

Evolution cannot explain how minds work

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ARTICLE INFO

Article history:

Available online 16 June 2015

Keywords:

Evolution
Cognition
Learning
Memory
Birdsong
Songbirds
Birdsong learning
Speech
Language

ABSTRACT

Following Jerry Hogan, I argue that questions of function and evolution, and questions of mechanism should be seen as logically distinct. Evolution is concerned with a historical reconstruction of traits, while the actual underlying mechanisms are the domain of cognitive neuroscience and psychology. Functional and evolutionary considerations may be used to generate hypotheses regarding the underlying mechanisms. But these hypotheses may be false and should always be tested empirically. Many researchers still hold that common descent implies cognitive closeness. Studies on birds suggest that evolutionary convergence may be the rule rather than the exception in animal cognition. Neurocognitive differences between classes of individuals are often thought to be the result of adaptive specialisation. In the case of learning and memory, however, empirical results are more consistent with a 'general process' interpretation, without qualitative differences between different taxa. Evolutionary psychology (EP) argues that the mind of modern humans was formed as a result of selection pressures in the Stone Age. The empirical data are often overinterpreted, and EP is mostly based upon an outdated view of evolutionary biology. In human speech and language, both neurogenetic homology and evolutionary convergence are involved regarding speech, but human language has a unique combinatorial complexity.

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1. Introduction: two evolutionary fallacies

Among many other things, Jerry Hogan has taught us that cause and function are logically distinct categories (Hogan, 1988, 1994, 2009). Some might argue that the cause/function distinction is a trivial one, and that ‘Teleology [...] can be said to have ceased to be a source of confusion in its cruder forms, in which function was given as a proximate cause [...]’, as Tinbergen (1963), (p. 413) put it. I beg to differ, and I would maintain that Hogan’s arguments for a distinction of cause and function in the study of behavioural processes are not only very sensible, but that this distinction is crucial for a proper understanding of animal behaviour in all its facets. Failure to distinguish between these two categories has led to considerable confusion in the brain and behavioural sciences. In fact, I would argue that there are complete disciplines – cognitive ecology, neuroecology and evolutionary psychology – that are based on an erroneous confounding of cause and function.

Evolutionary and/or functional analysis might be brought to bear on behaviour or cognition in two different ways. First, functional or evolutionary considerations could be used to explain the mechanisms underlying a particular trait. This approach is fraught with difficulties. As Hogan (1988, 1994) has argued, questions of evolution or function are fundamentally different from those relating to mechanism, so evolution can never ‘explain’ mechanisms (Bolhuis and Wynne, 2009). This is because evolution by natural selection is not a causal factor of either cognitive or neural mechanisms (Bolhuis and Wynne, 2009; Bolhuis et al., 2014). Natural selection can be seen as one causal factor for the historical process of evolutionary change – but, as Bolhuis et al. (2014) argued, that is merely stating the essence of the theory of evolution. It is the case that evolutionary considerations – in particular, reconstructing the evolutionary history of relevant traits – might provide clues or hypotheses as to mechanisms, even though such hypotheses have frequently been shown to be false or misleading (Bolhuis and Wynne, 2009; see also below). A good example of such an evolutionary clue is provided by analyses of the possible evolution of language, as discussed in Section 4, below.

The second, more traditional way of applying evolutionary analysis to behaviour or cognition is to attempt to reconstruct its evolutionary history. In my view, this is essentially what an evolutionary analysis of behaviour should be about. However, here too, we are confronted with major explanatory obstacles. For a start, the evolution of a particular trait may have proceeded in different ways, such as via common descent, convergence or exaptation, and it is not easy to establish which of these possibilities (or a combination of them) is relevant (Bolhuis, 2005; Bolhuis and Wynne, 2009; Bolhuis et al., 2014). One of the cornerstones of evolutionary analysis is the comparative method, which generally relies on features that are shared by virtue of common descent. Alternatively, in convergent evolution similar traits, such as birds’ wings and bats’ wings, arise independently to ‘solve’ functionally analogous problems. As we shall see in Section 2, below, vocal imitation learning is an example of a trait that has had convergent evolution. It is present in humans and songbirds, *inter alia*, but not in our closest relatives, the great apes. Bolhuis et al. (2014) have argued that a likely reconstruction of the evolution of the faculty of language is consistent with a contemporary view of language’s syntactic structure.

The study of brain, behaviour and cognition has been plagued by two major misinterpretations of the theory of evolution. First, emphasis on common descent has led to what, I would call an ‘ancient’ view of evolution, involving the idea of a ‘scala naturae’ (Hodos and Campbell, 1969). Second, there is often a confounding of evolutionary (and functional) considerations on the one hand, and considerations of mechanism on the other. I will discuss these two problems in turn.

2. An ancient view of evolution

2.1. *Scala naturae* thinking leads to anthropomorphism

In a classic paper, Hodos and Campbell (1969) discuss the originally Aristotelian concept of the ‘scala naturae’, a hierarchy of complexity within the animal kingdom, with man at the top. The concept was widely adopted in medieval times as a way of classifying Creation, with, in this case, angels at the top, followed by man and the ‘higher mammals’ and so on, until we reach the bottom of the hierarchy, with worms and sponges. In a different form, this kind of hierarchical thinking is still prevalent in contemporary behavioural biology, where, attempts are made to neatly arrange the cognitive capacities of animals along a continuous phylogenetic scale. Darwin himself suggested as much when he wrote: “[...] there is a much wider interval in mental power between one of the lowest fishes, [...] and one of the higher apes, than between an ape and man.” (Darwin, 1871).

In this approach, the emphasis is clearly on common descent, where closely related species will have similar cognitive abilities. I will discuss a number of examples to suggest that this is often not the case. In addition, this approach often leads to anthropomorphism, where human cognitive or emotional traits are attributed to non-human animals, particularly to our closest relatives. A prominent example of this can be found in the work of Frans de Waal and colleagues, as discussed below (de Waal, 1997, 1999, 2009; Wynne, 2004a,b, 2007; Bolhuis and Wynne, 2009).

