INTERNATIONAL
JOURNAL OF COMPARATIVE PSYCHOLOGY

2018, 31
David Washburn
Special Issue Editor
Peer-reviewed

Assessing Distinctiveness Effects and "False Memories" in Chimpanzees (*Pan troglodytes*)

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There are many parallels between human and nonhuman animal cognitive abilities, suggesting an evolutionary basis for many forms of cognition, including memory. For instance, past research has found that 2 chimpanzees exhibited an isolation effect, or improved memory for semantically distinctive items on a list (Beran, 2011). These results support the notion that chimpanzees are capable of semantic, relational processing in memory and introduce the possibility that other effects observed in humans, such as distinctiveness effects or false memories, may be present in nonhuman species. The Deese-Roediger-McDermott (DRM) paradigm is a commonly-used task to explore these phenomena, and it was adapted for use with chimpanzees. We tested 4 chimpanzees for isolation effects during encoding, distinctiveness effects during recognition, and potential "false memories" generated by the DRM paradigm by presenting a serial recognition memory task. The isolation effect previously reported (Beran, 2011) was not replicated in this experiment. Two of four chimpanzees showed improved recognition performance when information about distinctiveness could be used to exclude incorrect responses. None of the chimpanzees were significantly impaired in the "false memory" condition. However, limitations to this approach are discussed that require caution about assuming identical memory processes in these chimpanzees and in humans.

Keywords: *chimpanzees, memory, DRM illusion, isolation effect, false memory, distinctiveness, relational processing*

Research in the 20th century redefined our understanding of ape minds, especially the pioneering work of Dr. Duane Rumbaugh that highlighted many similarities in the thinking processes of human and nonhuman primates (Rumbaugh, 2013). For instance, there are a number of similarities in memory processes between humans and their closest living evolutionary relative, the great apes (e.g., Beran, 2011; Martin-Ordas & Call, 2011; Menzel, 1973; Menzel, 1999; Schwartz, Meissner, Hoffman, Evans, & Frazier, 2004; Tinklepaugh, 1932; Yerkes & Yerkes, 1928). In recent years, this has included reports of episodic-like memory in great apes (e.g., Hampton & Schwartz, 2004; Kano & Hirata, 2015; Martin-Ordas, Haun, Colmenares, & Call, 2010; Menzel, 1999; Schwartz & Evans, 2001), autobiographical memory (e.g., Martin-Ordas, Berntsen, & Call, 2013), and prospective memory (e.g., Beran, Perdue, Bramlett, Menzel, & Evans, 2012; Osvath & Osvath, 2008; Perdue, Evans, Williamson, Gonsiorowski, & Beran, 2014). This overlap suggests that many aspects of memory may serve, or have served, an adaptive purpose during humans' evolutionary history.

One of the features of human memory that increases its capacity and efficiency is the ability of the individual who is encoding or recalling information to do so by relating that information to other things also stored in memory (Craik & Lockhart, 1972; Hyde & Jenkins, 1973). The use of conceptual categorization is a central process in a number of cognitive domains, including memory (Anderson, 1976; Roediger, Balota, & Watson, 2001). In particular, spreading activation across semantic networks has been a crucial feature of important memory theories and models (e.g., McClelland & Rumelhart, 1986). Evidence for the importance of semantic organization can be seen early in the lifespan. For example, when young children learn lists of

https://doi.org/10.46867/ijcp.2018.31.03.05

items, they tend not to organize those lists, whereas older children begin to organize the lists on the basis of categorical information situated among the items in the list (e.g., Paris, 1978). Research with young children on free-recall tasks also demonstrates that as children get older, they are more likely to cluster their responses by categories (see Jablonski, 1974). It is likely that what is occurring here is the use of conceptual information that helps structure that organization and this might be an important mechanism in increasing memory capacity (e.g., Calfee & Peterson, 1968; Jablonski, 1974; Vonk & Mosteller, 2013). For example, when seeing a list of individual foods, it is beneficial to recognize that all items are in the food category because at the time of recall or recollection one can remember not only the exemplars, but also the conceptual category as a means of generating and evaluating information that comes from the search of memory.

Despite the importance of semantic processing for human memory, it remains relatively unexplored in nonhuman animal memory research (Vonk & Mosteller, 2014). Certainly, there is clear evidence that nonhuman animals can form concepts ranging from concrete to highly abstract (Roberts & Mazmanian, 1988; Vonk & MacDonald, 2002, 2004; Zentall, Wasserman, & Urcuioli, 2014), but the extent to which these concepts might influence memorial processing continues to be an important empirical question (Vonk & Mosteller, 2014). Perhaps due to language-related constraints in nonhuman animals, examining the role of semantic organization in memory processes has been understudied. There are at least two well-studied paradigms in the human memory literature that can help elucidate the role of semantic organization in nonhuman memory: (1) the distinctiveness effect, and (2) associative false memory paradigms.

