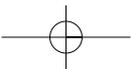
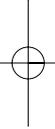
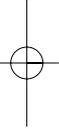
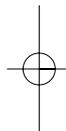
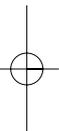
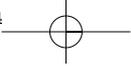


Part II

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# **Rational versus associative processes**





## Chapter 7

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# **Transitive inference in animals: Reasoning or conditioned associations?**

Colin Allen

### **Abstract**

It is widely accepted that many species of non-human animals appear to engage in transitive inference, producing appropriate responses to novel pairings of non-adjacent members of an ordered series without previous experience of these pairings. Some researchers have taken this capability as providing direct evidence that these animals reason. Others resist such declarations, favouring instead explanations in terms of associative conditioning. Associative accounts of transitive inference have been refined in application to a simple five-element learning task that is the main paradigm for laboratory investigations of the phenomenon, but it remains unclear how well those accounts generalize to more information-rich environments such as primate social hierarchies, which may contain scores of individuals. The case of transitive inference is an example of a more general dispute between proponents of associative accounts and advocates of more cognitive accounts of animal behaviour. Examination of the specific details of transitive inference suggests some lessons for the wider debate.

### **7.1 Transitive inference**

Transitive relationships are frequently important to animals, especially those living in social groups. Some of these relationships are manifest in perception: if A is larger than B, and B is larger than C, then simple inspection of A next to C will reveal that A is larger; no reasoning is required. But it is also possible to draw the inference that A is larger than C without having to see A and C side by side. Most adult humans have the capacity for such reasoning, demonstrating their understanding of the transitivity of the larger-than relationship. Other transitive relationships are not directly manifest in perception. If A is a faster runner than B and B is a faster runner than C, it will not always be able to tell just by looking at them. But once these relationships are known,

the judgement that A is a faster runner than C is an inference that can be based on the transitivity of the *faster-than* relationship.

Social dominance relationships are also typically not manifest in perception (Martin *et al.* 1997), providing a domain in which a capacity for transitive inference would seem to be very useful. If animal A dominates B, and B dominates C, there need be no common perceptual marker of this dominance, and no direct comparison of A to C will reveal the relationship between them. Being able to infer A's dominance of C in a linear dominance hierarchy could be very advantageous in an environment in which losing a struggle could result in injury, and reduced access to food and other resources, with potentially serious consequences for fitness (see, for example, Beaugrand *et al.* 1997).

Transitive relationships define orderings:  $A > B > C$ , etc. Cognitive approaches to transitive inference postulate that animals explicitly represent such orderings and use these representations to infer relationships between pairs of non-neighbouring elements (Zentall 2001).<sup>1</sup> Behaviouristically-trained psychologists favour explaining apparent transitive inferences in terms of the past reinforcement history of the individual elements without invoking any explicit representation of the entire series. This characterization of the distinction between cognitive and associative approaches to transitive inference will suffice for my present purposes; I will have more to say about the distinction below.

## 7.2 Explaining (the appearance of) transitive inference

The simplest experiment that generates the appearance of transitive inference consists of training an animal with two pairs of (arbitrarily-labelled) stimuli,  $A+B-$  and  $B+C-$ . (Here '+' means that selection of this item is rewarded and '-' means this item is not rewarded. The letters A through C are our labels for the stimuli, not the actual stimuli themselves, which may be arbitrary shapes, smells, etc.) When trained in this way using standard operant conditioning procedures, pigeons and rats presented with the novel pair AC are highly likely to select A. However, this particular result admits of a very simple associative explanation. In training, A was always rewarded and C never rewarded. Hence the preference for A over C can be explained entirely in terms of the past reinforcement history for the individual elements; the animal is simply picking the one that has been rewarded in the past.<sup>2</sup>

<sup>1</sup> Editors' note: see also Pepperberg (this volume) on transitive inference.