2.2. *Scant consolation*

In his study of the behaviour of the chimpanzee colony in Arnhem zoo, Frans de Waal noticed that the animals often behaved in a particular way after agonistic interactions (e.g. de Waal and van Roosmalen, 1979; cf. Aureli and de Waal, 2000). When two chimpanzees had been involved in an agonistic interaction, often a third individual would arrive and perform certain behaviours towards one of the two participants in the fight. The third party could, for instance, put its arm around the participant, or otherwise touch it. De Waal and collaborators called this third-party affiliative behaviour ‘consolation’, arguing that it is similar to the behaviour of humans in a similar situation (de Waal, 1997, 1999). This would seem to be the kind of anthropomorphism that Tinbergen (1951) suggested would ‘kill our urge for continued research’ (p. 4).

Subsequent research by Sonja Koski on the same chimpanzee colony proved Tinbergen’s point (Koski and Sterck, 2007). Koski reported similar behaviour patterns to the ones that de Waal had observed decades before her. However, she reached quite different conclusions, which prompted her to use the term ‘triadic post-conflict affiliation’ to characterise the chimps’ behaviour. Koski confirmed that the behaviour that de Waal had termed ‘consolation’ was performed roughly equally towards the ‘victor’ and the ‘loser’ of an agonistic interaction. In addition, ‘consolation’ behaviour did not reduce stress (measured behaviourally) in the ‘consoled’ animals, and it was also directed to participants without increased levels of post-conflict stress (Koski and Sterck, 2007). The authors conclude that “[...] it seems that consolation does not ‘console’” (p. 140), and that it may be that this third-party behaviour is performed to reduce the likelihood of future aggression from either of the two participants (Koski and Sterck, 2007). They suggest that the term ‘consolation’ be replaced by ‘triadic postconflict affiliation’. These results suggest that a characterisation of behaviour in anthropomorphic terms should be avoided, as it can indeed prevent further research (Tinbergen, 1951; Wynne, 2004a,b; 2007). The work by Koski and Sterck (2007) suggests that the chimps’ behaviour is not so much an indication of human-like ‘empathy’ (de Waal, 2009), but more likely the result of more ‘selfish’ motives (cf. Bolhuis, 2009).

A 'scala naturae' interpretation of third-party affiliative behaviour is further put in doubt by research by Amanda Seed and colleagues (Seed et al., 2007) concerning the social behaviour of rooks (*Corvus frugilegus*). These authors found clear evidence of third-party affiliative behaviour after conflicts between two individuals in a colony of rooks. In this case, the behaviour consisted of 'bill twining', which was performed with both 'victors' and 'losers' of an agonistic confrontation, as was the case in de Waal's chimpanzees. In an anthropomorphic interpretation, the rooks' behaviour could be seen as an instance of 'consolation'. In that case, it would be unlikely to be the outcome of common descent, but rather be a case of convergent evolution – unless 'consolation' would be widespread in the animal kingdom. Alternatively, it may be that third-party affiliation has a similar 'selfish' explanation in rooks and in chimpanzees. In either case, this behaviour would not fit a 'scala naturae' interpretation of the evolution of cognition.

2.3. Twitter evolution: birdsong and human speech

From a *scala naturae* perspective, with common descent being the crucial factor, the animal species most likely to have some kind of equivalent of human speech would be our closest relatives, chimpanzees. However, chimpanzees do not acquire their vocalisations by imitation learning, in the way that human infants do. Vocal imitation learning is a relatively rare ability in the animal kingdom. So far, only a few mammalian taxa have been identified as vocal learners, namely humans, certain marine mammals and bats, while vocal learning appears to be absent in our closest relatives, non-human primates (Hauser et al., 2002; Moorman and Bolhuis, 2013). In contrast, nearly half of the approximately 10,000 bird species are songbirds or oscine Passeriformes, that can vocally imitate species-specific communication sounds. In addition, parrots (Psittaciformes) and hummingbirds (Apodiformes) are also vocal imitators.

Songbirds learn their songs from an adult conspecific 'tutor' through a process that has parallels with human speech acquisition (Bolhuis et al., 2010; Bolhuis and Everaert, 2013; Moorman and Bolhuis, 2013; Bolhuis and Moorman, 2015). In many songbird species, song learning has two phases. In the memorisation phase, auditory-vocal information contained in the tutor song is stored in long-term memory, while in the sensorimotor phase the bird's own vocal output is 'matched' with the information stored in memory. In socially reared birds, during auditory learning an internal representation of the tutor song is formed that has been called a 'template' (Konishi, 1965). It should be pointed out that the term 'template' is essentially a metaphor for the internal representation of the memory of the tutor song (Bolhuis and Gahr, 2006), and not identical with the neural substrate of this memory. During the sensorimotor phase the young bird starts to vocalise, and it is thought that its song output is matched with the template that was formed in the memorisation phase. When birds are surgically deafened at this stage, they cannot match their own vocal output to the template, and eventually they will sing a rudimentary song that bears little resemblance to that of the tutor (Konishi, 1965). When a juvenile songbird is reared in auditory isolation, the crude template is not altered by experience with adult song. When such an isolation-reared bird is adult, it will sing a highly abnormal song that is based only on the information contained in the crude template, and feedback from the bird's own vocalisations. This so-called isolate song (Marler, 1970; Fehér et al., 2009) does have some recognizable species-specific features, but it has a relatively simple structure and does not sound like the songs of socially raised birds. Birds that are reared normally will eventually sing a crystallised song that does not change substantially during adulthood in the case of age-limited learners such as the zebra finch (Catchpole and Slater, 2008; Moorman and Bolhuis, 2013).

At the behavioural level, there are at least three ways in which song learning in songbirds and speech acquisition in human infants are similar (Bolhuis et al., 2010; Moorman and Bolhuis, 2013; Bolhuis and Everaert, 2013; Bolhuis and Moorman, 2015). First, both human infants and songbirds acquire their speech and song repertoire, respectively, through a combination of predispositions and learning. Second, in both songbirds and humans there is a sensitive period early in development, during which auditory-vocal learning is optimal. Third, in both human infants and juvenile songbirds there is a transitional phase at the start of vocal production, when the vocalisations are quite different from those of adult conspecifics. During this transitional phase, which is called 'babbling' in human infants and 'subsong' in songbirds, the young individual's vocalisations gradually come to resemble the adult form. Interestingly, none of these parallel features of auditory-vocal acquisition learning occur in our closest relatives, the great apes. To date, there is no evidence to suggest that great apes acquire their vocalisation by imitating conspecifics. It has been argued that vocal imitation learning is a prerequisite for the evolution of spoken language or speech (Hauser et al., 2002). Remarkably, then, this evolutionary prerequisite is absent in our closest relatives, but present in quite a similar form in songbirds. Thus, we have another example of the *scala naturae* being turned upside down.

