Matchmaker Genes:
Can Automatic Pattern Recognition Trigger Speciation?
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The puzzle of mate matching during speciation

Arguably, the defining feature of a eukaryotic animal species is that females and males recognise each other sufficiently well to ensure that inappropriate mating with other sympatric species (living in the same area) is rare. The focus here will be on birds, where recognition of males as suitable mates by females is thought to be crucial, but in other groups recognition by either or both sexes may be important. In birds, differences in appearance between sister species are often limited to shifts in detailed pattern of plumage or song of no obvious immediate survival value. The puzzle is how, assuming for the present that both male appearance (visual or auditory) and female recognition of that appearance as ‘suitable’ are genetically determined, a mutation that alters the pattern of one of these traits as part of speciation gets to be matched with a mutation that alters the other precisely enough to avoid confusion with other species. Whichever trait shift comes first it seems extraordinarily unlikely that a random matched shift in the other trait would occur within thousands of generations, and without it the first would be selected against and die out. Many suggestions have been made to try to avoid the problem [Lande, 1981; Price, 1998; Arnegard and Kondrashov, 2004; Burley, 2006; Butlin et al., 2012] but, as discussed below, they all raise difficulties.

There is a simple solution, but one that has generally been considered implausible until recently [Lande, 1981; Arnegard and Kondrashov, 2004; Shaw et al., 2011; Singh and Shaw, 2012]: that the mutation that shifts female preference and the mutation that shifts the male appearance are one and the same. The general term for coupling of different traits in the same gene is pleiotropy (of the gene). In recent years evidence for possible pleiotropic genes has been found in relation to butterfly wing colour, cricket song rhythm, drosophila pheromone production and fish colouration [Shaw et al., 2011]. Perhaps the most striking finding is that the same gene encodes for either a white or a yellow spot on a butterfly wing in different species, and for preference for the conspecific spot colour by a mate.

Despite this renewed interest, the sceptic might argue that these cases are occasional quirks, not too surprising given the simple recognition apparatus likely to exist in invertebrate nervous systems and the fact that many genes show pleiotropy in the general sense of affecting multiple organ systems; cytokine genes are obvious examples. Effects of single genes on appearance and selective mating can have simple explanations. A gene for a large beak that allows male and female birds to feed on trees with large seeds may lead to females with a large beak gene mating with males with the same gene simply from proximity. Nevertheless, we would like to propose here that there is a good case for considering a much more systematic and specific form of pleiotropy similar to that for the butterfly wing pattern, which may be of considerable significance to vertebrate neurobiology.

The proposal is that there are certain genes whose sole function is to systematically encode both species-specific appearances and their detection and preference within the nervous system and that in certain vertebrate groups, in particular certain bird and tropical fish families, these genes have evolved to allow use of complex pattern differentiation in mate choice. We have termed these Matchmaker genes since they would not only serve the traditional function of appropriate pairing but also match two very different functions in neural and non-neural tissues. Matchmaker genes will not be the only triggers for speciation or the only determinants of plumage pattern or song structure. There is good evidence for things being more complicated. However, for certain groups like New World orioles the Matchmaker gene model seems a particularly attractive hypothesis.

Pleiotropy seems worth revisiting in terms of a Matchmaker gene model partly because mechanisms of speciation are still uncertain and it provides a very simple solution to the dynamics. In addition, it seems worth pursuing because it may provide clues for an even more difficult puzzle: that of the structural, or syntactic, basis of signaling patterns within the brain used for recognition and choice. If a single gene allele can code both for outward appearance and for preference for that appearance some sort of systematic isomorphism between the processes involved seems needed. Genetic coding of species-specific recognition might provide a useful clue to the way the brain signals the presence of valued objects.
The case of New World orioles

Long-term evolutionary diversification in birds clearly involves divergences in structural features of relevance to fitness and natural selection – as in the split between avocets and oystercatchers. However, at the fine-grained level of speciation, as between the four avocet species, differences in appearance often look to be fitness-neutral. Several families or tribes show rapid radiation of species without major structural change. These include the estrildid finches [Gomes et al., 2016], African starlings [Maia et al., 2013] and a number of groups, including the oriole tribe Icterini, in the Neotropics, where diversity is particularly high.