The von Restorff (1933) effect, or isolation effect, refers to the empirical finding that items that stand out from their context (perceptually or semantically) are remembered with greater accuracy (Hunt, 1995). Isolate items within a list are distinctive, usually in terms of their category membership (e.g., a fruit name in a list of vehicle types). In humans, isolation effects are robust as they have been found among all age groups (Howe, Courage, Vemescu, & Hunt, 2000; Smith, 2011), with various materials (pictures and words; Kishiyama & Yonelinas, 2003), and with various memory formats such as recall, recognition, and cued-recall tests. Recent work with chimpanzees suggests that a semantic distinctiveness effect might arise in tasks presenting isolate stimuli (Beran, 2011; Vonk & Mosteller, 2013). Vonk and Mosteller (2013) reported that an adult male chimpanzee selected a studied distinctive item during a recognition test at above chance levels in two of the three category conditions. Beran (2011) studied chimpanzees who were proficent at identifying real world items from two dimensional photographs (e.g., Beran, Savage-Rumbaugh, Brakke, Kelley, & Rumbaugh, 1998). They were presented with a sequence of categorically related or unrelated photographs. In the isolation effect condition, subjects were presented with three photographs of familiar items (people, animals, or objects) from the same category and one distinct item from a different category (e.g., a photograph of a hammer presented in a list of different fruits). In the control condition, all four items were from the same category (e.g., four tools). Then, given two photos, the chimpanzees chose the photo that was in the list to receive a food reward. Critically, those two photos came from the same category themselves (e.g., hammer and wrench) so that the response could not be made on the basis of selecting whatever choice item was less like the majority of the list items. The results demonstrated that two of the chimpanzees showed more accurate recognition for the isolate item compared to an item from the same serial position in the control lists. This suggested that the isolate was remembered at high levels because the chimpanzees noticed its distinct conceptual nature within the list at the time of encoding.

An interesting possibility is that the significant differences reported in Beran (2011) not only reflected a distinctiveness effect but were driven in part by a specific type of memory error in the control condition. Specifically, the control condition may have been susceptible to false memories. These memory errors occur because of semantic confusions due to the relatedness of foil (incorrect) options to the items on the list. It is an interesting question then, if nonhuman animals might be susceptible to false memories in the way that humans are.

In the human literature, false memories refer to a number of phenomena. Here, we are using the term as it is commonly studied within the Deese-Roediger-McDermott task (DRM; Deese, 1959; Roediger & McDermott, 1995). In the standard DRM task, human participants are presented with a series of words that are conceptually related. There is also a nonpresented lure that is conceptually related to the list of words. At test, participants are asked to recall or recognize items from the list. The typical finding in these tasks is that participants falsely retrieve or recognize the nonpresented critical lure at high levels (Gallo, 2013). In the Beran (2011) control condition, chimpanzees were presented with photographs of four categorically related items, and the foil was also from the same category. Thus, poorer performance on the control condition may have resulted from subjects sometimes falsely remembering the foil in addition to more proficient remembering of the distinctive item in the test condition. It is not possible to disentangle the potential effects of false memory and distinctiveness using the Beran (2011) comparison. However, there may be ways to independently assess these phenomena using a similar methodology.

In addition to enhancing memory for certain distinct items, the presence and potential expectation of distinctiveness can also be used to help avoid making recognition errors during test (Israel & Schacter, 1997; Schacter, Israel, & Racine, 1999). Specifically, the correct rejection of a probe item because it does not meet the expectation that an item would be remembered (e.g., "I would have remembered seeing that") is referred to as the *distinctiveness heuristic*. Although there are other explanations in addition to the distinctiveness heuristic that explain this phenomenon (e.g., Gallo, Weiss, & Schacter, 2004), research with humans makes clear that distinctiveness can be used in a disqualifying manner during recognition. By addressing whether animals also use distinctiveness in an exclusionary manner in this type of testing scenario, we can broaden our understanding of distinctive processing in nonhumans and further explore similarities between human and nonhuman memory systems.

Identifying the overlap in primate memory processing can help reveal the extent to which these systems share the same evolutionary origins. Based on previous research demonstrating similarities in memory organization between humans and chimpanzees (e.g., Beran, 2011; Martin-Ordas & Call, 2011; Menzel, 1999; Vonk & Montseller, 2013), we expected that the chimpanzees could show some evidence of distinctiveness effects and false memories. Finding positive results for these memory biases in chimpanzees would suggest that these effects have an adaptive value, at least in an evolutionary context, or are a byproduct of other adaptations such as the rapid memory retrieval afforded by semantic networks. A better understanding of the ultimate and proximate factors influencing memory (and errors of memory) has important theoretical and practical implications. However, such errors may be less likely in other species, again owing to a number of possible explanations. At present, there are limited empirical data to guide theoretical efforts to explain the evolutionary bases for human memory errors and processes such as false memories. Our experiment with four chimpanzees was largely exploratory to document the extent to which some of these phenomena might be present.

Method

Subjects

Four chimpanzees participated in this study: (*Females*: Lana – 33 years old, Panzee – 17 years old; *Males*: Sherman – 20 years old, Mercury – 16 years old). These data were collected shortly after the data reported in Beran (2011) using the same approach that was used in that experiment. All chimpanzees were housed together in the same building and spent time together in social groups daily, but they were observed separately during test sessions. Chimpanzees worked for preferred food treats. Otherwise, they were maintained on their normal diet of fruit, vegetables, and primate chow. Food or water deprivation was not used. Three of the four animals (excluding Mercury) had been involved in language acquisition research in which they learned to associate geometric forms called lexigrams with different foods, locations, objects, and people (see Brakke & Savage-Rumbaugh, 1995, 1996; Rumbaugh, 1977; Rumbaugh & Washburn 2003; Savage-Rumbaugh, 1986). These chimpanzees had experience in performing symbolic matching-to-sample tasks in which comparison stimuli differed from samples (including tasks that involved selecting lexigrams to match spoken English words or photographs; Beran & Heimbauer, 2015; Beran et al., 1998).