3. Confounding evolution and mechanism

3.1. Tinbergen's four questions

In his groundbreaking paper, Tinbergen (1963) proposed that the four main problems in behavioural biology concerned causation, function (survival value), development (ontogeny) and evolution. Roughly speaking, causation and development are essentially causal or 'how' questions, while function and evolution are functional or 'what for' questions (cf. Hogan, 1994; Bolhuis and Macphail, 2001). When Tinbergen wrote his paper, the prevailing emphasis in behavioural biology was on causation. In his article he argued that more effort should be directed to the study of development, function and evolution. With regard to function and evolution, the behavioural ecology revolution in the 1970's was a somewhat delayed response to Tinbergen's clarion call. Recently, there have been increasing attempts to integrate the four questions. For example, many researchers studying cognitive and neural mechanisms increasingly appeal to the evolutionary history or the functional significance of behaviour to better understand its causation (e.g. Kamil, 1988; Shettleworth, 1998; Healy and Braithwaite, 2000; Sherry, 2005). This has led to a number of new fields of research, dubbed 'evolutionary psychology', 'cognitive ecology', and 'neuroecology', respectively.

In all three cases, functional or evolutionary considerations are used in an attempt to understand or explain the cognitive or neural mechanisms underlying behaviour (see Bolhuis, 2005 and Bolhuis and Verhulst, 2009; for detailed discussion). At face value, this seems to be a laudable approach. All of Tinbergen's four questions are important, so they should all be addressed when investigating a particular behavioural problem. Hogan (1988, 1994) has pointed out, however, that cause and function are logically distinct categories. Bolhuis and Macphail (2001), following Hogan (1994), suggested that problems of mechanism (i.e. causation and development) cannot be solved by functional considerations (i.e. evolution and function). Shettleworth (1998), (p. 574) has attempted to integrate causal and functional approaches to animal cognition, in what she called a 'deep synthesis' of the 'ecological program' and the 'anthropocentric, traditional or general-process program'. The author explicitly asked the question, "Can function explain mechanism?" (p. 42). From the remainder of her book it would seem

that the answer to that question is affirmative. Although she says that “Throughout this book we will be concerned with the adaptive value and evolution of cognitive mechanisms”, at the same time “In terms of Tinbergen’s four questions, cognition – defined as information processing – is one of the proximate causes of behaviour” (p. 13). Not surprisingly, the author suggests that “[...] animal intelligence should ultimately be defined in terms of fitness” (p. 10). In contrast to Shettleworth’s ‘deep synthesis’, Bolhuis and Macphail (2001) maintained that “[...] it should be clear that functional questions and questions about mechanisms are fundamentally different, and furthermore, that results from one domain cannot be used as explanations in the complementary domain. Thus, for example, a functional interpretation of why an animal performs a certain behavior does not explain the cognitive and neural mechanisms governing that behaviour” (p. 426). Bolhuis (2005) has argued that functional or evolutionary considerations may provide clues (or hypotheses) as to a possible causal analysis of mechanisms, but these clues can be misleading as they do not necessarily reveal the actual mechanisms involved.

3.2. Integrating function and mechanism

Integration of the four questions in the investigation of a particular behavioural problem is uncontroversial. Tinbergen et al. (1963) have done precisely that on several occasions, most notably in their classic study of egg shell removal in black-headed gulls, *Larus ridibundus*. Integration in this sense means investigating several of the four questions with respect to the same behavioural problem. Tinbergen (1963) himself was cautious concerning a conceptual integration of causation and function (cf. Bolhuis, 2005; for a detailed discussion). More recent investigators have been more assertive concerning an integration of causal and functional questions. In fact, there is an increasing tendency to integrate Tinbergen’s four questions in the study of brain, behaviour, and cognition, particularly in the new fields of evolutionary psychology, cognitive ecology and neuroecology. These fields are part of a more general trend in biology which has been termed the ‘ecological’ ‘adaptationist’ or ‘synthetic’ approach (Kamil, 1988; Shettleworth, 1998).

3.3. Cognitive ecology and neuroecology

Real (1993) introduced the term ‘cognitive ecology’, to indicate the adaptationist approach to the study of animal cognition. More recently, Healy and Braithwaite (2000), (p. 22) described cognitive ecology as: “[...] work that attempts to integrate functional explanations of behaviour, such as those provided by behavioural ecology, with an understanding of the underlying psychological and neural mechanisms.” (cf. Bolhuis, 2005).

Bolhuis (2000) characterised some recent research into food storing and song in birds as “a ‘neuroecological’ approach to the study of the neural mechanisms of learning and memory.”. He stated that: “In a neuroecological approach, a functional or evolutionary principle is used for a comparative analysis of brain mechanisms of behavior [...]. For instance, by comparing the brains of a food storing bird species with those of a closely related species that does not store food, it is hoped that the neural substrate for the memory of stored food items will be revealed [...].” (p. 89). In their critique of the adaptationist approach to the study of the brain mechanisms of learning and memory, Bolhuis and Macphail (2001) define ‘neuroecology’ as: “The study of the neural mechanisms of behaviour guided by functional and evolutionary principles” (p. 426). The most extreme version of neuroecology was formulated by Healy et al. (2005), when they described it as “This approach

of linking the size of specific regions of the brain to adaptations in behaviour and cognition” (p. 17).

