INTERNATIONAL JOURNAL OF COMPARATIVE PSYCHOLOGY
2014, 27 (1), 31-49
Lance Miller & Heather Hill
Special Issue Editors
Peer-Reviewed

The Comparative Study of Learning from 1994-2013

Rachel E. Blaser and Carolina Bellizzi
University of San Diego, U.S.A.

The study of learning has long held a central position in the field of comparative psychology. Here we present a survey of the past 20 years of comparative learning research, covering publications from 1994 to 2013. We selected seven journals with a strong focus on comparative learning, and identified five major topics of study represented by the publications in those journals: non-associative learning, associative learning, perceptual/object learning, social learning, and neural correlates of learning. Of these topics, associative learning was by far the most popular, comprising about 85% of the research in comparative learning. We therefore subdivided this topic into seven subcategories of research questions, which included causal reasoning, compound cue interactions, extinction, stimulus control, outcome learning and motivation, spatial learning, and temporal integration or timing. The number of publications addressing each topic or research question, as well as the number of citations received by these publications, was examined for the combined seven journals across the 20 year period of review. The subject of spatial learning has grown rapidly over the past 20 years, and has attracted robust interest by researchers both in and outside of the field of comparative psychology. Although much less popular in terms of publication number, recent growth was also identified for studies of causal reasoning, social learning, and perceptual or object learning.

Throughout its history, the field of comparative psychology has been nearly synonymous with the study of learning. Since Thorndike (1911) proposed simple associative learning tasks as a standardizable metric for comparing cognitive abilities across species, the majority of comparative research has employed learning as a primary measure. Although comparative psychology has now expanded to include additional areas of study such as communication, social dynamics, and perception, learning research remains central to the field. Moreover, learning is a subject of interest to scholars outside the bounds comparative psychology, such as neuroscientists examining the biological bases of learning and memory as well as clinical and educational psychologists studying practical methods for behavioral change. As such, the number of questions being asked about learning is tremendous, and the range is varied. A Web of Science® search for 'learning' as a topic of research produced well over a million scholarly papers for the 20 year period spanning from 1994-2013. Moreover, the numbers are steadily growing, with the yearly publication count in Web of Science® more than tripling from 1994 to 2013. While much of this growth may well be attributable to changes in journal publishing and indexing standards, our results are largely consistent with those of an earlier report by Domjan and Krause (2002) indicating that the field of learning has not languished over the past century.

In order to produce a review that would be manageable and relevant to comparative psychologists, the review parameters needed to be narrowed considerably. Therefore, we first decided to take a comparative perspective, and include only studies of learning in nonhuman animals, or if human subjects were used, only those which addressed learning phenomena amenable to comparative study (e.g., classical conditioning, habituation, imitation). Next, we excluded studies using learning merely as a tool for the investigation of other questions, such as using self-administration procedures to study drug addiction, or the use of a spatial task to study the function of the hippocampus, including only experiments that were designed to address novel questions about learning. Finally, we limited our search to a subset of academic journals whose focus most closely fit the previous criteria. This review therefore by necessity encompasses only a small sample of the available research on learning, but a sample that is representative of current trends and directions in the field. Academic Search Complete® (through EBSCO) and Web of Science® databases were primarily used to extract the numbers summarized here, occasionally in conjunction with the journals' own websites or archives.

Given the breadth of scientific interest in learning, countless journals accept articles on the topic as it relates to their specific focus. However, only a handful of journals make comparative learning a high priority for publication. We selected seven journals to include in the review, all of which regularly publish articles on non-human animal learning from a behavioral, comparative perspective. The selected journals include (in

Correspondence concerning this article should be addressed to Rachel E. Blaser, Department of Psychological Sciences, University of San Diego, 5998 Alcala Park, San Diego, CA 92110, Phone: (619) 260-7736, Fax: (619) 260-6867.(rblaser@sandiego.edu)

alphabetical order): *Animal Cognition* (AC); *International Journal of Comparative Psychology* (IJCP); *Journal of Comparative Psychology* (JCP); *Journal of Experimental Psychology: Animal Behavior Processes* (JEP:ABP); *Learning and Behavior* (L&B: previously *Animal Learning and Behavior*); *Learning and Memory* (L&M); and *Quarterly Journal of Experimental Psychology* (QJEP: Section B prior to 2006). The top publishers of comparative learning research include the American Psychological Association and Springer press. Of these journals, JEP:ABP, L&B, and QJEP focused almost exclusively on questions central to learning, and publish the largest proportion of relevant research.

In the seven listed journals, roughly 2600 articles have been published on the subject of learning in the period from 1994 to 2013, averaging about 18 articles each year per journal. The absolute number of learning articles has risen steadily over the 20 years of the review period, roughly doubling in each decade (see Figure 1a). As noted, however, this apparent growth may well be due to growth in the total number of articles published and indexed in these databases, rather than an increase in the relative popularity of learning research. When 'learning' articles are considered as a proportion of the total number of articles indexed in those seven journals each year, that proportion remains roughly constant across the past 20 years (see Figure 1b).

Within the general field of learning, we identified five major topics that were commonly studied. These include non-associative learning (habituation and sensitization), perceptual and object learning (or learning in the absence of explicit reinforcement), associative learning (including both classical and operant conditioning), social or observational learning, and neural correlates of learning and memory. Of these five, the topic of associative learning encompassed about 85% of the research, so we further subdivided this category into seven subcategories: causal learning/reasoning, compound cue interactions, extinction, stimulus control, outcome learning and motivation, spatial learning, and timing/temporal integration. For each topic and subcategory, we identified the number of articles on that topic published each year (combined across the seven journals). To obtain a clearer sense of the impact of the research questions, we then identified the total number of times that those articles have been cited, and the proportion of citations (compared to the total for all learning articles in the reviewed journals). Although the citation count produces a substantial bias for articles published earlier in the review period, it may still provide a useful index of which topics are currently most popular. Finally, we identified the 10 most cited learning articles in the reviewed journals (from 1994-2013), as well as the most relevant articles on learning published in *Science* and *Nature*, to determine which research topics attract the most interest from the broader scientific community. See Table 1 for a summary of these data.

Non-Associative Learning

The study of non-associative learning comprised only about 3% of learning research, which remained roughly constant across 20 years (see Figure 2a). These publications account for about 4% of the citations of the reviewed papers (see Table 1). There was no clear directional focus within non-associative learning, with articles covering miscellaneous topics such as the neural basis of habituation (Bristol & Carew, 2005; Paranjpe, Rodrigues, VijayRaghavan, & Ramaswami, 2012) and sensitization (Barbas, DesGroseillers, Castellucci, Carew, & Marinesco, 2003), novel techniques or animal models (Bee, 2001; Riedel, 1998), or habituation as a component of other questions (e.g., the effects of habituation to an outcome in an associative learning task (De Brugada, González, Gil, & Hall, 2005)). Although there were a few studies asking direct questions about the mechanisms of habituation (e.g., Bee, 2001; Hawkins, Cohen, & Kandel, 2006; Sanderson & Bannerman, 2011), overall this has not been a common topic for research within the field of comparative learning. This is unfortunate, since a thorough understanding of basic non-associative learning processes is essential for subsequent interpretation of other phenomena such as perceptual and associative learning. A number of unanswered questions remain on issues such as the differences in mechanism between long- and

