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April 19, 2011

Cognitive Mechanisms for Transitivity in Rhesus Monkeys (*Macaca mulatta*)

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Abstract

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By Nicholas W. Chee

Knowing that Ben is taller than Emily and Emily is taller than Dina, one can infer that Ben is taller than Dina. This is called transitive inference (TI). In TI experiments, subjects are trained with adjacent overlapping pairs of discriminations that create an implicit order (e.g. if $A+B-$ and $B+C-$ then $A+C-$). TI is evaluated with never-before-seen non-adjacent pairs of stimuli from the implicit order (e.g. AC). Often subjects select the higher ranked item, suggesting logical inference. However, because nonhuman subjects are reinforced with food during training, individual stimuli may acquire associative values consistent with the implicit order that control choice behavior in a way that mimics inference. We assessed the contribution of logical inference and associative strength to performance of rhesus monkeys on a TI test. We manipulated associative values in a within-subjects experimental design by rewarding some choices with 2 food pellets and others with 1 pellet. This manipulation was presented in two conditions: in the congruent condition, associative values were consistent with the implicit order (e.g. A was rewarded with two pellets, D was rewarded with one); in the incongruent condition, associative values conflicted with the order of the implicit order (e.g. D was rewarded with two pellets, A with one). We found that when differences in reinforcement are salient, associative values exert significant control over choice behavior.

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Cognitive Mechanisms for Transitivity in Rhesus Monkeys (*Macaca mulatta*)

Given that Ben is taller than Emily, and Emily is taller than Dina, one can logically infer that Ben is taller than Dina. To link overlapping relations in this way is called transitive inference (TI). In traditional TI studies, subjects are trained on overlapping adjacent pairs of stimulus discriminations ($A+B-$, $B+C-$, $C+D-$, $D+E-$, $E+F-$, $F+G-$; Figure 1; Vasconcelos, 2008). To test for inference, subjects are presented with never-before-seen pairs of non-adjacent stimuli (e.g. BD , CE , and DF ; Figure 1) and show TI if they select the item higher in the inferred order ($A > B > C > D > E > F > G$). Many nonhuman species, including rodents (DeVito, Kanter, & Eichenbaum, 2010; Dusek & Eichenbaum, 1997), birds (Bond, Kamil, & Balda, 2003; Bond, Wei, & Kamil, 2010; Hogue, Beaugrand, & Lague, 1996; Lazareva, Smirnova, Raevskii, & Zorina, 2000; Lazareva, Smirnova, Zorina, & Rayevsky, 2001; Lazareva & Wasserman, 2006; Paz-y-Mino, Bond, Kamil, & Balda, 2004; Vonfersen, Wynne, Delius, & Staddon, 1991; Weiss, Kehmeier, & Schloegl, 2010; Wynne, 1997), and monkeys (Bryson & Leong, 2007; Maclean, Merritt, & Brannon, 2008; Merritt & Terrace, 2011; Treichler, Raghanti, & Van Tilburg, 2003, 2007; Treichler & Van Tilburg, 1996, 2002) successfully select the correct items on these test trials, which suggests that they are able to use inference to determine relations between stimuli (e.g. Lazareva & Wasserman, 2006).

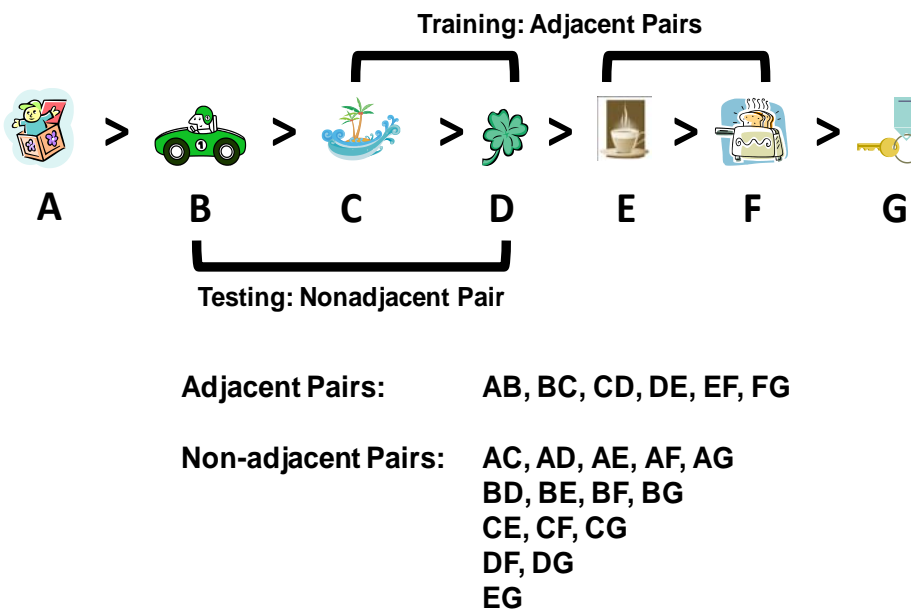


Figure 1. Example of Training and Testing Pairs of Stimuli. This figure illustrates what pairs of stimuli are used in training and testing in TI experiments.

In addition to above chance performance on test pairs, subjects regularly show the Symbolic Distance Effect (SDE) on TI tasks. The SDE is the observation that as the distance between items in a test pair increases, accuracy on test trials increases and response latency decreases (Figure 2B). In other words, inference becomes easier the further apart test items are in the implicit order. Occurrence of SDE may suggest that the training stimuli are mentally represented in a linear order, which may underlie performance on test pairs.