Materials

Trials were presented on a Compaq DeskPro computer with an attached joystick. The program was written in Visual Basic 6.0 for Windows. Joysticks were mounted on the chimpanzees' home cages so that they could manipulate the joysticks with their hands to control a cursor on the screen, and all chimpanzees were familiar with the use of this procedure. The stimuli that were presented during trials were colored photographs taken of real world items and individuals using a digital camera.

Beran (2011) outlined the critical nature of the photographic stimuli. These photographs were sufficiently variable in their color and features that photos within a category were not perceptually distinct on the basis of color or form from all others from outside that category. Thus, perceptual distinctiveness was accounted for, and the details are offered in Beran (2011). In brief, analyses of the images using software that "clustered" perceptually similar stimuli showed that the clusters did not fall consistently into the same categorical classifications that were used to denote the semantic nature of the stimuli. Thus, the photo categories used here could not be reduced to simple perceptual similarities that defined any category exclusively.

Procedure

The task. The methodology was identical to that used in Beran (2011). List items (photographs – 7.5 cm × 7.5 cm) were presented in the center of the screen for 2 s each. At the end of the list presentation, there was a 1-s delay and then the comparison stimuli (5.5 cm × 5.5 cm) appeared on the screen. These comparison stimuli were located at the left center and right center of the screen, and the cursor was returned to the bottom center of the screen. The chimpanzee observed the list stimuli, followed by the delay, and then selected one of the two choice stimuli by moving the cursor into contact with that stimulus. Correct responses led to a melodic tone, and incorrect selections led to a buzz tone, followed by an intertrial interval of approximately 15-30 s. Food reward was given only for correct selections by an experimenter who was not able to view anything on the computer screen and thus could not cue the chimpanzees in any way during trials. Chimpanzees were tested in their familiar home enclosures and were free to leave the test area at any time during testing.

The stimuli. The stimuli used in the experiment consisted of 90 photographs from 10 experimenter-defined categories (see Table 1). All of the chimpanzees were familiar with all of the items in the photographs.

Study lists of these photographs were constructed in one of three ways that we called the *list type*: (1) *Homogeneous*, (2) *Isolate*, or (3) *Mixed*. For the Homogeneous List, all four stimuli were from the same category (i.e., all items were from one of the columns in Table 1). For the Isolate List, three items were from the same category, and one item was from a different category (i.e., the isolate). In this condition, the isolate was always presented as the probe item. For the Mixed List, each photo was from a unique category but from the same supercategory (either foods, objects, or individuals; see Table 1).

Table 1
The Photographic Stimuli Used in the Lists

Foods				**Objects**				**Individuals**	
Vegetables	**Fluids**	**Fruits**	**Treats**	**Toys**	**Utensils**	**Husbandry**	**Tools**	**Apes**	**Humans**
Tomato	Cola	Kiwi	Cereal	Ball	Bowl	Shot	Screw	Panzee	C1
Carrot	Coffee	Strawberry	Cracker	Crayons	Knife	Oil	Dustpan	Austin	C2
Onion	Water	Banana	Peanuts	Mask	Plate	Mirror	Nails	Lana	S
Celery	Koolaid®	Pineapple	M&Ms®	Paper	Pan	Toothbrush	Lever	Sherman	J
Lettuce	Lemonade	Apple	Pretzel	Paint	Cup	Thermometer	Hose	Panbanisha	M1
Broccoli	Juice	Pear	Jelly	Bear	Spoon	Stethoscope	Broom	Tamuli	D1
Potato	Orange soda	Peach	Yogurt	Balloon	Fork	Toothpaste	Lighter	Kanzi	D2
Sweet potato	Milk	Grapes	Raisins	Bubbles	Straw	Clippers	Wrench	Matata	M2
Green beans	Orange Juice	Orange	Goldfish®	Clay	Can opener	Brush	Hammer	Mercury	S
Peas	Perrier®	Blackberry	Cheese	Chalk	Box	Medicine	Keys	Nyota	L

The relationship between the probe item and the foil during the response phase was also varied in three ways that we called the *test foil type*: A) *Same Category*, B) *Same Supercategory*, or C) *Different Supercategory*. For the Same Category condition, the foil was from the same category as the probe (e.g., banana and apple; both are high preference fruits as well as foods). For the Same Supercategory condition, the foil was from the same supercategory as the probe, but a different category (e.g., banana and carrot; both are foods, but one is a preferred fruit and other is a low-preference vegetable). For the Different Supercategory condition, the foil was from a different supercategory than the probe (e.g., banana and hammer). We used these different trial types to provide a lot of variability for the chimpanzees across trials while ensuring that we did not need to present photographs more than once within a session. We intended to combine some of the trials to specifically focus on distinctiveness and false memory effects if those occurred.

The three levels of list type and test foil type were fully crossed to create nine trial types, as outlined in Table 2. In each daily session, 15 trials were completed. Session duration was approximately 15 min. Each chimpanzee completed only one session per day (with an average of 4 sessions per week) and a total of 30 sessions (450 trials). Importantly, each photograph was shown only once (or not at all) in a session to reduce the chances of proactive interference within a session by ensuring that each trial contained all session-unique stimuli.