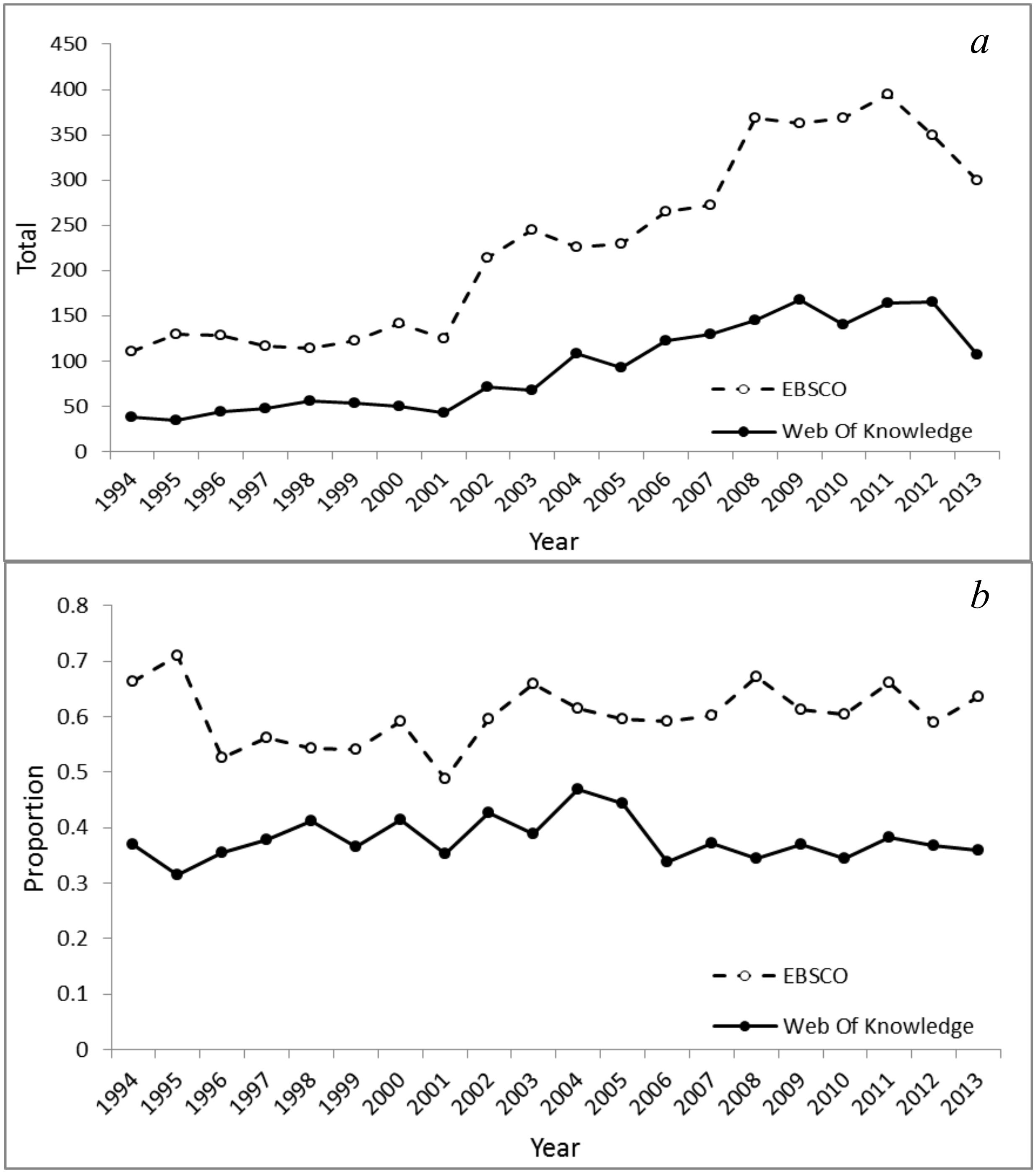

Figure 1. In the upper panel of Figure 1 (a) are plotted the total number of papers on the topic of learning published in the seven reviewed journals over the past 20 years, as reported by two major databases. In the lower panel of Figure 1 (b) are plotted the same set of publications, converted into a proportion of the total number of articles indexed by those two databases for the seven reviewed journals. Although the total number of learning articles has grown rapidly, the proportion of published/indexed articles devoted to learning has remained roughly constant.

short-term habituation, interactions between habituation and sensitization, and stimulus effects such as habituation to different stimulus modalities or generalization across stimuli. Therefore, while non-associative learning is not currently a popular topic of study, this is one area in which further research would likely be quite beneficial to the field of comparative psychology.

Table 1

Proportion of publications and citations received by each learning subtopic

Research Topic	Proportion of Publications 1994-2013	Proportion of Publications 2009-2013	Proportion of Citations 1994-2013	Most Cited Learning Publications*
Non-Associative Learning	0.03	0.03	0.04	
Perceptual and Object Learning	0.04	0.05	0.05	McLaren & Mackintosh, 2000
Associative Learning				Bouton, 1994
Causal Reasoning	0.06	0.07	0.05	
Compound Cue Interactions	0.10	0.10	0.07	
Extinction	0.11	0.09	0.09	Bouton, 2004
Stimulus Control	0.07	0.07	0.06	
Outcome Learning and Motivation	0.10	0.12	0.08	Dickinson & Balleine, 1994
Spatial Learning	0.30	0.38	0.23	
Temporal Integration and Timing	0.15	0.18	0.12	
Social and Observational Learning	0.04	0.05	0.04	Laland, 2004 Whiten, 1996 Farabaugh, 1994
Neural Correlates of Learning	0.16	0.14	0.28	Sara, 2000 Hammer & Menzel, 1998 Christian & Thompson, 2003

* This column represents the ten publications most frequently cited (as of October 2013) from the seven reviewed journals on the topic of learning

Perceptual and Object Learning

Perceptual learning and object recognition, or related questions of recognition memory and object perception that may occur in the absence of explicit reinforcement, comprised about 4% of learning research, with some growth in recent years; there were almost no articles on this subject in the reviewed journals during the first 5-year span from 1994-1998, but the topic grew to about 5% of learning papers in the most recent span from 2009-2013 (see Figure 2a). These publications account for about 5% of the citations for the reviewed articles (see Table 1).

Perceptual learning refers to enhanced discrimination between stimuli following pre-exposure to them, and research on this topic has focused on explaining this effect. Although most perceptual learning studies use associative learning procedures, the key processes involved may be non-associative in nature (i.e., resulting from familiarity or salience of stimulus elements), so we chose to categorize it separately. A commonly reported effect is that discrimination of stimuli A and B is enhanced when they are pre-exposed in alternation rather than separately (e.g., Artigas, Sansa, Blair, Hall, & Prados, 2006; Blair & Hall, 2003; Blair, Wilkinson, & Hall, 2004). A good deal of research on perceptual learning has therefore aimed to explain this effect, either as a result of changes in the salience of stimulus elements of A and B, through the establishment of inhibitory associations between A and B, or other possible mechanisms (e.g., Artigas, Contel, Sansa, & Prados, 2012; de Zilva & Mitchell, 2012; Mundy, Dwyer, & Honey, 2006; Rodriguez, Blair, & Hall, 2008). One of the most

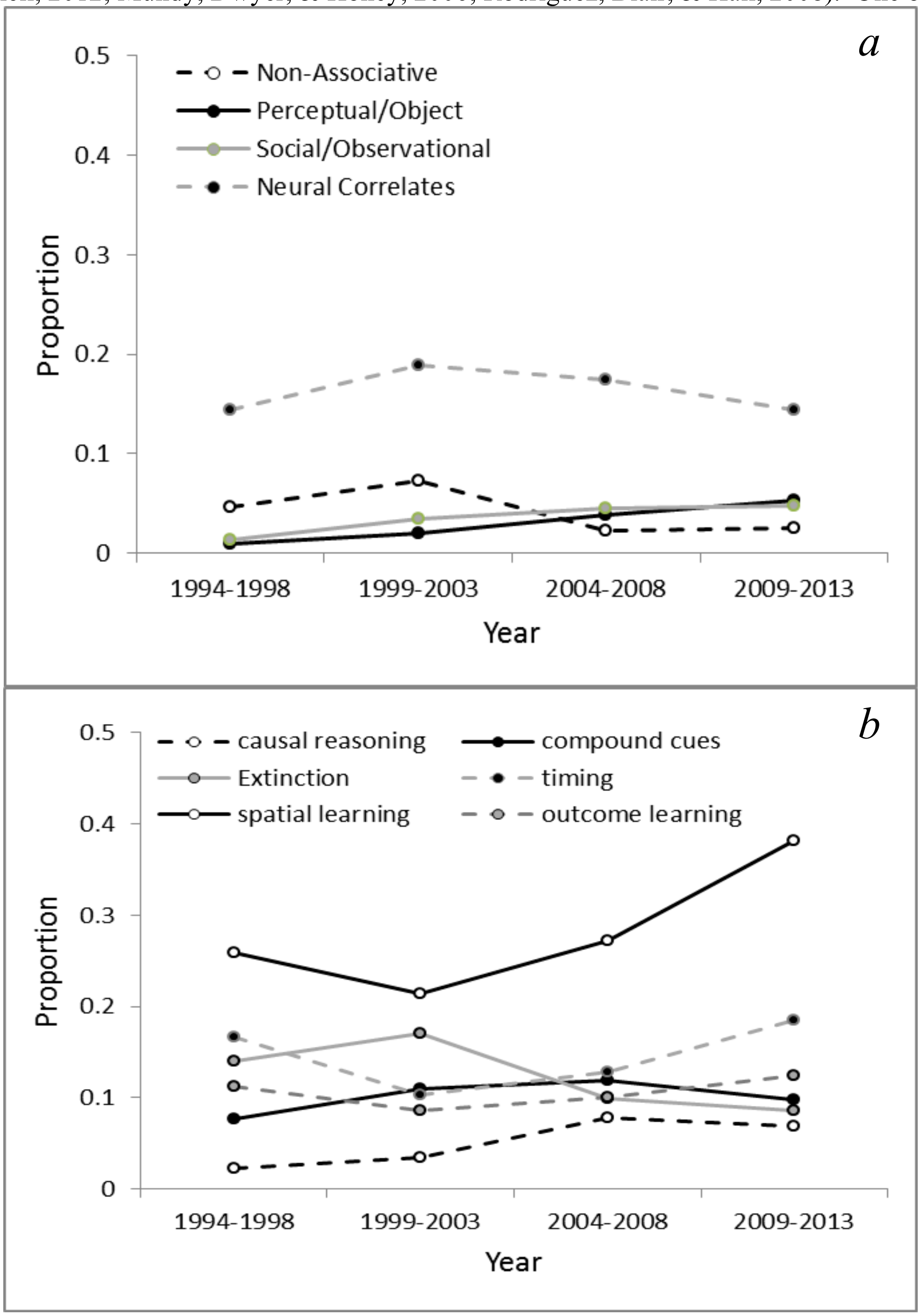

Figure 2. In the upper panel of Figure 2 (a) are plotted four of the five major topics of study in learning, in terms of the proportion of total learning publications devoted to that topic. In the lower panel of Figure 2 (b), the subcategories of the fifth major topic (associative learning) are plotted in terms of the proportion of total learning publications devoted to that subtopic.

highly cited publications from the past 20 years, although primarily a theoretical article introducing a new model of learning, did so from the perspective of perceptual learning (McLaren & Mackintosh, 2000).