<sup>2</sup> Editors' note: Allen is concerned here with the character of the processes supposedly required by PP-rationality for genuine transitive inference. Compare this with Kacelnik's worry (this volume) that very little behaviour is ruled out by transitivity of revealed preference in E-rationality, given the possibility of state- or context-dependent preferences. Given behaviour that apparently expresses transitive inference, Allen is concerned with the distinction between rational or associative accounts explanations of the processes that generate such behaviour. Kacelnik's concern is rather with how such behaviour can be identified in the first place.

This result leads to a slightly more sophisticated experiment, that has become the industry standard for laboratory investigations of transitive inference in animals. In the five-element procedure, the animals are trained with four pairs of stimuli:  $A+B-$ ,  $B+C-$ ,  $C+D-$ , and  $D+E-$ . Once they have reached a certain criterion level of correct performance on these pairs, the subjects are then tested with the novel pair  $BD$ . Many kinds of animal (e.g. rats, pigeons, monkeys) tested in this way reliably select  $B$ . In the training set,  $B$  is rewarded exactly as frequently as  $D$  (on average, 50 per cent of the time—that is always when paired with  $C$  and  $E$  respectively, and never when paired with  $A$  and  $C$ ). Consequently there is no explanation of the preference for  $B$  over  $D$  simply in terms of the past history of direct reinforcement of selections of each of these individual elements. Successful transfer on this test has been taken by many to provide strong evidence for inference by animals. Hence, for example, Dusek and Eichenbaum (1997, p. 7109) write: 'An appropriate choice between the two non-adjacent and non-end elements,  $B$  and  $D$ , provides unambiguous evidence for transitive inference.'

Despite this claim, however, ambiguity between associative and cognitive accounts remains. Fersen *et al.* (1991) had already suggested that differential conditioning effects could account for the selection of  $B$  over  $D$  through a mechanism of 'value transfer'. According to the theory of value transfer, in any simultaneous discrimination task, some of the value associated with the  $S+$  is transferred to the accompanying  $S-$ . According to the value transfer theory, in the  $A+B-$ ,  $B+C-$ ,  $C+D-$ ,  $D+E-$  training set, even though both  $B$  and  $D$  are individually rewarded at the same rate,  $B$  is seen in association with  $A$ , which is always a winner. This is hypothesized to give  $B$  a positive boost in comparison to  $D$ .

A test of positive transfer theory is described by Zentall (2001; see also Zentall and Sherburne 1994). Pigeons were trained on just two pairs:  $AB$  and  $CD$ .  $B$  and  $D$  were never rewarded when selected. Selection of  $A$  was rewarded on 100 per cent of the occasions it was selected (represented by  $A100B0$ ), whereas selection of  $C$  was rewarded on just 50 per cent of the occasions it was selected (represented by  $C50D0$ ). Once the pigeons had reached a criterion level of performance—reliably selecting  $A$  over  $B$  and  $C$  over  $D$ —they were tested with the novel pair  $BD$ . The training set does not justify a transitive inference, but pigeons trained in this fashion nevertheless tend to select  $B$  over  $D$ , hence confirming the value transfer hypothesis that  $B$  gains simply by being paired with the reliably rewarded  $A$ .

Despite these results, Zentall (2001) does not entirely discount the possibility that a cognitive explanation of the pigeons' behaviour might be correct. At the very least, he accepts the utility of a cognitive perspective as a heuristic for devising novel experiments, with the ultimate goal of constructing better associative models. Describing ongoing work that might support an account in terms of explicit representation of the  $ABCDE$  series, he writes, 'Whether this line of research will provide evidence in support of a cognitive account is less important than the fact that the investigation of the transitive inference effect led to a series of experiments that clarified the interaction

between the S+ and S− in a simultaneous discrimination.’ In a similar vein, DeLillo *et al.* (2001) show that the BD generalization is modelled by a standard associative learning mechanism: backward error propagation in an artificial neural network (Rumelhart and McClelland 1986). DeLillo and colleagues conclude that ‘a simple error-correcting rule can generate transitive behaviour similar to the choice pattern of children and animals in the binary form of the five-term series task without requiring high-order logical or paralogical abilities.’ The implication here is that the burden of proof lies with those who would argue that animals are engaged in reasoning with an explicitly represented ordering.

