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Preparedness in cultural learning

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Abstract

It is clear throughout *Cognitive Gadgets* (2018) Heyes believes the development of cognitive capacities results from the interaction of genes and experience. However, she opposes *cognitive instincts* theorists to her own view that uniquely human capacities are *cognitive gadgets*. Instinct theorists believe that cognitive capacities are substantially produced by selection, with the environment playing a triggering role. Heyes's position is that humans have similar general learning capacities to those present across taxa, and that sophisticated human cognition is substantially created by our socioculturally transmitted environment. It is a core strategy of Heyes (Cognitive gadgets: the cultural evolution of thinking. Harvard University Press, Cambridge, 2018) to provide evidence of learning altering a cognitive capacity to conclude that a capacity is a cognitive gadget and not an instinct. We draw on recent work on the evolution of learning preparedness to examine the adequacy of this strategy. In particular, we analyse experimental evolution work showing how selection affects cognition within the laboratory. First, this work reveals that change due to learning can still be retained under genetic assimilation. This suggests that domain-specific adaptation can coexist with learning, *moderate nativism*, an option missed by the *instinct* versus *gadget* distinction. Second, we describe the conditions that select for increased preparedness in learning: certainty, reliability, and particular costs. We consider how these conditions can be used when conducting evolutionary reasoning about cognition, applying them to the important capacity for imitation. We find that the conditions lend theoretical support to moderate nativism about the capacity to imitate, which is supported by psychological evidence.

Keywords Preparedness · Social learning · Imitation · Learning · Evolution of cognition · Evolutionary psychology

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1 Introduction

There is still little consensus on how to apply evolutionary theory to psychology (Laland and Brown 2011). In her 2018 book, *Cognitive Gadgets*,[1] Cecilia Heyes defines two theoretical positions regarding the evolution of uniquely human psychology. The first is the *cognitive instinct* position. The key theorists targeted here are those with a strong *nativist* outlook, particularly, those of the Santa Barabra School of Evolutionary Psychology, who argue that human uniqueness is explained by cognitive mechanisms or modules, which are substantially hardwired and inherited genetically (Barkow et al. 1995; Buss 2001; Confer et al. 2010; Pinker 1997). On this view, humans have many modules, specialised to solve the problems faced by our ancestors, produced through evolution by natural selection on genes (hereafter *evolution* or *selection*). Other cognitive instinct theorists targeted are those who have strong nativist views in their main domain of cognitive theorising: for instance, Chomsky in the domain of language (e.g., Berwick and Chomsky 2017), and Meltzoff in imitation (e.g., Meltzoff 2002). Indeed, even the California School Cultural Evolutionists (c.f. Sterelny 2017), who endorse the view that much of our psychology is culturally inherited, have suggested social learning is underpinned by cognitive instincts (Henrich 2015; Henrich and McElreath 2003).

Heyes occupies the second position. The critical hypothesis of Heyes (2018) is that human psychology is largely explained by *cognitive gadgets* that are substantially constructed by social learning. Heyes focuses on four capacities thought to be central to uniquely human forms of social learning and cumulative culture: selective social learning, imitation, theory of mind, and language. It is regarding these *cultural learning* capacities that Heyes (2018) provides a radical view, arguing that these capacities are themselves largely socially learned. Namely, cultural learning capacities develop via domain-general cognitive processes and associative learning, in concert with the transmitted sociocultural environment.

In principle, Heyes clearly does not advocate for a naïve nature versus nurture, or nativist versus empiricist, dichotomy. She provides a chapter-length discussion of how genetically inherited structure and learning interact and together contribute to the formation of a mature cognitive capacity (Chapter 3). Heyes also thinks it is possible and important to determine the role each plays in producing a cognitive mechanism. However, in practice, the *core strategy* of Heyes (2018) collapses discussion of the nativist structure of the mind to an opposition between highly nativist cognitive instincts versus highly empiricist cognitive gadgets. Heyes's core strategy is to present evidence of covariation between cultural learning capacities and learning opportunities to infer that these capacities are cognitive gadgets rather than cognitive instincts. By presenting evidence of learning in the formation of cultural capacities, her strong empiricist account is meant to be vindicated over the strong nativist alternative.

In making this argument, Heyes leans on *poverty of the stimulus* reasoning (Chomsky 1965). According to poverty of the stimulus reasoning, we can infer that a cognitive mechanism is a cognitive instinct if it is underdetermined by any experience through which it could be learned. Heyes extends: if there are learning opportunities that could

[1] Unless otherwise specified all page and chapter references refer to Heyes (2018).

create a cognitive mechanism—that is, if there is *wealth of the stimulus*—then we should favour a learning-based explanation and infer that a mechanism is a cognitive gadget. She further argues that we can use patterns of covariation between cognitive capacities and learning opportunities to assess the poverty or wealth of a stimulus. So, if a capacity covaries with learning opportunities, then learning should be favoured as an explanation. Alternatively, if a cognitive capacity does not covary with learning opportunities, then a nativist explanation should be favoured.

In our view, where it is often assumed human social cognition and cultural learning is the result of substantial genetic inheritance, Heyes has been successful in showing that learning is more important than has previously been considered. However, her core strategy of presenting evidence of learning to discredit a strong nativist account and to support her strong empiricist account is not as powerful as it first appears. We will argue that the plasticity of cognitive capacities in response to learning does not warrant excluding a more *moderate nativist* account. This will be done by presenting evidence of learning that appears to have been specialised for a specific domain by selection, along with recent experimental evolution and modelling work showing how this specialisation occurs. Together, this work suggests that plasticity can be reduced, but still retained, under genetic assimilation produced by selection on cognition (Pigliucci et al. 2006). It suggests that evolution may establish domain-specific biases to guide adaptive behaviour, but such biases are still *defeasible* and can be changed by learning. Experimental evolution provides an exceptional line of evidence for discussions about how evolution affects cognition, as experimenters control the selection pressures present and observe evolution as it occurs.

