Experiments with humans indicate that decision accuracy drives the evolution of niche width

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One theory to explain the high incidence of niche specialization in many animals is that it reduces attentional load during resource-seeking behaviour and thus leads to more accurate resource selection. A recent neural network model refined the predictions of this theory, indicating that a cognitive advantage in specialists is likely to occur under realistic ecological conditions, namely when ‘mistakes’ (i.e. selection of non-host resources) contribute moderately but positively to fitness. Here, we present a formal empirical test of the predictions of this model. Using a human–computer interactive, we demonstrate that the central prediction of the model is supported: specialist humans are more accurate decision-makers than generalists when their mistakes are rewarded, but not when mistakes are punished. The idea that increased decision accuracy drives the evolution of niche width in animals has been supported in almost all empirical systems in which it has been investigated. Theoretical work supports the idea, and now the predictions of a key theoretical model have been demonstrated in a real biological information-processing system. Considering these interlocking pieces of evidence, we argue that specialization through increased decision accuracy may contribute significantly, along with other mechanisms, to promote niche specialization in animals.

Keywords: human; decision; specialization

1. INTRODUCTION

One idea to explain the high incidence of niche specialization in many animals is that specialization reduces attentional load during resource-seeking behaviour, and thus leads to more accurate resource selection [1,2]. This idea has been supported in most of the empirical systems in which it has been tested [3–8] (but see [9,10]), and Tosh et al. [11] recently provided firm theoretical underpinning for the idea through the use of an artificial neural network. This model can be used to optimize the relationship between stimulus and behavioural response, but, unlike many alternative models, the optimization is embodied in fundamental aspects of neural information processing. Tosh et al. [11] trained the model to specialize or generalize on a subset of shapes (called ‘hosts’) in a larger ecosystem of shapes by making these host shapes particularly valuable within the training algorithm. They also varied the punishment/reward for the network selecting the less valuable shapes (called non-hosts).

This punishment/reward could be positive or negative and was always less than the high positive value of the hosts. Here, we define punishment as a consequence of a decision that makes a negative contribution to overall performance (negative points value in the model and present study), and reward as a consequence of a decision that makes a positive contribution to overall performance (positive points value in the model and present study). After optimizing networks, Tosh et al. [11] tested the decision accuracy (i.e. ability to distinguish host from non-host) of all networks using a standardized task. What they found was, at first glance, counterintuitive. Generalists outperformed specialists in terms of decision accuracy when punishment/reward for selecting non-hosts during network training was negative; specialists outperformed generalists when punishment/reward was positive. Although the authors did not formally investigate a mechanism underlying the effects owing to the fundamental difficulties of dissecting mechanism in a complex system, they suggested that these effects may be due to trade-offs between the processes of host acceptance and non-host rejection within the network. Most resources that a specialist encounters are non-host resources, and, if these are harmful, fitness can be
maximized by focusing the neural apparatus on the process of non-host rejection at the expense of host acceptance. Of course, the opposite is true of generalists. Increasing the benefits of non-host resources probably liberates the process of acceptance in specialists (all resources can now be accepted without serious fitness consequences) and discrimination of a single resource from the rest is probably a simpler task than discrimination of a group of different resources from the rest. The model predictions are important because they are the first to indicate that some degree of non-host suitability is a necessary central component in the evolution of specialization. Non-host suitability in most previous models of the evolution of niche width has hampered specialization [11–16]. As many non-host resources in nature are quite suitable for utilization by specialists if they are artificially forced to use them [17–19], model predictions are fundamentally in agreement with observations in nature.

In fact, the idea of a negative trade-off between behavioural efficiency and niche width, while recently synthesized and applied to the issue of the evolution of niche width, has been recognized and applied more widely for many years. Specialist individuals in a resource-limited population of sea otters, for example, handled prey such as snails and crabs significantly more efficiently than generalists in the same population [20]. Experiments with the cabbage butterfly, Pieris rapae, show that individuals that have learned to use the plant Lotus corniculatus, when then presented with another plant, Campanula rotundifolia, must relearn the task of exploiting the original host, thus promoting flower constancy [21]. This idea is also central to the field of individual specialization where it is proposed that many instances of niche generalization are numerous instances of individual specialization, with attendant consequences for fundamental ecological and evolutionary processes in such populations (reviewed in [22]). An economist in the 18th century also appears to have been familiar with the idea when he stated that ‘... the division of labour, by reducing every man’s business to some one simple operation, and by making this operation the sole employment of his life, necessarily increases very much the dexterity of the workman’ (Book 1, Chapter 1 of [23]).