3.3.1. Food storing birds

A prominent paradigm for both neuroecology and cognitive ecology is that of food-storing birds. Many bird species store food when it is abundant and retrieve it during periods of food shortage. Some species of jays, nutcrackers, nuthatches and titmice store many thousands of seeds and nuts in autumn and rely on these stores for winter sustenance (see Brodin and Bolhuis (2008), for review). Food storing in birds has become an important paradigm for the study of memory and brain for two reasons. First, it has been demonstrated experimentally that caching birds rely on spatial memory to retrieve caches. Second, lesion experiments have suggested that a specific region of the avian brain, the hippocampus, is important for spatial learning and memory. Most researchers investigating food hoarding in birds consider this behaviour to be an adaptive specialisation. For instance, Shettleworth (2003) states that “[...] an attractive and plausible hypothesis is that food storing birds possess an adaptation specific to spatial memory and its neural substrate. Many of the data resulting from attempts to test this hypothesis are consistent with it.” (p. 115).

An extensive series of studies seemed to confirm Shettleworth (2003)’s ‘attractive and plausible’ hypothesis (see Bolhuis, 2005; Macphail and Bolhuis, 2001; Bolhuis and Macphail, 2001; Shettleworth, 1998, 2003; Healy et al., 2005; Brodin and Bolhuis, 2008; for reviews). Several studies reported that food-storing birds performed better in spatial memory tasks than their non-storing counterparts (see Macphail and Bolhuis (2001), for review). In addition, in a number of studies a significant correlation was found between food storing capacity and the relative size of the hippocampus, although the number of species used in any particular study was often limited (see Brodin and Bolhuis (2008), for review).

In an extensive review of the extant literature, Macphail and Bolhuis (2001) demonstrated that, for both corvids and parids, overall there is no consistent relationship between food-storing capability and performance in spatial memory tasks, compared to non-spatial memory tasks. Thus, the authors concluded that the results of research into food-storing in birds did not support the hypothesis of adaptive specialisation of spatial memory. Rather, the behavioural findings are consistent with a general process view, according to which the same central processes of learning and memory are used across an extensive range of problems involving very different inputs (Macphail and Bolhuis, 2001). Brodin and Bolhuis (2008) reviewed the extant literature on relative hippocampus volume in relation to food storing behaviour in both parids and corvids. They used the data of an earlier survey by Brodin and Lundborg (2003) and added some data of their own, thus providing the most comprehensive review of the data at that time. The authors’ meta-analysis did not show any evidence of a significant relationship between relative hippocampus volume and food-storing capability (see Fig. 1). Thus, also in the neural domain, the results taken together do not support the hypothesis of adaptive specialisation of (the neural substrate of) spatial memory in food-storing birds.

3.4. Evolutionary psychology

Evolutionary psychology attempts to analyse human cognition and the underlying brain mechanisms using evolutionary considerations (e.g. Cosmides and Tooby, 1995; Daly and Wilson, 1999, 2005; Duchaine et al., 2001). According to the most extreme version of evolutionary psychology, the human mind and brain can only be understood properly if selection pressures acting on our pleistocene hunter-gatherer ancestors are taken into account (Cosmides

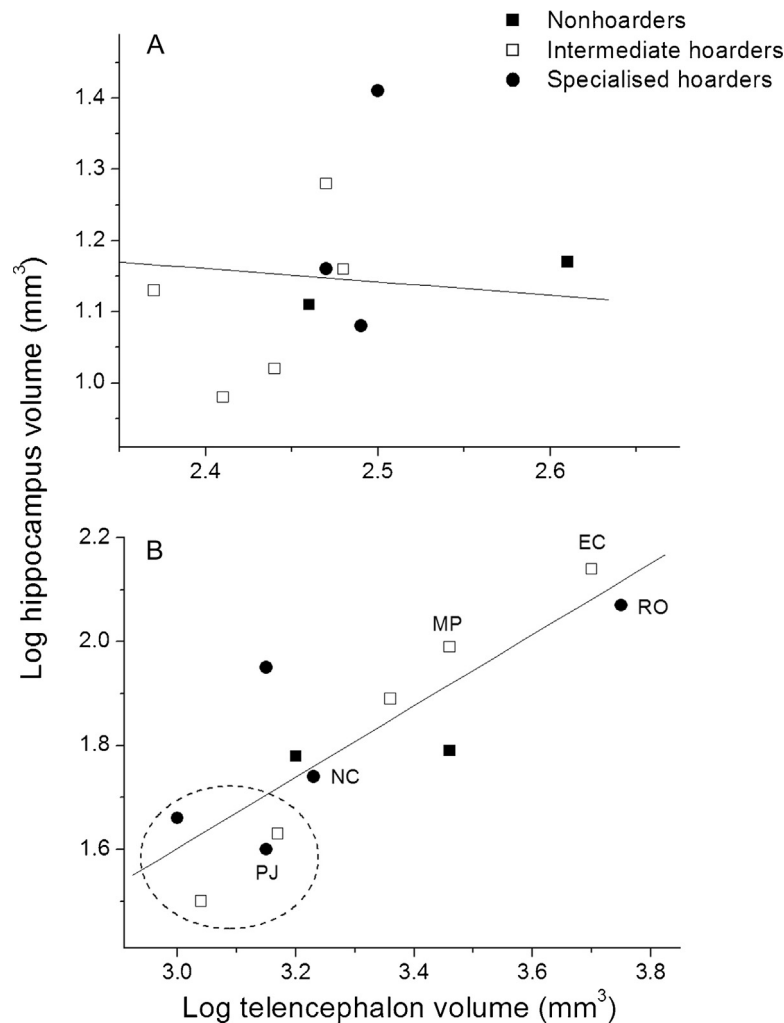


Fig. 1. Log hippocampal volume regressed on log telencephalon volume in (a) parids and (b) corvids. Non-hoarders are represented by black squares, hoarders of intermediate specialisation by white squares and highly specialised hoarders by black dots. Species specifically shown are Clark's nutcracker (NC), pinyon jay (PJ), magpie (MP), rook (RO) and Eurasian crow (EC). The monophyletic American 'blue jay group' is indicated by a dotted ellipse. From Brodin and Bolhuis (2008), with permission.

and Tooby, 1995; Duchaine et al., 2001; cf. Laland and Brown, 2002; Buller, 2005a,b).