Moreover, research on perceptual learning is clearly of interdisciplinary interest; perceptual learning, often from the perspective of cognition, computer modeling, or neuroscience, was the learning subtopic to most frequently appear in *Science* and *Nature* (e.g., Ahissar & Hochstein, 1997; Dinse, Ragert, Pleger, Schwenkreis, & Tegenthoff, 2003; Law & Gold, 2008; Tsodyks & Gilbert, 2004; Watanabe, Náñez, & Sasaki, 2001).

Object recognition and memory studies address a similar question of which features are used in object perception and how these are bound together (Cook & Katz, 1999; Peissig, Kirkpatrick, Young, Wasserman, & Biederman, 2006; Spetch, Friedman, & Vuong, 2006), and of how familiar objects are discriminated from novel objects (Whitt, Haselgrove, & Robinson, 2012). Although the study of object perception/recognition and perceptual learning is still rather limited, it does appear to be growing in popularity. Moreover, it represents a relatively focused set of questions and hypotheses that is amenable to real progress over the next decade of research.

Associative Learning

Experiments on associative learning processes account for roughly 85% of learning experiments, growing slightly from about 80% to about 90% over the past two decades. Including experiments on both classical and operant conditioning, associative learning is by far the most popular subject of study. This broad topic includes several popular subcategories, including causal learning/reasoning, compound cue interactions, extinction, stimulus control, outcome learning and motivation, spatial learning, and timing/temporal integration.

Causal Reasoning

Studies on causal learning, propositional reasoning, and dissociations between explicit and implicit associative processes account for about 6% of learning research. These publications account for about 5% of the citations for the reviewed articles (see Table 1). Although by no means a new question, the publication of Blaisdell et al.'s controversial article in *Science* (2006) on causal reasoning in rats prompted widespread proliferation of research on related questions, growing substantially from virtually 0% in the first 5 year period to roughly 10% in the most recent 5 years (see Figure 2b). The general question here is whether dissociable mechanisms exist for implicit conditioning and explicit causal or propositional reasoning, and how widespread the latter is across species (Dwyer, Starns, & Honey, 2009; Polack, McConnell, & Miller, 2013; Simms, McCormack, & Beckers, 2012). One central issue is whether apparent causal reasoning, in humans or in non-human animals, can be parsimoniously explained using simple associative models such as the Pearce (Pearce, 2002) or Rescorla-Wagner (Rescorla & Wagner, 1972) models of learning (Dwyer et al., 2009; Polack et al., 2013; Simms et al., 2012). Results so far have indicated that human performance on causal tasks closely resembles that of rats, suggesting that there is unlikely to be a clear divide between human and non-human capabilities. However, a variety of conflicting results makes interpretation difficult, and the degree to which similarities are based on common associative processes or more complex propositional reasoning is still debated. Additionally, the dissociation between implicit and explicit learning, and the role of awareness in human learning, is of widespread interest, having also appeared several times in top journals (e.g., Bayley, Frascino, & Squire, 2005; Clark & Squire, 1998; Rugg et al., 1998). This topic has grown dramatically over the past decade and appears to be a promising and interesting direction for future research.

Compound Cue Interactions

Questions about compound cue interaction effects comprised about 10% of learning research each year (see Figure 2b). These publications account for about 7% of the citations for the reviewed articles (see Table 1). These include questions of how manipulation of one cue may affect learning about another cue with which it is simultaneously reinforced (e.g., overshadowing, potentiation), with which it has been previously paired (e.g., sensory preconditioning, retrospective revaluation), or with which it is subsequently paired (e.g., forward blocking). This general set of questions involves theoretical issues of whether compound stimuli are processed elementally or configurally (e.g., Allman & Honey, 2006; Gonzalez, Quinn, & Fanselow, 2003; Harris, Gharaei, & Moore, 2009; Lachnit, Schultheis, Konig, Ungor, & Melchers, 2008), under what conditions stimulus elements compete with each other for associative strength (Pearce, Graham, Good, Jones, & McGregor, 2006; Urcelay & Miller, 2009), and in what ways reinforcement of one stimulus can affect responding to an absent but associated stimulus (Blaser, Couvillon, & Bitterman, 2004; Bradfield & McNally, 2008; Dopson, Pearce, & Haselgrove, 2009; Luque, Flores, & Vadillo, 2013). The results of these experiments suggest that a number of parametric variables such as the CS-US interval, pairing frequency, US intensity, and stimulus modality, may affect cue interactions, although in most cases additional exploration and replication are required to establish these effects. While this topic of research encompasses a very broad set of experimental questions and designs, most of the work is bound by a common theoretical basis which has allowed for some degree of progress over the past two decades. Although it has not grown significantly in popularity, the question of compound cue interactions remains a robust topic of research for which we have some promise of future progress. In particular, as more empirical data are collected concerning factors that affect cue interactions, it will be imperative to develop new theories that can successfully incorporate these results and provide direction for future inquiry.

Extinction

About 10% of learning studies each year have dealt with questions of extinction, making this a consistently popular subject of research (see Figure 2b). These publications account for about 9% of the citations for the reviewed articles (see Table 1). Despite its popularity, and in contrast to the topic of cue competition, there is not a clear central focus to the extinction research. This is likely due to applied pressures on research in this domain – many of the experiments addressed issues relating to reinstatement, spontaneous recovery, or neural mechanisms of extinction as they relate to drug addiction, post-traumatic stress disorder, phobias, and other psychiatric disorders. To this end, there have been a large number of studies presenting the effects of various parametric variables, such as trial number, trial spacing, outcome intensity or exposure, and experimental context on the efficiency of extinction or probability of recovery (e.g., Cain, Blouin, & Barad, 2003; Li & Westbrook, 2008; McAllister & McAllister, 2006; Morris, Furlong, & Westbrook, 2005; Rauhut, Thomas, & Ayres, 2001; Westbrook, Iordanova, McNally, Richardson, & Harris, 2002), without a centralized attempt to integrate these variables into new theoretical predictions. Nonetheless, a number of studies were also designed to address the mechanisms by which extinction occurs – and even those not so designed can provide results with theoretical implications. Although the suggestion that extinguished associations remain intact is not new, there were additional demonstrations of this retention as well as further inquiry into the nature of the associative changes that occur during extinction (Kehoe & White, 2002; Leung, Bailey, Laurent, & Westbrook, 2007; Rescorla, 2001, 2004, 2006). As is the case for the study of compound cue interactions, the past 20 years have led to an accumulation of empirical data that are not yet accommodated by current learning theories. Here again there has been recent progress, the continuation of which will be facilitated by an effort to incorporate the data into a set of theoretical predictions for future research. The popularity of this topic outside of narrow associative learning is illustrated by the fact that the most highly cited article from the reviewed publications is on the topic of extinction (Bouton, 2004).

Stimulus Control

Nearly 35% of learning articles were classified by the search databases as addressing stimulus control, although this is likely due to the applicability of stimulus questions to nearly all of the other domains of research. When only experiments with a central focus on the mechanisms of stimulus control are included, this number is closer to 4-8% of learning research (not included in Figure 2, since accurate values were difficult to determine). These publications account for about 7% of the citations for the reviewed articles (see Table 1).

There were four basic topics within stimulus control research: category formation, sequence/serial learning, concept learning (such as same/different) and a miscellaneous category including how choice of stimuli affects other learning processes. The first included stimulus equivalence and category formation – how animals perceive or learn categories, and how this information is encoded and used (e.g., Astley, Peissig, & Wasserman, 2001; Honey & Ward-Robinson, 2002; Jitsumori, Shimada, & Inoue, 2006; Loidolt, Aust, Meran, & Huber, 2003; Urcuioli, 2007). Included in this topic are the more basic questions about how animals discriminate stimuli and manipulations that affect generalization gradients (Lazareva, Miner, Wasserman, & Young, 2008; Livesey & McLaren, 2009; Pearce, Esber, George, & Haselgrove, 2008). The second topic is of serial or sequence learning, and how animals encode and correctly select sequences of stimuli or behaviors. The question here is whether standard associative processes can account for serial ordering, and which cues (e.g., position of stimuli, previous stimuli or responses) control behavior in these tasks (e.g., Burns, Dunkman, & Detloff, 1999; Capaldi, Alptekin, Miller, & Birmingham, 1997; Capaldi & Miller, 2004; Swartz, Chen, & Terrace, 2000; Treichler, Raghanti, & Van Tilburg, 2003). The third topic is concept formation, with the goal of determining how abstract concepts – virtually always the concept of same/different – are learned and used (e.g., Blaisdell & Cook, 2005; Gibson & Wasserman, 2003; Smith, Redford, Haas, Coutinho, & Couchman, 2008; Wasserman, Frank, & Young, 2002). The final category involves the relationship between generalization or discrimination and perceptual learning or other processes such as cue competition or spatial learning (Blaser, Couvillon, & Bitterman, 2006; Chamizo, Rodriguez, Espinet, & Mackintosh, 2012; Gonzalez et al., 2003; Thorwart & Lachnit, 2009). The popularity of the core question (basic mechanisms of generalization) has not changed much and has in fact remained rather low, but its relevance to growing areas of research, such as spatial learning, numerical cognition, temporal discrimination, and perceptual learning, have supported continued widespread interest in this domain (Brannon & Terrace, 1998; Giurfa, Zhang, Jenett, Menzel, & Srinivasan, 2001; Kamil & Jones, 1997; Ohl, Scheich, & Freeman, 2001).