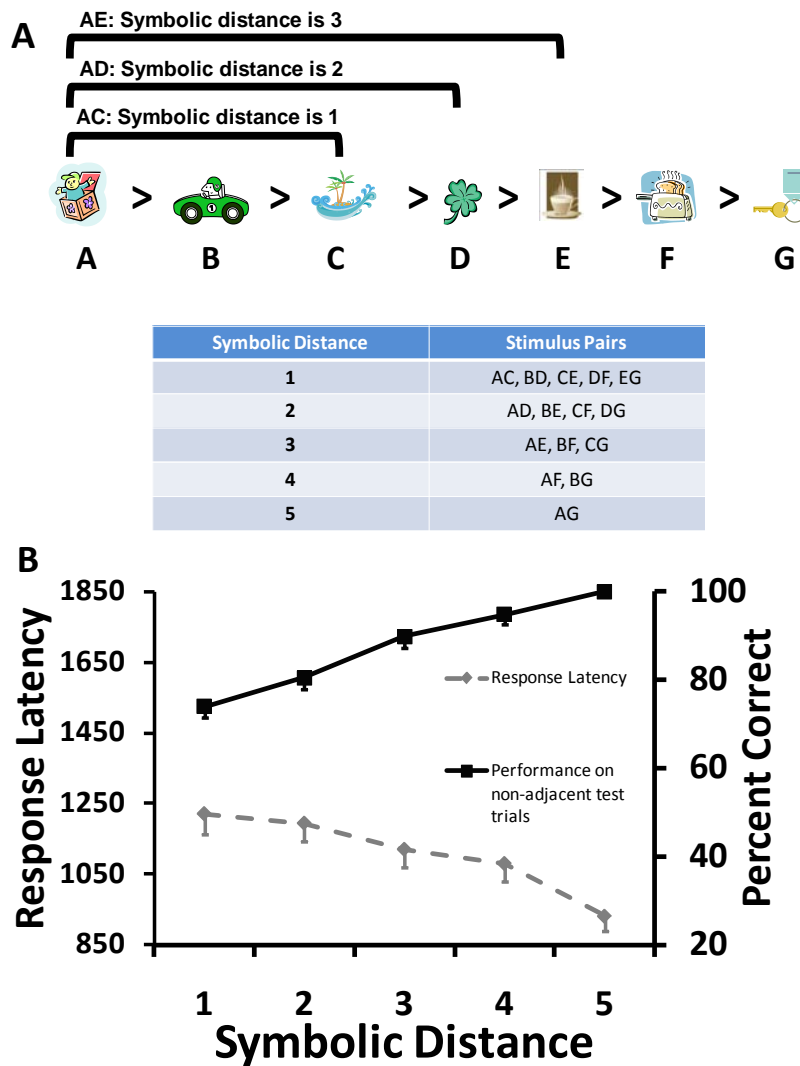


Figure 2. Symbolic Distance Effect. *A* illustrates how symbolic distance is determined and what pairs of stimuli correspond to specific symbolic distances. *B* illustrates the Symbolic Distance Effect (SDE) in terms of performance and response latency (Data from a standard TI task data with the subjects used in this experiment; Paxton and Hampton, in prep.)

In laboratory TI studies in nonhumans, premise discriminations are trained using food reinforcement, such that in pair *AB*, selection of *A* is reinforced with food while *B* is not. In pair *BC*, *B* is reinforced but *C* is not. This pattern continues through all training pairs (Vasconcelos, 2008). Before this training, all stimuli are presumably equivalently associated with food reward; but as training progresses, stimuli are reinforced and not reinforced based on the subjects' performance and can therefore acquire different associative values (AV). If these values

correspond with the implicit order of the stimuli, then subjects could show a pattern of performance consistent with TI simply by selecting the item with the higher reward value. For instance, in a set of ordered stimuli (e.g. Figure 1) if stimulus *B* has a higher associative value than stimulus *D*, subjects could choose *B* over *D* on test trials without the need for inference. Thus, although performance on TI tasks often looks like inference, it is possible that associative values control the choice behavior of subjects.

Recent studies have shown that social animals including fish, chickens, and birds can perform TI with social dominance relations, in which there is no explicit food reinforcement (Grosenick, Clement, & Fernald, 2007; Hogue, et al., 1996; Paz-y-Mino, et al., 2004). Because there is no food reward in these tasks, these data cannot be explained by AVs. These findings suggest that some animals can order stimuli using inference.

Additional evidence that performance in TI tests cannot be fully accounted for by AVs comes from studies on list linking (Paxton & Hampton, in prep; Treichler & Van Tilburg, 1996). Monkeys learned two separate lists and then were trained that the lowest ranking stimulus of one list ($A > B > C > D > E > F > G$) was ranked above the highest ranking stimulus of another list ($H > I > J > K > L > M > N$) through presentation the linking pair *GH* only. Afterwards, monkeys were presented with test pairs using images that spanned the two lists (e.g. *BK*, *DM*). Because the two lists were learned separately, the stimuli occupying the same relative list positions in the two lists would have roughly equivalent associative values (e.g. item *B* in the first list should have an equal associative value to *I* in the second list). Subjects who use associative values would not perform above chance when presented with cross-list pairs of images where the correct item held a lower place in its list than the incorrect item held in its list (e.g. *E* paired with *I*). However, monkeys performed above chance on these between list trials

and showed a SDE that spanned all twelve symbolic distances, suggesting that they may have used inference to link the two lists into one large list.

Advocates of associative value models contend that responses on transitive inference tasks result from the associative values of stimuli that accrue as a result of reinforcement during training (Lazareva & Wasserman, 2010). There have been many different models proposed to explain how associative values might be acquired and in turn could mimic the pattern of performance that would result from inference. The Rescorla-Wagner model stipulates that the resulting value of a stimulus can increase or decrease every time it is presented in a stimulus comparison (Rescorla, 1972). Wynne's configural model (Wynne, 1995) is very similar to the Rescorla-Wagner Model (Vasconcelos, 2008) but stipulates that stimuli are treated differently depending on which other stimuli are presented with them. In turn, every stimulus has a portion of its value that can vary depending on context. There is also Value Transfer Theory, which stipulates not only do associative values result in part from individual reinforcement history (similar to the Rescorla-Wagner Model) but they also depend on the "transfer" of values from adjacent stimuli (e.g. *A* has a high value, which partially transfers to *B* during their co-presentation, and increases *B*'s associative value (Vonfersen, et al., 1991)).

