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8	SIMPLE MINDS:
9	A QUALIFIED DEFENCE OF ASSOCIATIVE LEARNING
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#### 1 Abstract

2 Using cooperation in chimpanzees as a case study, this article argues that research on animal 3 minds needs to steer a course between 'association-blindness' - the failure to consider 4 associative learning as a candidate explanation for complex behaviour - and 'simple-5 mindedness' - the assumption that associative explanations trump more cognitive 6 hypotheses. Association-blindness is challenged by the evidence that associative learning 7 occurs in a wide range of taxa and functional contexts, and is a major force guiding the 8 development of complex human behaviour. Furthermore, contrary to a common view, 9 association-blindness is not entailed by the rejection of behaviourism. Simple-mindedness is founded on Morgan's canon, a methodological principle recommending 'lower' over 'higher' 10 11 explanations for animal behaviour. Studies in the history and philosophy of science show 12 that Morgan failed to offer an adequate justification for his canon, and subsequent attempts to justify the canon using evolutionary arguments and appeals to simplicity have not been 13 successful. The weaknesses of association-blindness and simple-mindedness imply that there 14 15 are no short-cuts to finding out about animal minds. To decide between associative and more cognitive explanations for animal behaviour, we have to spell them out in sufficient detail to 16 17 allow differential predictions, and to test these predictions through observation and experiment. 18

#### 1 1. Simple-mindedness and association-blindness

2

3 There is a current of opinion in the study of comparative cognition suggesting we should 4 assume that animals have simple minds. This current takes a variety of forms. Sometimes there is an explicit appeal to Lloyd Morgan's canon, parsimony, or Ockham's Razor. These 5 6 principles are usually taken to indicate that, when animal behaviour could be due to two 7 different psychological processes, and these processes vary in complexity, it is more 8 scientifically healthy or legitimate to assume that the behaviour is due to the less complex 9 option. Another, related principle is Macphail's null hypothesis (1). This hypothesis suggests that there are no differences in intelligence among nonhuman species, and implies 10 11 that there is a burden of proof on any study attempting to show that behavioural differences 12 are due to intellectual rather than 'contextual' variables. Whether they are discussing 13 alternative explanations for behaviour in one species, or species differences, proponents of the simple-mindedness tend to emphasise the importance of associative learning. In the most 14 15 extreme cases, the claim that animals have simple minds amounts to the claim that associative learning is the only way in which animals can think about the world. 16

17

In marked contrast with the simple minds lobby, many contemporary scholars of comparative 18 19 cognition appear to assume that animals do not engage in associative learning, or that associative learning is not even a candidate explanation for much of their behaviour. This 20 21 view is implied by the many recently published studies reporting that animals 'understand' a particular aspect of the world (e.g. causality, intentions, reciprocity, or the needs of others), or 22 23 'have' a particular psychological attribute (e.g. theory of mind, shared intentionality, social motivation), without mentioning associative learning. These studies, which very often 24 involve primates, are not designed to test an 'understanding' hypothesis against an 25

associative learning hypothesis, and do not discuss the possibility that associative learning
 could produce the focal, intelligent behaviour.

3

In this article I suggest that research on comparative cognition needs to steer a course
between simple-mindedness and association-blindness. I offer a qualified defence of
associative learning, arguing that it should be treated as a contender – a candidate explanation
for intelligent behaviour in all animals – but not as a default winner. When behaviour can be
explained by both associative and more cognitive mechanisms, we need to do more empirical
work; we can't assume that associative processes are responsible.

10

I begin by outlining a recently published experiment that reported some interesting prosocial 11 12 behaviour in chimpanzees, and did not refer to the possibility that this behaviour could be due to associative learning (2). I chose this experiment by Horner and colleagues as a focal 13 example of association-blindness because it is excellent in all other respects. It addressed a 14 15 timely and important question with meticulous care, obtained interesting results, and was published in a high profile journal. After outlining the case study, I shall discuss three 16 17 reasons why associative learning should be considered as a candidate explanation, not only for the behaviour reported in the case study, but in all other studies of intelligent behaviour in 18 19 animals, including primates. These reasons draw on evidence that associative learning 1) 20 occurs in a wide range of vertebrate and invertebrate taxa and across a variety of functional domains, 2) has been conserved in primates including humans, and 3) cannot be dismissed on 21 historical grounds. In the final part of the article, I turn from association-blindness to simple-22 23 mindedness, arguing that, although they are important candidates, associative hypotheses do 24 not have a privileged status in the explanation of animal behaviour.

25

#### 1 2. Case study: Prosocial behaviour in chimpanzees

2

3 Altruism or prosocial behaviour is currently a hot topic in comparative cognition. In the last 4 decade, increasing numbers of observational and experimental studies have investigated the extent to which other primates share the cognitive and motivational processes that underwrite 5 6 human cooperation. In one of the latest studies of this kind (2), Horner and colleagues tested 7 six female chimpanzees using a sophisticated version of the Prosocial Choice Test. In every 8 trial of this test, the focal chimpanzee (the actor) was offered a bucket containing a jumble of 9 plastic pipes, and allowed to remove one of them from the bucket. Half of these 'tokens' was 10 of one colour, and the other half was of a different colour. If the actor selected a token of one 11 colour (e.g. purple), the experimenter gave a food reward to the actor, and to another 12 chimpanzee in an adjacent enclosure (the partner). If the actor selected a token of the other colour (e.g. green), the actor was given a food reward but the partner was not. The actors had 13 been given the opportunity to learn the outcomes of their token choices immediately before 14 15 the test. In this contingency training session, the procedure was the same as the one used for testing, but the bucket contained just one token (e.g. green or purple) in each trial. During 16 17 both contingency training and the Prosocial Choice Test, actors and partners were able to see and hear one another through a wire mesh window between their enclosures. Slices of 18 19 banana, wrapped in paper, were used as rewards. "Unwrapping the paper made a loud noise 20 (like eating bonbons), so that actors did not need to rely on vision alone to know whether the 21 partner had been rewarded" ((2)p.13850).