In this paper, we describe a formal test of the above neural network model using analysis of short-term learning in humans. This is the first formal test of this model and, given the overall weight of evidence discussed above, agreement between model predictions and empirical data would indicate that specialization through increased decision accuracy could contribute to the evolution of the niche width of consumer organisms, along with other mechanisms [17–19]. While the model used an evolutionary process to optimize networks, network training can in fact represent either behavioural evolution or learning within the lifetime of the individual. The performance surface of a neural network (the multivariate relationship between network weights and task efficiency) is determined by the task at hand, the network architecture and the functions chosen to embody artificial neurons. The optimization algorithm simply traverses this surface, and evolutionary and ontogenetic optimization methods will ideally reach the same point on the surface. Moreover, evolution and learning will arguably operate on the same or similar components of the sensory and decision-making apparatus of animals, and so analysis of short-term learning processes is justified. The use of humans is principally an issue of utility: humans will play games in which experimenter-defined goals are pursued with strong motivation. The use of humans as a study organism is consistent with the general structure of the model, and has been used successfully in previous studies of sensory ecology [24,25]. The network previously used was a very simple connectionist model, embodying the most fundamental and general aspects of neural processing. It is thus assumed that most or all organisms employing neural information processing (even very complex ones) will be subject to the constraints predicted by the model.

2. MATERIAL AND METHODS
We sampled four points from the previously published [11] performance surface generated by the model (relevant parts of this surface shown in figure 1a). These four points best illustrate the key biologically meaningful phenomena predicted by the model. The line between the first two points (figure 1a, black) occurs where networks were moderately rewarded for choosing non-host resources during training. Here, specialists outperform generalists in terms of decision accuracy in a standardized task. The line between the second pair of points (figure 1a, grey) occurs where networks were severely punished for choosing non-host resources during training. Here, generalists outperform specialists in terms of decision accuracy in a standardized task. We developed a human–computer interaction based around these four points in which the fundamentals of the modelling procedures were replicated, but now with evolutionary optimization of networks replaced by optimization through short-term learning in humans. The game consisted of 70 screen presentations in which a random selection of letters from the Roman (or Latin) alphabet (selection size random between 1 and 26) appeared on the screen in each presentation. Users could click on a letter and obtain a positive or a negative score, or they could refrain from clicking on a letter and obtain a zero score. Only by clicking on an example of a certain letter could the user identify that letter’s value. Such values were consistent between screens, so users could apply knowledge learned from earlier screens to later screens. They were informed at the start of the interaction that the purpose of the game was to accumulate as many points as possible based on the value of previous letters clicked. We did not introduce material reward (such as money) for high scores within the game; however, we present strong evidence in the electronic supplementary material that users were sufficiently motivated to develop efficient resource location strategies. Four different treatments were created, corresponding to the four points on the model performance surface (figure 1a). In all treatments, certain ‘host’ letters were rewarded +10 points when selected. In treatments 1 and 2, non-host selection was rewarded with +2 points. In treatments 3 and 4, non-host selection was punished with −10 points. Treatments 1 and 3 represented specialists where two randomly selected letters were chosen as hosts. Treatments 2 and 4 represented generalists where six randomly selected letters were chosen as hosts (table 1). In all treatments, screens 71–100 of the game consisted of a standardized decision-accuracy task. Each screen comprised two hosts (randomly selected from the set of letters rewarded +10 within screens 1–70) and 10 non-hosts, and we
measured the ability of users to recognize and select host letters from this standardized mix of hosts and non-hosts. We measured this ability in two ways: the time taken to locate a host letter within the first successful screen presentation in which a host letter was selected after presentation 70, and the proportion of screen presentations in which a host letter was located just after initiating the standardized task (screens 71–75). A full description of the interactive game is available within the electronic supplementary material.

The model predictions we test in this paper (generalists outperform specialists in terms of decision accuracy when punishment/reward for selecting non-hosts during network training is negative; specialists outperform generalists when punishment/reward is positive; §1) can only be tested definitively using independent tests of relative performance of the generalist and specialist treatments under the two different punishment regimes. We undertake these tests using t-tests. An alternative test of the strength of effects that tests model predictions under a narrower range of potential results is the interaction of treatments (specialization/generalization and punishment/reward) in a two-way ANOVA, and we also present these analyses. Data in figure 1b were inversely transformed prior to statistical analysis to normalize data. Data in figure 1c could not be normalized using common transformations and so were analysed in an untransformed manner.