Outcome Learning and Motivation

Learning about outcomes, differential learning between outcomes, or the effects of motivation for specific outcomes, accounted for about 10% of learning research each year (see Figure 2b). These publications account for about 8% of the citations for the reviewed articles (see Table 1). A central question was which qualities of an outcome are learned during conditioning (e.g., sensory vs. motivational qualities (Bonardi & Jennings, 2009; Delamater, Campese, LoLordo, & Sclafani, 2006; Delamater, LoLordo, & Sosa, 2003; Scarlet, Campese, & Delamater, 2009)), or similarly how different outcomes (or different motivational drives for a particular outcome) affect what is learned (Balleine & Dickinson, 2006; Le Pelley, Mitchell, & Johnson, 2013; Lotz & Lachnit, 2009). Results have indicated that associations are frequently outcome-specific, in that the animal learns to associate a particular stimulus or response with both the sensory and motivational consequences of a particular outcome, but the precise nature and degree of specificity of these associations remains unclear. Although this was a relatively small area of research, one of the ten most highly cited publications was on the topic of motivation and goal-directed behavior (Dickinson & Balleine, 1994).

Spatial Learning

Spatial learning has been one of the largest areas of research, as well as the fastest-growing. Overall, spatial learning experiments comprised about 30% of learning studies across the past 20 years, growing from about 25% in the first five years to nearly 40% in the most recent five (see Figure 2b). These publications account for about 23% of the citations for the reviewed articles (see Table 1). Within the domain of spatial learning, one of the central questions is how well it fits into a standard associative learning framework, or to what degree spatial learning is unique from other forms. Although the results of some experiments have suggested that spatial learning may be unique (Brown, Yang, & DiGian, 2002; Kamil & Jones, 2000; McGregor, Horne, Esber, & Pearce, 2009), with a specialized module for integrating geometric cues, more recent research has suggested that this may not be the case. In fact, many familiar effects involving compound cue interactions, such as blocking and overshadowing, have also been observed in the domain of spatial learning (Kosaki, Austen, & McGregor, 2013; Pearce et al., 2006; Sansa, Rodrigo, Santamaria, Manteiga, & Chamizo, 2009). An additional set of studies has addressed the integration of spatial and temporal cues, with mixed evidence for integration depending on the experimental design and species (Clayton, Yu, & Dickinson, 2001; Crystal & Miller, 2002; Hoffman, Beran, & Washburn, 2009; Pizzo & Crystal, 2004; Skov-Rackette, Miller, & Shettleworth, 2006; Thorpe & Wilkie, 2006). A model attempting to integrate spatial and associative learning has been proposed (Miller & Shettleworth, 2007), although its validity is still being tested (Dawson, Kelly, Spetch, & Dupuis, 2008; McGregor et al., 2009; Miller & Shettleworth, 2008).

Spatial learning has also become the darling of neuroscientists interested in the biological basis of learning and memory (Bannerman, Good, Butcher, Ramsay, & Morris, 1995; Moser, Krobert, Moser, & Morris, 1998). Most of this research fell outside of the reviewed literature, since the focus was not on the mechanisms of spatial learning per se but rather on the function of the hippocampus or some other physiological system. Still, there is the potential for neurobiological manipulations to inform our understanding of the learning processes themselves (e.g., Pearce, Good, Jones, & McGregor, 2004), and the wider interest in spatial learning has likely helped to stimulate the considerable behavioral research in this domain.

Timing

Questions of temporal integration and timing comprised about 15% of learning experiments, having grown from about 12% to nearly 18% over the past two decades (see Figure 2b). These publications account for about 12% of the citations for the reviewed articles (see Table 1). The relative popularity of this topic is likely because it is widely applicable to other areas of learning; timing studies range from the role of inter-stimulus and inter-trial interval on the formation of associations (Amundson & Miller, 2008; Denniston, Blaisdell, & Miller, 2004; Stout, Chang, & Miller, 2003; Urcelay, Wheeler, & Miller, 2009) to the integration between time/place cues in spatial learning (Clayton et al., 2001). As such, most of the research on timing was not focused around a central question of how time is perceived or learned, but instead on a rather miscellaneous set of questions about how temporal manipulations affect other aspects of learning. Nonetheless, within this category was a core set of experiments designed to test models of temporal discrimination, including manipulations that affect perception and discrimination of temporal cues (Bizo & McMahon, 2007; Guilhardi & Church, 2005; Kirkpatrick & Church, 2003; Machado & Pata, 2005), or models of temporal coding of associations (Arcediano, Escobar, & Miller, 2003; Balsam, Fairhurst, & Gallistel, 2006; Denniston et al., 2004).

Social/Observational Learning

Experiments on imitation, observational learning, and social facilitation comprise about 4% of learning research in the surveyed journals. Over the past two decades, interest in social aspects of learning has grown, with numbers increasing from about 1% to about 5% over the past two decades (see Figure 2a). These publications account for about 4% of the citations of the reviewed papers (see Table 1). In the past 10 years, three special issues have been published on social learning – two by Learning and Behavior in 2004 and 2010, and a third in 2012 by the Journal of Comparative Psychology – which may account for the relatively large number of publications in the second half of the review period. Questions about social learning employed a much more varied selection of model species than those of associative learning, so one of the common research questions entailed the description of novel species or techniques for examining social learning (e.g., Davis & Burghardt, 2011; Gajdon, Fijn, & Huber, 2004; Holzhaider, Hunt, & Gray, 2010; Suboski et al., 1990). Within social learning, there was a strong focus on imitation (Akins, Klein, & Zentall, 2002; Carrasco, Posada, & Colell, 2009; Dorrance & Zentall, 2001, 2002; Klein & Zentall, 2003; Mottley & Heyes, 2003; Saggerson, George, & Honey, 2005; Stoinski, Wrate, Ure, & Whiten, 2001; Yunger & Bjorklund, 2004);

primarily including attempts to demonstrate imitation (as opposed to other forms of social facilitation) in a particular species or under certain conditions (Mottley & Heyes, 2003; Stoinski et al., 2001), but also with some questions about the mechanisms of imitation, or which features of a task are learned during imitation (e.g., Saggerson et al., 2005). Although far less common than imitation, there were also studies of cultural transmission of behavior (Freeberg, 2004; McGuigan, 2012), as well as experiments involving observational effects on the kinematic features of motor responses (Hardwick & Edwards, 2011, 2012; Salama, Turner, & Edwards, 2011). Although the total number of social learning articles was rather low, three of the ten most highly cited articles from the reviewed journals were on the topic of social learning (Farabaugh, Linzenbold, & Dooling, 1994; Laland, 2004; Whiten, Custance, Gomez, Teixidor, & Bard, 1996). Additionally, a paper on imitation in nonhuman primates was published in *Science* (Subiaul, Cantlon, Holloway, & Terrace, 2004) suggesting that this subject is of substantial general interest.

Neural Correlates of Learning and Memory

Neural correlates of learning comprised about 16% of papers in the surveyed articles (see Figure 2a), although the question is addressed more widely in other journals with a stronger focus on neuroscience or physiology. This is reflected in the citation count – nearly 28% of citations are to this topic, which is clearly of interest to researchers outside of the reviewed journals (see Table 1). At least within these journals, most articles had a focus on applied questions such as the physiological mechanisms of extinction or reward pathways for understanding the neurobiology of drug addiction, post-traumatic stress disorder, and other human pathologies (e.g., Lebron, Milad, & Quirk, 2004; Milton, Lee, & Everitt, 2008; Peters, Kalivas, & Quirk, 2009; Sokolowska, Siegel, & Kim, 2002; Stafford, Maughan, Ilioi, & Lattal, 2013; Twining, Tuscher, Doncheck, Frick, & Mueller, 2013). However, some researchers were also interested in using neurobiological techniques to attempt to unravel the processes that produce various forms of associative learning (Berman, Hazvi, Stehberg, Bahar, & Dudai, 2003). Overall, nearly every other topic of learning was represented from a neurobiological perspective to some degree, so the identification of a single unifying direction of research is difficult. However, some direction may be provided by three articles on this general subject which were among the 10 most highly cited publications; one was on the neurobiology of retrieval and reconsolidation (Sara, 2000), one was on the neurobiology of olfactory learning in honeybees (Hammer & Menzel, 1998), and one was on the neural substrates of eyeblink conditioning (Christian & Thompson, 2003). While the largest number of papers may therefore have dealt with miscellaneous applied topics, the most highly cited articles address the biological mechanisms of basic associative processes. Additionally, within the journals *Science* and *Nature*, a popular topic was on the role of dopamine in basic error-correction or reinforcement processes, which may have considerable relevance to the study of fundamental learning mechanisms (Flagel et al., 2010; Pessiglione, Seymour, Flandin, Dolan, & Frith, 2006; Stuber et al., 2008; Waelti, Dickinson, & Schultz, 2001).