22

The study yielded four key findings: 1) In the Prosocial Choice Test, the actors chose a dualreward token, resulting in the provision of food to both actor and partner, in significantly more trials than they chose a single-reward token, resulting in the provision of food to the

1 actor only. 2) In control trials, where the actors were tested in the same way, but no partner 2 was present in the adjacent enclosure, the actors selected dual-reward and single-reward 3 tokens at random. 3) Analysis of the partners' reactions showed that they exhibited more 4 'attention-getting behaviour' (e.g. self-scratching, noise, hitting the caging) and made more 'directed requests and pressure' (e.g. poking paper through the mesh partition, begging with 5 6 an open hand, staring at the bucket with tokens) after single-reward than after dual-reward 7 choices by the actor. 4) Actors were more likely to choose dual-reward than single-reward 8 tokens on trials immediately following attention-getting behaviour, but not on trials 9 immediately following directed requests and pressure. This suggests that the actors' dual-10 reward choices were not provoked by threats from their partners.

11

In combination, these results were interpreted as evidence that chimpanzees are capable of "prosocial choice"; as undermining claims that chimpanzees are "marked by indifference to the welfare of others", and have "a limited sensitivity to the needs of others"; and as "indicating that the partners were not passive food recipients but understood the difference between selfish and prosocial token choices". Couched in a positive way, these statements imply that the results of the study provide evidence that, at least as actors, chimpanzees know (cognition) and care (motivation) about the needs of conspecifics.

19

Here is another interpretation of the findings, inspired by research on associative learning:
When a chimpanzee in this experiment got a food reward, she heard loud rustling as she
unwrapped the treat, immediately before she slipped the juicy slice of banana into her mouth.
Consequently, just as Pavlov's dogs got to like the sound of a bell, the chimpanzees got to
like the sound of paper rustling. In other words, as a result of being presented with the
banana, the sound of paper rustling became a 'conditioned reinforcer', a previously neutral

1 event which has acquired reward value through 'Pavlovian' or 'classical' conditioning. Now, 2 single-token choices yielded one shot of this conditioned reinforcer – the sound of the actor 3 unwrapping her own treat - but dual-token choices yielded two shots - the sound of both the 4 actor and the partner unwrapping their treats. Dual-token choices were more richly rewarding for the actor than single-token choices, and therefore, via a process known as 5 'instrumental learning' or 'operant conditioning', the frequency of dual-token choices 6 7 increased relative to the frequency of single-token choices. This associative explanation for 8 the chimpanzees' prosocial behaviour is consistent with the fact that actors did not show a 9 bias towards dual-token choices in control trials, when no partner was present. In these trials, which used a new pair of token colours, dual-token choices were not followed by the sound 10 11 of a second treat being unwrapped.

12

On the associative learning account, the chimpanzees can still be said to have shown 13 prosocial choice because the effect of their bias towards dual-token selection was to benefit 14 15 their partners. However, the associative account implies that the chimpanzees' behaviour was controlled purely by the 'selfish' reward value of the events (paper rustling and banana 16 17 consumption) that followed their choices. 'Selfish' is in cautionary quotes because, although this description may seem appropriate from the human perspective, the associative account 18 19 does not imply that the actors represented their behaviour as selfish. Furthermore, and 20 crucially, the associative account does not imply that the chimpanzees knew or cared about the needs of their partners. It implies that the effect of their choices was prosocial, but that 21 the underlying representations and motivations were not. 22

23

I have suggested in this section that the prosocial behaviour reported by Horner andcolleagues could have been due to associative learning. A critic might concede that this is

1	possible in principle, but argue that the chances of it being true in practice are so remote that
2	it would not have been productive for Horner et al. to discuss the associative learning
3	hypothesis, or to design their experiment so that associative learning could be distinguished
4	empirically from the hypothesis that chimpanzees know and care about the needs of others.
5	After all, it would not be rational for scientists to devote time and energy to testing
6	hypothesis that are already known to have a very low probability of being correct. In the next
7	three sections I suggest that this line of argument is not persuasive; that, given what we know
8	about associative learning, it should be considered as a candidate explanation – a major
9	contender – for all new observations of intelligent behaviour in animals.
10	
11	3. Associative learning is everywhere
12	
13	Associative learning is ubiquitous. Evidence of associative learning has been found in every
14	major taxon where it has been sought, and in a huge range of functional contexts, from
15	foraging, through predator avoidance, to mate choice and navigation.
16	
17	The last major survey of the taxonomic distribution of associative learning was published by
18	MacPhail in his book 'Brain and intelligence in vertebrates'(1) (see also (3, 4)). That survey
19	focussed on carefully controlled laboratory experiments, and applied exacting criteria to
20	decide whether the members of a particular species were capable of associative learning.
21	MacPhail first asked whether they had provided evidence of Pavlovian and instrumental
22	conditioning, and then whether they had shown compound conditioning effects characteristic
23	of associative learning in mammals. Operationally defined, Pavlovian conditioning is a
24	change in behaviour due to exposure to a contingency (or predictive relationship) between
25	two events in the world – a conditioned stimulus (CS), such as a flash of light, and an

1 unconditioned stimulus (US) or reinforcer, such as the delivery of food. Instrumental 2 learning is a change in behaviour due to exposure to a contingency between an action, such as 3 pressing a lever, and a stimulus that follows the action (an outcome or reinforcer), such as the 4 delivery of food (5). The changed behaviour is known, in both cases, as the 'conditioned response' (CR). To be sure that a change in behaviour is really due to contingency exposure, 5 6 conditioning experiments need to control for the possibility that the animal is merely altering 7 its behaviour as a result of repeated exposure to stimuli or repeated performance of responses. 8 The ideal way to do this is using a 'random control'(6). For example, in a Pavlovian 9 conditioning experiment, animals in a 'contingent group' might see a flash of light just before their receive each of a series of food pellets, whereas animals in a 'random control group' 10 would see the same number of light flashes, and receive the same number of food pellets, but 11 12 the occurrence of the two types of event would be uncorrelated.