The New World orioles are perhaps an ideal group for studying changes in pattern of appearance during speciation. Plumage changes have been documented in association with genetic studies, which also looked at song differences [Omland and Lanyon, 2000; Kondo et al., 2004; Price et al., 2007]. Icterus species all have contrasting black and yellow or orange (yo) plumage areas (occasionally maroon) (see Table 1) [Omland and Lanyon, 2000]. About ten main areas are either black or yo, in about thirty species-specific combinations [see del Hoyo and Collar, 2017]. (Omland identifies more areas, including white wing areas but these are simplified here.) As documented by mitochondrial DNA, on multiple occasions speciation has involved a switch of colour in one or more areas, in some cases reverting to earlier patterns [Omland and Lanyon, 2000]. Apart from differences in colour the orioles are similar in structure. It seems likely that this variation has evolved because it has allowed birds of different species to recognise conspecific individuals, and avoid hybridisation. It is difficult to envisage what other adaptive advantage it could confer.

Most oriole species occupy fairly extended geographic domains, often favouring central or coastal regions, with significant overlap with other species. Bullock’s and Baltimore orioles breed across wide ranges of latitude, whereas black-backed oriole is restricted to central Mexico and orange oriole to Yucatan [Kondo et al., 2004; del Hoyo and Collar, 2017]. A few are restricted to specific island groups.

How would female preference for male appearance be encoded genetically?

With the exception of pigment acquisition from food crustacea, plumage pattern is believed to be genetically determined and some aspects of mechanism are reasonably well understood [Maia et al., 2013]. As for other morphogenetic processes we can expect domains of epidermal cells (such as crown or rump) to acquire some form of ‘positional information’ [Wolpert, 2016] during embryonic growth, perhaps through gene methylation, that makes cells respond in a site-specific way to transcription factors activating genes involved in feather production.

In contrast, genetic determination of recognition of, and value assignment to, visual or auditory appearance, has proved more difficult to demonstrate empirically and little is known about possible mechanism. There must be genetic mechanisms relevant to mate choice in order to explain successful pairing in Old World brood parasitic cuckoos but studies of genetic determination in cage birds such as canaries have not yielded simple answers [Trösch, 2017]. This discrepancy may have directed attention away from the possibility that the same genes might mediate both processes. Nevertheless, in the light of what is now known of the systematic interactions between genes in encoding phenotypes, this may not be as implausible as at first appears.

The survival advantage of a complex nervous system lies in an ability to identify spatial and temporal differences, or asymmetries, in dynamic patterns, or in simple terms, ‘objects’, in the environment, of relevance to optimal behaviour. It is significant that what our perceptions track when we think we are tracking ‘objects’ are differences. Individual signals from receptors tell us nothing. The colour constancy effect emphasises the fact that even the simple sense of the property of yellowness, which we attribute to a lemon in many types of lighting, is based on a systematic difference from background that allows us to identify a tendency to reflect a certain spectrum [Logvinenko et al., 2015]. Having extracted evidence for properties like reflectance spectrum we can then identify classes of object by these properties in terms of different patterns of difference.

To achieve the specificity of online behavioural response that we see in vertebrates, recognition of hierarchies of difference almost certainly requires both compositionality and systematicity of representation (as seen with e.g. verbs composing systematically with nouns in natural languages). Recognition of fellow creatures, predators and prey requires identification of combinations of invariant patterns including colours, shapes and movements. These need to combine systematically in the sense that all colours relate in the same way to shapes and all shapes the same way to movements, and so on. Classic studies from Hubel and Wiesel’s [1959] work on early vision pathways to Tsao’s group’s work [Grimaldi et al., 2016] on face recognition are
consistent with systematic stepwise extraction of invariant patterns of difference. How patterns of neural signals ultimately represent objects is poorly understood [Edwards, 2016]. However, as David Marr [1982] proposed, arguments from informational parsimony suggest that the representations familiar as ‘percepts’ are likely to be constructed more in the way a sentence is constructed out of nouns and adjectives than the way a screen image is constructed out of pixels, i.e. in a systematically compositional way. Recent studies on face recognition lend support such a view [Grimaldi et al., 2016].