The aim of this paper is to communicate the reasoning and evidence for moderate nativism, and show it is a plausible alternative within the current discussion of the evolution of cultural learning capacities. We do this both by critiquing Heyes (2018) to argue that this option is missed within the work, and by giving an example of how evolutionary psychological reasoning can be conducted about cultural learning from a moderate nativist perspective.

The structure of the paper is as follows. First, in Sect. 2, we present work on the evolution of learning, which establishes how selection may affect cognition. Specifically, this work examines the evolution of biased learning or *preparedness*, in which certain associations or responses become more rapidly learned due to selection. In Sect. 3, we note from this work that, even though preparedness may evolve within a cognitive capacity, defeasibility or responsiveness to learning can still be retained. Further, this work has been done in concert with modelling that argues for the importance of environmental certainty, reliability of cues, and costs and benefits, to the evolution of this preparedness. In Sect. 4, we present implications For Heyes' view and describe a position that fits with work on the evolution of preparedness: moderate nativism. Finally, in Sect. 5, we deploy our findings to give an example of how to reason about the degree of preparedness in cultural learning capacities, focusing on the imitation capacity. We argue that there is good support for the hypothesis that the capacity to imitate is more prepared than Heyes's apparent strong empiricist account suggests.

2 Plasticity and preparedness

2.1 In principle

A widely supported view is that plasticity emerges in response to particular kinds of environmental variation (Dunlap and Stephens 2016; Godfrey-Smith 1996). When the environment can take on many different states that affect the agent, it may be adaptive for an agent to be plastic and to match their responses to states. However, in order to match adaptive responses to a changing environment, the agent must be able to track the relevant state of the world such that it can choose the best response (Sterelny 2003). If, for example, some cue C does not closely co-vary with a state of the world W, either because C is present when other states obtain or because C is absent when W obtains, then C is not a reliable guide to W.[2] The consequences of matching responses to different states of the world is thought to be central in selecting for plasticity. For instance, even if the world is nearly always in W_i, if the state of the world W_j is infrequent but highly consequential, this can also select for plasticity.

Studying this idea further, a family of formal models has revealed two particularly important features of the environment that are important for the evolution of plasticity and preparedness (reviewed Dunlap and Stephens 2016; also see Godfrey-Smith 1996). Dunlap and Stephens (2009), provide a simple model calling these two features (1) the *certainty* of the environment p, and (2) the *reliability* of experience in the environment q. A highly certain world has few different states which affect the agent; it is homogenous or simple. Certainty means that actions have consistent outcomes: when a bee encounters a lavender flower it often has nectar. The reliability of experience is high when the state of the world can be inferred from the cues available: the bee can tell which lavender flowers contain nectar. Here, p and q are probabilities: p is the prior probability the world is one state, and q is the probability it is in that state given experience. Learning is favoured when $q > p$, and using a fixed action is favoured when $q < p$. That is, when there is high certainty there is less of a need to learn, and when there is low reliability learning is not efficacious. Conversely, when there is a lot of uncertainty and high reliability, it is an ideal time to learn.

Costs and benefits crucially bear on the advantage gained by learning (Dunlap and Stephens 2016). First, the opportunity cost involved with time spent learning and the possibility of making an error select against learning. Errors are an unavoidable consequence of learning and decision-making under uncertainty (Godfrey-Smith 1996; Wiley 2006). The role of errors while learning has been studied in the exploration–exploitation literature. The central question in this work is: how should the agent spend their effort learning about various options? For instance, given several food-patches that may differ in productivity, what is the optimal combination of time spent foraging at a known patch and time spend exploring others? There is no consensus on the optimal strategy to use in such a scenario (in a finite timespan). However, a sensible result

[2] Sterelny uses the terms *stable* to describe cues that co-occur with only one relevant state of the world, and *reliable* to describe cues that always co-occur when that state obtains. Since we will be investigating their model throughout this section, we follow (Dunlap and Stephens 2009, 2016) in using "reliable" as a catch-all term that does not distinguish between these two sources of correlation between cues and states of the world.

is that, if errors are large or likely, then refraining from exploring unknown options should be favoured. And, if benefits are large and likely, then learning is adaptive (Sherratt 2011). Second, there may be metabolic costs associated with maintaining plasticity; however, there are arguments that this may not always hold and it has not been well tested (see Godfrey-Smith 1996, §8.4).

Let us consider a toy example to further explain the logic of the models. Imagine we have a low-certainty social environment where conspecifics are either trustworthy co-operators or self-interested defectors. Let us also imagine that conspecifics come in two colours: orange and yellow. Let the parameter p determine the proportion of time the agents are good social partners, so if $p = 1$ or 0, then we have a homogenous world in which invariant responses of indiscriminate trust or distrust will be effective. As $p \rightarrow 0.5$, the world becomes more heterogeneous and discrimination is adaptive. (Instead, p could be considered the probability of an agent switching social quality, and so certainty could be temporal.)

Finally, imagine that the colours orange and yellow are indicators of good and bad social partners. Real markers of partner quality might include their accent or dress. Let q be the probability that an orange conspecific is a co-operator, so $q = P(cooperator|orange)$. If $q = 1$, then orange gives a perfect cue for tracking the distal causal state that the agent is cooperative. If $q = 0.5$, on the other hand, then orange gives no information as to the quality of the social partner. And, if $q = 0$, then yellow gives a perfect cue to a co-operator. Under the conditions that the world is heterogeneous in ways that matter to the agent and there is reliable information regarding the changing state of the world, then the optimal response is to learn the state of the world, such as *cooperate conditional on orange*.