Each of these models has free parameters such that values of the individual stimuli can be changed to fit the data, giving them the flexibility to fit most performance patterns. Therefore, in general, these models can predict performance on standard TI test trials. Successful models should also be able to predict the SDE. Although the Value Transfer theory does not always predict this effect, the configural and Rescorla-Wagner models are able to reasonably predict the SDE and are therefore reasonable models to explain TI performance (Wynne, 1995). However,

there are instances where they fail to predict TI tasks performance, such as in list linking studies and TI experiments that manipulate or eliminate food reinforcers.

Lazereva and Wasserman (2004; 2006) purposefully manipulated the reinforcement histories of stimuli to go against the order of the stimuli in an effort to put associative and inference mechanisms at odds with one another. In their experiments, they trained 5 overlapping pairs of stimuli (i.e. $A+ B-$, $B+ C-$, $C+ D-$, $D+ E-$); then presented the well known $D+ E-$ pairing by itself for many trials, in an effort to increase the associative value of stimulus D . Because subjects correctly choose D so often on these trials, they argue that D 's associative value would increase. According to associative value models, stimulus D would therefore be more likely to be chosen when presented with stimulus B , even though that would be "incorrect." Instead, pigeons and crows correctly chose stimulus B in these trials, suggesting that current associative models cannot entirely predict TI behavior. However, the manipulations of reinforcement in this experiment were subtle. In fact, it is not certain that further training the DE pair, after it was already at asymptote, would increase the associative value of D . It is also possible that the model calculated associative values as a function of reinforcement history differently from how the values actually accrued in test subjects. Therefore, experiments that directly and dramatically alter associative values are needed to fully address the contribution of associative mechanisms to TI performance.

With this study, we attempted to assess the contribution of two possible cognitive mechanisms for TI performance: associative value and logical inference. We explicitly manipulated the associative values of stimuli by rewarding performance with some premise pairs with two food pellets and performance with other premise pairs with just one food pellet. Rhesus monkeys learned six overlapping premise pairs comprising an implicit ordering of 7 stimuli on a

touch-screen computer apparatus. We employed two distinct reinforcement schemes during this training (Figure 3). In the first condition, the associative values of the stimuli were *congruent* with the implicit order. Premise pairs including images *A*, *B*, and *C* were rewarded with 2 pellets; those including *D*, *E*, and *F* with 1 pellet. As a result, the associative value of *B* should be greater than that for *D*, for example. In the other reinforcement scheme, the associative values of some stimuli were *incongruent* with the implicit order. Premise pairs including *A*, *B*, and *C* stimuli were rewarded with 1 pellet; those including *D*, *E*, and *F* with 2 pellets. As a result, the associative value of *D* should be greater than that for *B*. We hypothesized that if monkeys used logical inference exclusively, performance on the non-adjacent test trials would not differ between the congruent and incongruent conditions. However, if associative values control choice in the non-adjacent test trials, we expect subjects to perform poorly in the *incongruent* condition but very well in the *congruent* condition.

Methods

Subjects

Subjects used in this experiment were ten male rhesus monkeys at the Yerkes National Primate Research Center in Atlanta, Georgia. All but two subjects were pair-housed and all were given a daily allowance of monkey chow and fruit and ad libitum access to water. All subjects had previous experience on computerized cognitive tasks, including transitive inference tasks. All procedures were approved by the Institutional Animal Care and use Committee of Emory University (protocol number 042-2008Y) and were in compliance with National Institutes of Health guidelines for the care and use of laboratory animals.

Apparatus and Stimuli

Subjects performed tests on touch-screen displays that were attached to their home cages for seven hours per day, 6 days per week. Attached to each structure encompassing a touch-screen was a laptop with built-in speakers and two food reward dispensers. The laptop was connected to the touch-screen that presented stimuli using Presentation® software. Below the display were two compartments where food rewards were dispensed.

Two sets of stimuli consisting of seven 350 X 350 pixel clip art images were used, one set in the *congruent* condition and one in the *incongruent* condition. The images were randomly assigned to locations in an order (i.e. images *A*, *B*, *C*, *D*, *E*, *F*, and *G* in Figure 1) and image sets were counterbalanced across conditions.

Procedure

Presentations of pairs of stimuli appeared on the left and right touch-screen displays. The appearance of stimuli on the left or right sides of the screen were counterbalanced. On 80% of training trials, correct responses in these comparisons resulted in a positive auditory reward

paired with a food reward of flavored nutritionally complete pellets; on the other 20% of correct trials, subjects received just a positive auditory reinforcer. All incorrect responses resulted in a negative sound and a time out of 5 seconds before the next trial. Intermittent reinforcement was equally distributed across all the premise pair training.

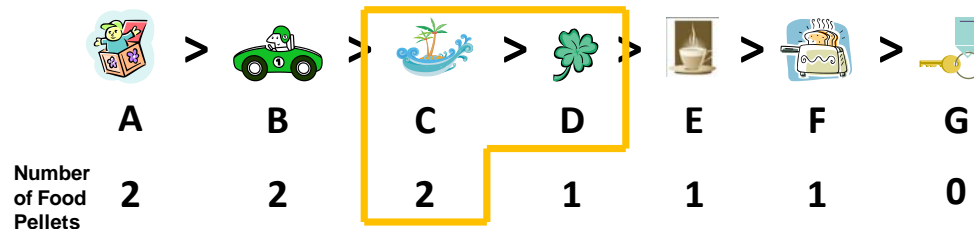
Premise pair training

Subjects trained with adjacent pairs of images only (i.e. *AB*, *BC*, *CD*, etc), where choice of the higher ranking item in each pair was rewarded. Training began with learning the pair lowest in the order (*FG*) and ended with learning the pair highest in the order (*AB*). As subjects learned each pair to a criterion of 80 percent, they moved on to the next phase of training. For example, monkeys were first trained on the *FG* pair and achieved 80 percent correct (21 of 26 trials). The next pair (*EF*) was then learned to criterion. Subjects were then presented *EF* and *FG* intermixed in each session until they reached criterion of 80 percent correct for both pairs. Then pair *DE* was introduced. This training scheme (consisting of learning a new pair alone then mastering all previously learned pairs) continued through to the presentation of pair *AB*, until the subject learned all six premise pairs to 80 percent.