A key aspect of relevant environment is the presence of conspecific individuals and especially potential mates. Recognition of the patterns of potential mates presumably entails a general ability to recognise creatures in terms of combinations of features like eyes, beaks and limbs. Vertebrate brains include areas programmed to interpret incoming stimuli in terms of eyes, mouths, heads, and limbs. Primate brains have specific areas that recognise visual patterns as faces [Arcurio et al., 2012; Grimaldi et al. 2016]. Innate recognition of food sources like nipples and parental beaks is common [ten Cate, 2009]. It is worth remembering that mating itself must require very sophisticated genetically programmed expectations about complex dynamic relations involving body parts. Put simply, if we know there must be a complex system of genes providing instructions for finding a mate and how to mate, then a few more genes to say which colour pattern is right adds no further implausibility. Doing it with ‘feather genes’ might seem tricky, but is it?

The Matchmaker gene model

The central proposal of the Matchmaker gene model is that female recognition of patterns of male appearance and the male appearance itself can be programmed by the same set of genes because both the sensory nervous system and the skin can read off their respective functions from a single set of allelic options that interact in a systematic way to form a dual-purpose functional blueprint. Like any system of interacting genes, this blueprint does not need to have any clearly delimited location or arrangement on the chromosomes. All that is required is that a cascade of transcription factor binding can be tapped in to for two different, but functionally matched, purposes. However, as for the Major Histocompatibility Complex, it is likely that many of the relevant genes lie close together, if, as likely, arising by gene reduplication.
It would be too speculative to suggest a detailed molecular structure for a set of Matchmaker genes but certain likely options can be considered. In skin it seems likely that the proteins encoded would be transcription factors that directly or indirectly switch on enzymes involved in pigment synthesis or keratin micro-organisation. The model is framed in terms of genes and alleles. However, a significant option is that elements of a black/yo plumage pattern are determined by binding affinities of a series of transcription factor binding sites on the promoter of a single gene, each subject to domain specific silencing. Thus, for ten binding sites a thousand patterns could be encoded through variations in a single gene with initial speciation steps involving perhaps a single base change in one binding site. Such an arrangement would help explain the stereotyped pattern of variation seen in orioles and also perhaps the tendency for patterns to re-appear [Omland and Lanyon, 2000]. Tribes such as *icterini* with marked plumage diversity may have acquired relative lability within the sequences of particular promoter regions.

During brain development, it is suggested that groups of high-level sensory neurons are endowed with ‘positional information’ analogous to that for skin cells, that guides a suitable pattern of gene transcription relevant to setting up connections for handling data from a particular body part. Moreover, just as the pattern of permitted transcription will for the skin encode what the differences in colour of the feathers will be, for the relevant high-level sensory neurons the pattern of transcription will determine a recognition response based on what the differences in colour of body parts of a suitable mate ‘should be’.

This concept of a dual-purpose functional blueprint might seem implausible. However, we know that innate recognition occurs, at least in some cases. Moreover, since species-specific plumage patterns and the ability for females to recognise them are likely to be under only one selection pressure – to match up – an automatic matching mechanism would be very strongly selected for. A possible objection might be that neuroscience has moved away from allocating very specific recognition tasks to specific neuron populations. However, this movement has, if anything, been recently reversed by the findings of Quian Quiroga [2016] and others who have identified cells in human brain with very specific recognition capacities.

The concept may be counterintuitive in part because of an assumption that plumage recognition mechanisms have evolved as an adaptive response to plumage colour patterns. Yet the reverse is likely to be true. Systematic representation of patterns is central to all sensory neural function, including avoidance of danger [see also Greenfield, 2016]. It is not unreasonable to suggest that, perhaps specifically in dinosaurs, and in parallel in tropical fish, a set of systematically interacting genes used by the brain have been functionally ‘borrowed’ to set up a complementary body surface signaling system that matches neural powers. Functional borrowing of this sort is a commonplace phenomenon between the immune and musculoskeletal systems, for instance [Edwards, 2000].