In defence of animal reasoning, McGonigle and Chalmers (1992) exclaim in their title ‘Monkeys are rational!’ This follows up an earlier paper that, in its title, asked ‘Are monkeys logical?’ (McGonigle and Chalmers 1977). Building on the standard five-element test, McGonigle and Chalmers don’t base their case solely on BD generalization, but also on various effects of series position on performance, such as end anchoring, where performance is better on comparisons where the pair includes an item from the start or finish of the series, and the symbolic distance effect (SDE), where increased separation in the series between the pair of elements tested leads to degraded performance. To tease apart different components of the SDE, McGonigle and Chalmers (1992) also used a triadic version of the five-element task. In this variant, animals were trained with triples of stimuli—AAB, ABB, BBC, BCC, CCD, CDD, DDE, DEE—and tested with BCD. Monkeys do generalize a correct response to the novel BCD stimulus, but curiously, their performance is somewhat worse on this task than in generalizing to BD in the standard five-element task, despite the explicit presence of C between B and D. McGonigle and Chalmers (1992, p. 224) conclude that ‘the SDE has been over-interpreted as a ranking phenomenon’. Nevertheless, they write of their monkeys that ‘some sort of explicit seriation ability may be within their scope’.

De Lillo *et al.* undermine the significance of arguments based on serial-positioning effects by claiming that their artificial neural network model displays SDE, end-anchor, and other effects reported in the literature on transitive inference on animals and children. They concede that certain features of adult human learning are not captured by their model—for instance the fact that young children do equally well whether the training pairs are presented randomly or in serial order, whereas adult performance is seriously degraded by random presentation (De Boysson-Bardies and O’Regan 1973). Referring to the work by McGonigle and Chalmers, De Lillo *et al.* also admit that they know of no ‘connectionist implementations of the task robust enough to deal with both binary and triadic versions’ (p. 67). In their final remarks, they take the proven capacity of a simple, randomized neural network to perform the basic BD generalization task to suggest that ‘the binary, non-verbal, five-term-series task might not be suitable for detecting ontogenetic or phylogenetic trends in the development of the cognitive skills underlying inferential abilities. In order to find behavioural differences of potential comparative significance, it might prove a more fruitful exercise

to manipulate the training procedures . . . and the structure of the task itself (such as the triadic testing introduced by McGonigle and Chalmers 1977, 1992), instead of extending the same binary version of the paradigm to yet more non-human species or younger children.' (p. 68).

A muffled 'Hurrah!' might be heard at this point coming from ethologists who have never been particularly impressed with the weight that comparative psychologists have placed on the five-element task. Muffled, because replacing one simplistic paradigm with another would be only limited progress and the DiLillo recommendation might not seem to go far enough in overthrowing the grip that simplistic lab experiments have on thinking about the mechanisms underlying animal behaviour.

Although not directly targeting the work I have described above, Seyfarth and Cheney (2002) offer a naturalist's critique of those who would extend the results of similar associative learning experiments to explaining the capacities of animals living in complex natural societies. They point out that social dominance hierarchies can be quite large—a typical troop of baboons might consist of '80 or more individuals drawn from eight or nine matrilineal families arranged in a linear dominance rank order' (p. 379). In the five-element paradigm, the number of possible pairs (treating AB the same as BA, etc.) is ten. The five-element task artificially limits the number of pairs actually encountered during training to four, whereas baboons living in an 80-member troop may confront any of the 3160 different possible dyads. Furthermore, because of alliances where two animals may combine forces against another, dominance interactions may often take place among triads, of which there are 82 160 possible combinations (Seyfarth and Cheney 2002; see also Connor, this volume, who conveys the further complexity introduced by second-order alliances among bottlenose dolphins). Also, dominance hierarchies have to be rapidly relearned whenever there is a reversal in dominance. (For a description of this phenomenon in coyotes, see Bekoff 1977.) Whereas pigeons may take months to learn just four dyads, monkeys rapidly learn a much bigger hierarchy and flexibly adjust to changes in the hierarchy.