13

The compound conditioning effects examined by MacPhail (1) included overshadowing and blocking. In Pavlovian conditioning procedures, these effects occur when more than one CS (e.g. a light and a noise) is presented in a contingent relationship, or 'paired', with the US (e.g. electric shock). Overshadowing refers to a reduction in conditioning to a CS when it is presented with another CS, than when it is presented alone (7). Blocking refers to a reduction in conditioning of one CS as a result of its being presented with a second CS that had previously been paired with the US (8).

21

Using these exacting standards, MacPhail found evidence of associative learning, not only in
mammals, but in all other major vertebrate taxa: fish, amphibians, reptiles and birds. The fish
examples included lemon sharks, goldfish, Siamese fighting fish, golden shiner minnows,
green sailfin mollies, guppies, Beau glory, carp and many more. Fewer well-controlled

experiments have been conducted with amphibians and reptiles, but MacPhail found evidence
of conditioning in leopard and green frogs; spadefoot, African clawed and Woodhouse's
toads; salamanders and crested newts (amphibians); and in Bengal monitor, collared and tegu
lizards; red-eared turtles; tuatara; indigo and garter snakes; alligators and crocodiles
(reptiles). Most studies of conditioning in birds have used the pigeon, but MacPhail's survey
also found evidence of associative learning in chickens, doves, quail, magpies and mynah
birds.

8

A contemporary survey of vertebrates would add many new species to these lists. Of yet
more interest, however, is recent work providing evidence of associative learning in
invertebrate species. For example, demonstrations, not only of conditioning, but also of
blocking, have been reported in insects (honey bee (9) (10)), molluscs (garden snail (11)
(12)), and platyhelminthes (planarian flatworms (13)). Evidence of basic conditioning has
even been reported in the unicellular paramecium (14).

15

To secure precise experimental control, many studies of associative learning use arbitrary or 16 17 'unnatural' stimuli and responses, such as electric shock and lever pressing. However, there is also a rich supply of more naturalistic studies indicating that associative learning is a motor 18 19 of adaptive plasticity in a wide variety of species and behavioural contexts. For example, the 20 flavour-aversion learning paradigm first developed by Garcia and colleagues (15), and now a standard laboratory procedure, uses distinctively flavoured foods as conditioned stimuli, 21 rather than lights or tones, and poison as the unconditioned stimulus, rather than electric 22 23 shock. The results obtained using this paradigm show that associative learning enables rodents and birds to enhance foraging efficiency and to promote survival by avoiding foods 24 that are potentially toxic (16). Similarly, studies of bees have shown that they acquire flower 25

colour preferences through associative learning, and that these preferences enhance foraging
 efficiency by enabling the bees selectively to sample flowers that are most likely to contain
 rich supplies of nectar and pollen (17).

4

Associative learning also enables animals to recognise and to avoid predators. In one study 5 6 demonstrating the role of associative learning in predator avoidance, Wisenden and 7 colleagues used damselfly larvae that were initially unresponsive to chemical stimuli from 8 pike (18). After the pike stimuli (CS) had been paired with cues from injured damselflies 9 (US), the larvae made fewer approach responses to the pike stimuli than control larvae that 10 had encountered the pike cues with distilled water. Similarly, there is evidence that 11 blackbirds learn to recognise predator birds, such as owls, by observing those birds (CS) 12 being mobbed by conspecifics (US) (19) (20), and, from a carefully controlled series of analytic experiments, that monkeys acquire fear of snakes in the same Pavlovian way (21). 13 In all of these cases, the US (injured damselflies, mobbing behaviour by blackbirds, and 14 15 fearful behaviour by monkeys) had a social source; it came from members of the same species as the learner. Thus, these are also examples of what is known as 'observational 16 17 conditioning'; they show that associative learning plays a major role in social learning and the transmission of behaviour across generations and extant members of social groups (22). 18

19

Navigation is another domain in which associative learning has been shown to play a
significant role. In this case, animals are able to find their way back to a rewarding location –
a place at which they found food or escaped danger – by learning that the rewarding location
(US) is marked by a distinctive stimulus (a 'beacon'; CS) that is visible from some distance
away. Evidence that it is associative learning that allows animals to use a beacon for
navigation comes from experiments showing that learning about the beacon can block and

overshadow learning about the relationship between other, more spatially distinct cues and the rewarding location. For example, Roberts & Pearce (23) gave rats the opportunity to learn the location of an invisible escape platform in a swimming pool. In principle, the rats could have learned the location of the platform relative to a beacon (a visible sphere attached to the platform) and to a range of objects surrounding the pool. However, when the rats had prior experience in which the beacon alone had signalled the location of the platform, they learned very little about the location of the platform relative to the other objects.

8

9 Associative learning can also enhance the effectiveness of territorial behaviour. For example, 10 Hollis and colleagues exposed one group of male blue gourami fish to a contingency between 11 a red light (CS) and the arrival of a territorial rival (US). In comparison with a random 12 control group, these fish provided evidence of conditioning by showing more aggressive displays during the presentation of the light. Furthermore, when pairs of conditioned and 13 control males were exposed simultaneously to the red light, and then allowed to fight one 14 15 another, the conditioned males delivered more bites and tail-beating responses than their rivals, and consequently won more of the fights (24) (25). 16

17

18 Finally, in the domain of sexual behaviour, there is evidence not only that associative 19 learning makes an important contribution to behavioural development, but also that it 20 enhances reproductive fitness (16). For example, after conditioning trials in which a light (CS) predicted the arrival of a female (US), presentation of the light resulted in male blue 21 gouramis making fewer aggressive responses, and more courtship responses, to approaching 22 23 females. As a consequence, the conditioned males spawned sooner, and fathered 24 approximately 10 times more young, than the control males (26). Conditioning also enhances reproductive success in male and female Japanese quail. When they mate in the presence of 25

cues that have been paired with the presence of a potential sexual partner, males release more
 sperm (27), and females produce more fertilized eggs (28).