Conclusions

As might be expected given the long history and widespread interest in questions about learning, recent comparative learning experiments are extremely diverse in both techniques and research goals. This diversity of questions and approaches has led to some fragmentation of the field, although many of the questions are quite interrelated even across category divisions. In some cases, such as perceptual learning, the various research questions represent a genuinely unified series of experiments driven by a central theoretical question or controversy. In others, such as non-associative learning, the primary unifying characteristic is simply a common procedure with little theoretical focus. Central theoretical controversies could be readily identified in the subjects of spatial learning, perceptual learning, and causal learning – three areas demonstrating especially strong recent growth (in terms of publication number) as well as better than average scientific progress. The results of experiments across several domains, including extinction (or non-reinforcement more generally), cue compounding, and perceptual learning, provide instructive data that are inconsistent with old learning models, and invite the development of new ones. For example, it may be necessary to better integrate acquisition and performance effects, to better incorporate temporal and stimulus modality information, to re-think the representation of extinction, and to develop more complex associations between stimuli than are currently accommodated. Some recent efforts have been devoted to model development (e.g., Harris, 2006; Le Pelley, 2004; McLaren & Mackintosh, 2000; Miller & Shettleworth, 2007), but given the utility of models in directing future research, further efforts are warranted.

From the perspective of comparative psychology, it is notable that relatively little learning research was truly comparative in nature – certainly not a sufficient number of experiments to warrant a separate topic of species differences or generality. In this, our results parallel those of a similar review by Shettleworth (2009) of the entire field of comparative psychology, in which only 5-10% of surveyed publications compared more than one species. As was reported by Bitterman (2006) for the field of classical conditioning, the vast majority of experimenters assumed generality of effects across techniques and species, and employed traditional animal models (rats and humans for associative learning, pigeons, non-human primates and humans for perceptual learning and stimulus control) for reasons of convention or convenience. The exception to this might be the question of causal reasoning, in which one focus is whether human causal reasoning is unique from that of other species (Dwyer et al., 2009; Mitchell, Harris, Westbrook, & Griffiths, 2008; Polack et al., 2013; Simms et al., 2012), although even here most experiments used either humans or rats, and were not explicitly comparative in design. Some of the research topics, most notably social learning, did employ a wider diversity of animal models (e.g., Davis & Burghardt, 2011; Gajdon et al., 2004; Holzhaider et al., 2010), but the goal was often to simply demonstrate some effect in a novel species (or to review results obtained with that species) rather than a systematic attempt to analyze similarities or differences in some learning phenomenon across species. Given the often conflicting results that have led to theoretical controversies, it may be well to revisit the question of generality more explicitly, particularly as it applies to different conditioning techniques and experimental parameters.

Finally, although learning continues to be a strong focus of research within comparative psychology, nearly all of the questions are also directly or indirectly relevant to related disciplines including neuroscience and clinical psychology. Experiments on the neurobiology of learning accounted for a relatively low proportion of publications within the surveyed journals (since those with an explicitly neurobiological rather than behavioral focus were excluded from review), but this was by far the most highly cited set of papers. For this reason, journals publishing a larger number of papers with a neurobiological focus have higher impact factors than those with a stronger focus on behavioral, comparative research, and may therefore attract some of the more innovative papers. In fact, given the prevalent interest in learning research, there are surprisingly few journals that publish purely behavioral experiments on the topic. Even the best of these journals (e.g., L&B, JEP: ABP, QJEP) do not appear to be widely read and cited by researchers outside of the domain of comparative learning. Therefore, one challenge for future research may be ensuring that the results of purely behavioral learning studies are accessible and even promoted to researchers from other disciplines to which they are relevant. At the same time, it is important that the nature of the research questions themselves be driven internally rather than imposed by funding or other priorities from outside of the field.

In conclusion, comparative learning has continued for over 100 years to be a robust field of scientific inquiry, in which hundreds of experiments are undertaken each year. Topics of research in which there has been sustained interest over the past 20 (or more) years include those about the mechanisms of extinction, temporal integration, and compound cue interactions. Questions of recently growing interest include the mechanisms of spatial learning, perceptual learning, and causal reasoning, all of which have received substantial interest from interdisciplinary researchers outside of the field of learning. In addition to identifying popular research questions, we also suggest two major challenges for researchers in comparative learning. The first challenge is to resist further fragmentation within the field, by maintaining a focus on theoretical questions that provide structure to the research process. This effort might be further improved by careful consideration and standardization of the species, techniques, and parameters employed when designing experiments, to ensure that results can be compared across laboratories (Bitterman, 2006). The second challenge is to improve the accessibility of learning research to scientists from related disciplines, without sacrificing the integrity of the research questions. One approach to accomplishing this goal might be to employ high-quality review articles and special issues in behavioral journals that discuss how progress in our understanding of basic learning mechanisms can be applied in other disciplines.

References

Ahissar, M., & Hochstein, S. (1997). Task difficulty and the specificity of perceptual learning. *Nature, 387*, 401-406.

Akins, C. K., Klein, E. D., & Zentall, T. R. (2002). Imitative learning in Japanese quail (*Coturnix japonica*) using the bidirectional control procedure. *Animal Learning & Behavior, 30*, 275-281.

Allman, M. J., & Honey, R. C. (2006). Transfer of configural learning between the components of a preexposed stimulus compound: implications for elemental and configural models of learning. *Journal of Experimental Psychology: Animal Behavior Processes, 32*, 307-313.

Amundson, J. C., & Miller, R. R. (2008). CS-US temporal relations in blocking. *Learning & Behavior, 36*, 92-103.

Arcediano, F., Escobar, M., & Miller, R. R. (2003). Temporal integration and temporal backward associations in human and nonhuman subjects. *Learning & Behavior, 31*, 242-256.

Artigas, A. A., Contel, D. M., Sansa, J., & Prados, J. (2012). Salience modulation in serial preexposure: Implications for perceptual learning. *Journal of Experimental Psychology: Animal Behavior Processes, 38*, 66-73.

Artigas, A. A., Sansa, J., Blair, C. A., Hall, G., & Prados, J. (2006). Enhanced discrimination between flavor stimuli: roles of salience modulation and inhibition. *Journal of Experimental Psychology: Animal Behavior Processes, 32*, 173-177.

Astley, S. L., Peissig, J. J., & Wasserman, E. A. (2001). Superordinate categorization via learned stimulus equivalence: quantity of reinforcement, hedonic value, and the nature of the mediator. *Journal of Experimental Psychology: Animal Behavior Processes, 27*, 252-268.

Balleine, B. W., & Dickinson, A. (2006). Motivational control of blocking. *Journal of Experimental Psychology: Animal Behavior Processes, 32*, 33-43.

Balsam, P. D., Fairhurst, S., & Gallistel, C. R. (2006). Pavlovian contingencies and temporal information. *Journal of Experimental Psychology: Animal Behavior Processes, 32*, 284-294.

Bannerman, D., Good, M., Butcher, S., Ramsay, M., & Morris, R. (1995). Distinct components of spatial learning revealed by prior training and NMDA receptor blockade. *Nature, 378*, 182-186.

Barbas, D., DesGroseillers, L., Castellucci, V. F., Carew, T. J., & Marinesco, S. (2003). Multiple serotonergic mechanisms contributing to sensitization in aplysia: evidence of diverse serotonin receptor subtypes. *Learning & Memory, 10*, 373-386.

Bayley, P. J., Frascino, J. C., & Squire, L. R. (2005). Robust habit learning in the absence of awareness and independent of the medial temporal lobe. *Nature, 436*, 550-553.

Bee, M. A. (2001). Habituation and sensitization of aggression in bullfrogs (*Rana catesbeiana*): Testing the dual-process theory of habituation. *Journal of Comparative Psychology, 115*, 307-316.

Berman, D. E., Hazvi, S., Stehberg, J., Bahar, A., & Dudai, Y. (2003). Conflicting processes in the extinction of conditioned taste aversion: behavioral and molecular aspects of latency, apparent stagnation, and spontaneous recovery. *Learning & Memory, 10*, 16-25.

Bitterman, M. (2006). Classical conditioning since Pavlov. *Review of general psychology, 10*, 365.

Bizo, L. A., & McMahon, C. V. (2007). Temporal generalization and peak shift in humans. *Learning & Behavior, 35*, 123-130.

Blair, C. A., & Hall, G. (2003). Changes in stimulus salience as a result of stimulus preexposure: evidence from aversive and appetitive testing procedures. *Learning & Behavior, 31*, 185-191.