Data analysis. We first compared performance across all conditions as a function of list position at the point of recognition testing. We compared performance for each chimpanzee for lists where the first, second, third, or fourth item was presented as the probe item using a 4 × 2 chi-squared test. We predicted a strong recency effect given the very short delay before recognition testing, as past research with monkeys has shown that short delays do not tend to evoke primacy effects (e.g., Wright, 1999). We also compared the overall performance level of each chimpanzee to chance levels of responding using a binomial test. Then, we compared specific test conditions for the proportion or correct responses in those conditions using a Fisher's exact test in each case and for each chimpanzee. More details about the specific comparisons are offered below along with predictions for those comparisons. In these cases, we used a one-tailed test to account for the directional predictions we made.

Table 2
Description of Conditions

	Same Category Foil	**Same Supercategory Foil**	**Different Supercategory Foil**
Homogeneous List	<u>Homogeneous-Same</u> All four stimuli are from the same list. The foil is from the same category. *Sample List:* ***Juice, Cola, Milk, Coffee*** *Probe:* ***Juice*** *Foil:* ***Water***	<u>Homogeneous-Super</u> All four stimuli are from the same list. The foil is from the same supercategory. *Sample List:* ***Juice, Cola, Milk, Coffee*** *Probe:* ***Juice*** *Foil:* ***Banana***	<u>Homogeneous-Different</u> All four stimuli are from the same list. The foil is from a different supercategory. *Sample List:* ***Juice, Cola, Milk, Coffee*** *Probe:* ***Juice*** *Foil:* ***Fork***
Isolate List	<u>Isolate-Same</u> Three list stimuli are from the same category. The fourth (not necessarily in terms of order) is from a different supercategory. The foil is from the same category as the probe, which is always from the unique category. *Sample List:* ***Juice, Cola, Milk, Fork*** *Probe:* ***Fork*** *Foil:* ***Spoon***	<u>Isolate-Super</u> Three list stimuli are from the same category. The fourth (not necessarily in terms of order) is from a different supercategory. The foil is from the same supercategory as the probe item. *Sample List:* ***Juice, Cola, Milk, Fork*** *Probe:* ***Fork*** *Foil:* ***Keys***	<u>Isolate-Different</u> Three list stimuli are from the same category. The fourth (not necessarily in terms of order) is from a different supercategory. The foil is from the same category as the three non-probe items. *Sample List:* ***Juice, Cola, Milk, Fork*** *Probe:* ***Fork*** *Foil:* ***Water***
Mixed List	<u>Mixed-Same</u> Each list stimulus is from a unique category but the same supercategory. The foil is from the same category as the probe. *Sample List:* ***Juice, Apple, Jelly, Peas*** *Probe:* ***Peas*** *Foil:* ***Carrot***	<u>Mixed-Super</u> Each list stimulus is from a unique category but the same supercategory. The foil is from the same supercategory. *Sample List:* ***Juice, Apple, Jelly, Peas*** *Probe:* ***Peas*** *Foil:* ***Kiwi***	<u>Mixed-Different</u> Each list stimulus is from a unique category but the same supercategory. The foil is from a different supercategory. *Sample List:* ***Juice, Apple, Jelly, Peas*** *Probe:* ***Peas*** *Foil:* ***Keys***

Note. In the Isolate-Different trial type, the isolate was always presented as the probe item.

Assessing the isolation effect during encoding. We combined Isolate-Same and Isolate-Super conditions to form our isolate condition and compared this to a control condition (Mixed-Same and Mixed-Super). In both the isolate and control conditions, chimpanzees were given a probe item and foil item from the same category or supercategory. Importantly, the study lists differed in that the isolate condition involved one distinctive item that could be noticed during list presentations and which was used as the probe, whereas the mixed list never presented an isolate that would “stand out” against the rest of the list conceptual organization (because the list was mixed). We predicted better performance in the isolate list condition, which would suggest that distinct items were better remembered as reported by Beran (2011). If this was true, it would suggest that, during list presentation, the isolate was encoded in a way that led to better recognition without being the result of the isolate being categorically different (and therefore more salient) from its foil at the time of the recognition test.

Prediction: Isolate-Same + Isolate-Super > Mixed-Same + Mixed-Super

Assessing foil distinctiveness effects. When the study list was homogeneous (all from the same category) or mixed (all from the same supercategory), performance should have been better when the foil was from a different category or supercategory than the probe (and the rest of the list) than when the foil was from the same category or supercategory if distinctiveness can be used in an exclusionary way. In other words, the foil might be excluded on the basis of its distinctiveness (i.e., it is the only item not categorically related to the rest of the list). Thus, we predicted that subjects would perform better when the probe and foil were from different categories when the study list was homogeneous.

Prediction: Homogeneous-Different + Mixed-Different > Homogeneous-Super + Mixed-Super

Assessing "false memories." Given the possibility that distinctiveness at the time of encoding or at the time of test might affect performance, we needed a comparison in which distinctiveness was controlled so that we could test for false memory. In the Mixed-Same and Mixed-Super conditions, the lists contained items of the same supercategory, whereas Homogenous-Same and Homogeneous-Super lists contained all items of the same category. Thus, no item was categorically distinct at the time of encoding. In both cases, the foil item was from the same category as the probe, controlling for distinctiveness of the foil contributing to response biases. All that differed was the degree to which the lists were categorical or supercategorical, with the prediction being that false memories would occur if more errors were made when the lists were of all the same category (and the same foil category) than when lists contained more variety as in the mixed conditions.