The final pathways of gene transcription that determine sensory neuron connection patterns and feather microstructure will be very different. Morphogenesis remains a poorly understood area. However, significant progress has been made in identifying genes such as the homeobox and notch groups [Holland, 2013; Wang et al., 2015] and building plausible models of tissue differentiation in terms of these, particularly in terms of encoding asymmetrical forks in differentiation pathways. In brain, tactic factors called Slits and Netrins have been identified that mediate connectivity, although we are a long way from understanding how this relates to object representation [Jaworski et al., 2015]. Major differences can be expected in the local use of chemical gradients or contact ligands in brain and skin but there seems to be no reason why both should not draw on a common blueprint encoding isomorphic decision forks. Moreover, one of the characteristics of genes associated with morphogenesis like the homebox group is that they are highly conserved and appear to be deployed in a wide variety of contexts. Matchmaker-style pleiotropy may be such a useful acquisition that it has arisen in parallel in crickets, butterflies, fish and birds, rather like eyes and acoustic organs, making use of a complex mixture of function borrowing and idiosyncratic tissue expression mechanisms.

Each New World oriole species is identifiable by a specific pattern of block colouration of areas such as crown, breast, or rump. If sensory neurons are allocated to such areas then alleles coding for a binary colour choice for each is straightforward. Neotropical wrens show similar interspecies variation but also involving barring and streaking, which might seem more difficult to explain [del Hoyo and Collar, 2017]. These patterns are likely to arise in plumage from alleles of genes encoding a general colour plan together with alleles of genes that set up some sort of local cross-inhibition fields within feather-generating cells that produce regular colour alternations. How would that detail be matched in sensory recognition? Marr’s proposal for neural signals combining like adjectives may be relevant again here. A neural code for a general colour scheme
such as brown and white combined ‘adjectively’ with a code for close barring would deal with the problem, even if superficially counterintuitive. Pixelated visual representations are unlikely to exist anywhere in the nervous system, not even at the retina, because the colours and shapes we experience are derived at a higher level from differentials between signals conveying information about invariances.

Recognition of block colours, barring and streaking would be likely to have evolved in the early vertebrate nervous system for general navigation purposes. Exploitation of this by skin cells might depend to some degree on progressive evolution of colour or texture options over time. Thus, Maia et al. [2013] have suggested that a novel development in melanin micro-distribution has provided the option for more colours in recent starling plumage. Such a development would need to be matched by novel preferences (not just recognition), which might seem difficult to explain. However, there is evidence for ‘hidden’ preference existing that might be tapped in to and then refined, as in the zebra finch females found to prefer red plastic leg rings in mates [Burley, 2006].

In comparison to the co-programming of plumage patterns and their recognition the situation for song may be much simpler. If a bird learns to sing a particular way by making random vocalisations and persisting with those its neurons recognise as ‘our sort of song’ then song production and recognition become almost the same thing. Pleiotropy becomes almost a redundant description. Nevertheless, the implications for neural recognition and evaluation systems are just as intriguing.

In finches song is probably learned to a significant extent by mimicry but for the more stereotyped songs of wrens genetic programming may be more important. And even in canaries there is evidence for parental genetic influence on song, even if through sometimes rather paradoxical responses to learning from others [Trösch et al., 2017]. Recognition of conspecific appearance can be encoded in a set of binary options for rhythms and pitches. The song of the musician wren sounds spectacularly complex and musical but could probably be programmed relatively simply using rhythm and pitch harmonic rules, with the male responding to recognition of appropriate patterns with persistence and the female with sexual interest.

The key challenge for a dual-use blueprint is that over evolutionary time local gene expression systems in two tissues need to give rise to correctly matched alternatives. If the skin reads a blueprint as coding black above yellow it is no good if the sensory system reads the blueprint in terms of preference for yellow above black or black above blue. Binary options cannot be matched to ternary options, and so on.