3.4.1. Love, sex and jealousy

A popular topic in evolutionary psychology research is that of the alleged behavioural differences between men and women. That there should be differences is derived from Bateman (1948)'s conclusions from his experiments with fruitflies that selection should universally favour "an indiscriminating eagerness in the males and a discriminating passivity in the females" to obtain mates (Brown et al., 2009), a view that is quite consistent with Darwin's (Darwin, 1871). That is, males are thought to attempt to fertilise as many females as they can, whilst females will try to bond with their male partner so that he can assist in the care of the offspring. As Brown et al. (2009) note, "The conventional view of promiscuous, indiscriminating males and coy, choosy females has also been applied to our own species". Buss et al. (1992, 1996) investigated sex differences in jealousy in humans, using questionnaires. These authors concluded that the attitude of the two sexes to infidelity is consistent with the Bateman/Darwin view. Buller (2005b, 2009) reviewed the data of Buss et al. (1992) and that of a number of other studies (see Table 1). One of the questions asked was "Please think of a serious committed romantic relationship that you have had in the past, that you currently have, or that you would like to have.

Imagine that you discover that the person with whom you have been seriously involved became interested in someone else. What would distress or upset you more? (please circle only one):

(A) Imagining your partner forming a deep emotional attachment to that person [emotional infidelity].

(B) Imagining your partner enjoying passionate sexual intercourse with that other person [sexual infidelity].

The results of a number of studies are shown in Table 1. Buller concluded that the results of the questionnaire studies are 'questionable', as he put it. First, the males did not find sexual infidelity more upsetting than emotional infidelity; the average of all the different studies was 51%. Second, and more importantly, the variation between subjects in different countries was greater than that between the sexes. Thus, it would seem that cultural differences in attitudes towards sexuality and sex roles is a more important factor than possible biological differences between men and women (see Buller, 2005a,b, 2009 for a detailed discussion).

3.4.2. Speed-dating

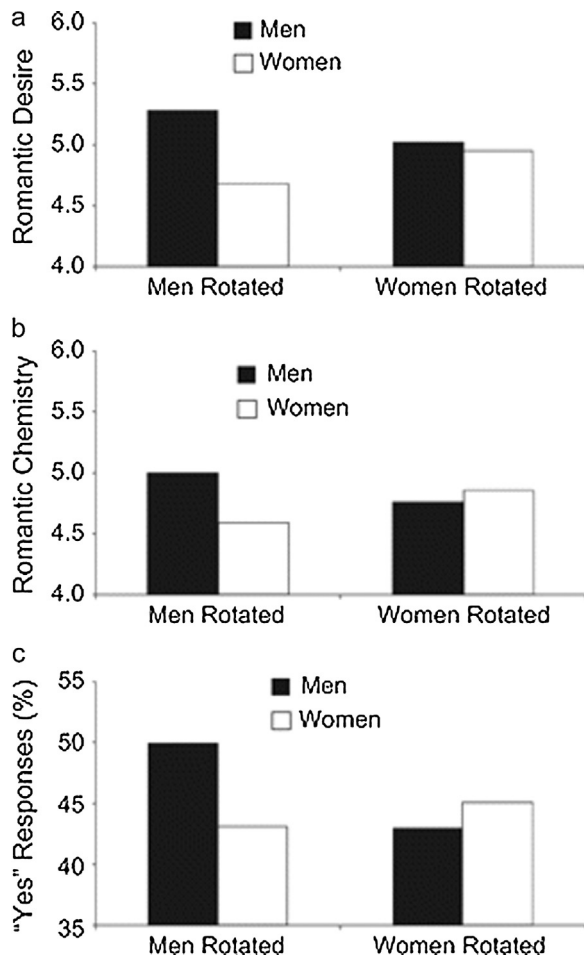
Another example of evolutionary psychological interpretations of alleged behavioural differences between the sexes involves studies of speed-dating. At such events, males and females have brief 'dates' (4–5 min) during which they can engage in conversations. The females are seated at tables, while the males rotate

Table 1

Percentage choosing sexual infidelity as more upsetting than emotional infidelity.

	USA	USA	USA	USA	USA	USA	China	Netherlands	Germany	Korea	Japan
Male	60	76	61	55	53	73	21	51	28	59	38
Female	17	32	18	32	23	4	5	31	16	18	13

Adapted from Buller (2005b), with permission.

**Fig. 2.** Men's and women's (a) romantic desire for their speed-dating partners, (b) romantic chemistry with their partners, and (c) percentage of "yes" responses to their partners as a function of which sex rotated. From Finkel and Eastwick (2009), with permission.

(Fisman et al., 2006; Kurzban and Weeden, 2005; Todd et al., 2007). After the event, both sexes indicate whether or not they would like to meet their conversation partners again. Overall, men respond with 'yes' to a larger proportion of their speed-date partners than women, consistent with the conventional image of 'choosy' females and 'promiscuous' males. However, Finkel and Eastwick (2009) found that a slight modification of the speed-dating procedure yielded quite different results. In addition to a conventional procedure, they reversed the sex-roles in that the men were sat at tables and the women rotated. As Fig. 2C shows, when the women rotated, the relative proportion of 'yes' responders changed quite considerably, in favour of women. That is, rather than females being more choosy, there was a trend for males to be the more choosy sex. The authors suggest that rotating and approaching boosted subjects' self-confidence and made them less selective. Interestingly, when the authors asked speed-date organisers why they had men rotate, the reply was that (a) women often have more accessories (e.g. handbags) with them, (b) men never seem to mind rotating, and (c) "it just seems more chivalrous". So, again, cultural bias about

the supposed role of men and women, rather than biological differences, seems to play a large role.

On the basis of their review, Brown et al. (2009) challenge the view "[...] that evolutionary theory prescribes stereotyped sex roles in human beings". The authors review the literature on mating behaviour and reproductive success in animals as well as in current and historic human populations. They conclude that "human mating strategies are unlikely to conform to a single universal pattern".

4. Evolution of speech and language

4.1. How could language have evolved?

Recently, the evolution of the faculty of language has been the topic of considerable debate (e.g. Berwick et al., 2013; Hauser et al., 2014; Bolhuis et al., 2014, 2015; Lieberman, 2015). Bolhuis et al. (2014) suggested that, although it is uncontroversial that language has evolved, there is considerable disagreement as to how it did. There are two main reasons for this lack of agreement. First, there is no general consensus as to the nature of the language faculty. Second, there is a lack of agreement as to the process of evolution itself. Clearly, equating language with 'communication' or speech will yield completely different answers to the evolutionary question than a conception of language as a computational cognitive system (Bolhuis et al., 2014, 2015). Also, viewing common descent as the crucial factor in the evolution of traits (such as language) is going to yield different answers than an approach that also allows for convergence, exaptation and other factors, as I discussed above (see Bolhuis et al. (2014); for a more detailed treatment of these issues).