In order to assess the contribution of AV to task performance, we manipulated the quantity of reinforcement associated with the individual stimuli. These reinforcement values were manipulated in two conditions. Subjects were split into two groups and received either the *congruent* training condition or the *incongruent* training condition. In the *congruent* condition, reinforcement values were consistent with the implicit order. High ranking items *A*, *B*, and *C* were reinforced with 2 pellets, while lower ranking items *D*, *E*, and *F* were reinforced with 1 pellet. When a subject correctly chose image *A* during a trial that showed images *A* and *B*, he was

rewarded with a *higher* quantity of food reinforcement (2 pellets) than if he chose image *E* during a trial that showed images *E* and *F* (1 pellet).

Congruent Condition



Incongruent Condition

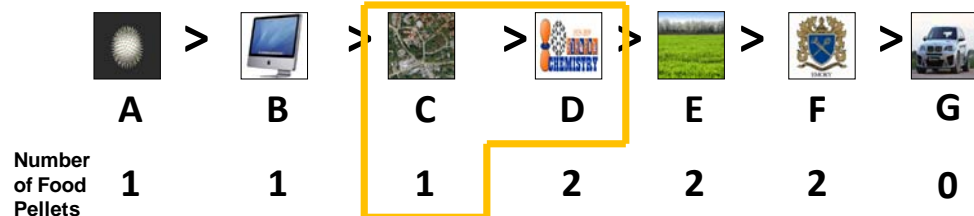


Figure 3. The manipulation in the number of food rewards earned for correct choices on training trials in the Congruent and Incongruent conditions. The boxed sections of figures are read as follows: if the adjacent pairing *BC* is presented and *B* is correctly chosen, then 2 food pellets are dispensed. If *C* is chosen, no pellets are dispensed.

In the *incongruent* condition, the reinforcement values of the stimuli were inconsistent with the implicit order. High ranking items *A*, *B*, and *C* were reinforced with 1 pellet, while low ranking items *D*, *E*, and *F* will be reinforced with 2 pellets. When a subject correctly chose image *A* in pair *AB*, he was rewarded with a *lower* quantity of food reinforcement (1 pellet) than if he chose image *E* when presented with pair *EF* (2 pellets). In both conditions incorrect choices always resulted in a negative sound, a timeout of 5 seconds, and no food reward.

Non-adjacent test trials

Once training was complete, we assessed the contributions of associative values and transitive inference to the monkeys' knowledge of the relations between the trained pairs by presenting trials containing never-before-seen pairs of non-adjacent images (e.g. *BD*, *CE*, *DG*)

intermixed with training trials (e.g. *AB*, *BC*, *CD*). Ten test sessions were conducted. In each test session fifteen pairs of non-adjacent images were presented semi-randomly intermixed with 26 trials of each of the training pairs for a total 171 trials. To prevent learning on test trials, all test trial choices (correct or incorrect) resulted in positive auditory reinforcement but no food reward. Since subjects were used to getting auditory feedback but no food reward on 20% of training trials, probe trial reinforcement did not stand out. After test trials were run, the subjects who were trained with the congruent condition were trained on a new set of images in the incongruent condition, and vice versa.

Data analysis

One-sample t-tests were used to compare performance to chance in both the *congruent* and *incongruent* conditions. Paired samples t-tests were used to compare performance between the *congruent* and *incongruent* conditions. All response latency analyses used median latencies from correct trials only. Performance data were arcsin transformed before analyses (Aron & Aron, 1999). All analyses were conducted using an alpha level of .05.

Results and Discussion

We first examined if the order in which subjects received the two training conditions impacted results on test trials by comparing performance on non-adjacent test trials by subjects who received congruent training first ($M = 95$ percent, $SD = 5.87$) to performance by subjects who received congruent training second ($M = 75$ percent, $SD = 24$). We also compared performance on non-adjacent test trials for subjects who received incongruent training first ($M = 54.8$ percent, $SD = 17.1$) with subjects who received incongruent training second ($M = 39.7$ percent, $SD = 6.85$). We ran two independent samples t-tests, one for each comparison. Training order did not significantly impact non-adjacent test trial performance in the incongruent condition ($t(8) = 1.967$, $p = 0.085$). However, a significant difference was found when comparing performances following congruent training ($t(8) = -2.488$, $p < 0.05$). This difference in performance may be an artifact of the small number of subjects trained first on the incongruent condition and second on the congruent condition who have so far completed testing ($N = 4$, instead of $N = 6$ in the reverse training order). Therefore, for all subsequent analyses presented all data within a condition, regardless of training order (all congruent, all incongruent) were combined.

Premise Pair Training

In the congruent condition, the *CD* pair is the first pair where correct responses are rewarded with 2 pellets instead of 1, while in the incongruent condition this is the first pair that is rewarded with 1 pellet instead of 2. Specifically, this pair in the incongruent condition trained subjects to learn that correct selection of stimulus *C* resulted in one pellet, while selection of stimulus *D* was incorrect and therefore not rewarded. Stimulus *D* was previously trained as the correct stimulus in pair *DE* and rewarded with 2 pellets. Therefore, if associative values control

choice of the stimuli in training, rhesus monkeys may take longer to learn the *CD* pair to criterion in the incongruent condition than in the congruent condition, because it requires inhibition of choice of a stimulus previously rewarded with 2 pellets, in favor of choice of a stimulus being rewarded with only 1 pellet.

The number of sessions to reach criterion did not differ in the two conditions for any test pairs except for this critical *CD* pair. Subjects took significantly longer to reach criterion in the incongruent condition than in the congruent condition in both the single pair training ($t(9) = -2.29, p < .05$; Figure 4) and the first mixed training session to included pair *CD* ($t(9) = -2.52, p < .05$; Figure 4), suggesting that it was difficult for monkeys to overcome their tendency to select a previously rewarded stimulus with more reinforcement value.