In general, this modelling work suggests that when the state of the world does not change, it is more adaptive to produce a single phenotype that matches it, rather than taking time to learn its state, which is advantageous only when it changes frequently (see the model of Chater et al. 2009). Indeed, the model of Thompson et al. (2016) found that, when environmental change is frequent, defeasible biases that can be overwhelmed by learning are more adaptive than those that tightly constrain action. With certainty and reliability considered, the value of using a plastic strategy must bring benefits that outweigh these costs. By corollary, if there is one highly important state, then matching that state will be selected. Further note, the modelling above makes relatively few assumptions about the mechanisms which produce biased learning.

These theoretical results give firm arguments that selection will favour plasticity in some circumstances and constrain it in others. Particularly early in the study of learning, there was a line of thinking that argued that all associations were equally learnable. However, there now exists much evidence, across diverse species and domains, indicating adapted design works with learning (Seligman 1970; Krause 2015). This turn began with the discovery of the classic Garcia effect. Garcia and colleagues found that rats who were nauseated by radiation would more quickly associate this nausea with sweetened water than with light and sound (Garcia et al. 1955,1966). Conversely, rats more quickly associated light and sound with an electric shock. Garcia suggested that the more rapid learning of certain associations showed evolutionary design: things an animal eats may make them nauseous, and things an animal sees may attack them externally. Following the literature, we refer to the adaptive constraining of learning

such that an association or response is produced more readily as preparedness. So note, we do not specify in the definition of preparedness what mechanisms selection alters to bring about a change to learning. Further note, an increase in preparedness seems to entail a reduction in defeasibility. This is not a logical entailment, as speed in acquisition does not logically entail slowness in the breaking of an association or reduction of a response, called *extinction*. However, as we present in the next section, apparent instances of adaptively biased learning have the features of rapid acquisition and resistance to extinction (Krause 2015). So an increase in the defeasibility of a bias may mean a reduction in speed of acquisition and an increase in speed of extinction. Although this is a matter of ongoing research, we suggest the reason for this connection is the following. If the evolutionary purpose of biasing learning is to increase the likelihood of certain responses because they are generally (but not always) adaptive, it makes sense that an animal requires more evidence to assume it will be adaptive to produce an alternative to the prepared response.

In the next section, we will touch on the major sources of evidence for preparedness. We then focus on recent experimental evolution work that purports to create preparedness within the laboratory. These studies test the role of certainty and reliability in the evolution of learning, with selection regimes which mirror the toy scenario above (Dunlap and Stephens 2009, 2014; Mery and Kawecki 2002, 2004).

2.2 Evidence for the evolution of preparedness

2.2.1 Signatures of selection in prepared learning

The recent empirical review of Krause (2015) draws attention to three domains in which a selective account of preparedness has been most evidenced: taste aversion (reviewed by Lin et al. 2017), fear response systems (reviewed by Ohman and Mineka 2001), as well as mating systems (reviewed by Domjan and Akin 2011). For most associations to be learned it is necessary for stimulus and response to occur on the order of seconds; however, fitting the adaptive requirements of a harmful-food avoidance system, taste aversion is associated with food eaten hours beforehand. This association is also made specifically with the food, and not other elements of the scene in which the eating took place. Comparative evidence also suggests the hand of selection. For instance, Ratcliffe et al. (2003) tested three bat species that are dietary generalists, as well as the vampire bat. They found that taste aversion could be induced in the generalist bats, but that the vampire bats did not show taste aversion, making them a rarity among animals. The vampire bat is a dietary specialist, subsisting exclusively on the blood of live mammals, which, since it is harvested from a live animal, should not be toxic. We may conclude that selection produces conditioned taste aversion in situations where it is necessary, which is lost when it is not necessary.

The kinds of stimuli that acutely provoke fear also show adaptive specialisation. Humans rapidly learn to associate fear with snakes and spiders, rather than other biological stimuli, like mushrooms, or things which are a larger threat in most parts of the modern world, such as guns (Ohman and Mineka 2001). The fear of snakes is common among primates, except for those that have had little coexistence with

snakes (Isbell 2006), suggesting selection. It is notable that snakes and spiders form the basis of common phobias, which, with little exposure, produce irrational fears that are difficult to overcome.

Domjan and colleagues have conducted a wide range of studies examining how the mating behaviour of the Japanese quail shows more preparedness towards ecologically relevant stimuli than arbitrary stimuli. For instance, Krause et al. (2003) showed sex-deprived male quails a mannequin female that was either ecologically accurate (a taxidermied quail) or less ecologically accurate (a fluffy cylinder with no head). Particularly when paired with the presentation of a female nearby, the males learned to mate with the mannequin. When the stimulus was ecologically accurate, the association was learned more quickly, and its extinction took longer.

2.2.2 The experimental evolution of preparedness

The evidence for the existence of prepared learning has been established over many studies, through multiple methods, and may be treated as relatively uncontroversial (Krause 2015). However, an exciting development in recent years is the inducing of changes to the plasticity and preparedness of learning through experimental evolution (Dunlap and Stephens 2009, 2014; Mery and Kawecki 2002, 2004). This work allows direct testing of theories regarding how evolution affects learning, and makes implausible alternative explanations that can be drawn on when arguing for a selective of account of a cognitive capacity through evidence produced by probing it in the present.

Mery and Kawecki (2002) presented successive generations of the fruit-fly *Drosophila melanogaster* with Petri-dishes containing agar mixed with either orange or pineapple juice concentrate, observing the medium they chose to lay their eggs on. In an initial phase, flies in the experimental condition were exposed to both dishes, with one of the two paired with the adverse chemical quinine, which flies readily identify and have a strong preference against laying on. In a second phase, the flies were exposed to the two food types without quinine present and could lay eggs on the medium of their choosing. If the flies had learned the quinine-medium association in the first phase, then in the second phase they should lay on the medium that was not earlier paired with quinine. Experimenters then collected only eggs laid on the non-quinine paired medium to populate the next generation. Importantly, experimenters alternated the medium paired with the quinine between successive generations. Thus, the flies who learned not to lay on quinine, no matter which medium it was paired with, were selected. This created an environment where there was low certainty ($p = 0.5$) regarding the medium on which it was best to lay eggs, but high reliability ($q = 1$) regarding the quinine cueing the maladaptive state of the world.