Prediction: Mixed-Same + Mixed-Super **>** *Homogeneous-Same + Homogeneous-Super*

There is another way to assess possible "false memories" using the conditions we generated. If lists always contained an isolate, which was the probe stimulus (i.e., the three Isolate conditions), one would predict more errors in the Isolate-Different condition compared to the two other conditions because in that condition the foil was more categorically related to the rest of the list items; however, in the Isolate-Same and Isolate-Super conditions, the foil was only related to the isolate. If, at the time of test, the list category influenced memory, the chimpanzees might be more likely to erroneously choose the item that was related to the majority of the list items compared to choice of the isolate, even given that the isolate might experience differential encoding compared to the other list items.

Prediction: Isolate-Different > Isolate-Same + Isolate-Super

Results

Serial List Position Effects and Overall Performance

All chimpanzees showed the classic recency effect, with performance being highest for probe stimuli from the fourth list position compared to the others. In general, later list items were recognized more accurately than earlier list items (Lana, X^2 (3, N = 450) = 24.65, $p < 0.01$; Mercury, X^2 (3, N = 450) = 37.47, $p < 0.01$; Panzee, X^2 (3, N = 450) = 19.51, $p < 0.01$; Sherman, X^2 (3, N = 450) = 61.97, $p < 0.01$; see Figure 1). Overall, Lana was correct on 78% of the trials, Mercury was correct on 65% of the trials, Panzee was correct on 84% of the trials, and Sherman was correct on 70% of the trials. These performance levels all exceeded chance levels, $p < 0.05$ (binomial test).

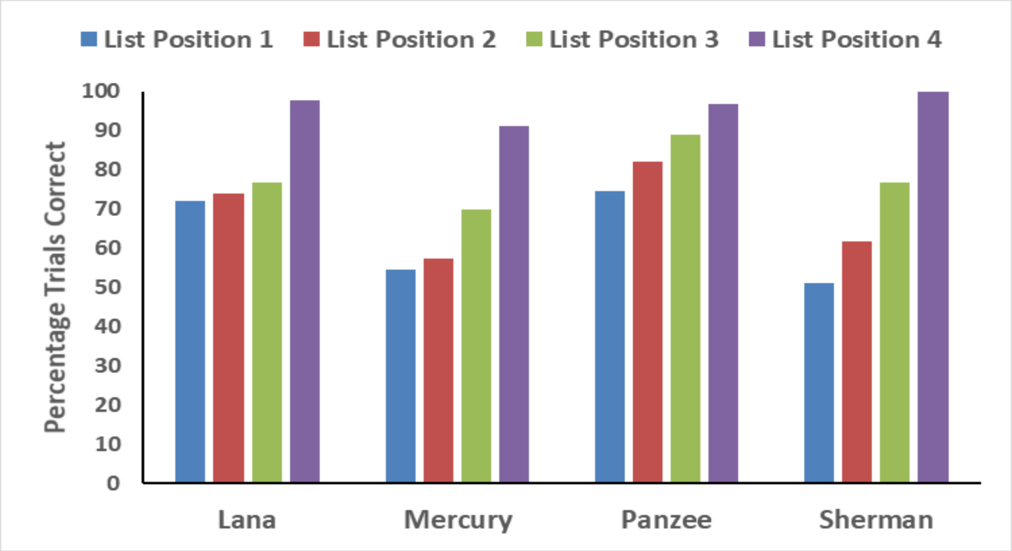

Figure 1. **Performance of each chimpanzee for probes from each serial list position.** This figure shows the data from all trial types combined.

Isolation Effect

Figure 2 shows that none of the chimpanzees showed better performance in the Isolate-Same + Isolate-Super conditions compared to the Homogenous-Same + Homogenous-Super conditions (Lana, p = 0.36; Panzee, p = 0.42; Mercury, p = 0.23; Sherman, p = 0.08). Thus, we failed to replicate the isolation effect in this experiment.

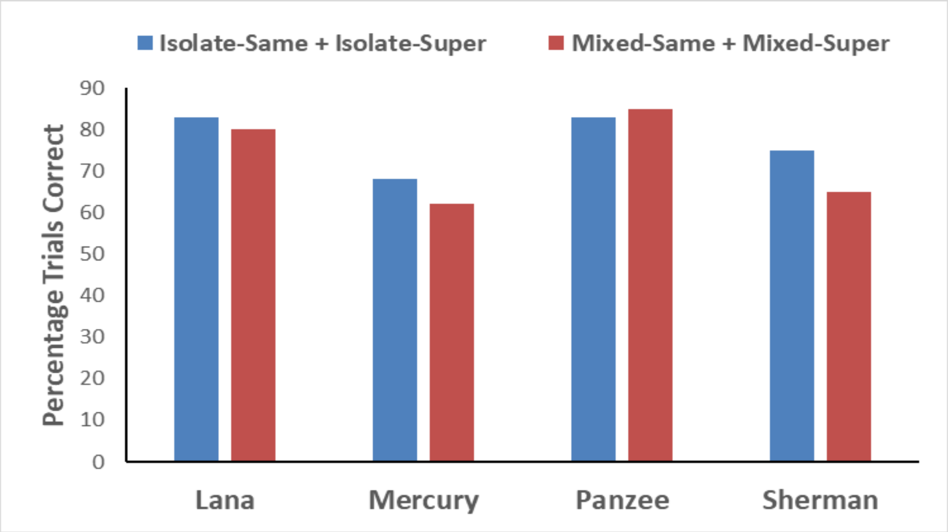

Figure 2. **Performance for the Isolate-Same and Isolate-Super trials compared to the Mixed-Same and Mixed-Super trials.** No chimpanzees showed a difference for this comparison.