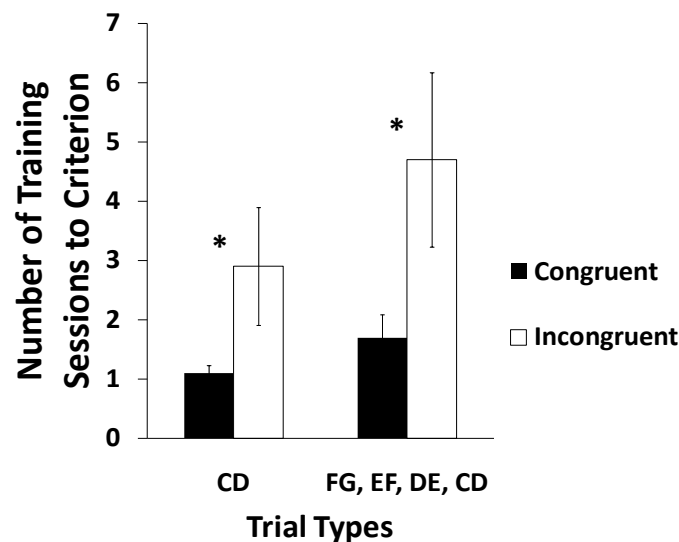


Figure 4. Training data for the *CD* pair in single pair sessions (*CD*) and the corresponding mixed training trial session (*FD, EF, DE, CD*). This figure illustrates that subjects took longer to learn the *CD* pair in the incongruent condition than in the congruent condition in both kinds of training trials. $*p < .05$ between training conditions.

While *CD* could have been more difficult to learn in the incongruent condition, we also investigated the possibility that the difference between learning rates on *CD* may have been due

to this pair being learned more easily in the congruent condition. Comparison of learning rates for the *CD* pair to learning rate for the pair learned immediately before it (*DE*) shows that subjects took significantly longer to learn the *CD* pair than the *DE* pair in the incongruent condition ($t(9) = 2.478, p < .05$), but learned these pairs at the same rate in the congruent condition ($t(9) = 1.000, p = .343$). This indicates that it was the increased difficulty in learning this pair in the incongruent condition that led to the difference between congruent and incongruent performance, not a decrease in difficulty in learning this pair in the congruent condition. Therefore during training, monkeys are attending to the reinforcement values of the individual stimuli, and these values are affecting premise pair learning.

Non-adjacent test trials

We hypothesized that if choices are primarily controlled by associative values, they would perform poorly in the *incongruent* condition but very well in the *congruent* condition. To examine performance on non-adjacent test trials, we averaged accuracy across all internal test pairs that did not include stimuli *A* and *G*, which could easily be solved based on a history of being always (*A*) or never (*G*) correct. Performance in the congruent condition was significantly above the 50 percent chance level (Figure 5A, $t(9) = 0.957, p < .001$), while performance in the incongruent condition was not significantly different from chance ($t(9) = -0.97, p = .357$). Additionally, performance in the congruent condition was significantly better than performance in the incongruent condition ($t(9) = 5.09, p < .001$). Figure 5A clearly shows this pattern of performance between both training conditions. These results, along with data summarized in Figure 4, suggest that subjects are attending to the associative values of the stimuli in training and in testing, and that associative values may seem to be driving choice behavior on this TI task.

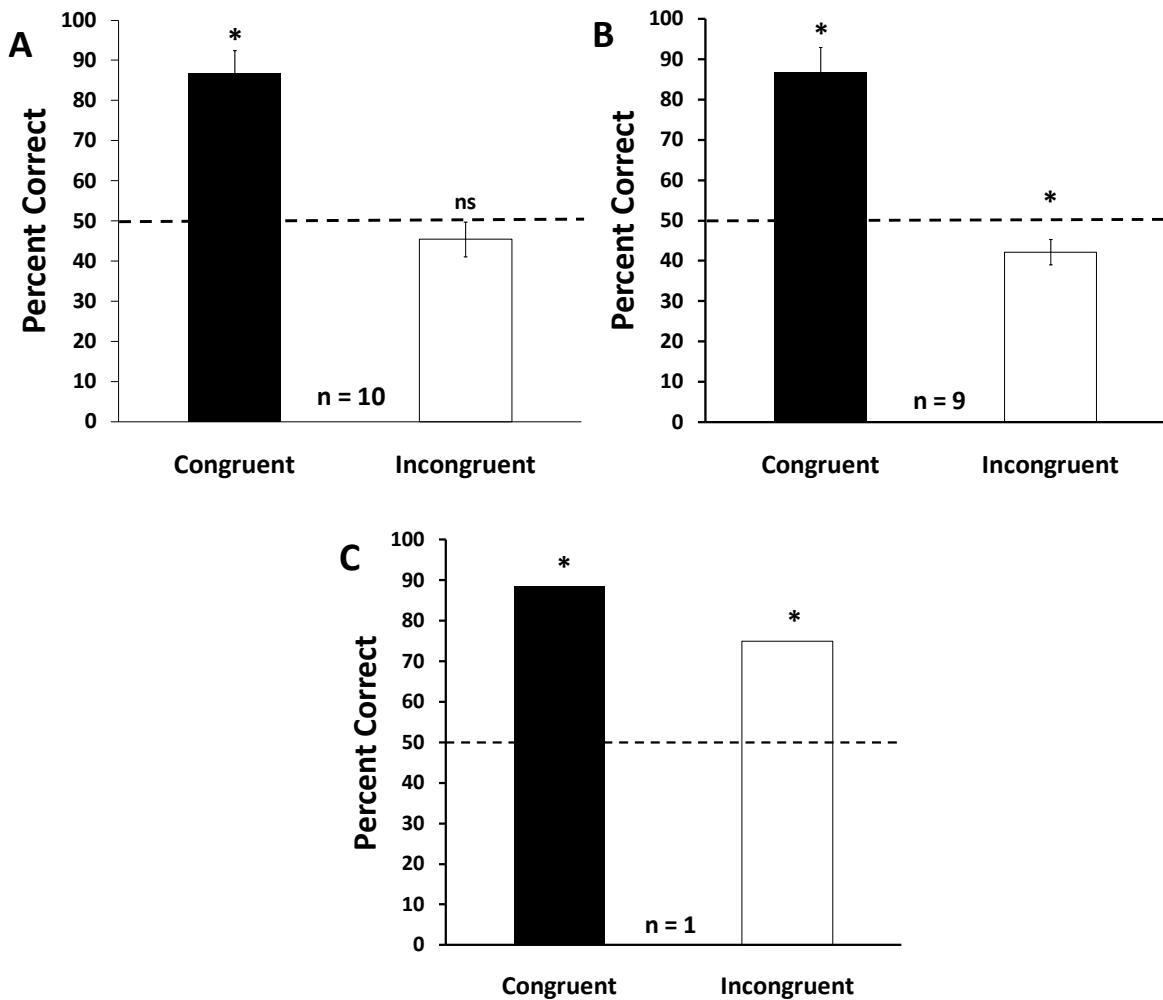


Figure 5. Performance data on non-adjacent test trials. *A* shows overall performance on non-adjacent test trials for congruent and incongruent conditions encompassing all subjects. *B* shows overall performance excluding data from the subject who showed a different pattern of performance, whose data is in *C*. ns = not significant, $*p < .05$ with respect to chance.