3

4 In this section I have tried to give some sense of the wide range of taxa and functional domains in which associative learning is known to occur. Although the survey is brief and 5 6 very far from complete, it highlights the fact that conditioning has been found in every major 7 vertebrate taxon, as well as several invertebrate groups. It also shows that associative 8 learning is not just something that happens in laboratories. Rather, there is compelling 9 evidence that associative learning contributes to the ontogeny of adaptive behaviour in a wide 10 range of domains, including foraging, predator avoidance, navigation, territoriality and sexual 11 behaviour.

12

### 13 **4.** ...even in (human) primates

14

15 The evidence surveyed in the previous section suggests that associative learning is an important candidate explanation for adaptive behaviour in a wide range of taxa and functional 16 17 contexts. However, by itself it does not imply that associative learning is an important contender to explain the prosocial behaviour of chimpanzees - behaviour of the kind 18 19 observed in our case study (2) - or, more generally, to explain complex behaviour in primate 20 species. To be persuaded of this, we need evidence that associative learning has been conserved in primates, and that it doesn't just control "spit and twitches" (29), but contributes 21 to the development of subtle, voluntary patterns of primate behaviour. A sample of this 22 23 evidence is reviewed below. The examples are all taken from recent studies of associative learning in humans. This is necessary because very little contemporary research examines 24 associative learning in other apes. (Indeed, the reasons for this omission are, in its most 25

general form, the puzzle examined in this article.) Fortunately, in this case, the focus on
humans is not a problem. If associative learning plays an important role in guiding complex
human behaviour, in spite of the many ways in which our lives differ from those of all other
animals, there is no reason to doubt that it remains a powerful force in shaping the behaviour
of other primates.

6

7 Let's start with a couple of particularly striking examples where associative learning has been 8 implicated in cognitive functions that many would regard as characteristically human. First, 9 recent research on individual differences shows that, alongside working memory and processing speed, associative learning makes a substantial independent contribution to IQ. 10 11 How well people perform on standardised tests of general intelligence - such as Raven's 12 matrices, the Differential Aptitudes Test of verbal reasoning, and the mental rotations test – is predicted by the efficiency of their associative learning (30). Second, associative learning 13 has recently been implicated in the development of 'sense of agency', the phenomenal 14 15 experience of producing events through one's own intentional action. In a study measuring 'temporal binding' – a strong index of sense of agency – a blocking effect, characteristic of 16 17 associative learning, was observed when people were exposed to flashes of colour on a computer screen that may or may not have been produced by their finger movements (31). 18 19

Another recent study implicated associative processes in human geometry learning (32). In a computer-based task, participants were required to learn the location of a goal (food for three blind mice) within a room using geometric information available on the screen. Consistent with an associative model (33), when the goal location was defined by two shapes that differed in salience, the more salient shape overshadowed the less salient shape, and when

the shape was pre-trained as a signal for the goal location, learning about the geometric cues
 of the other shape was blocked.

3

4 Turning to the social domain, a series of studies in my own laboratory has provided evidence that associative learning drives the development of mirror neurons (34), and of the capacity to 5 imitate (35) (36). For example, using transcranial magnetic stimulation (TMS) and functional 6 7 magnetic resonance imaging (fMRI), these studies have shown that the action of the mirror 8 neuron system can be reversed – such that it is active during the observation of one action 9 and the performance of a *different* action – by training on a nonmatching sensorimotor 10 contingency (e.g. foot movement stimulus > hand movement response, and vice versa (37)). Providing more specific evidence for the involvement of standard associative processes, 11 12 behavioural experiments examining the effects of training on automatic imitation have shown that it is sensitive to contingency, and shows context effects characteristic of counter-13 conditioning (38, 39). 14

15

Mathematical modelling of fMRI data has also shown that associative learning is important in 16 17 a variety of human decision-making tasks. These studies typically identify associative learning through the footprint of 'prediction error' (40). Following the Rescorla-Wagner 18 19 model (41), most contemporary models of associative learning assume that there is a change 20 in the strength of an association between two event representations (learning occurs) when the sequel or outcome of the first event differs from the predicted outcome, i.e. when there is 21 a prediction error. Therefore, when people are engaged in decision-making, and the blood 22 23 oxygen dependent (BOLD) response in focal areas of the brain both correlates with 24 behavioural responses, and fits a prediction error model better than alternative models, this shows that the decision-making is mediated by associative learning. Using this approach, 25

brain imaging studies have demonstrated that in humans, as in other animals, associative
learning plays a fundamental role in learning about relationships between actions and their
outcomes (42); in learning higher-order relationships between outcomes (43); in incidental
encoding of relationships among stimuli (44); in updating perceptual representations (45);
and in tracking the value of social cues (i.e. advice) as well as asocial cues in decisionmaking (46).

7

8 As a focal example, illustrating the complexity of the decisions in which associative learning 9 has been implicated, consider the last of these experiments. In each trial, Behrens and 10 colleagues (46) asked people to choose between a blue and a green option to earn points that 11 would be later turned into money. At the beginning of a trial, the options were marked with 12 numbers. At certain times in the experiment, these numbers gave a very accurate guide to how many points would be received if the participant selected the option, and at other times 13 they were misleading. Later in the trial, the participant was offered some advice - to choose 14 15 blue or green - by an unseen confederate. Like the numbers, this advice was trustworthy in some phases of the experiment and untrustworthy in others. Finally, the participant made her 16 17 choice, and was told how many points she was going to get on that trial. Modelling of choice behaviour showed that people used both of the sources of information, the numbers and the 18 19 confederate's advice, in a broadly rational way. For example, the weights of the two varied 20 with the recent trustworthiness of the source, and the volatility of the environment - how rapidly the trustworthiness of each was currently changing. Of primary interest, modelling of 21 the BOLD responses in two areas of the anterior cingulate cortex suggested that the 22 23 information value assigned both to the numbers and to the confederate's advice was being computed on the basis of prediction error; that choice behaviour in this complex decision-24 making task was based on associative learning. 25