Foil Distinctiveness Effect

Figure 3 shows that Lana and Panzee showed improved performance when a distinctive foil was presented (Lana, $p < 0.01$; Panzee, $p < 0.05$), suggesting that the distinctiveness of the foil may have been used in a disqualifying manner to improve performance. This was not true for Mercury ($p = 0.38$) or Sherman ($p = 0.05$).

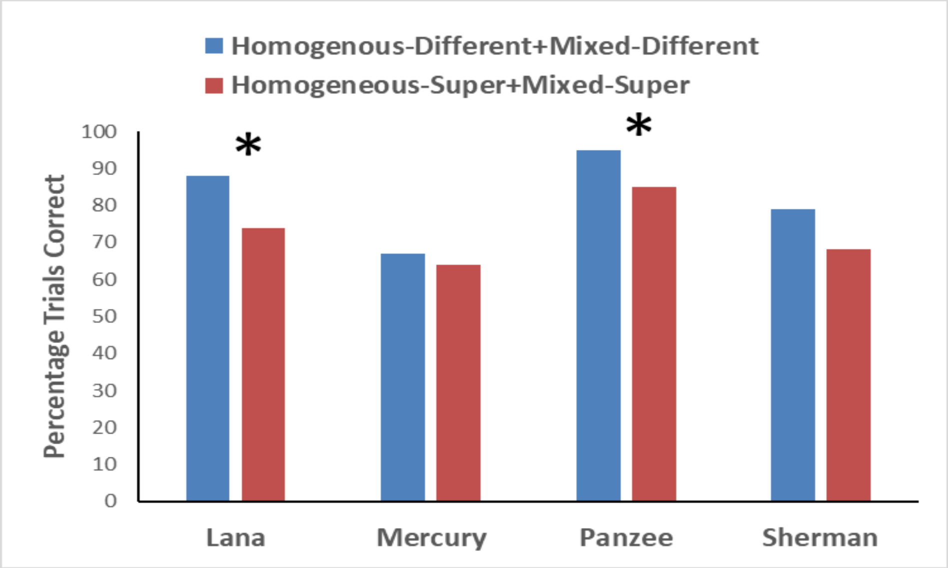

Figure 3. **Performance for the Isolate-Same and Isolate-Super trials compared to the Mixed-Same and Mixed-Super trials.** Asterisks indicate chimpanzees that showed a statistically significant difference.

False Memory

Figure 4 shows that performance was not different when comparing the Mixed-Same and Mixed-Super trials to the Homogenous-Same and Homogeneous-Super trials (Lana, $p = 0.16$; Mercury, $p = 0.23$; Panzee, $p = 0.29$; Sherman, $p = 0.38$). However, when comparing the Isolate-Same and Isolate-Super trials to the Isolate-Different trials, Lana ($p < 0.01$) and Sherman ($p = 0.03$) showed poorer performance when the foil came from the same category as the majority of the list items compared to when the foil was instead related to the isolate probe item. Mercury ($p = 0.37$) and Panzee ($p = 0.21$) did not show this effect (Figure 5).

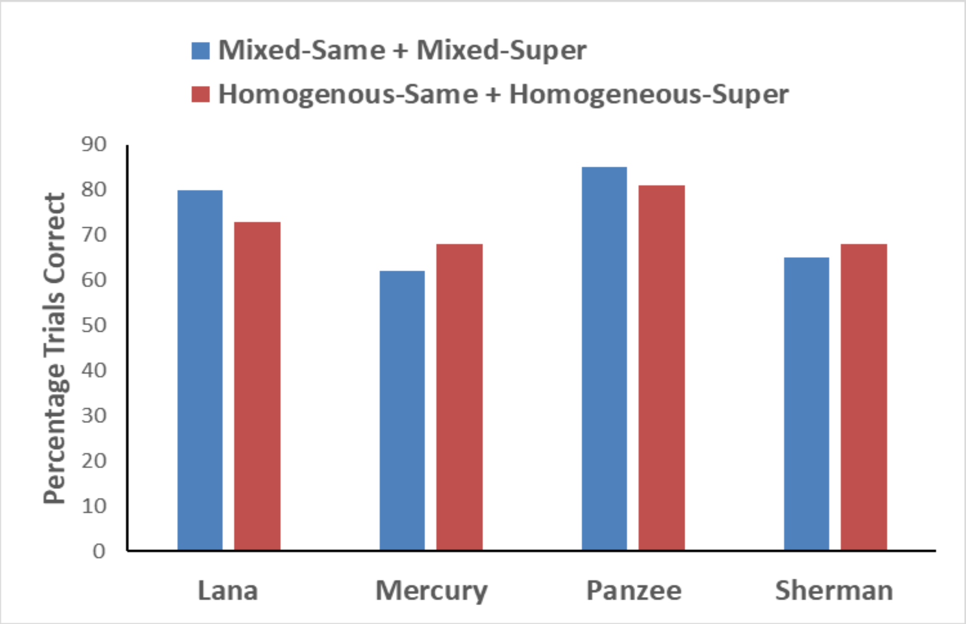

Figure 4. **Performance for the Mixed-Same and Mixed-Super trials compared to the Homogenous-Same and Homogeneous-Super trials.** No chimpanzees showed a difference for this comparison.