The laborious way in which lab animals learn the key associations in the five-element task could be due to the lack of any natural ordering among the stimuli. Typical visual stimuli used with pigeons include, for example, square symbols distinguished by arbitrary shading patterns in black and white. Unlike dominance hierarchies, the experimenter-imposed ordering on these stimuli has no intrinsic biological significance to the animals, nor any connection to any naturally transitive relationship. In this way, they are like the conventional ordering of the letters of the alphabet, which must be laboriously learned by young children; imagine trying to teach the alphabet by giving the elements only in adjacent pairs, possibly randomized: WX, DE, JK, BC, etc. (and definitely no singing!).

These issues become extremely significant when trying to think of ways in which one might like to extend the existing experiments. For instance, to address the positive transfer hypothesis put forward by Fersen and tested by Zentall, an obvious suggestion

is to train the animal on the pairs that define a seven-element series, ABCDEFG and then test on the middle span CE. Because the nearest neighbours of C and E have equivalent reinforcement histories, successful generalization of the correct response to CE could not be accounted for by the positive transfer theory (although there could be a secondary transfer theory that accorded positive transfer to C on the basis of its association with B, which gets direct positive transfer from A; this move can of course be iterated to the point of implausibility, although the location of that point might be the subject of considerable differences among commentators depending on their commitment to the hegemony of associationist principles). Some psychologists with whom I have discussed the seven-element experiment have remarked only somewhat facetiously that the experiment might well be impracticable with pigeons as one could approach the pigeon's life span in trying to train it to reach criterion performance on all six pairs simultaneously. But Bond *et al.* (2003) have recently trained five representatives each of two different corvid species, pinyon jays and the less intensely social scrub jays, on the seven-element task. Although the pinyon jays reached criterion performance levels much more quickly than scrub jays, a three-stage training process involving hundreds of exposures to the training set was required for members of both species to reach the criterion level of performance.

Lest it be thought that these relatively slow learning rates reflect some sort of inherent limitation of the avian brain with respect to transitive inferences, it is worth pointing out that Beaugrand *et al.* (1997) demonstrate the occurrence in domestic chickens of rapid observational learning of dominance relations, apparently involving a transitive inference, as the result of watching a single aggressive interaction between a familiar dominant and an unfamiliar conspecific. When the stranger dominates the familiar dominant, observers never initiate an attack on the unfamiliar animal, and submit immediately if attacked. But when the familiar dominant is observed to defeat the stranger, observers are much more likely to attack and defeat the stranger than in circumstances where no information is available about the stranger.

The relatively slow learning rate in the standard operant conditioning paradigm may, then, have much to do with the nature of the task. In the original Piagetian version of the five-element paradigm, designed to test transitive inference in young human children, arbitrary symbols or colours are paired with different length rods. During training and testing the length of the rods is obscured and the children are rewarded for choosing the longer rod from pairs that are distinguishable only by the associated symbol or colour. Unlike the typical task that pigeons are confronted with, here the arbitrary relationship among the visual cues is mapped onto a naturally transitive relationship in the length of the rods. It is quite possible, then, that the arbitrary markers acquire significance as proxies for the properties (specific lengths) underlying the transitive ordering. I am unaware of any similar attempts to pair stimuli with real transitive relationships within a traditional, behaviouristic animal learning paradigm.