Blair, C. A., Wilkinson, A., & Hall, G. (2004). Assessments of changes in the effective salience of stimulus elements as a result of stimulus preexposure. *Journal of Experimental Psychology: Animal Behavior Processes, 30*, 317-324.
Blaisdell, A. P., & Cook, R. G. (2005). Two-item same-different concept learning in pigeons. *Learning & Behavior, 33*, 67-77.
Blaisdell, A. P., Sawa, K., Leising, K. J., & Waldmann, M. R. (2006). Causal reasoning in rats. *Science, 311*, 1020-1022.
Blaser, R., Couvillon, P., & Bitterman, M. (2004). Backward blocking in honeybees. *Quarterly Journal of Experimental Psychology Section B, 57*, 349-360.
Blaser, R., Couvillon, P., & Bitterman, M. (2006). Blocking and pseudoblocking: New control experiments with honeybees. *The Quarterly Journal of Experimental Psychology, 59*, 68-76.
Bonardi, C., & Jennings, D. (2009). Learning about associations: evidence for a hierarchical account of occasion setting. *Journal of Experimental Psychology: Animal Behavior Processes, 35*, 440-445.
Bouton, M. E. (1994). Conditioning, remembering, and forgetting. *Journal of Experimental Psychology: Animal Behavior Processes, 20*, 219.
Bouton, M. E. (2004). Context and behavioral processes in extinction. *Learning & Memory, 11*, 485-494.
Bradfield, L., & McNally, G. P. (2008). Unblocking in Pavlovian fear conditioning. *Journal of Experimental Psychology: Animal Behavior Processes, 34*, 256-265.
Brannon, E. M., & Terrace, H. S. (1998). Ordering of the numerosities 1 to 9 by monkeys. *Science, 282*, 746-749.
Bristol, A. S., & Carew, T. J. (2005). Differential role of inhibition in habituation of two independent afferent pathways to a common motor output. *Learning & Memory, 12*, 52-60.
Brown, M. F., Yang, S. Y., & DiGian, K. A. (2002). No evidence for overshadowing or facilitation of spatial pattern learning by visual cues. *Animal Learning & Behavior, 30*, 363-375.
Burns, R. A., Dunkman, J. A., & Detloff, S. L. (1999). Ordinal position in the serial learning of rats. *Animal Learning & Behavior, 27*, 272-279.
Cain, C. K., Blouin, A. M., & Barad, M. (2003). Temporally massed CS presentations generate more fear extinction than spaced presentations. *Journal of Experimental Psychology: Animal Behavior Processes, 29*, 323-333.
Capaldi, E., Alptekin, S., Miller, D. J., & Birmingham, K. M. (1997). Is discriminative responding in reward outcome serial learning mediated by item memories or by position cues? *Learning and Motivation, 28*, 153-169.
Capaldi, E., & Miller, R. M. (2004). Serial learning in rats: A test of three hypotheses. *Learning and Motivation, 35*, 71-81.
Carrasco, L., Posada, S., & Colell, M. (2009). New evidence on imitation in an enculturated chimpanzee (*Pan troglodytes*). *Journal of Comparative Psychology, 123*, 385-390.
Chamizo, V. D., Rodriguez, C. A., Espinet, A., & Mackintosh, N. J. (2012). Generalization decrement and not overshadowing by associative competition among pairs of landmarks in a navigation task. *Journal of Experimental Psychology: Animal Behavior Processes, 38*, 255-265.
Christian, K. M., & Thompson, R. F. (2003). Neural substrates of eyeblink conditioning: acquisition and retention. *Learning & Memory, 10*, 427-455.
Clark, R. E., & Squire, L. R. (1998). Classical conditioning and brain systems: the role of awareness. *Science, 280*, 77-81.
Clayton, N. S., Yu, K. S., & Dickinson, A. (2001). Scrub jays (*Aphelocoma coerulescens*) form integrated memories of the multiple features of caching episodes. *Journal of Experimental Psychology: Animal Behavior Processes, 27*, 17-29.
Cook, R. G., & Katz, J. S. (1999). Dynamic object perception by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 25*, 194-210.
Crystal, J. D., & Miller, B. J. (2002). Simultaneous temporal and spatial processing. *Animal Learning & Behavior, 30*, 53-66.

Davis, K. M., & Burghardt, G. M. (2011). Turtles (*Pseudemys nelsoni*) learn about visual cues indicating food from experienced turtles. *Journal of Comparative Psychology, 125*, 404-410.

Dawson, M. R., Kelly, D. M., Spetch, M. L., & Dupuis, B. (2008). Learning about environmental geometry: a flaw in Miller and Shettleworth's (2007) operant model. *Journal of Experimental Psychology: Animal Behavior Processes, 34*, 415-418.

De Brugada, I., González, F., Gil, M., & Hall, G. (2005). The role of habituation of the response to LiCl in the US-preexposure effect. *Learning & Behavior, 33*, 363-370.

de Zilva, D., & Mitchell, C. J. (2012). Effects of exposure on discrimination of similar stimuli and on memory for their unique and common features. *Quarterly Journal of Experimental Psychology, 65*, 1123-1138.

Delamater, A. R., Campese, V., LoLordo, V. M., & Sclafani, A. (2006). Unconditioned stimulus devaluation effects in nutrient-conditioned flavor preferences. *Journal of Experimental Psychology: Animal Behavior Processes, 32*, 295-306.

Delamater, A. R., LoLordo, V. M., & Sosa, W. (2003). Outcome-specific conditioned inhibition in Pavlovian backward conditioning. *Learning & Behavior, 31*, 393-402.

Denniston, J. C., Blaisdell, A. P., & Miller, R. R. (2004). Temporal coding in conditioned inhibition: analysis of associative structure of inhibition. *Journal of Experimental Psychology: Animal Behavior Processes, 30*, 190-202.

Dickinson, A., & Balleine, B. (1994). Motivational control of goal-directed action. *Animal Learning & Behavior, 22*, 1-18.

Dinse, H. R., Ragert, P., Pleger, B., Schwenkreis, P., & Tegenthoff, M. (2003). Pharmacological modulation of perceptual learning and associated cortical reorganization. *Science, 301*, 91-94.

Domjan, M., & Krause, M. A. (2002). Research productivity in animal learning from 1953 to 2000. *Animal Learning & Behavior, 30*, 282-285.

Dopson, J. C., Pearce, J. M., & Haselgrove, M. (2009). Failure of retrospective revaluation to influence blocking. *Journal of Experimental Psychology: Animal Behavior Processes, 35*, 473-484.

Dorrance, B. R., & Zentall, T. R. (2001). Imitative learning in Japanese quail (*Coturnix japonica*) depends on the motivational state of the observer quail at the time of observation. *Journal of Comparative Psychology, 115*, 62-67.

Dorrance, B. R., & Zentall, T. R. (2002). Imitation of conditional discriminations in pigeons (*Columba livia*). *Journal of Comparative Psychology, 116*, 277-285.

Dwyer, D., Starns, J., & Honey, R. (2009). "Causal reasoning" in rats: A reappraisal. *Journal of Experimental Psychology: Animal Behavior Processes, 35*, 578-586.

Farabaugh, S. M., Linzenbold, A., & Dooling, R. J. (1994). Vocal plasticity in budgerigars (*Melopsittacus undulatus*): Evidence for social factors in the learning of contact calls. *Journal of Comparative Psychology, 108*, 81.

Flagel, S. B., Clark, J. J., Robinson, T. E., Mayo, L., Czuj, A., Willuhn, I., . . .Akil, H. (2010). A selective role for dopamine in stimulus-reward learning. *Nature, 469*, 53-57.

Freeberg, T. M. (2004). Social transmission of courtship behavior and mating preferences in brown-headed cowbirds, *Molothrus ater*. *Learning & Behavior, 32*, 122-130.

Gajdon, G. K., Fijn, N., & Huber, L. (2004). Testing social learning in a wild mountain parrot, the kea (*Nestor notabilis*). *Learning & Behavior, 32*, 62-71.

Gibson, B. M., & Wasserman, E. A. (2003). Pigeons learn stimulus identity and stimulus relations when both serve as redundant, relevant cues during same-different discrimination training. *Journal of Experimental Psychology: Animal Behavior Processes, 29*, 84-91.

Giurfa, M., Zhang, S., Jenett, A., Menzel, R., & Srinivasan, M. V. (2001). The concepts of 'sameness' and 'difference'in an insect. *Nature, 410*, 930-933.

Gonzalez, F., Quinn, J. J., & Fanselow, M. S. (2003). Differential effects of adding and removing components of a context on the generalization of conditional freezing. *Journal of Experimental Psychology: Animal Behavior Processes, 29*, 78-83.