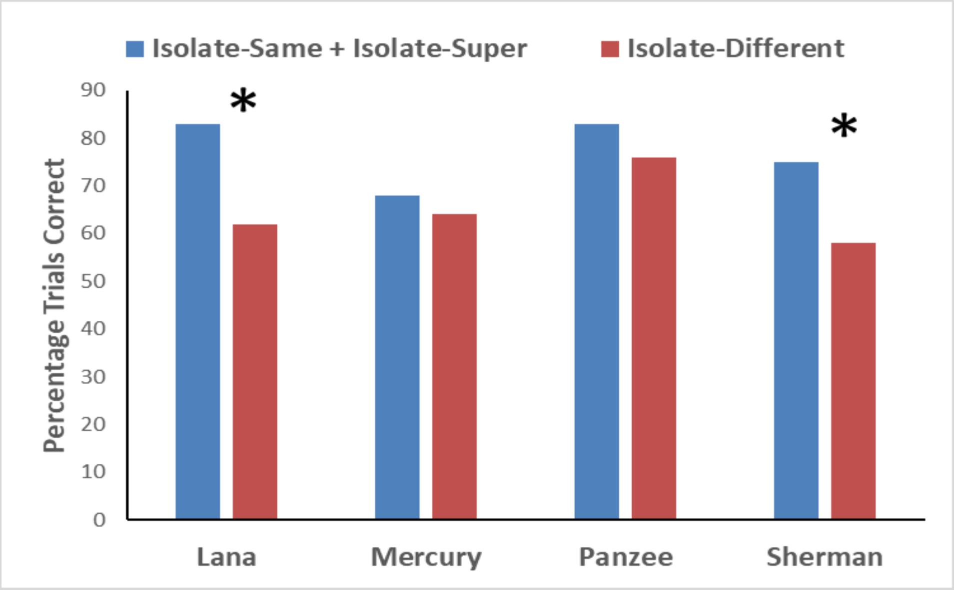

Figure 5. **Performance for the Isolate-Same and Isolate-Super trials compared to the Isolate-Different trials.** Asterisks indicate chimpanzees that showed a statistically significant difference.

Discussion

The results of this study were mixed and, in a few cases, reflected some trends toward human-like memory effects. A previous study found evidence of isolation effects in two of these subjects (Beran, 2011), whereas this experiment failed to replicate that outcome in any of the four chimpanzees. As noted, the results of Beran (2011) could have come from the joint contribution of not only an isolation effect, but also from some type of "false memory" experience by the chimpanzees. Isolate items were unique within lists, but the foil (incorrect) choices also were closely related to the other three list items. Thus, both effects might have contributed to that previous outcome.

The present work also expanded the same approach to separately identify DRM-like false memory and distinctiveness effects in the memory processing of nonhuman primates. Two of three language-trained chimpanzees showed improved performance when the foil (incorrect) stimulus presented at test was categorically distinct from the list. Sherman also trended in this direction but did not reach conventional levels of statistical significance. This outcome reflects a distinctiveness effect that is largely about exclusion of choices based on those items having not been in the list rather than accurate memory for what was in the list.

Finally, the evidence was inconsistent for false memory trials. In one comparison, there was no evidence that list organization and the similarity of a foil option to that list category affected performance. However, in another comparison, in which an isolate had been presented and was the correct stimulus at test, two chimpanzees showed more errors when the foil was related to the other three list items. This may indicate some categorical confusion at test, which is striking given that the isolate was the correct response option. This pattern is consistent with the robust finding in the DRM literature that people falsely recognize or recall items that were never actually presented (Roediger & McDermott, 1995).

There are several explanations for why individuals falsely recall or recognize items (Gallo, 2010). The associative activation model suggests that the critical lure becomes activated (either at encoding or retrieval) through spreading activation of a semantically organized conceptual system. The gist representation model suggests that individuals construct a gist representation, which summarizes the common semantic feature, and in turn activates the critical lure. Importantly, both models posit a critical role for an intact semantically organized conceptual network in establishing this memory error, a condition that has not been well established in nonhuman primates. Although there are clear indications that nonhuman animals are capable of various levels of categorization of stimuli (e.g., Bovet & Washburn, 2003; Vonk, 2003; Vonk & MacDonald, 2004; Wasserman et al., 2001), our findings extend the capacity of nonhuman primates to include semantic categorization similar to that demonstrated by humans, even if not all chimpanzees in all cases showed this.

Language undoubtedly plays a positive role in the ability of humans to use concepts to help structure and organize memory for lists of items. Given the extensive work and research program of Dr. Duane Rumbaugh, the chimpanzees Lana, Sherman, and Panzee all had unique experiences that involved language training in the form of symbol-referent learning, and these experiences may have aided in their use of conceptual framing of these lists. Their rearing histories and their abilities to use symbols may have led to unique memory processes; although with so few studies of conceptual list organization having been conducted with nonhuman animals and with the inconsistencies between and even within chimpanzees (across comparisons), this conclusion remains tentative. Chimpanzees (and other animals) may structure lists in ways that allow for false recognition or recall or enhanced recall because of distinctiveness, but, if they do, it is to a degree well below that to which human adults structure and organize lists in memory.