### 7.3 Reasoning or conditioned associations?

It appears to be a shared presupposition among many comparative psychologists and cognitive ethologists that behaviourism and cognitivism are exclusive alternatives. This is echoed by Dennett's (1983) early suggestion that behaviourism is the null hypothesis against which cognitive accounts are tested. But is this a correct representation of the dialectical situation? Why should the availability of an associative model trump the adequacy of a serial-representation model? Are associationist explanations *always* to be preferred? A certain Cartesian residue might be detected here: if we have an associative 'mechanism' we can avoid attributing (unsubstantiated) rational thought. That residue seems apparent when Clayton *et al.* (Ch. 9, this volume) write: 'the issue of whether an animal is psychologically rational turns on the nature of the processes causing its behaviour; specifically on whether this behaviour is caused by psychological mechanisms or by intentional processes.' In these days of computers, we know perfectly well how to build mechanisms to represent arbitrary sequences of elements, so characterization of a mechanist/mentalist dichotomy does not apply to the current debate about transitive inference. I agree with Papineau and Heyes (Ch. 8, this volume) that contemporary psychology is premised on materialism. This means that rational (or intentional, or cognitive) processes, whether in humans or other animals, have to supervene on psychological mechanisms. (For reasons I'll explain shortly, we can embrace the slippage between 'cognitive', 'rational', and 'intentional' that is present in other contributions to this volume.)

The question, then, is whether anything worthwhile can be made of the distinction between different kinds of psychological process or mechanism. Heyes and Papineau rightly ask this question about the distinction between 'associative' and 'rational', and, after critiquing two suggestions for making the distinction in very general terms, they declare themselves sceptical about its utility. Earlier in this paper I adopted a rough and ready distinction between associative and cognitive explanations of transitive inference. Cognitive approaches to transitive inference, I wrote, postulate that animals explicitly represent such orderings and use these representations to infer relationships between pairs of non-neighbouring elements. This did not, and was not intended to, supply a general account of the distinction between cognitive and associative mechanisms; instead it merely reflected the categories employed by the psychologists themselves (especially Zentall) who draw distinctions between putative explanations of the behavioural phenomena.

We can certainly 'put on our philosophical hats' and ask whether the distinction between 'associative' and 'cognitive' is generally defensible. But, in my view, the resulting discussion is likely to be too abstract to be instructive. Cognitive approaches to a variety of psychological phenomena are likely to bear family resemblances rather than being analytically definable. Elements of reasoning (hence rationality) and meaning or semantic content (hence intentionality) appear in specific cognitive explanations (hence the

acceptable slippage among these terms) but it would be a mistake to say that cognitive approaches stand or fall with the practical syllogism or a commitment to unlimited inferential power. Even if a generalized distinction between cognitive (or rational, or intentional) and associative mechanisms is not tenable, it is nevertheless the case that the distinction between the different kinds of explanation of transitive inference is specifically defensible. Cognitive approaches to transitive inference appeal to a retrievable unified representation of an entire ordered series which functions as a template for specific inferences about the relative ordering of arbitrary pairs of elements drawn from the series. Whatever efficiencies might be provided by such representations (Cheney and Seyfarth, for example, suggest that cognitive accounts but not standard associative accounts can deal adequately with the fact that individuals may be simultaneously classified in multiple ways), a cognitive mechanism that exploits such a representation of the series might, nevertheless, be quite limited. It may not have a completely general transitive inference capability for its ability to store sequences will almost certainly be limited by length of the series, and may also be limited in the content domains to which it can be applied. But this does not detract from the fact that, from an engineering/programming perspective, the distinction is clear enough between, on the one hand, how one would go about building the kind of system that builds and uses a unified representation of a transitively governed series and, on the other hand, how one would build a system that is limited to associating stimuli with actions to various degrees of strength.

DeLillo *et al.* (2001) demonstrate that the latter approach is capable of something akin to transitive inference. Their model has limitations, but associative mechanisms are clearly a very important part of the psychological make up of all animals, including humans. So it is not a stretch to imagine that associative mechanisms play a role in many behaviours that appear to conform to norms of transitive inference. Rather than this excluding a role for cognitive mechanisms, it is quite possible that multiple mechanisms may coexist in a single organism. Indeed there is direct evidence from Dusek and Eichenbaum (1997) that the training used in the standard five-element transitive inference paradigm engages two different systems in rats. Comparing rats with hippocampal lesions to controls, Dusek and Eichenbaum found that lesioned rats retained the ability to learn pairwise discriminations between (olfactory) stimuli, but were impaired in their ability to make some of the transitive generalizations about these pairs made by intact rats, including the BD generalization. Given the importance of the hippocampus for declarative memory, Dusek and Eichenbaum suggest that it plays a role in 'representation of orderly relations among stimulus items' (p. 7113). (See also Wu and Levy 1998, for a computational model of transitive inference inspired by the hippocampus.)