Guilhardi, P., & Church, R. M. (2005). Dynamics of temporal discrimination. *Learning & Behavior, 33*, 399-416.
Hammer, M., & Menzel, R. (1998). Multiple sites of associative odor learning as revealed by local brain microinjections of octopamine in honeybees. *Learning & Memory, 5*, 146-156.
Hardwick, R. M., & Edwards, M. G. (2011). Observed reach trajectory influences executed reach kinematics in prehension. *Quarterly Journal of Experimental Psychology, 64*, 1082-1093.
Hardwick, R. M., & Edwards, M. G. (2012). Motor interference and facilitation arising from observed movement kinematics. *Quarterly Journal of Experimental Psychology, 65*, 840-847.
Harris, J. A. (2006). Elemental representations of stimuli in associative learning. *Psychological review, 113*, 584-605.
Harris, J. A., Gharaei, S., & Moore, C. A. (2009). Representations of single and compound stimuli in negative and positive patterning. *Learning & Behavior, 37*, 230-245.
Hawkins, R. D., Cohen, T. E., & Kandel, E. R. (2006). Dishabituation in Aplysia can involve either reversal of habituation or superimposed sensitization. *Learning & Memory, 13*, 397-403.
Hoffman, M. L., Beran, M. J., & Washburn, D. A. (2009). Memory for "what", "where", and "when" information in rhesus monkeys (*Macaca mulatta*). *Journal of Experimental Psychology: Animal Behavior Processes, 35*, 143-152.
Holzhaider, J. C., Hunt, G. R., & Gray, R. D. (2010). Social learning in New Caledonian crows. *Learning & Behavior, 38*, 206-219.
Honey, R. C., & Ward-Robinson, J. (2002). Acquired equivalence and distinctiveness of cues: I. Exploring a neural network approach. *Journal of Experimental Psychology: Animal Behavior Processes, 28*, 378-387.
Jitsumori, M., Shimada, N., & Inoue, S. (2006). Family resemblances facilitate formation and expansion of functional equivalence classes in pigeons. *Learning & Behavior, 34*, 162-175.
Kamil, A. C., & Jones, J. E. (1997). The seed-storing corvid Clark's nutcracker learns geometric relationships among landmarks. *Nature, 390*, 276-279.
Kamil, A. C., & Jones, J. E. (2000). Geometric rule learning by Clark's nutcrackers (*Nucifraga columbiana*). *Journal of Experimental Psychology: Animal Behavior Processes, 26*, 439-453.
Kehoe, E. J., & White, N. E. (2002). Extinction revisited: similarities between extinction and reductions in US intensity in classical conditioning of the rabbit's nictitating membrane response. *Animal Learning & Behavior, 30*, 96-111.
Kirkpatrick, K., & Church, R. M. (2003). Tracking of the expected time to reinforcement in temporal conditioning procedures. *Learning & Behavior, 31*, 3-21.
Klein, E. D., & Zentall, T. R. (2003). Imitation and affordance learning by pigeons (*Columba livia*). *Journal of Comparative Psychology, 117*, 414-419.
Kosaki, Y., Austen, J. M., & McGregor, A. (2013). Overshadowing of geometry learning by discrete landmarks in the water maze: effects of relative salience and relative validity of competing cues. *Journal of Experimental Psychology: Animal Behavior Processes, 39*, 126-139.
Lachnit, H., Schultheis, H., Konig, S., Ungor, M., & Melchers, K. (2008). Comparing elemental and configural associative theories in human causal learning: a case for attention. *Journal of Experimental Psychology: Animal Behavior Processes, 34*, 303-313.
Laland, K. N. (2004). Social learning strategies. *Learning & Behavior, 32*, 4-14.
Law, C.-T., & Gold, J. I. (2008). Neural correlates of perceptual learning in a sensory-motor, but not a sensory, cortical area. *Nature Neuroscience, 11*, 505-513.
Lazareva, O. F., Miner, M., Wasserman, E. A., & Young, M. E. (2008). Multiple-pair training enhances transposition in pigeons. *Learning & Behavior, 36*, 174-187.
Le Pelley, M. E. (2004). The role of associative history in models of associative learning: A selective review and a hybrid model. *Quarterly Journal of Experimental Psychology Section B, 57*, 193-243.

Le Pelley, M. E., Mitchell, C. J., & Johnson, A. M. (2013). outcome value influences attentional biases in human associative learning: dissociable effects of training and instruction. *Journal of Experimental Psychology: Animal Behavior Processes, 39*, 39-55.
Lebron, K., Milad, M. R., & Quirk, G. J. (2004). Delayed recall of fear extinction in rats with lesions of ventral medial prefrontal cortex. *Learning & Memory, 11*, 544-548.
Leung, H. T., Bailey, G. K., Laurent, V., & Westbrook, R. F. (2007). Rapid reacquisition of fear to a completely extinguished context is replaced by transient impairment with additional extinction training. *Journal of Experimental Psychology: Animal Behavior Processes, 33*, 299-313.
Li, S. H., & Westbrook, R. F. (2008). Massed extinction trials produce better short-term but worse long-term loss of context conditioned fear responses than spaced trials. *Journal of Experimental Psychology: Animal Behavior Processes, 34*, 336-351.
Livesey, E. J., & McLaren, I. P. (2009). Discrimination and generalization along a simple dimension: peak shift and rule-governed responding. *Journal of Experimental Psychology: Animal Behavior Processes, 35*, 554-565.
Loidolt, M., Aust, U., Meran, I., & Huber, L. (2003). Pigeons use item-specific and category-level information in the identification and categorization of human faces. *Journal of Experimental Psychology: Animal Behavior Processes, 29*, 261-276.
Lotz, A., & Lachnit, H. (2009). Extinction of conditioned inhibition: effects of different outcome continua. *Learning & Behavior, 37*, 85-94.
Luque, D., Flores, A., & Vadillo, M. A. (2013). Revisiting the role of within-compound associations in cue-interaction phenomena. *Learning & Behavior, 41*, 61-76.
Machado, A., & Pata, P. (2005). Testing the scalar expectancy theory (SET) and the learning-to-time model (LeT) in a double bisection task. *Learning & Behavior, 33*, 111-122.
McAllister, W. R., & McAllister, D. E. (2006). Recovery of conditioned fear by a single postextinction shock: effect of similarity of shock contexts and of time following extinction. *Learning & Behavior, 34*, 44-49.
McGregor, A., Horne, M. R., Esber, G. R., & Pearce, J. M. (2009). Absence of overshadowing between a landmark and geometric cues in a distinctively shaped environment: a test of Miller and Shettleworth (2007). *Journal of Experimental Psychology: Animal Behavior Processes, 35*, 357-370.
McGuigan, N. (2012). The role of transmission biases in the cultural diffusion of irrelevant actions. *Journal of Comparative Psychology, 126*, 150-160.
McLaren, I., & Mackintosh, N. (2000). An elemental model of associative learning: I. Latent inhibition and perceptual learning. *Animal Learning & Behavior, 28*, 211-246.
Miller, N. Y., & Shettleworth, S. J. (2007). Learning about environmental geometry: an associative model. *Journal of Experimental Psychology: Animal Behavior Processes, 33*, 191-212.
Miller, N. Y., & Shettleworth, S. J. (2008). An associative model of geometry learning: a modified choice rule. *Journal of Experimental Psychology: Animal Behavior Processes, 34*, 419-422.
Milton, A. L., Lee, J. L. C., & Everitt, B. J. (2008). Reconsolidation of appetitive memories for both natural and drug reinforcement is dependent on beta-adrenergic receptors. *Learning & Memory, 15*, 88-92.
Mitchell, C. J., Harris, J. A., Westbrook, R. F., & Griffiths, O. (2008). Changes in cue associability across training in human causal learning. *Journal of Experimental Psychology: Animal Behavior Processes, 34*, 423-436.
Morris, R. W., Furlong, T. M., & Westbrook, R. F. (2005). Recent exposure to a dangerous context impairs extinction and reinstates lost fear reactions. *Journal of Experimental Psychology: Animal Behavior Processes, 31*, 40-55.
Moser, E. I., Krobert, K. A., Moser, M.-B., & Morris, R. G. (1998). Impaired spatial learning after saturation of long-term potentiation. *Science, 281*, 2038-2042.
Mottley, K., & Heyes, C. (2003). Budgerigars (Melopsittacus undulatus) copy virtual demonstrators in a two-action test. *Journal of Comparative Psychology, 117*, 363-370.

Mundy, M. E., Dwyer, D. M., & Honey, R. C. (2006). Inhibitory associations contribute to perceptual learning in humans. *Journal of Experimental Psychology: Animal Behavior Processes, 32*, 178-184.

Ohl, F., Scheich, H., & Freeman, W. (2001). Change in pattern of ongoing cortical activity with auditory category learning. *Nature, 412*, 733-736.

Paranjpe, P., Rodrigues, V., VijayRaghavan, K., & Ramaswami, M. (2012). Gustatory habituation in Drosophila relies on rutabaga (adenylate cyclase)-dependent plasticity of GABAergic inhibitory neurons. *Learning & Memory, 19*, 627-635.

Pearce, J. M. (2002). Evaluation and development of a connectionist theory of configural learning. *Animal Learning & Behavior, 30*, 73-95.

Pearce, J. M., Esber, G. R., George, D. N., & Haselgrove, M. (2008). The nature of discrimination learning in pigeons. *Learning & Behavior, 36*, 188-199.

Pearce, J. M., Good, M. A., Jones, P. M., & McGregor, A. (2004). Transfer of spatial behavior between different environments: implications for theories of spatial learning and for the role of the hippocampus in spatial learning. *Journal of Experimental Psychology: Animal Behavior Processes, 30*, 135-147.

Pearce, J. M., Graham, M., Good, M. A., Jones, P. M., & McGregor, A. (2006). Potentiation, overshadowing, and blocking of spatial learning based on the shape of the environment. *Journal of Experimental Psychology: Animal Behavior Processes, 32*, 201-214.

Peissig, J. J., Kirkpatrick, K., Young, M. E., Wasserman, E. E., & Biederman, I. (2006). Effects of varying stimulus size on object recognition in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 32*, 419-430.

Pessiglione, M., Seymour, B., Flandin, G., Dolan, R. J., & Frith, C. D. (2006). Dopamine-dependent prediction errors underpin reward-seeking behaviour in humans. *Nature, 442*, 1042-1045.