1 Brain imaging studies of this kind follow and support a substantial body of behavioural 2 experiments, initiated by Dickinson, Shanks and colleagues (47), showing that associative 3 learning contributes to human causality judgements. This on-going programme of research 4 (see (48) for a recent review), has tackled two issues that have led some researchers to doubt that associative learning is an important determinant of human behaviour. The first issue 5 relates to conscious awareness. In a widely cited paper, Brewer (49) defined conditioning as 6 7 something that occurs in the absence of contingency awareness, and, finding no evidence of 8 conditioning without contingency awareness in adult humans, declared that human behaviour 9 is not susceptible to conditioning. One response to this challenge has been to find evidence of human conditioning in the absence of awareness; for example, in studies of difficult 10 11 discriminations (50), evaluative conditioning (the transfer of affect or value from one 12 stimulus to another as a result of pairing, e.g. (51)), or in patients under anaesthesia (52). Another, more compelling response has been to question Brewer's premise: Given that so 13 little is known about the taxonomic distribution and functions of consciousness, why should 14 15 we assume that the consequences of associative learning - knowledge of a contingency between events – will never be available to conscious awareness? 16

17

The second and more substantial issue relates to the role of 'inferential' or 'propositional' 18 19 processes, rather than associative processes, in producing basic (Pavlovian and instrumental) 20 and complex (e.g. blocking, overshadowing) conditioning phenomena in human subjects (see (53), including commentaries, for a recent survey of this debate). The most important thing 21 to note about this debate is that even the most enthusiastic contemporary supporters of 22 23 associative learning would not deny that inferential processes play crucial roles in human 24 cognition. They are all subscribers to some kind of 'dual-process' theory, assuming that humans use both associative learning and inference processes to find out about the world. 25

1 Furthermore, the majority would readily agree that, at least in humans under some 2 circumstances, conditioning phenomena can be produced by inferential rather than 3 associative processes (54-60). However, along with the brain imaging data discussed above, 4 carefully designed experiments on human causality judgements have shown that, in many cases, complex human decision-making is controlled by associative learning. For example, 5 this (highly technical) literature shows that blocking occurs, not only when people have a 6 7 chance to reflect, but also in speeded, unintentional learning tasks (61); that cue-outcome 8 contingency has an impact on probability estimates even when variations in contingency do 9 not affect the objective probabilities (62, 63); and that human conditioning shows trial order effects that would not occur if it was based on reasoning about events stored in memory (56, 10 64). 11

12

This short survey of recent research with human subjects makes clear that the mechanisms of associative learning have been conserved in primates, and that they contribute, not just to basic functions – such as the development of preferences and motor skills – but to complex decision-making, and to high-level functions such as IQ, sense of agency, navigation and imitation. This evidence therefore suggests that associative learning is an important contender to explain complex behaviour in non-human primates, including the kind of prosocial behaviour reported in our case study.

20

## 21 5. But isn't this just behaviourism?

22

Association-blindness – failure to consider associative learning as a candidate explanation for
 complex behaviour – could not be due solely to scepticism of the kind addressed in the
 previous two sections; to doubts about whether ancient, taxonomically general psychological

processes contribute to animal cognition. This is made clear by a recent paper which calls for
a "bottom-up perspective on animal and human cognition" (65). This paper explicitly
advocates a research strategy in which complex cognition is explained by identifying the
conserved, taxonomically general "building blocks" from which it is constructed. But the
paper makes no mention of one of the most important and well-understood building blocks of
them all - associative learning. Why might this be?

7

8 A possible answer is suggested by the common, and typically pejorative, use of the term 9 'behaviourist' to describe associative explanations and the people who deal in them. If associative learning were merely 'behaviourist', and if behaviourism had been shown to be 10 11 false by the 'cognitive revolution' in psychology, then association-blindness would be 12 justified. We could safely assume that associative learning is a fiction, something like phlogiston, dreamed up by previous generations of scientists to explain data that can now be 13 explained in a much more rigorous and felicitous way. The trouble is that neither of the 14 15 premises of this argument is sound. Associative learning is not merely behaviourist (29), and the cognitive revolution of the 1950s and 1960s revealed that behaviourism was wildly over-16 17 ambitious, not that it was false (66).

18

Contemporary research on associative learning does retain some elements of behaviourism.
For example, it still makes use of operant chambers and other components of the technology
developed by Skinner, and it commonly assumes that the events that enter into associations
(stimuli and responses) are represented only in a 'thin' sense; by copies or traces of the
sensory stimulation they produce, rather than in a way that makes them semantically
evaluable – that can be characterised as true or false, correct or incorrect. This commitment
to thin representation, although it dates back to the "sense impressions" of the British

1 Empiricists, is reminiscent of the operationalism popular among behaviourists. However, in 2 most respects, contemporary associative learning theory is thoroughly cognitive, and has 3 been for at least 40 years. For example, rather than defining learning as a change in 4 behaviour, contemporary associative theory assumes that learning is something that happens in an animal's mind, and that changes in behaviour, rather than being constituitive of 5 6 learning, are signs that learning is taking place. In other words, associative learning theory embraces evidence of 'behaviourally silent' learning (5). Furthermore, memory is assumed 7 8 to play a crucial role in associative learning (67), and most models assume that attention is 9 both a major determinant of associative learning, and a process that can itself be modulated 10 by associative learning (68, 69). The hybrid character of research on associative learning – 11 the fact that it includes traces of behaviourism as well as solid cognitivist credentials - is 12 unsurprising when one reflects on the broad sweep of its history. Yes, the study of 13 associative learning was dominated by behaviourism from the 1920s to the 1950s, but it originated in the work of the British Empiricists some 300 years earlier; was converted into 14 15 an experimental science by Pavlov in the pre-behaviourist era; was pursued by cognitivists such as Tolman even at the height of the behaviourist period; and has been making rapid 16 17 progress throughout the 50 years since that vainglorious period ended.