In line with theory, after 20 generations, the flies showed a substantially increased preference against laying on a medium paired with quinine. This proclivity was flexible, occurring when they were tested on the novel mediums of apple and tomato. Moreover, when compared to unselected controls, the selected flies learned the quinine association more quickly and the influence it had on behaviour decayed more slowly. The experimenters suggested this was not due to quinine recognition alone,

but deeper changes to the cognitive system, as the rate at which the flies laid on quinine did not change over the course of the experiment.

Dunlap and Stephens (2009) replicated the key finding of Mery and Kawecki (in addition see Dunlap and Stephens 2014). They also exposed flies to a high certainty ($p = 1$) and low reliability ($q = 0.5$) selective environment, by selecting lines of flies from only one medium (e.g., orange), but varying the quinine-medium paring. In this *high-certainty/low-reliability* condition, flies were found to ignore the quinine association and lay preferentially on the medium on which their line was selected.

These results suggest that when there are fitness-affecting states of the world that the agent can detect, there will be increased preparedness to take the course of action that utilises these states. Take the *high-certainty/low-reliability* selective regime, in which orange-laying flies were always selected and quinine varied between orange and pineapple. In the first generation, flies had an approximately equal preference for the orange and pineapple mediums, perhaps owing to these being approximately equally good mediums for laying over the history of the natural evolution of the fly. After the experimenters imposed selection for *orange only*, the flies had an evolutionary motivation to discriminate between the mediums, becoming prepared to use the orange medium. Since quinine was an unreliable cue in this condition, the flies did not evolve to use it; the behaviour of not laying on a quinine-paired medium was not being selected. However, orange cues to the orange medium were perfectly reliable and this is what the flies evolved to use. In the *low-certainty/high-reliability* condition, flies were reared at random from orange and pineapple mediums, but experimenters never reared offspring laid on the medium paired with quinine. This also meant that orange and pineapple cues were not reliable guides about which medium to lay on, but quinine was, so flies displayed increased preparedness to use quinine.

In summary, the studies above suggest that when there is a high-certainty or homogenous environment, there will be selection against plasticity and towards preparedness for producing a single response. If there is a low certainty or a heterogeneous environment, plasticity will be selected, and agents will have the proclivity to initially explore options equally. Importantly, there must be reliable cues to the state of the environment to allow environmental matching.

Given the experimental rigour involved, it would be difficult to argue that the experimental evolution studies presented in this section do not show *bona fide* examples of selection acting on cognition (in the broad sense of information processing). These results do not admit of the alternative explanations possible when giving selective accounts of cognitive capacities that are observed only in the present. As this experimental evolution work is still in its infancy, the conservative reader might still be unpersuaded that this work induces preparedness such as is described by the taste aversion, fear and mate learning research presented. We are persuaded that preparedness is evolving in these experimental evolution studies because the selected lines of Drosophila showed both (1) faster learning of the association and (2) that this association is more enduring. These are both central features of the preparedness in domains in which a selective explanation has been inferred from signatures of selection alone (Krause 2015).

Table 1 Conditions selecting for increased preparedness

1	High distal environmental certainty or homogeneity (p); one action-state combination is superior to others
2	High cue reliability (q); the states of the environment can be determined
3	The benefits of increased preparedness outweigh the costs
a	High opportunity costs associated with time spent learning should increase preparedness
b	High error costs associated with mistakes in learned behaviour select for increased preparedness
c	Low metabolic costs of building preparedness in a capacity may increase preparedness

3 A lesson and conditions for cognitive evolution

We believe there are two main insights to draw from this work on the evolution of preparedness. First, an important outcome of this work is that, although learning capacities can undergo genetic assimilation under selection, this selection can take the form of biasing actions rather than producing complete fixed actions. Such biases are defeasible, in that learning can still alter them, although such reversals are generally more difficult. Fear-based phobias can take a lot of work to change, but such change is possible (Ohman and Mineka 2001). Similarly, as mentioned, Krause et al. (2003) found that more prepared associations were more difficult, but not impossible, to extinguish in the mating domain. Even imprinting, in which young animals may rapidly learn which individual is their mother from a single event, has been shown to be extinguishable (Bolhuis 1991). The existence of a continuum of preparedness makes sense given if a primary role of cognition is to find adaptive courses of action in a complex and often changing world (Godfrey-Smith 1996). Rather than ingrained courses of action which may soon become maladaptive in a changing environment, it is more adaptive to have defeasible biases (Chater et al. 2009; Thompson et al. 2016).

The evidence supplied of plasticity being retained in even a highly selected cognitive capacity weakens the force of Heyes's core strategy, as such findings weaken the inference that evidence of the presence of learning excludes a selection-based or more nativist explanation. It is reasonable to reduce expectations that selection will produce complete invariance to learning and that evidence of learning supports the strongly empiricist account of Heyes (a point we will elaborate on in the next section).

The second important take-away from this work on the evolution of preparedness is the particular conditions that increase preparedness. We display these conditions in Table 1, with the understanding they can no doubt be improved with further research. Note, when assessing the preparedness of a cognitive capacity, current work gives no reason to think any one condition is more important than any other. Rather, they work together, so if a cognitive capacity has faced a selective environment which meets all conditions we have good reason to infer it is more prepared. We will deploy these conditions in Sect. 4 to demonstrate that cultural learning may be more prepared than Heyes argues. This will give an example of how such conditions can be used in evolutionary reasoning about cognition.