However, one subject did not show this performance pattern. Instead, his performance on test trials in the incongruent condition was high (75 percent; Figure 5C). Binomial tests show that both performances in the congruent and incongruent conditions were significantly above chance (congruent condition: $p < 0.001$, incongruent condition: $p < 0.001$). If we exclude his performance and combine performance from the other 9 subjects that show the same performance patterns, non-adjacent test trial performance in the incongruent condition is significantly below chance ($t(9) = -2.41, p < .05$; Figure 5B). Performance in the congruent

condition is still above chance ($t(9) = 5.28, p < .001$). Because his performance was so different from the other 9 subjects, this indicates he may solve this task differently than the rest of the subjects. In fact, this subject's data reflected a pattern of performance that was predicted if subjects primarily used TI instead of associative values on TI tasks. These findings suggest that although most subjects relied on AVs to solve this task, they may be capable of using TI to solve these tasks as well. Therefore, there may be individual differences in strategies used to solve TI tasks.

We also examined non-adjacent test trial performance with respect to food reinforcements received by each stimulus in the pair during training in order to discover the mechanisms driving this below chance performance on non-adjacent test trials in the majority of subjects. On some test trials, the stimuli paired had both been reinforced during training with the same number of pellets, *Same Pairs* (Pairs *AC* and *DF*; Figure 3). For example, during congruent training, stimuli *A* and *C* are both reinforced with 2 pellets in their individual training pairs (*AB* and *CD*), and stimuli *D* and *F* were both reinforced with 1 pellet in their training pairs (*DE* and *FG*). In the incongruent condition, stimuli *A* and *C* are reinforced with 1 pellet while stimuli *D* and *F* are reinforced with 2 pellets. However on other test trials, the stimuli paired were reinforced with different numbers of pellets during training, *Different Pairs* (Pairs *AD*, *AE*, *AF*, *BD*, *BE*, *BF*, *CE*, and *CF*; Figure 3). For instance, during congruent training, stimulus *B* was reinforced with 2 pellets in its training pair (*BC*) while stimulus *D* was reinforced with 1 pellet in its training pair (*DE*). During incongruent training, however, stimulus *B* is reinforced with 1 pellet and stimulus *D* is reinforced with 2 pellets. To be clear, choices on non-adjacent test trials did not result in food reinforcement regardless of choice, so any choices based on reinforcement values were based on the values accrued during premise pair training.

We hypothesized that if the reason most monkeys were significantly below chance on test trials was that associative values controlled choices on test trials, then on *Different Pairs*, where the stimuli were reinforced with different numbers of rewards, subjects should select the stimulus with the higher reward value, and on *Same Pairs*, in which the reinforcement values of the stimuli were the same, subjects should show no preference for either item. Therefore on *Different Pairs* monkeys should be above chance in the congruent condition, where the “correct” items were reinforced with the higher number of pellets, but below chance in the incongruent condition, where the “correct” items were reinforced with the lower number of pellets. However, on *Same Pairs*, subjects should perform at chance in both conditions.

As predicted, performance on the *Different Pairs* in the incongruent condition was below chance ($t(8) = -2.918, p < .05$), while performance on these pairs in the congruent condition was above chance ($t(8) = 7.822, p < .001$). Performance on *Different Pairs* in the two conditions were significantly different ($t(98) = 7.558, p < .001$). However, contrary to predictions, subjects did not perform at chance on *Same Pairs*, but were above chance in both conditions (Congruent: $t(8) = 8.151, p < .001$; Incongruent: $t(8) = 5.119, p < .01$). Therefore, differences in overall performance on non-adjacent test trials were due to below chance performance on the *Different Pairs* in the incongruent condition. Above chance performance on *Same Pairs*, however, suggests that although choice is controlled by associative values when the stimuli have very different values, when those values are the same, subjects can select the correct item, suggesting some knowledge of the TI trained order even in the incongruent condition.

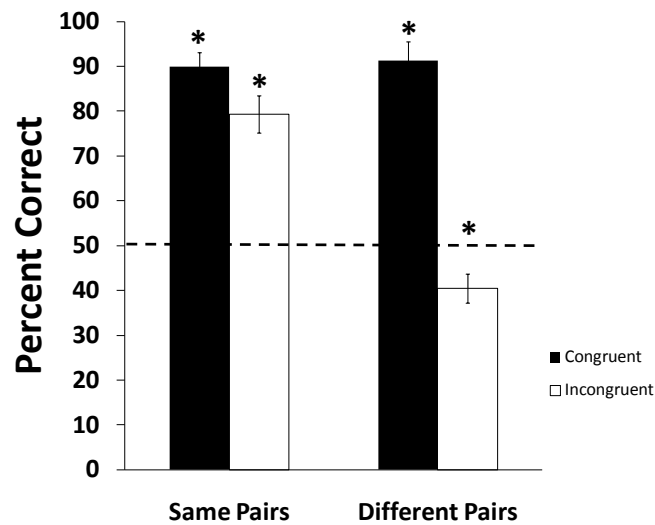


Figure 7. *Same Pairs* and *Different Pairs*. This figure illustrates same pairs and different pairs in both training conditions in terms of percent correct on non-adjacent test trials. $*p < .05$ with respect to chance.

