a closely related peptide called vasopressin is more important. As with oxytocin in the female, the distribution of this peptide within the brain is very similar in different mammals. It is also very similar to that of oxytocin.

However, once again it is the pattern of one of vasopressin's receptors - the V1a receptor - that is altered in monogamous mammals. Thus, in marmosets, prairie and pine voles and the Californian mouse this receptor is more highly expressed in another region of the brain associated with reward - the ventral pallidum. As with oxytocin in the female, brain infusions of vasopressin can only increase the formation of a partner preference, and general social behaviour, in species that have this pattern of receptor localisation. Indeed, by increasing the level of expression in this region in a monogamous vole they can bond with a partner without sex.

An important discovery has been that this altered pattern of V1a receptors is directed by an additional sequence inserted into the gene for this receptor. When Larry Young and Tom Insel at Emory University created transgenic mice with this version of the vole gene the animals developed a monogamous pattern of V1a receptor distribution in the brain. While they did not become monogamous they did start to show increased social behaviours in response to brain infusions of vasopressin. Needless to say this work was widely reported by the media as the discovery of a "monogamy gene".

Vasopressin also facilitates the process whereby two individuals learn to recognise each other. Indeed, David de Wied claimed in the 1960s that this peptide was the memory hormone and its agonists have even been used with some benefit in the treatment of Alzheimer's disease.

The changes undergone by these oxytocin and vasopressin genes to link the peptides concerned into the brain's pleasure

centres are clearly the crucial step in promoting social bonds in animals. Indeed, the pattern of brain activation seen in response to them in monogamous species is very similar to that reported with drugs like cocaine. Perhaps we have become "bonding junkies"!

Not surprisingly developmental and neuropsychiatric conditions associated with social dysfunction - autism and schizophrenia for example - are also often associated with altered oxytocin and vasopressin systems in the brain.

While we are beginning to understand how bonds are formed in monogamous species the question of what maintains them even following the death of a partner in some circumstances, is less clear. Presumably it is this combination of stimulation of both individual recognition and social reward that results in a particular partner - who you have had sex with often - providing you with the most frequent and greatest pleasurable high. This in itself would seem to be a compelling reason for sticking together.

Anything which acts to break up a mutual social and sexual relationship that gives pleasure, is also likely to promote frustrative aggression, leading to erosion of the hedonic value of that relationship. Interestingly, vasopressin in the brain can also stimulate aggression in both monogamous and non-monogamous species. This may, at least for males, provide the physiological basis for the perceived close proximity between love and hate reactions that the same individual can provoke.

Stress and social bonds

Stress is also important for driving social bonding. Studies on voles have shown that corticosterone releasing factor (CRF) - which facilitates the release of corticosterone and cortisol into the blood - can also stimulate pair-bonding in the absence of mating. Interestingly, human studies have shown that males and females become more attractive to one another if they meet in stressful circumstances - like in the middle of a high pedestrian suspension bridge!

Similarly the endogenous opiate systems (our body's own version of morphine) within the brain promote social and bonding behaviours in both sheep and monkeys. These substances are also released in stressful situations.

Shared experiences of stress during the course of a bond should therefore be a further way of cementing and maintaining it.

### **Q: Is there are monogamy gene?**

While it is clear that changes at the genome level have increased the propensity with which both social and sexual interactions between individuals and shared experiences of stress can lead to strong recognition and social bonds between individuals that are highly pleasurable, these are certainly not directly controlling sexual exclusivity.

Direct genetic control of sexual exclusivity in monogamy does not make compelling biological sense. Even though it has some obvious social and health advantages it would be a very dangerous step for any species to take and might seriously limit flexibility to adapt through sexual selection.

For this reason in monogamous humans sexual exclusivity is enforced legally or morally so that monogamy as a package maintains a strong, peaceful, well resourced, productive and democratic culture.

In humans and other animals it is also enforced at the individual level through the fear of losing all the other positive and pleasurable aspects of the social relationship.

Thus, social exclusivity in pairs is much more stably maintained than sexual exclusivity.

Some final thoughts

Monogamy has benefited both sexes, promoted sexual equality and improved female choice but it has not led to full arms decommissioning. The arsenals of biological weapons used for the purposes of sexual conflict in non-monogamous species have been reduced, at least by males, following the adoption of monogamy at a species level but none have, or are likely to be, completely abandoned.

Notably for females despite the benefits they have ultimately achieved through the adoption of monogamy we have yet to find real evidence that it has resulted in them decommissioning anything in the field of sexual conflict.

In short no monogamous mammal, including man, would be selectively disadvantaged in evolutionary terms if circumstances changed to make adoption of a different mating strategy imperative for survival.

So is there ever going to be a way to test biologically if you have met the ideal monogamous partner?

Human brain scans have revealed four specific regions that light up only when you view images of your beloved partner. Perhaps the future equivalent of a "lie detector" as regards successful indicator of a likely durable monogamy would be to put your prospective life-partner through one of these scans and compare how your image fares in comparison to previous partners or a clutch of male or female supermodels!

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