18

The second premise – that behaviourism has been shown to be false – misrepresents what happened in the phase of psychology's history known as the 'cognitive revolution'(66). The term 'cognitive revolution' implies that there was a Kuhnian scientific revolution, in which the old behaviourist 'paradigm' was swept away and replaced by a new, incommensurable cognitive 'paradigm' (70). However, close examination of the events of the 1950s and 1960s reveals that the discovery of what were subsequently known as 'biological constraints on learning' (15, 71), and increasing doubts about the capacity of associative learning theory to

explain linguistic behaviour (72, 73), stimulated rational changes in the content and ambition
of associative learning theory. For example, the discovery of biological constraints
contributed to the development of attentional theories of associative learning (74), and to the
recognition that attention can vary as a function of phylogenetic as well as ontogenetic factors
(22). Similarly, the controversy about language led students of associative learning to retreat
from the more grandiose claims of behaviourism, and to accept, as had many of their
forebears (75), that associative learning can explain some, but not all, behaviour.

8

9 So, association-blindness cannot be justified on historical grounds. For a period in its past, 10 research on associative learning kept bad company – it hung out with people who wanted to 11 explain all behaviour using highly impoverished theoretical resources - but the elements it 12 has retained from that behaviourist period are not the ones that history has shown to be false. It is likely that residual association-blindness – the kind that remains even when a sceptic is 13 reminded of the evidence reviewed in sections 3 and 4 - is due, not to bad company, but to 14 15 the fact that associative learning has had a bad press, and continues to have a bad complexion. The bad press was a direct result of the misinterpretations of history discussed 16 17 in this section. Regardless of the historical facts, generations of students have been told that associative learning equals behaviourism and that behaviourism is wrong. The bad 18 19 complexion comes from the fact that, for those without specialist training, research on 20 associative learning can appear to be exclusive and forbidding. It is an area of cognitive science in which common sense or 'folk' psychology is a poor guide, and that generally 21 values rigour of method over relevance of result. Partly as a consequence of this rigour, 22 23 research on associative learning has accumulated a substantial body of formal theory, a long 24 list of robust effects, and a highly technical vocabulary. These are scientific strengths, but they do not make research on associative learning easy to assimilate. Folk psychological 25

explanations for animal behaviour – referring to what the animal 'understands' – are much
easier even for specialists to generate and comprehend, and they send non-specialists –
including journalists and professional editors of journals such as *Nature* and *Science* – a
much more appealing message. The challenge of assimilating associative learning theory is
an understandable reason, but not a good reason, for association-blindness, especially when
lucid and accessible introductions to the subject are readily available (5, 16, 76).

- 7
- 8 6. A contender, but not the default
- 9

I have argued that association-blindness cannot be justified; given what is known about the 10 11 pervasive influence of associative learning, it should be considered as a candidate explanation 12 for all new examples of intelligent behaviour in animals. Some researchers would like to go further, to argue that associative learning should be regarded, not just as a contender to 13 explain intelligent behaviour, but as the default. According to these advocates of simple-14 15 mindedness, associative learning has an inherent edge. If a pattern of behaviour can be explained with reference to associative processes and in a (yet) more cognitive -i.e. if the 16 17 data are equally consistent with an associative and a 'super-cognitive' hypothesis - we should prefer the associative account. In this section I explain briefly why I do not think this is right; 18 19 why simple-mindedness is no better than association-blindness as a substitute for carefully 20 designed experiments testing associative against super-cognitive explanations for animal behaviour. 21

22

Supporters of simple-mindedness have appealed on various occasions to MacPhail's null
hypothesis, Ockham's razor, parsimony, and Morgan's canon to justify their preference for
associative explanations. However, the principle that is clearly most relevant to contests

1	between associative and super-cognitive explanations is Morgan's canon. MacPhail's null
2	hypothesis is a potential tie-breaker when there are two candidate explanations (intellectual
3	and contextual) for a behavioural difference between species, not when there are two
4	candidate explanations (associative and super-cognitive) for a behaviour observed in a single
5	species. Ockham's razor (typically rendered as "entities must not be multiplied beyond
6	necessity"), and the principle of parsimony, encourage explanations that postulate the
7	minimum number of causal entities or free parameters. In contrast, Morgan's canon is
8	concerned with kinds (e.g. associative and super-cogntive) rather than numbers of
9	explanatory devices (77), and not with explanation in general, but with the explanation of
10	animal behaviour in particular.
11	
12	In "possibly the most important single sentence in the history of the study of animal
13	behaviour" ((78) p.9), Morgan (79) rendered his canon:
14	
15	"In no case may we interpret an action as the outcome of the exercise of a higher
16	psychical faculty, if it can be interpreted as the outcome of the exercise of one which
17	stands lower in the psychological scale." (p. 53)
18	
19	Although "psychical faculty" is an antiquated term, and Morgan was far from clear in
20	explaining what he meant by the "psychological scale", many advocates of simple-
21	mindedness have interpreted his canon as endorsing associative explanations. To see why
22	this is so, let's return to the case study presented in section 2. In that study, Horner and
23	colleagues found that, in a Prosocial Choice Test, chimpanzees selected dual-reward tokens -
24	tokens that delivered a food reward to a partner, as well as to themselves - more often than
25	they chose single-reward tokens - which delivered a food reward only to themselves - and

they interpreted this choice behaviour as evidence that chimpanzees know and care about the needs of others. In contrast, I pointed out that the chimpanzees may have chosen the dualreward tokens more often than the single-reward tokens because the former choice was followed by two instances, rather than one instance, of a sound - paper rustling - that had acquired (selfish) reward value through Pavlovian conditioning, i.e. as a result of being paired with the consumption of banana.