The simple answer should be that any failure of matching will be selected against. There is, however, an issue of what maintains stable systematicity of the blueprint across speciations where particular pattern options are not exploited. This again points to the likelihood that plumage patterning arises as an adaptation to sensory capabilities. Systematicity of interpretation is essential for all sensory neural function, but may be optional for feather colouration. In addition, gene systems that give robustly systematic matching across multiple successful speciations are more likely to continue to give rise to successful speciations and that may contribute to the success of bird families as a whole. Matchmaker gene systems might be more extensive in some families than others, reflecting speciation rates and mechanisms.

Unlike Fisher’s [1930] ‘runaway’ proposal for sexual selection, the Matchmaker gene model does not predict a vicious cycle of more and more extreme male and female traits, since these are automatically matched. Nevertheless, male appearance will be matched with a female neural connection pattern that attaches value to a concept that might simply be ‘longer tail’. If there is competition between males there is no reason why they should not be selected for longer and longer tails indefinitely. The longest-tailed male will always be preferred. Matchmaker genes are not expected to be the only determinants of traits such as feather structure since these will also be under selection pressures relating to locomotion or insulation. Thus a Matchmaker gene system may tend to entail that female preference for size-related features such as tail length or crest extent may naturally tend towards extravagant male phenotypes, limited only by loss of fitness from encumbrance.

The establishment of a new species

The Matchmaker gene hypothesis provides a way of initiating isolated interbreeding. There remains the question of how a new interbreeding subpopulation becomes established as a substantial long-term population or new species. What might be called the strong Matchmaker gene hypothesis is that a single mutation, encoding for both male appearance and female
preference for that appearance, can be expected to trigger the formation of such a substantial long-term segregated population. We suggest that for many bird species we can expect such a mechanism to be available, in line with the widespread view that breeding isolation mechanisms are likely to interact with pre-existing natural selection pressures during speciation [Panhuis et al., 2001; Kirkpatrick and Ravigné, 2002; van Doorn et al., 2009; Butlin, 2011].

Most existing numerous bird species will inherit an environment that is heterogeneous in terms of temperature and rainfall and associated breeding and feeding opportunities. This will reflect geographical differences likely to lead to partial segregation of interbreeding groups. We can expect spontaneous mutation and natural selection within more populous species to generate a tension between adaptation to exploitation of a species-general environmental resource, say niche 1, and to exploitation of one of many localised resources: a niche 2. There should be dynamic equilibrium at each geographic location in frequencies for gene alleles conferring fitness for niche 1 and alleles conferring specific fitness for niche 2. (Niche 2-adapted alleles are expected to be suboptimal for other local niches and so not spread throughout the species.) Thus, niche 1 might involve availability of flying insects for food. Niche 2 might involve abundance of a late-flying local insect species ideal for chick feeding with genes favouring late nesting being adapted to this. The equilibrium would be influenced both by variation in environment and the distance over which individuals travelled to find mates. The latter would determine the rate of re-mixing of alleles selected for a particular niche 2 with alleles suited to niche 1.

We can now consider a female with a new mutation forming a new allele (taken as dominant in both sexes) encoding a preference for a new male plumage pattern, with that pattern in male descendants carrying the new allele, living in a locality where a niche 2-adapted lifestyle is optimal. We can expect her to find a mate from the original species on the grounds of fitting her preference better than other species, although not perfectly. (Work by Baker and Baker [1990] on Passerina buntings suggests that females compromise when faced with imperfect matches.) Her chicks will then include males and females with the new allele. Even if first degree relative mating is inhibited we can expect a second generation to produce second degree relatives of both sexes with the allele, with matched female preference and male plumage.

These new plumage allele-carrying individuals can be expected to form a near exclusive interbreeding subgroup. Assuming all these individuals carry a higher rate of niche 2-favouring alleles than members of the old species at a distance, the descendant population will not be subject to the dilution of these alleles by interbreeding with such distant members and will therefore be expected to further adapt to niche 2 more rapidly than other local individuals [see Panhuis et al., 2001; Butlin, 2012]. The restricted gene pool in the new interbreeding population should also accelerate changes in allele frequencies because high rates of homozygosity will tend to accentuate positive and negative fitness values for competing alleles. If a niche 2-adapted lifestyle is optimum in that locality we would expect the new interbreeding population with the new plumage pattern to outcompete the old population and become locally dominant.