At the same time, one could argue that our tests are not sensitive enough to measure these memory effects in chimpanzees; thus, to argue for uniquely human memory processes is premature. We were forced to choose photographs of things that we knew, objectively, were familiar to these chimpanzees. But, without being able to query them as to their interest in those items or to query the degree to which they organize things in the same clusters we do, we are faced with the possibility that some items (or lists) are not as coherent as categories for chimpanzees as they are for us. These assumptions had to be made, but might produce limitations in the extent to which memory phenomena are demonstrated. To give an historical anecdote, chimpanzee Sherman was in a study (Savage-Rumbaugh, Rumbaugh, Smith, & Lawson, 1980) in which he was trained to sort items into the categories of food and non-food. He became very proficient at this, but, during the crucial test, he called a sponge a food. Savage-Rumbaugh et al. noted that, for Sherman, sponges sometimes were used to soak up liquids that he would then consume by sucking on, and, in some cases, chewing the sponge. For humans, a sponge is not a food, at least typically, but for Sherman it was. This is not to argue that those instances in which no effect was seen should be discounted. To the contrary, the best interpretation is that these kinds of memory effects in chimpanzees are limited compared to humans, but it is possible that future designs will be more ideally suited to assessing such effects.

One limitation of the present study was the short interval between list presentation and test. Typically, in human studies, long-term memory is assessed through a longer delay. Thus, our study allows for the chimpanzees to engage working memory throughout a trial rather than to have to encode, store, and retrieve information about the list stimuli. Future studies will be required that make use of much longer delays, and such a manipulation may increase the memory effects that are seen. As noted, our use of a short delay likely influenced the limited primacy effects that we saw in the overall data as has been seen in other studies as well (e.g., Wright, 1999). Longer delays could produce very different results.

These findings are consistent with the argument that memory-based phenomena need to be understood in terms of both structure and function (Nairne & Pandeirada, 2010). Several researchers have argued that false memories are a direct consequence of a powerful but adaptive reconstructive memory system (Newman & Lindsay, 2009; Schacter, Geurin, & St. Jacques, 2011). Schacter and Addis (2007) suggested that this flexible episodic remembering system is critical for imagining the future. Furthermore, Howe et al. (2011) reported that committing the DRM illusion may improve insight-based problem solving, which suggests that the errors indicative of a reconstructive memory system may carry benefits for other cognitive tasks. Evidence for false memories in chimpanzees could indicate that these nonhuman primates might also exhibit similar cognitive capacities, and comparative research of these basic memory phenomena has the potential to further highlight the evolutionary function of memory. At the same time, the consistent failure of Mercury to show any of these effects suggests that language-training, or symbol use, or enriched early rearing may lead chimpanzees to better organize and associate stimuli in ways that allow for isolates to be better remembered when presented in lists, allow isolates to be more easily discounted as foils, and perhaps to more readily choose stimuli as having been part of a semantically organized lists when those stimuli fit the category of that list.

This research adds to other work showing that several species can benefit from perceptual distinctiveness (Parker, Wilding, & Ackerman,1998; Reed, Chih-Ta, Aggleton, & Rawlins,1991) by also highlighting that semantic distinctiveness effects can occur in some cases. These findings may reflect a semantic organization system in chimpanzees similar to that shown in humans, given that distinctiveness involves both item-specific and relational processing (Hunt, 1995). Lana and Panzee demonstrated that they could use the presence of a distinctive foil to avoid making recognition errors. This finding is relevant to the distinctiveness heuristic in which people can correctly reject a recognition probe because it fails to meet some detail-oriented criteria of remembering. Together, these findings suggest that chimpanzees' semantic organization sometimes allows them to benefit from the presence of distinctive information in the environment and use it to correctly identify items from memory and to reject items not in memory.

Overall, the findings of the current study suggest several parallels between human and nonhuman memory processing but also some inconsistencies that could reflect methodological constraints or psychological differences in the memory systems of humans and chimpanzees. We conclude that some chimpanzees likely engaged in relational categorical memorial processing, and patterns of performance reflected improvement or decline as a result of this processing, similar to that found in humans. However, not all subjects showed all effects, suggesting the subtle nature of these phenomena and the continued need for exploration of nonhuman primate memory and cognition. Nonetheless, the unique opportunities and insights afforded by testing nonhuman apes, especially those who have been language-trained, are extremely relevant and critical. We owe great credit and appreciation to Dr. Duane Rumbaugh for his work to establish such a critically important line of research that has extended beyond his lifetime. Without his powerful vision and experimental rigor, this work would not have been possible nor would have emerged the many other revolutionary lines of research. This line of inquiry could uncover exciting insights into the evolutionary origins of memory processing in humans, as well as memory biases, and it will help continue to define the nature of human memory.

Acknowledgements

All applicable institutional rules and regulations regarding animal care and use were followed in the care and testing of the chimpanzees, and the experiment complied with all laws of the United States of America. We thank David Washburn for inviting us to submit this paper for the special issue honoring Duane Rumbaugh. BMP and MJB had the honor to serve as Duane M. Rumbaugh Fellows at Georgia State University, and Professor Rumbaugh was a mentor to each of them. Dr. Rumbaugh spent his career advocating for nonhuman primates, and, over the years, he shared many conversations with us about chimpanzee memory and cognition more broadly. We are thankful to have had the chance to be a part of those conversations and to have had the chance to work with the chimpanzees that were such a big part of his life.

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Financial conflict of interest: This research was supported by Grant HD-060563 from the National Institute of Child Health and Human Development.

Conflict of interest: No stated conflicts.

Submitted: *June 21st, 2018*
Resubmitted: *October 14th, 2018*
Accepted: *October 22nd, 2018*