4 Between big special and small ordinary: domain-specific preparedness

All the theorists examined in Heyes (2018) are in fact *interactionists*, believing that learning and selection interact to produce cognitive capacities. This is explicitly the case with the Santa Barbara School Evolutionary Psychologists: "All evolved mechanisms require some environmental input for their activation" (e.g., Confer et al. 2010, p. 116). Similarly, Chomsky does not think that the entire capacity for language is innate, although he thinks this is the case for merge, the abstract capacity that underlies syntax (e.g., Berwick and Chomsky 2017). Moreover, Heyes (2018) herself remarks within her theory of Associative Sequence Learning (ASL) that some sensory and motor representations may be linked together genetically (pp. 122–123). The real disagreement between theorists is about the amount and sophistication of nativist structure or domain-specific cognitive adaptations.

Heyes cleaves theorists into two camps based on how much nativist structure they endorse (e.g., p 12). Cognitive instinct theorists are positioned to argue that cognition comes from the highly specified programs for the unfolding of sophisticated or *big special* cognitive capacities; for instance, mental maps, or the syntax of language. The environment is simply seen as triggering or evoking courses this program can take in cognitive development.

Heyes's own cognitive gadget position, on the other hand, suggests that human psychology is only endowed with *small ordinary* cognitive capacities: the same general learning mechanisms present in other taxa, for inferring relationships between events by their association in time. In addition, humans have superior *central processors*, which are again improvements to general capacities to combine and process information, present across taxa. For Heyes, humans may have some small tweaks to our social motivation, temperament and attention that mean more socially relevant information is filtered into these general learning capacities. Specifically, Heyes argues that humans may have faced selection to interact with, focus on, and empathise with others. The sophisticated cognitive capacities mature humans possess are constructed on the basis of high-quality information provided in social learning; culture plays a crucial role in recreating such cognitive capacities anew each generation, making them *gadgets*. Heyes denies practically all nativist structure for performing specific adaptive tasks.

What is left out of the *cognitive instinct-cognitive gadget* dichotomy is precisely the kind of domain-specific preparedness to learn evidenced in Sect. 2. The work reviewed stands as strong evidence of how cognitive evolution can occur. The flies in those experiments had their initially plastic egg-laying biased over the course of the evolution. We say this is an exemplar of natural evolution acting on cognition, in which evolutionarily relevant responses or associations have been prepared (Krause 2015). In doing so we endorse *genetic assimilation* as a pathway to modifying traits in evolution, which occurs in the following way (see Pigliucci et al. 2006; West-Eberhard 2003; relatedly see *canalisation* and the *Baldwin effect*). First, there is initial phenotypic plasticity within a population which is heritable. Second, the environment changes to makes a subset of possible plastic responses favourable compared to the others. Third, over repeated bouts of selection, the favourable response requires less environmental input to be produced, and this proclivity spreads through the population. This third

process is evidenced by evolutionary experiments (e.g., Dunlap and Stephens 2009, 2014; Mery and Kawecki 2002, 2004; Waddington 1942, 1953) and is the reason selective arguments bear on the discussion of the development of cognitive capacities in the current paper. We note, finally, that in the instances of preparedness that have been studied and discussed above, it is often the case that a prepared bias may be overturned or is defeasible. Indeed, as the strength of biasing within the fruit-fly experiments appeared to increase monotonically within repeated generations of selection, so it may be that the degree of preparedness is proportional to the strength and duration of its selection.

This *medium middling* approach to nativist structure is present in some contemporary theorising, and could be called *moderate nativism*. Perhaps the biggest proponent of such a view has been Barrett (2012, 2015; Barrett and Kurzban 2006). Specifically, Barrett and colleagues have argued that the mind comes equipped with domain-specific architecture to solve adaptive problems, but such architecture gets repurposed and reformatted in development by learning. The brain is argued to be structured hierarchically, such that there are centrally important functions used in many tasks, with some special adaptations working on top of these central functions dependent on the particular task. At the same time, these more specialised functional regions are plastic and interact with each other. Along these lines, Lotem and Halpern (2012) develop a formal model showing how evolution might tune learning capacities to allow more efficient learning from evolutionarily important domains. Indeed, it is not always clear that those positioned as cognitive instinct theorists believe that learning has such a minor triggering role. Meltzoff, the prime imitation-instinct theorist targeted by Heyes, states regarding his *starting-state nativism*:

> In the starting-state view, infants have innate knowledge and are endowed with tools for constructing an adult-like theory – but the newborn does not innately possess the adult theory. Evolution has provided the newborn with powerful discovery procedures for developing adult cognition, but the final state is not specified at birth or achieved through constraint removal (p. 8, Meltzoff 2002).

We argue that Heyes's (2018) core strategy misses the possibility of moderate nativism. The core strategy infers *from* evidence of learning influencing a cognitive capacity *to* the conclusion of a strong empiricist gadget, missing the possibility of moderate nativism and domain-specific preparedness. Further, the preparedness of a capacity can be assessed using conditions produced in Table 1. We will give an example of how such evolutionary reasoning can take place in Sect. 5 in the case of the imitation capacity. However, to make our presentation easier to understand, we must foreground two nuances in applying such evolutionary reasoning to cognition. First, we should think about the preparedness of cognitive capacities as a continuum. Just as the heritability of a trait is a value between 0 and 1, preparedness may be considered to be a value between 0 and 1. So values approaching 0 may mean that there is a large amount of plasticity within the capacity to be shaped by experience, whereas values approaching 1 identify traits that are more prepared and less plastic. Heyes's own (2018) discussion of two language-related capacities, language learning versus learning to read, is suggestive of such a gradient. While language learning occurs without concerted tutoring in all developmentally typical children and environments,

learning to read develops through laborious instruction and generally over a much longer period of time.