7

8 It is often difficult to tell exactly what a super-cognitive explanation is claiming about animal 9 minds. However, these hypotheses – the super-cognitive 'needs of others' and associative 'paper rustling' explanations – differ in at least two ways that seem to put the associative 10 11 explanation lower on Morgan's psychological scale. First, the paper rustling explanation 12 suggests that the chimpanzees' behaviour was based on associative processes, on the formation of excitatory and inhibitory links between representations, whereas the needs of 13 others explanation implies that the behaviour was based on reasoning or inferential processes, 14 15 involving the application of explicit rules to representations. Second, and relatedly, the associative account assumes that the representations supporting the focal behaviour were thin 16 17 or concrete; just sense impressions, or memory traces, of the sound of rustling paper and the taste of juicy banana. In contrast, the needs of others explanation suggests that the behaviour 18 19 was based on abstract or conceptual representations, with the structured or language-like quality necessary to support inference processes<sup>1</sup>. In *The Limits of Animal Intelligence*, 20 Morgan proposed "a threefold division [of mental activity] into instinct, intelligence, and 21 reason" (1893, p. 225), with instinct occupying the lowest rung of the ladder, intelligence 22 23 guided by associative learning in the middle, and reason at the top (80). Therefore, it seems likely that Morgan himself would have taken his canon to support the associative, paper 24

rustling interpretation of the chimpanzees' prosocial behaviour, over the super-cognitive,
 needs of others explanation.

3

But even if associative explanations in general, and the paper rustling explanation in
particular, would have received Morgan's imprimatur, there are at least three reasons to resist
the dictates of his canon. They concern history, evolution, and simplicity.

7

8 History. Historians and philosophers of science have identified errors in Morgan's work. For 9 example, Sober (81) has argued that Morgan founded his canon on the assumption that "psychical faculties" evolve by the "Method of Variation". The Method of Variation was 10 11 said by Morgan to imply a distribution of faculties across species in which "any one of the 12 faculties 1, 2, or 3, may in [species] b and c be either increased or reduced relative to its 13 development in [species] a" ((79) p. 57). Misled by his own graphical representation of this statement, Morgan took it to imply that a species could have a lower faculty without a higher 14 15 faculty, but not the reverse. If this were true, it would make possession of a lower faculty more probable than possession of a higher faculty, and therefore justify the canon. However, 16 17 as Sober pointed out, the quoted formula allows both possibilities – a higher faculty without a lower one, as well as a lower faculty without a higher one – and is therefore "too permissive 18 19 to justify the canon" ((81) p. 233).

20

Although Sober's analysis identified the most serious weakness in Morgan's thinking, further historical studies have revealed additional features that are also likely to worry contemporary students of animal behaviour (80, 82). For example, Allen-Hermanson (80) has argued that Morgan's ideas about a "psychological scale", and therefore his canon, were rooted in the idea that mental processes emerge from, or are "supervenient" on, physical processes in a

way that makes the relationship between the two fundamentally inexplicable. This kind of
view still has some currency in the philosophy of mind, where its adherents are known as
"Mysterians" (83), but it is not compatible with the reductive, mechanistic worldview that
underwrites much of contemporary biological and cognitive science.

5

Ghiselin ((84) p.362) noted that "Scientists tend to be quite vague when they invoke canons
of evidence, and often apply them mechanically, without giving much thought to the
underlying rationale". Reflecting on Morgan's veniality may help to counteract this
tendency, but it should not be enough to make us reject his canon. Perhaps the canon can be
justified, in a way that Morgan did not foresee, by appealing to evolutionary considerations or
to the virtues of simplicity.

12

*Evolution.* A number of evolutionary considerations might be thought to support Morgan's 13 canon. For example, it could be argued that associative processes are so widespread in the 14 15 animal kingdom, and so powerful in delivering behavioural adaptation across a variety of functional domains, that they are likely to screen-off selection in favour of higher or super-16 17 cognitive processes. Therefore, according to this evolvability argument, super-cognitive processes will evolve only in a narrow range of ecological conditions, where they bestow a 18 19 significant marginal benefit. Similarly, a cost argument would suggest that super-cognitive 20 processes are less likely to be present in any given species than associative processes because 21 they require larger brains, which are metabolically expensive. On a different tack, a phylogenetic argument might suggest that, if a super-cognitive process is absent in close 22 23 taxonomic relatives, it is unlikely to be present in the focal species.

24

1 As Fitzpatrick (85) has pointed out, rather than providing blanket support for the theoretical 2 conservatism of Morgan's canon, these evolutionary considerations cut both ways. Morgan's 3 canon is a general methodological principle. Therefore, to justify the canon we need reasons 4 that apply to *all* species in *all* cases, but the evolvability, cost and phylogenetic arguments only give us reasons to favour associative over super-cognitive explanations for some 5 6 behaviour in some species. In other cases they give us reason to favour super-cognitive over 7 associative explanations. If the species in question occupies an ecological niche where a 8 super-cognitive process would have a significant marginal benefit (e.g. theory of mind in an 9 especially complex social environment), or has a large brain (e.g. high encephalisation 10 quotient), or has relatives that appear to be running the super-cognitive process (e.g. humans 11 for other ape species), then the evolvability, cost and phylogenetic arguments militate in 12 favour of super-cognitive explanation and against the dictates of Morgan's canon.

13

Simplicity. The idea that explanations or theories should be simple is not without its 14 15 problems. In particular, it is no simple matter to explain why simplicity is an explanatory virtue. However, the idea is so pervasive in science and philosophy that it seems reasonable 16 17 to suppose that Morgan's canon would be justified if it could be shown to be a special case an animal behaviour-specific case - of the requirement to prefer simple explanations. 18 19 Unfortunately, attempts to do this have not been successful. The first problem harks back to 20 history: Morgan himself rejected the idea that simplicity is a proper criterion for theory choice in science, and argued that "higher" explanations, because they are more 21 anthropomorphic, are often simpler than "lower" explanations ((79), pp. 53-54). The second, 22 23 related and more general problem is that there are a great many kinds of simplicity, and, at best, Morgan's canon favours some kinds of simplicity at the cost of others (85). An 24 explanation can be simpler by virtue of being easier to generate and understand (ease of use, 25