Bolhuis et al. (2014, 2015) argued that the key distinguishing feature of language, and what evolutionary theory must explain, is hierarchical syntactic structure. On the basis of paleoanthropological evidence, these authors suggested that it is likely that the faculty of language emerged quite recently in evolutionary terms, some 70–100 thousand years ago, and that it does not seem to have undergone modification since. The recent emergence of language and its stability are both consistent with the Strong Minimalist Thesis (Chomsky, 2000), which has at its core a single repeatable operation, called 'merge', that takes exactly two syntactic elements *a* and *b* and assembles them to form the set {*a*, *b*}. Thus, in this case, evolutionary considerations (the recent emergence of language) may provide clues as to the mechanisms of a trait (i.e. the relatively simple core feature of the language faculty, *merge*).

A major obstacle for the comparative analysis of the evolution of language is that, to date, there is no evidence for human-like language syntax in any non-human species (Berwick et al., 2011, 2013; Bolhuis et al., 2014). In principle, there is no reason why a version of such a combinatorial computational system could not have evolved in non-human animals, either through common descent (e.g. in apes or monkeys) or convergent evolution (e.g. in parrots or songbirds). Although the auditory-vocal domain is just one possible external interface for language (with signing being another), it has been argued that the strongest animal candidates for human-like syntax are songbirds and parrots (Bolhuis et al., 2010; Berwick et al., 2011, 2012, 2013). This is because birds and parrots exhibit vocal imitation learning, a trait that is shared with certain marine

mammals and hummingbirds, but that seems to be absent in our closest relatives, the great apes (see above, Section 2.3).

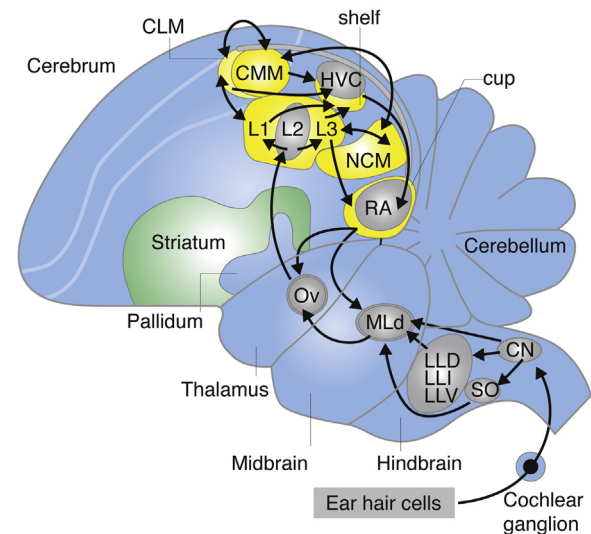
4.2. Neural similarities between birdsong and speech

In Section 2.3, above, I discussed the behavioural similarities between birdsong learning and the acquisition of speech in human infants. More recently, a number of neural parallels have been revealed (Bolhuis and Gahr, 2006; Bolhuis et al., 2010). There are interesting analogies with regard to the neural substrates underlying auditory processing and memory, and vocal production. Briefly, we have suggested that songbirds have 'Broca-like' brain regions involved in the production of song as well as in sensorimotor learning, and 'Wernicke-like' regions involved in auditory perception and memory (Bolhuis and Gahr, 2006; Bolhuis et al., 2010; Bolhuis and Moorman, 2015). In addition, these brain regions exhibit patterns of hemispheric lateralisation that are very similar to those in human speech- and language related regions (Moorman et al., 2012, 2015; Moorman and Nicol, 2015).

In humans, the neural substrate of motor representations of speech is considered to involve Broca's area in the inferior frontal cortex, while perception and memory of speech is thought to involve Wernicke's area and surrounding regions in the superior temporal cortex (Bolhuis and Everaert, 2013; Berwick et al., 2013). It should be emphasised that Broca's and Wernicke's areas serve more complex roles than just production or perception of speech, respectively (Bolhuis and Moorman, 2015). For example, Broca's area is activated during perception of syntactically complex sentences (Friederici, 2011; Berwick et al., 2013). There are many analogies and homologies between the brains of birds and mammals that have prompted a complete revision of the nomenclature of the avian brain (Jarvis et al., 2005). Similarities in connectivity and function would suggest at least analogies between the human neocortex and the avian pallium (including the hyperpallium, mesopallium, nidopallium and arcopallium; Bolhuis and Gahr, 2006; Bolhuis et al., 2010; see Fig. 3). Bolhuis and Gahr (2006) suggested that the NCM and the CMM may be analogous with the mammalian auditory association cortex. Doupe et al. (2005) have argued that the anterior forebrain pathway (AFP) loop in the song system bears strong similarities in connectivity, neurochemistry and neuron types to the mammalian basal ganglia, while both LMAN and HVC have been tentatively suggested to correspond functionally to Broca's area (see Bolhuis et al. (2010); for further discussion).

Apart from these neuroanatomical parallels, there is evidence for a similar neural dissociation between auditory recognition and vocal production regions in the brains of songbirds and humans (Bolhuis and Gahr, 2006; Gobes and Bolhuis, 2007; Bolhuis et al., 2010). I will briefly discuss evidence for such a neural dissociation in the songbird brain, obtained in a study by Gobes and Bolhuis (2007). These authors reasoned that, if the NCM of zebra finch males were to contain (part of) the neural substrate of tutor song memory, lesions to this structure should impair recognition of the tutor song, but should not affect song production. This is precisely what Gobes and Bolhuis (2007) found after they had placed small neurotoxic lesions in the NCM of adult male zebra finches (Fig. 4). While sham-operated controls continued to show a strong behavioural preference for the tutor song over a novel song, this preference was significantly impaired in birds with lesions to the NCM (Fig. 4A). At the same time, song production was completely unimpaired in the lesioned animals as it was in the controls (Fig. 4B). Thus, processing song information appeared to be impaired, while vocal production remained intact. This is reminiscent of the deficits in patients with aphasia as a result of damage to Wernicke's area, who are impaired in the processing of speech, while at the same time they can speak perfectly well.