In the oriole case it seems plausible that plumage variation between species has allowed separation of sub-populations so that genetic behavioural patterns suited to local ecological factors can be capitalised on in this way. The large numbers of similar species in the Neotropical may reflect, for instance, adaptation to local seasonal food availability and appropriate nesting schedules. Patterns of seasonal water availability vary dramatically over short ranges in Mexico and Middle America. Evidence for recent splitting between Baltimore and black-backed orioles would fit with the idea that a large domain species (Baltimore) has given rise to a more specialised local species (black-backed) [Kondo et al. 2004] through a Matchmaker gene shift.

Alternative explanations

The historical literature has often considered the role of mate choice in speciation in rather different ways and it may be useful to review these in the context of application to the New World oriole tribe.

The role of parental imprinting

While there is little doubt that male plumage is genetically encoded, female preference might be learned from parental appearances. There is some evidence for imprinting on parental appearance, although it is inconsistent, with a recent study finding only imprinting on maternal appearance [Burley, 2006]. There is also a concern that evidence for imprinting in captivity using techniques such as artificial ornamentation may not be relevant to species-specific cues in the wild.
Imprinting might seem more plausible than genetic encoding of preference because learning is more familiar to us than the idea of genes controlling neural mechanisms involving specific preferences. However, as indicated above, we have to assume complex genetic encoding of neural function either way and so there actually may be little to choose in terms of plausibility.

Imprinting may also be considered inherently less stable than genetic encoding. This may be hard to pin down but it is of interest that studies of song preference in canaries showed that females actually preferred song that was not like that of their foster father [Trösch et al., 2017], perhaps as part of a mechanism to avoid first degree relative inbreeding. Such an effect would certainly seem to entail instability of breeding isolation purely through imprinting.

Learning of suitable mate plumage and song patterns from parents remains plausible for some bird families and predicted effects on reproductive isolation would be similar to that for a Matchmaker gene model. Nevertheless, in a range of contexts in the animal kingdom genetic determination of recognition of conspecific mates does appear to be necessary to explain successful intraspecific pairing. In many arthropods, fish, reptiles and amphibians, and also brood parasitic birds such as Old World cuckoos and New World cowbirds, juvenile females have little or no opportunity to learn the appearance of conspecific males.

The relative importance of imprinting and genetic determination of preference still needs to be tested empirically but a genetic basis would have a theoretical advantage in terms of trait stability and seems the only option for some species, so seems worthy of exploration.

'Sexual selection'

The role of mate preference in speciation has often been considered in terms of the role for ‘sexual selection’ [Panhuis et al., 2001; Kirkpatrick and Ravigné, 2002; Butlin, 2012]. However, the formation of two distinct interbreeding communities need not involve ‘selection’ (of a gene or trait type ‘by’ an ecosystem) in the metaphorical Darwinian sense of differential survival. Actual mate selection in the sense of choices by females may have nothing to do with ‘which male is best’, only with ‘which male is of the right sort’. As indicated above, Darwinian selection must be involved if a new species is to establish but it may operate through a distinct mechanism, complementary to mate choice.

The differences between closely related bird species that females might use for recognition are often qualitative differences of plumage or song pattern rather than quantitative differences such as tail length or brightness of colour. Most seem unlikely to have any differential fitness value per se. Differential fitness for distinct niches between sister species are likely to involve behavioural patterns that may be quite inapparent during courtship. The role of mate choice in speciation is therefore a different issue from that of traditional sexual selection. As both Gomes [2016] and Maia [2013] indicate rich species radiation goes with the potential for difference, irrespective of whether more or less. The distinction between cues for ‘right sort of male’ and ‘best male’ has been nicely illustrated in frogs [Kime et al., 1998] where certain aspects of vocalisation are required for species recognition but others determine choice given those aspects being present. Song in birds has often been studied in terms of preference between conspecific males. Species cues may be rather different [see Price et al., 2007 for an analysis in orioles]. This may explain some of the puzzling findings in terms of song preferences in both sexes in studies of canaries [Trösch et al., 2017]. There may be genetic encoding of male song features admired by at least some females but, not being species specific, this encoding may be quite separate from encoding of species specific features by putative Matchmaker genes.