3. RESULTS

Results are shown in figure 1b,c. For both parameters, specialists performed better than generalists in terms of decision accuracy when non-host selection was rewarded, but there was no difference between generalist and specialists when non-host selection was punished. Thus, almost all key phenomena produced by the model were reproduced (although generalists did not outperform specialists when mistakes were punished), and specialists had a greater tendency to outperform generalists when non-host selection was rewarded rather than punished. Two-way ANOVA interactions between treatments for
both performance parameters in figure 1b,c were not significant at $p = 0.05$ (figure 1b, $F_{1,79} = 2.13$, $p = 0.15$; figure 1c, $F_{1,81} = 0.298$, $p = 0.59$). Results regarding selection for different absolute levels of specialization and generalization are presented in the electronic supplementary material, including additional discussion.

### 4. DISCUSSION

Our present study lends strong empirical support to the assertion that decision accuracy could promote the evolution of ecological specialization in animals. In contrast to many research programmes in ecology and evolution, which proceed by partial agreement and constant reformulation of original ideas, research on this idea has produced a positive and consistent picture of its importance. Almost all empirical studies investigating specialization in animals have shown that specialists outperform generalists in terms of decision accuracy [3–8] (but see [9,10]); a focused model has shown that specialist advantage is likely to occur under just the conditions seen in nature [11]; and now the key predictions of this model have been reproduced in a real organic information-processing system. The research programme into decision accuracy and the evolution of niche width should proceed by developing neural models around the process of olfaction to determine if the modelling results of Tosh et al. [11] and the present results hold for this sensory modality, because the great specialists in nature—the plant-eating insects—commonly use smell to locate hosts. It would also be informative to incorporate conclusions derived into traditional evolutionary genetic models of the evolution of niche width [12,26].

Despite the essential agreement between results from the present experiments and the predictions of the model of Tosh et al. [11], there were also some differences. In particular, the model predicted that generalists should outperform specialists when selection of non-hosts is punished, but the present experiments indicated no difference between generalists and specialists in this context. It would perhaps be surprising if there were no differences between the results of the present experiments and model predictions. The complexity of the human brain makes it one of the least well understood of all organic structures, whereas the neural network model consists only of a homogeneous population of 100 or so artificial neurons. The principal feature they share is the property of processing tasks in a distributed fashion. The success of the simple neural network model of Tosh et al. [11] and simple connectionist models used by other authors [27,28] indicates that this shared property is, however, one of the most fundamental determinants of the evolution of behaviour. In terms of the biological relevance of the model predictions, the differences between model predictions and experimental results are less serious than discrepancies in other specific predictions would have been. Fundamentally, because many specialist organisms can use non-host resources if artificially forced to do so [17–19], any mechanism promoting specialization through decision accuracy must favour specialists when non-host resources are beneficial, but not when they are harmful. This condition holds for both model predictions and experimental results, so the discussed discrepancy is not critical. It may be that the lower power of experimental procedures relative to modelling (unavoidably introduced by the logistical demands of experiments) could contribute to the observed discrepancy. Modelling allowed an almost infinite number of data points to be produced and powerful regressions could be applied to this output (figure 1a). Owing to the logistical demands of experimental procedures, however, we could only sample a few points from the model fitness surface and it may be that these points are not always representative of the underlying phenomenon, where the discrepancy between experiment and model occurs. This problem could be further exacerbated by the lower size (see $F$-statistics and slope values, figure 1a) of the effect where the discrepancy occurred, relative to the effect where model and experiment agreed fully. It should also be noted that the results we have obtained agree, in general, with model predictions when predictions are analysed independently; however, effects gauged as the interaction term of a two-way ANOVA are of lower statistical significance. As discussed in $\S2$, independent statistical analyses were considered appropriate to test model predictions as stated, but the limited statistical significance of the results indicates that effects are ‘weak’, and this may limit the extent to which observed effects translate into fitness consequences for organisms. Another factor that makes it difficult to predict how observed effects will translate into fitness consequences for organisms in nature is the concentration in the present and previous modelling studies on cognitive dynamics with the ecological conditions being considerably simplified. This has been done because, if cognitive processes are likely to drive the evolution of niche specialization, then results of the sort we have produced are likely to be necessary. It is also important to initially characterize the dynamics of these cognitive processes without other ecological variables obscuring results. It does, however, make it extremely difficult to predict if and how the present results might drive the evolution of specialization under realistic ecological conditions. Work to integrate cognitive dynamics into a realistic ecological and evolutionary genetic framework is the next logical step.