The second point of nuance we draw attention to is that different *aspects* of a cognitive mechanism may vary in their preparedness. For instance, the flies in Sect. 2 had their proclivity for learning medium type altered, but the rest of their egg-laying behaviour remained the same. We suggest that the conditions for increased preparedness should often be applied carefully to different aspects of a cognitive capacity rather than to a capacity wholesale (though, it might be possible to amalgamate the preparedness of subcomponents to talk about an entire capacity).

5 How learned is cultural learning? An imitation example

We have been arguing that Heyes's (2018) core strategy misses the possibility of moderate nativism and domain-specific preparedness. In this section, we apply this general argument to an example. Imitation has long been thought of as crucial in human forms of culture, and Heyes agrees it has this special role (p. 4). In this section, we will first examine the evidence Heyes deploys against a cognitive instinct account of imitation. We accept that her major sources of evidence eliminate the possibility of a highly fixed imitation mechanism which admits of little plastic change, and which can achieve its work with no error. However, we argue they do not challenge a more moderately prepared imitation mechanism that still permits of plastic change via learning.

Heyes contrasts her own *associative sequence learning* cognitive gadget (ASL) to Meltzoff's (e.g., 2002) *active intermodal matching* model of imitation (AIM), construed as a cognitive instinct. According to AIM, an imitation module takes a sensory representation of an observed body and calculates the topographic similarity between observed and executed actions. Moreover, the topographic similarity calculator module is innate, though Meltzoff (e.g., 2002) does suggest it gets revised by experience. On the ASL view, the capacity to imitate is constructed nearly entirely through sensorimotor experience. This sensorimotor experience is a mixture of self-observation as well as directed observation of models and the use of artefacts such as mirrors to ensure that one's own motor representations are paired with matching sensory representation of the same action.

We take it that there are no specific cognitive adaptations for imitation in Heyes's account because she states: (1) most of the cognitive systems linking observation of actions to performances of those actions are learned and not inherited genetically (p. 122); (2) this learning connects two systems that normally operate independently (p. 127); (3) cognitive instinct theorists predict that selection would have buffered imitation so it could not be reversed through brief periods of training (p. 134); (4) previous theorists have erroneously come to the conclusion that there is a uniquely human cognitive instinct that underlies the motivation to imitate (p. 138); and instead (5), the motivation to imitate is primarily created when adults reward children (p. 139). This final point also appears in her discussion of the human starter-kit "… developing humans are inclined to adopt those actions, beliefs, and ways of thinking that yield social rewards—nods, smiles, warm touches, kind words" (Heyes 2018, p. 58). We will give reasons to cast doubt on these points; in particular, we argue that children

have a prepared, intrinsic motivation to imitate observed actions, and this departs from Heyes' suggestion that extrinsic reinforcement creates this motivation.[3]

Heyes focuses much of her discussion on the capacity for *correspondence*: the ability for an individual to carry out the matching of their own actions to those of another. However, she also believes general learning mixed with the right sociocultural environment underlies the *motivation* to imitate: the proclivity to deploy imitation (pp. 138–140). Namely, it is the praise given to a young child when they imitate that constructs the motivation to imitate. We will argue that there is both good support for the position that humans come equipped with a prepared proclivity to imitate observed actions—humans have, at minimum, undergone selection on the motivation to imitate—and this may also extend to a greater correspondence capacity to imitate.

There are also reasons to think that a division between correspondence and motivational capacities may not be so clean. A basic feature of learning is that rewarded behaviours are performed more (Pearce and Bouton 2001). It follows that if an individual finds imitation more rewarding, it will be done more often, and they will become more practised at the skill. The reverse may also hold: once an individual is a highly proficient imitator (good at correspondence) they may open up greater rewards from imitation. Tweaking the intrinsic rewardingness of imitation—increasing preparedness—would be a simple mechanism by which evolution could expand the imitation capacity in our lineage.

In the remainder of this section, we will argue that the theorising across Sects. 2 and 3 supports more domain-specific preparedness than Heyes assumes, particularly in the motivation to imitate. We apply the conditions for increased preparedness described in Table 1 to the imitation capacity. Where the flies of Sect. 2 had their preparedness altered by certainty and reliability to asocial aspects of the environment, here we apply the conditions to the sociocultural environment (Sterelny 2003). Our aim here is not to fully elaborate a new theory of the cognition underlying imitation, nor can we compare and contrast every theory regarding imitation. Instead, our aim is to demonstrate how the lessons from the sections above may be applied to the imitation case and to show that domain-specific preparedness is a plausible alternative.

5.1 Evidence against an imitation cognitive instinct

Heyes provides two major lines of evidence to support her argument that imitation is not a cognitive instinct. The first line focuses on training studies of automatic imitation: the facilitation of copying actions when watching another perform the same action. These training studies show that this facilitation can be altered and reversed by learning. The second is work showing *signature limits* that shows specific limitations of our capacity to imitate, which are supposed to be indicative of its non-instinct status.

It has been shown that people's action-performance is facilitated while watching others performing the same action but hindered when an alternative action is observed.

[3] We are also happy for our comments here to be considered extension rather than critique, as the connections between her discussion of social motivation (Chapter 3) and imitation (Chapter 6) are, at best, unsatisfactorily explored. More differences between our position and Heyes's may be able to be exposed when more details of the psychological mechanisms involved are revealed by future research.

Heyes cites evidence that training can eradicate (Heyes et al. 2005) or reverse (e.g., Catmur et al. 2007) automatic imitation, such that observing an incongruent action becomes facilitating. Other sources of training evidence cited by Heyes show that imitative capacities can be enhanced by learning (e.g., Cooper et al. 2013). In line with her core strategy, she takes the influence of learning to indicate that automatic imitation is not a cognitive instinct.