Given the existence of parallel systems, it is also likely that these would be engaged somewhat differently depending on the context of learning. In the standard five-element task there is nothing in the stimuli or the training situation to suggest that the elements belong to a transitive ordering (the experimenter could, after all, follow

the three pairs  $A+B-$ ,  $B+C-$ ,  $C+D-$  with the transitivity destroying  $D+A-$ ). The animals in the experimental situation must discover an arbitrary transitive ordering of the stimuli in a situation where they would not be primed to expect such an ordering. In more natural contexts, where the cues to be learned are markers of real transitive relationships, it would be unsurprising to discover that learning of the series is facilitated by priming of the relevant brain areas. Nonetheless, if Dusek and Eichenbaum are correct, the five-element paradigm does lead eventually to explicit serial representation in the hippocampus, albeit through a more laborious process than might be triggered by more natural contexts.

### 7.4 Reflections on animal cognition

'Animal cognition' is nowadays a term embraced by scientists with a variety of methodological backgrounds, but it is clear that many of the old methodological divisions remain. Many laboratory-based psychologists are sceptical of the claims that field-based ethologists make about the cognitive abilities of their research subjects. Conversely, many ethologists remain deeply sceptical about the significance of results derived from laboratory studies of animal learning. The debate on transitive inference provides a microcosm of this dispute. From the behaviourists' perspective, the reinforcement history of animals studied under field conditions cannot be known in sufficient detail to permit reliable inferences about the animals' cognitive abilities. The ethologist doesn't know what experiences have shaped the behaviour of the 80 or so baboons in a troop. From the naturalists' perspective, laboratory studies are insufficiently rich to provide reliable knowledge of the mechanisms underlying the cognitive capacities of animals in the field. The comparative psychologist doesn't know how to train a rat or a pigeon to produce (or appear to produce) transitive inferences about an 80-element series. How to bridge this methodological divide is, in my view, one of the most important outstanding problems blocking the development of a unified scientific approach to animal cognition. Even though I have doubts about the abstract distinctions they draw, the empirical contribution of Clayton and her colleagues in this volume is important because it brings laboratory methods to bear on cognitive questions involving genuinely naturalistic problems.

Turning to neuroscience, it is appropriate to think (as Konrad Lorenz did) that it has an integral part to play in the development of a complete science of animal behaviour. The work of Dusek and Eichenbaum described above provides intriguing insights. But neuroscientists, being lab scientists, have so far tended to adopt the learning paradigms of comparative psychology, with scant regard for ecological validity (see also Chemero and Heyser 2003). Neuroscientists, after all, typically want to get home in time for the 6 o'clock news (or perhaps the 9 o'clock news if they are particularly driven). Not for them the rigours of 6 months in the bush following monkeys from tree to tree. Perhaps one day it will be possible to study the brain functions of animals non-invasively

and in real time under field conditions, and at that point we can match complex social behaviours to events in the nervous system. But we should probably not hold our breath waiting for that moment, which depends on the rate of technological progress exceeding the rate of habitat loss.

Lorenz imagined a grand synthesis of functional, evolutionary, developmental, and neurological approaches to animal behaviour (Lorenz 1981). Such a synthesis has not yet been achieved, and it remains questionable whether it ever will be so long as lab and field scientists keep attacking each other on methodological grounds rather than finding ways to work on common problems. If the answer to the question ‘Transitive inference in animals: reasoning or conditioned associations?’ is perhaps ‘Both’, then we should be asking how to study these processes in all the contexts in which animals naturally employ them using a variety of approaches. But the hope for a fully synthetic approach to animal behaviour may be forlorn given the cultural divide that exists between behaviouristic psychologists and neuroscientists on the one hand, and ethologists on the other. This divide goes much deeper than the methodological problems indicated so far. It extends to issues about the proper treatment of animals for scientific purposes—to whether keeping animals in cages or cutting into their brains is an acceptable corollary of our desire to understand how real animals think, reason, and act.