A) Auditory pathways in the avian brain



B) Vocal pathways in the avian brain

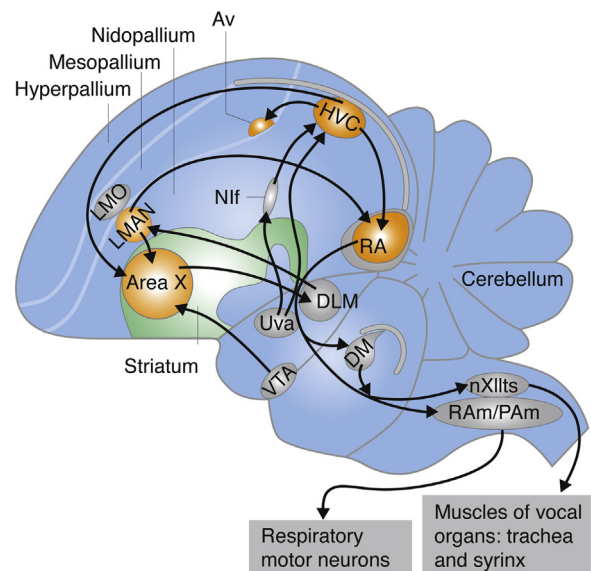


Fig. 3. Schematic views of the songbird brain. Two parasagittal sections show auditory (A) and vocal motor (B) pathways, indicating positions of brain regions and nuclei. (A) Brain regions depicted in yellow show increased neuronal activation when the bird hears song. The NCM and CMM regions are assumed to contain the neural substrate for tutor song memory. (B) The orange nuclei show increased neuronal activation when the bird is singing. Depicted are connections between the nuclei, of both the song motor pathway (SMP) and the anterior forebrain pathway (AFP). Area X, Area X of the striatum; Av, avalanche; CLM, caudolateral mesencephalic nucleus; CN, cochlear nucleus; DLM, medial subdivision of the dorsolateral nucleus of the anterior thalamus; DM, dorsomedial subdivision of nucleus intercollicularis of the mesencephalon; HVC, a letter-based name; L1, L2 and L3 are subdivisions of Field L; LLD, lateral lemniscus, dorsal nucleus; LLI, lateral lemniscus, intermediate nucleus; LLV, lateral lemniscus, ventral nucleus; LMAN, lateral magnocellular nucleus of the anterior nidopallium; LMO, lateral oval nucleus of the mesopallium; MLD, dorsal part of the lateral nucleus of the mesencephalon; Nif, interfacial nucleus of the nidopallium; nXIIIts, tracheosyringeal portion of the nucleus hypoglossus (nucleus XII); Ov, nucleus ovoidalis; PAm, nucleus paraambiguous medullaris; RA, robust nucleus of the arcopallium; RAm, nucleus retroambiguous medullaris; SO, superior olive; Uva, nucleus uvaeformis; VTA, ventral tegmental area. Reproduced, with permission, from Moorman et al. (2011).

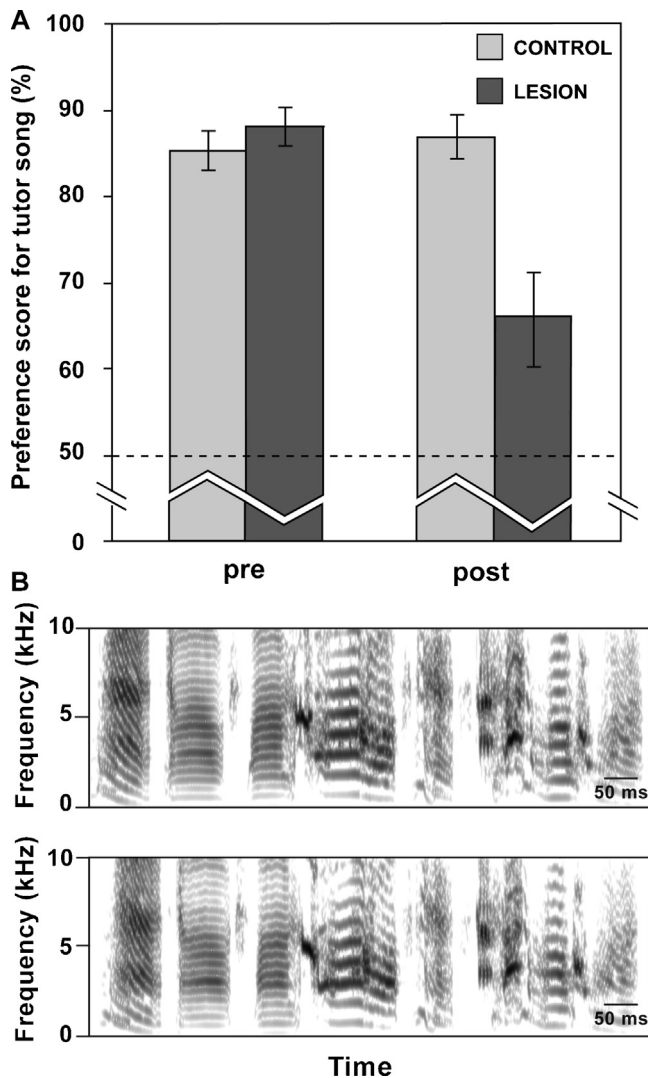


Fig. 4. Neural dissociation between birdsong recognition and production in the zebra finch. **A.** Lesions to the NCM impair song recognition in zebra finch males. Song preference scores (expressed as a percentage) were measured by calculating the amount of time spent near a speaker that broadcast the song of the bird's tutor compared to a speaker that broadcast a novel zebra finch song. Before surgery ("pre"), birds in both groups showed a strong preference for the song of the tutor over a novel song. After surgery ("post"), birds in the sham-operated group had maintained their preference, while this was significantly impaired in the group that received lesions to the NCM. **B.** Representative spectrograms of the song of a zebra finch male before (top) and after (bottom) surgery show that song production was not altered by lesions to the NCM.