The second major line of evidence Heyes draws on is signature limits, which is supposed to show that human imitation has limitations that mean it is "not as flexible or accurate as the cognitive instinct theory would lead us to believe" (Heyes 2018, p. 131). For instance, imitative ability does not readily generalise across the body (e.g., Leighton and Heyes 2010). One piece of evidence is that a complicated set of key-pressing movements can be imitated when the observer's hands are in the same position as the model's, but is disrupted when the observer's hands are crossed. As another example, it has been shown that people poorly replicate their own facial expressions in photos taken several months earlier (Cook et al. 2013).

The strength of both lines of evidence against a cognitive instinct view is dependent on the sophistication of the cognitive instinct capacity postulated. If the instinct view requires an innate mechanism that is invariant in response to experience and can perform any topographical transformation without error, then this evidence certainly eliminates that view. However, if a more moderately prepared imitative capacity is assumed, then this evidence can be accommodated. Such a capacity could have a bias to congruent actions, but this bias can be overcome with training. The strength of these studies as evidence against a moderate nativist account is weakened by the lesson that preparedness still allows plastic change; preparedness does not exclude altering by learning but may change the rate at which learning occurs. Such a capacity could also be assumed to make errors and improve with learning. Indeed, the fact that individuals start with a proclivity to replicate observed actions is consistent with the view a moderate degree of preparedness is present.

5.2 Preparedness in imitation

5.2.1 Conditions for preparedness in imitation

We have discussed the evidence Heyes presents that this is not a cognitive instinct; however, she also provides an evolutionary argument that considers what we called certainty. Heyes argues that alleles fixing the specific copying of actions could not be selected for, given the changing sociocultural environment humans occupy (p. 207). If we had a group bonding ritual that requires that one leans forward when another leans forward, individuals with alleles selecting for the matching lean-forward proclivity may have an advantage. However, leaning forward would be selected against when customs changed, and customs change relatively quickly to genetic time. We agree with this argument: the conditions required to make the imitation of specific actions sequences highly prepared in the human case are unlikely. However, this does not exclude the possibility of the preparedness of a proclivity to imitate observed action sequences in general.

First, we consider whether the heterogeneity or certainty of the environment is suitable to prepare the policy *often imitate observed actions*. There are many potential actions an individual could acquire. In a changing environment, it makes sense to stay relatively plastic with respect to these behaviours. However, there is reason to believe that, when cumulative culture is in place, the actions of others are an exceptional guide to which behaviours to perform. Cumulative culture produces behaviours that are fashioned to be highly productive. Tomasello (e.g., 2014) gives a substantial treatment of the argument that, of the many potential behaviours to acquire, imitating others gives access to many of the most valuable to be attained in the environment. What is more, the behaviours attained under cumulative culture are complex and unlikely to be stumbled upon without social learning. Thus, the policy of imitating others should be a certain and productive strategy.

We must also consider the reliability of cues leading to imitation. In general, social learning has been shown to be an efficacious strategy when others perform their most productive behaviours (Rendell et al. 2010). The social environment in which humans evolved is one marked by exceptional cooperation (e.g., Sterelny 2012). In a highly cooperative environment, individuals should allow others to observe their behaviour (Sterelny 2003); this does align well with Heyes' starter-kit item of social tolerance. Indeed, models may teach others, demarcating important actions and making cues even more reliable than the baseline. Furthermore, there is little risk of being taken advantage of by others. Specifically, in the case of imitation, it is likely that children can discern what behaviours are useful through adult signals, such as smiling, or their more direct attempts to get the child's attention. (Note that such smiling has the role of demarcating important actions and rather than simply giving reinforcement as Heyes suggests). Together, this supports the case for increased preparedness.

This is not to say that Machiavellian scheming does not occur. Individuals may deceive each other when the benefit outweighs that of cooperation. For instance, a model could purposely act on inferior food or have another produce a *faux pas*, in the hope they gain advantage from an unreflective imitator. This simply suggests that some plasticity should be retained and the fixed policy of *always imitate observed actions* should not be selected; defeasibility is beneficial.

Now to consider the relevant costs. In a highly cooperative environment, error costs will be low, for two reasons. First, models will often not take advantage of imitation errors. Second, models may help imitators avoid costly errors. Regarding opportunity costs, being accelerated in the ability to culturally learn stands to give a child advantages over their peers. According to Heyes's account, children must first identify that the praise they are being given is for imitating, rather than for any other part of the scenario they are in. Conversely, greater preparedness can fix cognition on the important cues in a situation to make such learning faster. Last, it would also be necessary for the metabolic cost of changes to cognition to prepare the rule *often imitate observed actions* to be outweighed by the benefit, it may be that the metabolic costs for greater preparedness are indeed cheaper than maintaining a plastic response.

5.2.2 Evidence for preparedness in imitation

In the previous section, we argued, based on the conditions which increase preparedness, that there are good evolutionary reasons to believe there is an elevation in humans' proclivity to imitate. We now present supporting evidence, which focuses on comparing the proclivity to imitate of humans with closely related primate species. It should be noted that these species have very different features regarding their selective environment. They are nowhere near as cooperative, thus should not provide cues that are as reliable to productive behaviours. Further, the possible behaviours to imitate are less valuable in comparison with those that can be discovered without imitation (Tomasello 2014), so there is less certainty as a result.

When compared to chimpanzees and monkeys, human children show an incredible use of imitation spontaneously when confronted with a novel task (Dean et al. 2012). Indeed, close examination of the cognition of chimpanzees and orangutans found they were equal or superior in most areas of non-social cognition when compared to young children, but that in the social domain, including in imitative ability, they were roundly outperformed by children (Herrmann et al. 2007). At first blush, our conclusion is well supported.