Symbolic Distance

Visual inspection of the results plotted by symbolic distance shows that the patterns of accuracy and latency in the congruent and incongruent conditions differ markedly (Figures 8A and 8B). In the congruent condition, accuracy climbs with a shallow slope as symbolic distance increases, while latency shows the opposite pattern. This pattern in the congruent condition is similar to what has been observed in previous studies (e.g. Figure 2B), but the slopes are shallower. The pattern in the incongruent condition is not like that observed in previous research, instead showing a “U” and inverted “U” shaped function for accuracy and latency, respectively.

Repeated Measures ANOVAs showed a main effect of symbolic distance on response latency and performance in both conditions (*Congruent Performance*: $F(4, 36) = 6.660, p < .001$; *Congruent Latency*: $F(4, 36) = 4.606, p < .01$; *Incongruent Performance*: $F(4, 36) = 65.29, p < .001$; *Incongruent Latency*: $F(4, 36) = 5.942, p < .001$). Paired-sample t-tests were performed in both conditions comparing symbolic distance of 1 and symbolic distance of 5 for performance and response latency. In the congruent condition accuracy was higher and latency

shorter with symbolic distance of 5 than symbolic distance of 1, consistent with the slopes of the lines evident visually (Performance: $t(9) = -4.380, p < .01$; Latency: $t(9) = 7.398, p < .001$). In the incongruent condition, performance was higher with symbolic distance of 5 ($t(9) = -14.95, p < .01$), but the difference in latency was not significant ($t(9) = 1.656, p = .132$).

These clear differences in symbolic distance curves between the present data and standard findings could be interpreted as a characteristic of use of AV, because presence of SDE has been used in previous studies as a way to suggest that ordered stimuli may be organized linearly, which in turn supports the view TI as the primary mechanism. Use of AV would not necessarily produce SDE. These results appear to support the view that subjects in this experiment used AV as the primary strategy for selecting stimuli on non-adjacent test trials.

However, the absence of clear SDE in this experiment compared to standard TI experiments also suggests that subjects may rely on different strategies to solve the task in this experiment than they have used in standard TI tasks. It is possible that the manipulation in AV by the changes in food reinforcement in this experiment may have driven choice behavior to be more AV-focused and in turn could overshadow the use of TI. Therefore, the present results may not really inform our understanding of the strategy subjects employ in traditional TI tasks at all, because past performance patterns produced are not the same.

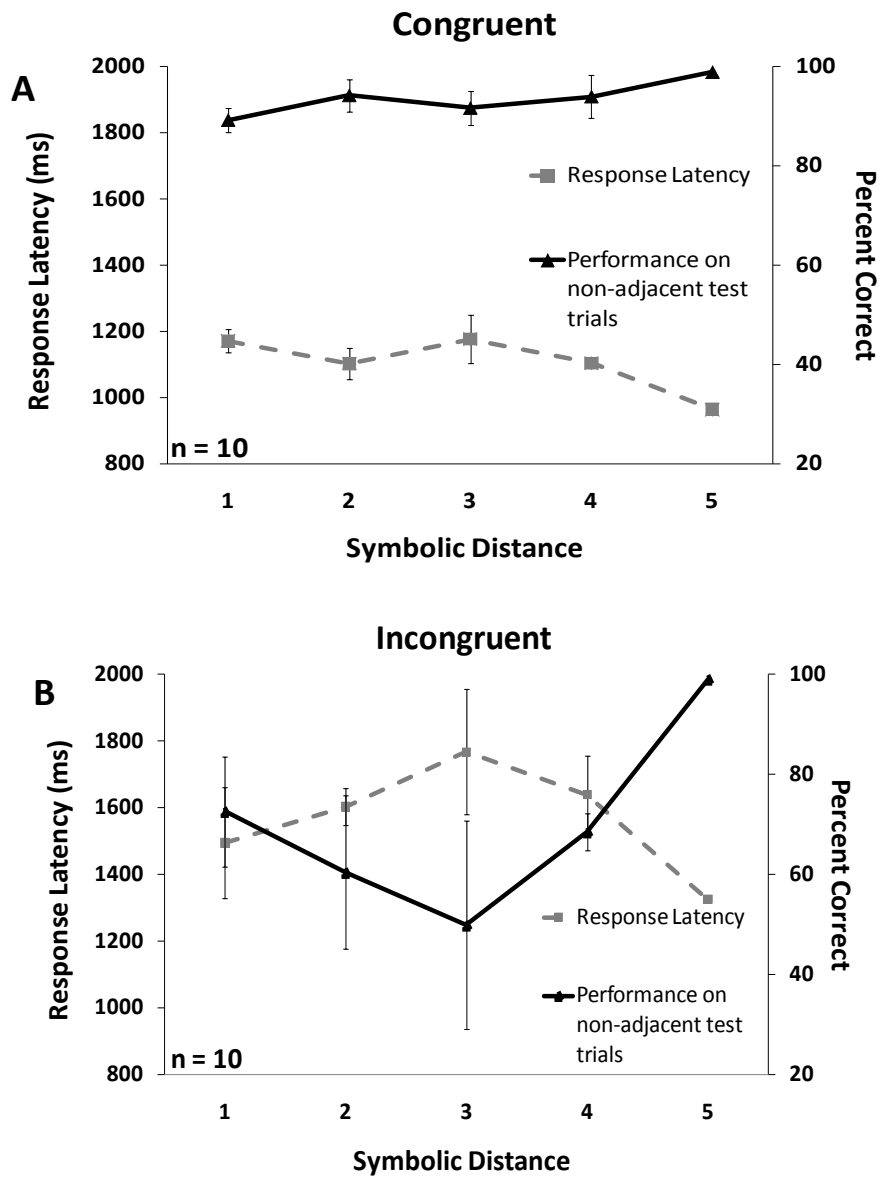


Figure 8. Symbolic distance curves. *A* and *B* show curves of response latency (ms) and performance in both congruent and incongruent conditions, respectively.

Conclusions

The results of this experiment show that associative values of the stimuli influenced learning of premise pairs and overall performance on non-adjacent test trials (TI trials). However, we also found evidence to suggest that TI may have also been used from analyzing individual subject data (Figure 5C) and from analysis of *Same Pairs*.