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**Table 1. A summary of experimental structure.**

<table>
<thead>
<tr>
<th>treatment</th>
<th>no. ‘host’ letters present</th>
<th>points value of host letters</th>
<th>points value of non-host letters</th>
<th>prediction (decision accuracy)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) specialist reward</td>
<td>2</td>
<td>10</td>
<td>2</td>
<td>$1 &gt; 3$ and $4 &gt; 2$</td>
</tr>
<tr>
<td>(2) specialist punishment</td>
<td>2</td>
<td>10</td>
<td>$-10$</td>
<td></td>
</tr>
<tr>
<td>(3) generalist reward</td>
<td>6</td>
<td>10</td>
<td>$-2$</td>
<td></td>
</tr>
<tr>
<td>(4) generalist punishment</td>
<td>6</td>
<td>10</td>
<td>$-10$</td>
<td></td>
</tr>
</tbody>
</table>
The development and the application of our interactive simulation have inspired us to speculate further on the mechanisms underlying the observed effects. However, ultimately, a definitive statement on those mechanisms will require further work. Explaining why specialists should outperform generalists does not seem problematic: recognizing a small number of resources in a complex scene is a simpler task for the attentional apparatus of organisms than recognizing many [1,2]. The difficulty arises in explaining why specialists should outperform specialists (or at least no longer be inferior to them) in terms of decision accuracy when selection of non-host resources results in punishment. One possibility is that the combination of resource rarity inherent in specialization and punishment discourages the user from searching for new host resources through random sampling. Specialists could be particularly curtailed in their search for host resources relative to generalists and could simply find a lower or similar proportion of potential host types relative to generalists. This could explain why specialists no longer outperform specialists under the punishment regime in terms of the parameter ‘proportion of screen presentations in which a host letter was located just after initiating the standardized task’ (screens 71–75). However, it does not explain the similar trend in the decision speed parameter. Presumably, location of fewer hosts would result in a lightening of the attentional load, which should lead to even faster decision-making by specialists than generalists when non-host selection is punished. If this explanation for results were true, we would also expect the results presented in figure 1c to be reflected in the proportion of potential host types (two in the case of specialist and six for generalists) located during the training period (presentations 1–70). A greater proportion of potential hosts should be located during training by specialists than generalists when selection of non-hosts is rewarded, but this effect should disappear when selection of non-hosts is punished. Data do not support this prediction, however. Four of 25 specialists located one of two possible hosts during training when selection of non-hosts was rewarded, and three of 22 generalists located three or fewer of a possible six hosts under the same treatment ($z$-test for two proportions, $z = -0.18, p > 0.4$). Twelve of 21 specialists located one of two possible hosts during training when selection of non-hosts was punished, and eight of 17 generalists located three or fewer of a possible six hosts under the same treatment ($z = 0.29, p > 0.6$). At present, the suggestion of Tosh et al. in the original modelling paper [11] is as plausible as any: the constant encountering of harmful non-hosts by specialists (bear in mind that their hosts are rare relative to generalists and most of the resources encountered by a randomly dispersing specialist are non-hosts) leads to a sensory processing and decision-making apparatus concentrating on the process of non-host rejection at the expense of host acceptance. This could be interpreted as ‘hesitancy’ or ‘caution’ in humans and could explain trends in both decision-accuracy parameters considered here under the regime of punishment for selection of non-hosts. A similar phenomenon called ‘dietary wariness’ is known in foraging animals, where they tend to show a transient aversion to approaching new food (neophobia), and many individuals also show a much longer-lasting reluctance to consume new food (dietary conservatism) [29]. This aversion to novel food items, in general, can be overcome by exposure to a single novel food item. This concept does not appear to fully explain the present results, however. It is clear that generalists should be less wary when mistakes are punished as, even when choosing letters randomly, the user in the generalist treatment will have a higher incidence of experiencing valuable, novel letters. When mistakes are rewarded, however, generalists should similarly encounter very beneficial letters more often than specialists, and while the abundance of mildly beneficial non-host letters in the treatment may equalize wariness between specialists and generalists to some extent, one cannot envisage why specialists should be less wary than generalists.

Of course, in the type of experiment presented here, it can be tempting to speculate on what results tell us about human nature, in addition to what they tell us about the evolution of niche width. Because at least some elements of the interactive involve simple (specialization) and difficult (generalization) memorization tasks, they appear to indicate that simple tasks respond well to rewarding ‘mistakes’ but difficult ones do not. Both simple and difficult memorization tasks respond equally well to punishment of mistakes. Caution is urged in the application of these results to real-life scenarios because, among other reasons, the process by which the overall memorization task develops is quite unusual and specific to the present experiment. Nevertheless, results such as these could potentially find application in educational theory, where an appropriate educator response to student mistakes is key, as well as the computer games industry, where they might inform on the correct strategy to improve gamer performance through time.

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