Adapted, with permission, from [Gobes and Bolhuis \(2007\)](#).

The results of [Gobes and Bolhuis \(2007\)](#), combined with a number of other studies (see [Bolhuis and Moorman \(2015\)](#) for review) suggest that regions in the songbird caudomedial pallium (including the NCM) contain the neural representation of tutor song memory that juveniles acquire ([Bolhuis and Gahr, 2006; Gobes and Bolhuis, 2007; Bolhuis et al., 2010; Gobes et al., 2010](#)), whereas nuclei in the song system are required for sensorimotor learning and song production ([Brainard and Doupe, 2000; Bolhuis et al., 2012](#)). This human-avian parallel is already in operation during speech and song acquisition (reviewed in [Bolhuis et al., 2010](#) and [Bolhuis and Moorman, 2015](#)).

4.3. Birdsong linguistics

Given the behavioural and neural parallels between birdsong and speech, the questions arises whether birdsong involves syntac-

tic structure. Birdsong and human spoken language both involve complex, patterned vocalizations ([Berwick et al., 2011, 2012; Moorman and Bolhuis, 2013; Bolhuis and Everaert, 2013](#)). An essential aspect of human language is syntax, defined by [Berwick et al. \(2011\)](#) as "the rules for arranging items (sounds, words, word parts or phrases) into their possible permissible combinations in a language". It is thought that human language can be distinguished from animal vocalisations by its syntactic complexity, where hierarchies can be assembled by combining words and word parts into higher-order phrases and entire sentences ([Berwick et al., 2011, 2013; Bolhuis et al., 2014](#)). The songs of songbirds also consist of discrete acoustic elements that occur in a certain temporal order. Individual notes can be combined as particular sequences into syllables, syllables into 'motifs', and motifs into complete song 'bouts' ([Moorman and Bolhuis, 2013](#)). In principle, variable song element sequences may be governed by sequential syntactic rules, as shown e.g. in the work of [Okanoya \(2004\)](#). [Marler \(1970, 1977\)](#) has called this 'phonological syntax'.

Recent claims that songbirds may have the ability to acquire context-free syntactic rules ([Gentner et al., 2006; Abe and Watanabe, 2011](#)) have been challenged ([Beckers et al., 2012; Everaert and Huybregts, 2013](#)), and [Beckers et al. \(2012\)](#) concluded that, although there is clearly evolutionary convergence between humans and songbirds regarding processes of auditory-vocal learning, birdsong is not a credible model for the study of the mechanisms of human language syntax. Extant evidence shows that birdsong does not have the combinatorial complexity that is characteristic of human language syntax ([Berwick et al., 2011, 2013; Bolhuis et al., 2014](#)).

4.4. Conclusions

Considering the evidence, [Berwick et al. \(2013\)](#) argued for an evolutionary scenario where three factors are important. First, there is homology, at both the neural and genetic levels, where similar brain regions and genes ([Bolhuis et al., 2010](#)) are involved in auditory learning and vocal production, not only in songbirds and humans, but also in other mammals (Section 4.2). Second, there is evolutionary convergence with regard to the mechanisms of auditory-vocal learning, which proceeds in essentially the same way in songbirds and human infants, but not in non-human primates (Section 2.3). Third, as yet there is no evidence to suggest that non-human animals possess the combinatorial complexity of human language syntax (Section 4.3). [Berwick et al. \(2013\)](#) speculated that it may be that the neural mechanisms that evolved from a common ancestor, combined with the auditory-vocal learning ability that evolved in both humans and songbirds, contributed to the emergence of language uniquely in the human lineage.

5. Conclusions

The evidence that I have reviewed here suggests that the answer to [Bolhuis and Wynne \(2009\)](#)'s question, 'Can evolution explain how minds work?', is a resounding 'no'. Attempts to use evolutionary or functional considerations to 'explain' mechanisms (in cognitive ecology, neuroecology or evolutionary psychology) have failed. The main reason for this failure is the fact that cause and function are logically distinct categories, as Jerry Hogan has argued repeatedly ([Hogan, 1988, 1994, 2009, 2015; Hogan and Bolhuis, 2009](#)). Thus, it is pointless to attempt to answer, say, a question about mechanisms using evolutionary considerations—which is essentially what cognitive ecologists, neuroecologists and evolutionary psychologists are trying to do. Evolutionary biology is essentially a historical science. That is, in behavioural biology, evolutionary analysis is concerned with a historical reconstruction of

brain, behaviour, and cognition, while the actual underlying mechanisms are the domain of cognitive neuroscience and psychology. Thus, 'evolution cannot explain how minds work', to paraphrase Bolhuis and Wynne (2009).

That is not to say that evolutionary or functional considerations are irrelevant when it comes to mechanisms. As I have argued above, such considerations may generate hypotheses as to the underlying mechanisms. As Niko Tinbergen put it: "Zoophysiology [...] derives much of its inspiration and guidance from knowledge or hunches about survival value" (Tinbergen, 1963; p. 423). We have seen, however, that such hypotheses have frequently shown to be false, whether it be in neuroecology, cognitive ecology or evolutionary psychology. Thus, evolutionary or functional hypotheses about mechanisms do not seem to have any particular advantage over 'mechanistic' hypotheses. Evolutionary considerations are made even more problematic because it is not always obvious how a particular trait has evolved. As we have seen, in the case of human speech and language, both common descent and evolutionary convergence have played a role in the evolution of speech, while the core aspect of human language, hierarchical syntactic structure, has no counterpart in non-human animals. The language example does suggest that evolutionary clues may be useful, in that the apparently very recent evolutionary emergence of the language faculty is consistent with contemporary minimalist concepts of the syntactic structure of language.

Given that, as we have seen, confounding causation and function has often led the field of behavioural biology astray, Jerry Hogan's continual reminder that cause and function are logically distinct categories is likely to be important for quite some time to come.

Acknowledgements

This review is dedicated to my good friend and colleague Jerry Hogan. I am grateful to the Netherlands Organization for Scientific Research (NWO) for financial support (NWO-Earth and Life Sciences Open Programme, NWO Gravity and Horizon Programmes).

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