It is clear from our findings that AV can impact choice behavior on TI tasks; however, it is possible that the AV may have been much more salient in this experiment than in standard inference experiments, which could have overshadowed any influence of inference on choice. It is also important to note that the results of this experiment that support AV as the primary mechanism controlling choice in TI tasks conflict with previously received results from experiments in our lab involving list linking (Paxton and Hampton, In prep), which cannot be solved using AV alone. In the future, effects of AV and TI could be better explored if reinforcement values were manipulated in a list linking experiment.

One limitation of this study was the lack of a control group that consisted of subjects who received the traditional TI training protocol, in which associative values were not explicitly manipulated. This control group could have been used to confirm that SDE was producible, since it was not observed in this experiment (Figures 8A and 8B). The control group could have also served as a comparison to the performances on non-adjacent test trials following congruent condition training. In this way, we could have seen if associative values augmented performance on test trials compared to control.

In summary, the results of this study do show that manipulation of associative values can influence choice behavior on test trials; however, this experiment also produces evidence to suggest that other cognitive mechanisms may influence choice behavior, including TI.

References

- Aron, A., & Aron, E. (1999). *Statistics for psychology*. Upper Saddle River, NJ: Prentice Hall.
- Bond, A. B., Kamil, A. C., & Balda, R. P. (2003). Social complexity and transitive inference in corvids. *Animal Behaviour*, *65*, 479-487.
- Bond, A. B., Wei, C. A., & Kamil, A. C. (2010). Cognitive representation in transitive inference: A comparison of four corvid species. *Behavioural Processes*, *85*(3), 283-292.
- Bryson, J. J., & Leong, J. C. S. (2007). Primate errors in transitive 'inference': a two-tier learning model. *Animal Cognition*, *10*(1), 1-15.
- DeVito, L. M., Kanter, B. R., & Eichenbaum, H. (2010). The Hippocampus Contributes to Memory Expression During Transitive Inference in Mice. *Hippocampus*, *20*(1), 208-217.
- Dusek, J. A., & Eichenbaum, H. (1997). The hippocampus and memory for orderly stimulus relations. *Proceedings of the National Academy of Sciences of the United States of America*, *94*(13), 7109-7114.
- Grosenick, L., Clement, T. S., & Fernald, R. D. (2007). Fish can infer social rank by observation alone (vol 445, pg 429, 2007). *Nature*, *446*(7131), 102-102.
- Hogue, M. E., Beaugrand, J. P., & Lague, P. C. (1996). Coherent use of information by hens observing their former dominant defeating or being defeated by a stranger. *Behavioural Processes*, *38*(3), 241-252.
- Lazareva, O. F., Smirnova, A. A., Raevskii, V. V., & Zorina, Z. A. (2000). Transitive inference formation in hooded crows: Preliminary data. *Doklady Akademii Nauk*, *370*(5), 698-700.
- Lazareva, O. F., Smirnova, A. A., Zorina, Z. A., & Rayevsky, V. V. (2001). Hooded crows solve a transitive inference problem cognitively. *Animal Welfare*, *10*, S219-S231.

- Lazareva, O. F., & Wasserman, E. A. (2006). Effect of stimulus orderability and reinforcement history on transitive responding in pigeons. *Behavioural Processes*, 72(2), 161-172.
- Lazareva, O. F., & Wasserman, E. A. (2010). Nonverbal transitive inference: Effects of task and awareness on human performance. *Behavioural Processes*, 83(1), 99-112.
- Maclean, E. L., Merritt, D. J., & Brannon, E. M. (2008). Social complexity predicts transitive reasoning in prosimian primates. *Animal Behaviour*, 76, 479-486.
- Merritt, D. J., & Terrace, H. S. (2011). Mechanisms of inferential order judgments in humans (*Homo sapiens*) and rhesus monkeys (*Macaca mulatta*). *J Comp Psychol*.
- Paz-y-Mino, G., Bond, A. B., Kamil, A. C., & Balda, R. P. (2004). Pinyon jays use transitive inference to predict social dominance. *Nature*, 430(7001), 778-781.
- Rescorla, R. A. (1972). Configural Conditioning in Discrete-Trial Bar Pressing. *Journal of Comparative and Physiological Psychology*, 79(2), 307-&.
- Treichler, F. R., Raghanti, M. A., & Van Tilburg, D. N. (2003). Linking of serially ordered lists by macaque monkeys (*Macaca mulatta*): list position influences. *J Exp Psychol Anim Behav Process*, 29(3), 211-221.
- Treichler, F. R., Raghanti, M. A., & Van Tilburg, D. N. (2007). Serial list linking by macaque monkeys (*Macaca mulatta*): list property limitations. *J Comp Psychol*, 121(3), 250-259.
- Treichler, F. R., & Van Tilburg, D. (1996). Concurrent conditional discrimination tests of transitive inference by macaque monkeys: list linking. *J Exp Psychol Anim Behav Process*, 22(1), 105-117.
- Treichler, F. R., & Van Tilburg, D. (2002). Premise-pair training for valid tests of serial list organization in macaques. *Animal Cognition*, 5(2), 97-105.

Vasconcelos, M. (2008). Transitive inference in non-human animals: An empirical and theoretical analysis. *Behavioural Processes*, 78(3), 313-334.

Vonfersen, L., Wynne, C. D. L., Delius, J. D., & Staddon, J. E. R. (1991). Transitive Inference Formation in Pigeons. *Journal of Experimental Psychology-Animal Behavior Processes*, 17(3), 334-341.

Weiss, B. M., Kehmeier, S., & Schloegl, C. (2010). Transitive inference in free-living greylag geese, *Anser anser*. *Animal Behaviour*, 79(6), 1277-1283.

Wynne, C. D. L. (1995). Reinforcement Accounts for Transitive Inference Performance. *Animal Learning & Behavior*, 23(2), 207-217.

Wynne, C. D. L. (1997). Pigeon transitive inference: Tests of simple accounts of a complex performance. *Behavioural Processes*, 39(1), 95-112.