We admit that more developmental evidence is needed, in particular showing how the amount of experience relates to increased motivation to imitate. Nonetheless, we draw attention to two lines of evidence that are highly suggestive of the endowment of more imitation-preparation in humans. First, enculturated nonhuman great apes (hereafter *apes*) do not show comparable motivation to imitate or corrospodance capacity that is anywhere near that of children, even when they are specifically trained for the task. Further, they do not show the same proclivity or flexibility in deploying imitation in new situations. If sociocultural experience was the key driver of the proclivity to imitate we should expect a similar dose-dependent response in each species to enculturation and training, and this is not what is observed. Second, although other animals can imitate, but often do not, they practically never overimitate, whereas humans do from a young age. That is, non-human animals never knowingly imitate causally irrelevant actions. The development of imitation is suggestive of a prepared proclivity to interpret much of observed actions as causally relevant, imitate these actions, and to then refine the deployment of the acquired behaviours.

The abilities of enculturated and trained apes give evidence about the effect social experience can have on the development of a cognitive system by comparison to our own. In a recent review of the effect of enculturation on imitative ability, Subiaul (2016) concludes that while enculturation does improve the imitative capacities of apes, differences in their imitation persist when compared to even infant children. Namely, apes will imitate familiar trained actions within their repertoire, but consistently fail to produce such imitation in new contexts and on their first attempt. Extreme cases of enculturation have shown there are fundamental capacities within language apes never acquire (Vauclair 1996); this also appears to be the case with imitation.

For example, Carrasco et al. (2009) studied the imitation of the 5-year-old chimpanzee Lili. Lili was raised by humans, in their house, until she was 2-years-old. She underwent a 4-week period in which the model she was to imitate visited her 5 times per day, used food, and played with her. She then underwent a training regime over

9 months in which she was trained for 30–40 min, 3 times a day, 5 days a week, on 20 specific behaviours to imitate. Only when she showed an 80% success rate on these behaviours for three days in a row was her imitative behaviour tested on 52 novel actions, which were similar to the trained set of actions. Throughout testing, praise and food were used as encouragement. Nonetheless, 50% of the actions were either not performed correctly or not performed at all on the first trial; the authors noted that Lili actually performed substantially better at imitation tasks than previous apes tested in comparable studies.

Compare this to human infants, who by the age of 18 months, are performing at ceiling on similar tasks, with little to no specific training and after only brief familiarisation with the task (e.g., 3-min demonstration; Jones 2007; Young et al. 2011). Further, chimpanzees can also imitate actions on a task in which a reward is extracted, but rarely do, especially compared to young children (Whiten et al. 1996). Together, this evidence suggests that enculturation does have a positive effect on ape imitative ability—learning is still a factor—but humans are more motivated towards and skilled at imitation.

While apes can be compelled to imitate, there is practically no evidence they overimitate (Whiten 2011). In a classic study by Horner and Whiten (2005), it was shown that young children, but not young chimpanzees, imitate even obviously causally redundant actions. The following study of Lyons et al. (2007) showed that it is fairly difficult to dissuade children from overimitating, even under time pressure or direct warnings. Lyons et al. (2007) conclude, "children who observe an adult intentionally manipulating a novel object have a strong tendency to encode all of the adult's actions as causally meaningful" (p. 19,751). Recently, Clay et al. (2018) showed that over the course of early development, children move from roundly overimitating to selectively overimitating. Together, this evidence supports the argument for increased preparation of the motivation to imitate in humans; a prepared tendency to imitate first and then refine the deployment of imitation at later ages (also see Flynn et al. 2016).

In summary, apes given substantial sociocultural input within human environments, and even with specific training, still perform far below typically-raised children with little to no concerted effort to train imitation. The ability to perform novel tasks calling on a cognitive capacity provides evidence that capacity is likely to have some domain-specific preparation, a point which Heyes highlights (p. 50), and is evident in the imitation case when comparing humans and close relatives. Young children, but not any non-human animals tested thus far, have demonstrated the propensity to overimitate, seemingly imitating first and refining acquired behaviours later. The conditions for preparedness of imitation obtain, and the evidence fits well with our expectations about how a prepared imitation system would operate. The present paper, therefore, suggests this a persuasive instance of prepared cognition in cultural learning, and provides an example of how such reasoning can be performed.

6 Conclusion

In applying evolutionary reasoning to psychology, researchers are often interested in drawing conclusions about how cognitive tasks will be performed on the basis of a

history of selection. A complicating factor is the influence of learning on shaping cognitive performance. Practically all theorists in the area recognise that selection and learning interact to produce mature cognitive capacities. Here, we have reviewed theory and recent experimental evolution evidence examining how selection affects the way in which learning operates. This work suggests that genetic assimilation produced by selection may reduce the scope of learning, but such selection does not necessarily remove the ability of learning to overturn evolutionarily induced biases. Indeed, this may often be the case, as selection that completely removes defeasibility may not be favoured in an environment that still contains some change.

In many ways, this lesson makes the challenge of applying evolutionary theory to psychology more difficult, as it shows plasticity via learning can coexist with an evolutionarily prepared proclivity. Therefore, evidence of learning does not eliminate an explanation based on selection; instead, we should often expect a continuum of preparedness (and plasticity) in cognitive capacities. We suggest, to help aid researchers in determining the degree of preparedness, that evolutionary conditions should be used alongside psychological evidence. Here, we focused on certainty, reliability, and particular costs and benefits that have been established as important in the evolution of preparedness. We took the imitation cultural learning capacity as a case study of how this might be conducted, concluding that theory and evidence were consistent with moderate preparedness. Developing theory that uses the understanding that intermediate levels of preparedness may often be present—that adaptive domain-specificity and learning can be present together—is a promising direction for the future of evolutionary reasoning about psychology.

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