Polygenic models

Models of speciation have often tended to assume that within a species there is often a wide range of polymorphic genes, with different alleles of each of several genes encoding slightly different quantities of a trait. That means that selection pressures, including female preference, without new mutations, can force the quantity up or down or split the population into polar groups, potentially forming new species. If there are numerous polymorphic genes for both female preference and male appearance then there is a natural tendency for matched traits to co-segregate [Lande, 1981]. A species with purple colouration might split into a group with red colour with corresponding female preferences and one with blue colour with corresponding preferences (assuming purple is recognised as a bit blue and a bit red) [Arnegard and Kondrashov, 2004].

There are several problems with this approach. Firstly, if significant polymorphisms affecting appearance are so numerous it is odd that appearances are so stereotyped within a
species over thousands of generations. One would expect by chance at least one in a flock of ten thousand starlings to look like a new species. Otherwise the effect of each individual allele would have to be so slight that effective population segregation seems likely to be swamped by random re-assortment of genes. Geographic variations do occur but even they tend to be stereotyped and they are not the rule. Improvement of domestic stock by cross breeding might seem to support a polymorphic gene base but changes in colour pattern tend to involve sudden gross phenotypic shifts, like leucism, unlike the subtle pattern changes seen between wild species.

Many shifts in appearance between sister species are quite minor and very specific. In the orioles considered above it may be replacement of one of ten areas with an opposite colour, leaving all other areas the same. It is very hard to see why such specific cues, the ones actually needed for speciation, should be encoded by multiple polymorphic alleles in a pre-existing population, when intermediate phenotypes are not seen.

Moreover, persisting polymorphisms within a wild population presumably represent some sort of dynamic equilibrium due to complementary fitness advantages from different alleles and slightly different environmental conditions, otherwise new alleles would never reach significant prevalence. If the dynamics were unstable one would expect alleles to either vanish or overrun a species within a relatively short evolutionary period. If stable then selection pressures would operate against any splitting into new species [see Arnegard and Kondrashov, 2004]. For this reason we think it is more realistic to attribute a speciation event to the appearance of novel gene alleles, rather than an instability in a pre-existing polymorphic gene population encoding appearance leading to a cascade of segregation. What does seem plausible is that within a local niche the formation of a local interbreeding population on the basis of a step shift in appearance should facilitate shifts in allele frequencies for multiple genes, unrelated to plumage or song, encoding fitness for the local niche.

Conclusion

The problem of how, during speciation, female preference for new male characteristics tracks efficiently to those characteristics remains unresolved. The proposal here is that in some cases the two functions are encoded in the same ‘Matchmaker’ genes encoding a dual-function blueprint accessible to neural and non-neural tissues. (For vocalisation a single sensorineural blueprint may suffice.) Whether this mechanism obtains in practice may be reasonably easily tested using cross-fostering and hybridisation in closely related Neotropical bird populations (perhaps contrasting subspecies) such as orioles, where genetic information has already been gathered. Almost certainly any mechanism of this sort would operate alongside traditional natural selection forces during speciation and imprinting as a further means for retaining isolation of breeding populations.

In addition to providing a possible partial solution to the speciation problem the concept of Matchmaker genes has broader implications of interest. It suggests that complex organisms with nervous systems may, metaphorically, like Meno’s slave, on seeing other individuals of their species ‘spontaneously recover knowledge known from a past life’ about unique features of the species. Matchmaker genes would provide an interesting molecular biological basis for Jung’s concept of archetypes – hidden amongst a network of homeobox, notch and netrin genes.

There could also be major implications for general questions about mental representation of the world. Marr’s proposal that such representations are constructed out of word-like components is at present a prediction based on parsimony of encoding information. If, however, it was possible to demonstrate the genetic basis of templates used for recognition of images we would have much more powerful and direct evidence for the compositional syntax of those internal images.

References


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