1 the sense in which anthropomorphic explanations are simple); postulating a smaller number 2 of causal entities or free parameters (ontological parsimony), iterations of a process (iteration 3 parsimony), or evolutionary changes (phylogenetic parsimony); implying a lesser burden on limited resources (load, e.g. metabolic, memory); or by allowing similar observations to be 4 5 explained by similar processes (uniformity, e.g. allowing superficially similar behaviour to be 6 explained by the same processes across species) (85). In any particular case, an explanation 7 that is "lower" in the context of Morgan's canon, and specifically an associative explanation, 8 might score well on ontological parsimony, phylogenetic parsimony and uniformity, but 9 poorly on ease of use, iteration parsimony, and memory load. Therefore, to vindicate Morgan's canon it would be necessary to show that it consistently favours a particular kind of 10 11 explanatory simplicity, and to argue that this kind of simplicity is of overriding importance. 12 Perhaps the best candidate for this queen of simplicities is ontological parsimony. However – and this is the third problem – Sober (77) has shown using 'model selection theory' that there 13 is no reason to suppose that "lower" explanations, in Morgan's sense, are generally more 14 15 ontologically parsimonious than "higher" explanations; surprisingly, even when a "lower" explanation postulates only first-order intentionality (e.g. beliefs) and the corresponding 16 17 "higher" explanation postulates both first-order and second-order intentionality (e.g. beliefs about beliefs), the latter may have fewer free parameters. 18

19

In summary: Advocates of simple-mindedness often assume that, when behaviour can be explained by associative processes and with reference to yet more cognitive processes, the associative account should be accepted. If any general methodological principle could justify this assumption, it is likely to be Morgan's canon, but Morgan's canon is not up to the task. Morgan's own justification for the canon is flawed, and subsequent attempts to support it with evolutionary arguments and by appeal to the virtues of simplicity have identified factors

that sometimes favour associative explanations and sometimes favour super-cognitive
explanations, depending on the species, behaviour and type of simplicity under examination.
They have not revealed considerations that consistently favour associative explanations; the
kind necessary to support the use of Morgan's canon as a tie-breaker, and thereby the
treatment of associative explanations as a default.

- 6
- 7

## 7. Where should we go from here?

8

9 I have argued that neither association-blindness nor simple-mindedness is a legitimate 10 strategy when investigating animal minds. Viewed from a certain angle, these are both 11 labour-saving devices; attempts to obviate the need for (further) empirical work. If neither 12 device is fit for purpose, we have to accept that in research on animal minds, as in other areas of science, the way to find out whether process X or process Y is producing a particular set of 13 phenomena is to look for differential evidence. To find out whether behaviour is mediated by 14 15 associative or super-cognitive processes we have to design and implement studies that test the two hypotheses against one another. More specifically, the two hypotheses need to be spelled 16 17 out in sufficient detail to allow differential predictions - behavioural (or neural) effects that one would expect to see if the associative account is correct and not if the super-cognitive 18 19 account is correct, and vice versa – and these predictions need to be tested through 20 observation and experiment.

21

Unfortunately, just as there is no general principle that allows us to choose between
associative and super-cognitive explanations without empirical work, there is no general
formula telling us how to test these explanations against one another. However, the nature of
the task can be illustrated with a final look at the study by Horner and colleagues on prosocial

1 behaviour in chimpanzees (2). One way to pit the associative, paper rustling explanation of 2 this behaviour against the super-cognitive, needs of others explanation, is to test whether the 3 prosocial bias is stronger with some partners than with others. The associative account 4 assumes that the actor's bias in favour of dual-reward tokens was supported solely by the sound of paper rustling – a cue that had been paired with the actor's own banana consumption 5 - and therefore predicts that the magnitude of the bias will not vary with the relationship 6 7 between actor and partner. In contrast, it seems reasonable to assume that, if chimpanzees 8 know and care about the needs of others, they might know and care *more* about the needs of 9 genetic relatives, close affiliates and individuals who recently did them a favour, than about 10 the needs of unrelated, unfamiliar or unhelpful partners. Therefore, the super-cognitive explanation predicts that the prosocial bias will be greater in the former cases than in the 11 12 latter. In effect, this test has already been conducted. Horner and colleagues did not make any reference to associative learning in their paper, but they provided support for the 13 associative account by seeking and failing to find any effect of kinship, affiliation or 14 15 reciprocity on the magnitude of the prosocial bias.

16

However, no single test is definitive. It is possible that the measure of prosocial bias used in 17 the study by Horner and colleagues was not sensitive enough to detect subtle variations due 18 19 to the relationship between the actor and partner. Another way to test the associative account 20 against the super-cognitive explanation would be to run 'ghost control' trials in which a partner is present in the cage adjacent to the actor, and the sound of unwrapping is heard from 21 that cage, but the actor is able to see that the partner did not do the unwrapping or get the 22 23 treat. Because the associative account assumes that the actor's bias was supported solely by the sound of paper rustling, it predicts that the bias would be sustained in these ghost control 24 trials. In contrast, the super-cognitive account assumes that the sound of paper rustling was 25

significant to the actors only as an indicator that the partner was receiving food, and therefore
that her needs were being met. If this is correct, the dual-token bias should disappear in the
ghost control condition.

4

5 Whatever the outcome of this particular test, or of the current debate about cooperation in 6 chimpanzees, the moral of my tale should by now be clear. If we really want to find out 7 about animals' minds, we can afford neither to ignore associative learning, nor to assume that 8 it reigns supreme. We need experiments – and then yet more experiments – to discover when 9 Mother Nature has left the job to associative learning, and when she has devised a new super-10 cognitive gadget to support behavioural adaptation.

- 1 Footnote 1
- 2

3 Horner and colleagues did not explicitly claim that the chimpanzees in their study provided 4 evidence of inferential processes or abstract representation. However, if these claims were not implicit in their 'needs of others' explanation, it is difficult to know exactly what they 5 6 were claiming about the minds of chimpanzees, or where they took the interest of their 7 findings to lie. There is no reason to doubt that chimpanzees can represent the behaviour of 8 conspecifics in a thin, concrete way. For example, that they can form a mental image of a 9 partner making a begging gesture. However, to suggest that an animal understands the needs of others implies a much more generic or conceptual form of representation, encompassing 10 11 many instances of need - for various commodities, in various circumstances - and with the 12 power to guide behaviour via some process of thought. If this process is neither associative 13 nor inferential, the authors of the study need to tell us what it could be.

14

15

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17

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