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## References

- Beaugrand, J. P., Hogue, M. E., and Lagüe, P. C. (1997). Utilisation cohérente de l’information obtenue par des poules domestiques assistant à la défaite de leur dominante contre une étrangère: s’agit-il d’inference transitive? *Processus cognitifs et ajustement écologique*, pp. 131–137. Société Française pour l’Étude du Comportement Animal, Toulouse: Presses de l’Université Paul Sabatier.
- Bekoff, M. (1977). Quantitative studies of three areas of classical ethology: social dominance, behavioral taxonomy, and behavioral variability. In: B. A. Hazlett, ed. *Quantitative Methods in the Study of Animal Behavior*, pp. 1–46. New York: Academic Press.
- Bond, A. B., Kamil, A. C., and Balda, R. P. (2003). Social complexity and transitive inference in corvids. *Animal Behaviour*, **65**: 479–487.
- Chemero, A., and Heyser, C. (2003). *What mice can do: affordances in neuroscience*. Presented at Society for Philosophy and Psychology, Pasadena, CA.
- De Boysson-Bardies, B., and O’Regan, K. (1973). What children do in spite of adults. *Nature*, **246**: 531–534.
- De Lillo, C., Floreano, D., and Antinucci, F. (2001). Transitive choices by a simple, fully connected, backpropagation neural network: implications for the comparative study of transitive inference. *Animal Cognition*, **4**: 61–68.

- Dennett, D. C. (1983). Intentional systems in cognitive ethology: The 'Panglossian paradigm' defended. *Behavioral and Brain Sciences*, **6**: 343–390.
- Dusek, A., and Eichenbaum, H. (1997). The hippocampus and memory for orderly stimulus relations. *Proceedings of the National Academy of the Sciences USA*, **94**: 7109–7114.
- Fersen, L. von, Wynne, C. D. L., Delius, J. D., and Staddon, J. E. R. (1991). Transitive inference formation in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, **17**: 334–341.
- Lorenz, K. (1981). *The Foundations of Ethology*. New York: Springer-Verlag.
- McGonigle, B., and Chalmers, M. (1977). Are monkeys logical? *Nature*, **267**: 694–696.
- McGonigle, B., and Chalmers, M. (1992). Monkeys are rational! *Quarterly Journal of Experimental Psychology*, **45B**: 198–228.
- Martin, F., Beaugrand, J. P., and Lagüe, P. C. (1997). The role of hen's weight and recent experience on dyadic conflict outcome. *Behavioural Processes*, **41**: 139–150.
- Rumelhart, D. E., and McClelland, J. L. (1986). *Parallel Distributed Processing*. Cambridge, MA: MIT Press.
- Seyfarth, R. M., and Cheney, D. L. (2002). The structure of social knowledge in monkeys. In: M. Bekoff, C. Allen, and G. M. Burghardt, eds. *The Cognitive Animal: Empirical and Theoretical Perspectives on Animal Cognition*, pp. 379–384. Cambridge, MA: MIT Press.
- Wu, X., and Levy, W. B. (1998). A hippocampal-like neural network solves the transitive inference problem. In: J. M. Bower, ed. *Computational Neuroscience: Trends in Research*, pp. 567–572. New York: Plenum Press.
- Zentall, T. R. (2001). The case for a cognitive approach to animal learning and behavior. *Behavioural Processes*, **54**: 65–78.
- Zentall, T. R., and Sherburne, L. M. (1994). Transfer of value from S+ to S- in a simultaneous discrimination. *Journal of Experimental Psychology: Animal Behavior Processes*, **20**: 176–183.