Peters, J., Kalivas, P. W., & Quirk, G. J. (2009). Extinction circuits for fear and addiction overlap in prefrontal cortex. *Learning & Memory, 16*, 279-288.

Pizzo, M. J., & Crystal, J. D. (2004). Time-place learning in the eight-arm radial maze. *Learning & Behavior, 32*, 240-255.

Polack, C. W., McConnell, B. L., & Miller, R. R. (2013). Associative foundation of causal learning in rats. *Learning & Behavior, 41*, 25-41.

Rauhut, A. S., Thomas, B. L., & Ayres, J. J. (2001). Treatments that weaken Pavlovian conditioned fear and thwart its renewal in rats: implications for treating human phobias. *Journal of Experimental Psychology: Animal Behavior Processes, 27*, 99-114.

Rescorla, R. A. (2001). Retraining of extinguished Pavlovian stimuli. *Journal of Experimental Psychology: Animal Behavior Processes, 27*, 115-124.

Rescorla, R. A. (2004). Spontaneous recovery varies inversely with the training-extinction interval. *Learning & Behavior, 32*, 401-408.

Rescorla, R. A. (2006). Deepened extinction from compound stimulus presentation. *Journal of Experimental Psychology: Animal Behavior Processes, 32*, 135-144.

Rescorla, R. A., & Wagner, A. R. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. *Classical conditioning II: Current research and theory*, 64-99.

Riedel, G. (1998). Long-term habituation to spatial novelty in blind cave fish (Astyanax hubbsi): role of the telencephalon and its subregions. *Learning & Memory, 4*, 451-461.

Rodriguez, G., Blair, C. A., & Hall, G. (2008). The role of comparison in perceptual learning: effects of concurrent exposure to similar stimuli on the perceptual effectiveness of their unique features. *Learning & Behavior, 36*, 75-81.

Rugg, M. D., Mark, R. E., Walla, P., Schloerscheidt, A. M., Birch, C. S., & Allan, K. (1998). Dissociation of the neural correlates of implicit and explicit memory. *Nature, 392*, 595-598.

Saggerson, A. L., George, D. N., & Honey, R. C. (2005). Imitative learning of stimulus-response and response-outcome associations in pigeons. *Journal of Experimental Psychology-Animal Behavior Processes, 31*, 289-300.

Salama, I. M., Turner, S., & Edwards, M. G. (2011). Automatic priming of grip force following action observation. *Quarterly Journal of Experimental Psychology, 64*, 833-838.

Sanderson, D. J., & Bannerman, D. M. (2011). Competitive short-term and long-term memory processes in spatial habituation. *Journal of Experimental Psychology-Animal Behavior Processes, 37*, 189-199.

Sansa, J., Rodrigo, T., Santamaria, J. J., Manteiga, R. D., & Chamizo, V. D. (2009). Conditioned inhibition in the spatial domain. *Journal of Experimental Psychology: Animal Behavior Processes, 35*, 566-577.

Sara, S. J. (2000). Retrieval and reconsolidation: toward a neurobiology of remembering. *Learning & Memory, 7*, 73-84.

Scarlet, J., Campese, V., & Delamater, A. R. (2009). Sensory-specific associations in flavor-preference reversal learning. *Learning & Behavior, 37*, 179-187.

Shettleworth, S. J. (2009). The evolution of comparative cognition: is the snark still a boojum? *Behavioural Processes, 80*, 210-217.

Simms, V., McCormack, T., & Beckers, T. (2012). Additivity pretraining and cue competition effects: developmental evidence for a reasoning-based account of causal learning. *Journal of Experimental Psychology: Animal Behavior Processes, 38*, 180-190.

Skov-Rackette, S. I., Miller, N. Y., & Shettleworth, S. J. (2006). What-where-when memory in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 32*, 345-358.

Smith, J. D., Redford, J. S., Haas, S. M., Coutinho, M. V., & Couchman, J. J. (2008). The comparative psychology of same-different judgments by humans (*Homo sapiens*) and monkeys (*Macaca mulatta*). *Journal of Experimental Psychology: Animal Behavior Processes, 34*, 361-374.

Sokolowska, M., Siegel, S., & Kim, J. A. (2002). Intraadministration associations: conditional hyperalgesia elicited by morphine onset cues. *Journal of Experimental Psychology: Animal Behavior Processes, 28*, 309-320.

Spetch, M. L., Friedman, A., & Vuong, Q. C. (2006). Dynamic object recognition in pigeons and humans. *Learning & Behavior, 34*, 215-228.

Stafford, J. M., Maughan, D. K., Ilioi, E. C., & Lattal, K. M. (2013). Exposure to a fearful context during periods of memory plasticity impairs extinction via hyperactivation of frontal-amygdalar circuits. *Learning & Memory, 20*, 156-163.

Stoinski, T. S., Wrate, J. L., Ure, N., & Whiten, A. (2001). Imitative learning by captive western lowland gorillas (*Gorilla gorilla*) in a simulated food-processing task. *Journal of Comparative Psychology, 115*, 272-281.

Stout, S. C., Chang, R., & Miller, R. R. (2003). Trial spacing is a determinant of cue interaction. *Journal of Experimental Psychology: Animal Behavior Processes, 29*, 23-38.

Stuber, G. D., Klanker, M., de Ridder, B., Bowers, M. S., Joosten, R. N., Feenstra, M. G., et al. (2008). Reward-predictive cues enhance excitatory synaptic strength onto midbrain dopamine neurons. *Science, 321*, 1690-1692.

Subiaul, F., Cantlon, J. F., Holloway, R. L., & Terrace, H. S. (2004). Cognitive imitation in rhesus macaques. *Science, 305*, 407-410.

Suboski, M. D., Bain, S., Carty, A. E., Mcquoid, L. M., Seelen, M. I., & Seifert, M. (1990). Alarm reaction in acquisition and social transmission of simulated-predator recognition by zebra danio fish (*Brachydanio rerio*). *Journal of Comparative Psychology, 104,* 101-112.

Swartz, K. B., Chen, S., & Terrace, H. S. (2000). Serial learning by rhesus monkeys: II. Learning four-item lists by trial and error. *Journal of Experimental Psychology: Animal Behavior Processes, 26*, 274-285.

Thorndike, E. L. (1911). *Animal Intelligence: Experimental Studies*. New York, New York: Macmillan.

Thorpe, C. M., & Wilkie, D. M. (2006). Rats' performance on an interval time-place task: increasing sequence complexity. *Learning & Behavior, 34*, 248-254.

Thorwart, A., & Lachnit, H. (2009). Symmetrical generalization decrements: configural stimulus processing in human contingency learning. *Learning & Behavior, 37*, 107-115.

Treichler, F. R., Raghanti, M. A., & Van Tilburg, D. N. (2003). Linking of serially ordered lists by macaque monkeys (*Macaca mulatta*): list position influences. *Journal of Experimental Psychology: Animal Behavior Processes, 29*, 211-221.

Tsodyks, M., & Gilbert, C. (2004). Neural networks and perceptual learning. *Nature, 431*, 775-781.

Twining, R. C., Tuscher, J. J., Doncheck, E. M., Frick, K. M., & Mueller, D. (2013). 17 beta-Estradiol is necessary for extinction of cocaine seeking in female rats. *Learning & Memory, 20*, 300-306.

Urcelay, G. P., & Miller, R. R. (2009). Potentiation and overshadowing in Pavlovian fear conditioning. *Journal of Experimental Psychology: Animal Behavior Processes, 35*, 340-356.

Urcelay, G. P., Wheeler, D. S., & Miller, R. R. (2009). Spacing extinction trials alleviates renewal and spontaneous recovery. *Learning & Behavior, 37*, 60-73.

Urcuioli, P. J. (2007). Sample and comparison location as factors in matching acquisition, transfer, and acquired equivalence. *Learning & Behavior, 35*, 252-261.

Waelti, P., Dickinson, A., & Schultz, W. (2001). Dopamine responses comply with basic assumptions of formal learning theory. *Nature, 412*, 43-48.

Wasserman, E. A., Frank, A. J., & Young, M. E. (2002). Stimulus control by same-versus-different relations among multiple visual stimuli. *Journal of Experimental Psychology: Animal Behavior Processes, 28*, 347-357.

Watanabe, T., Náñez, J. E., & Sasaki, Y. (2001). Perceptual learning without perception. *Nature, 413*, 844-848.

Westbrook, R. F., Iordanova, M., McNally, G., Richardson, R., & Harris, J. A. (2002). Reinstatement of fear to an extinguished conditioned stimulus: two roles for context. *Journal of Experimental Psychology: Animal Behavior Processes, 28*, 97-110.

Whiten, A., Custance, D. M., Gomez, J.-C., Teixidor, P., & Bard, K. A. (1996). Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 110*, 3-14.

Whitt, E., Haselgrove, M., & Robinson, J. (2012). Indirect object recognition: Evidence for associative processes in recognition memory. *Journal of Experimental Psychology-Animal Behavior Processes, 38*, 74-83.

Yunger, J. L., & Bjorklund, D. F. (2004). An assessment of generalization of imitation in two enculturated Orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology, 118*, 242-246.

Submitted October 1, 2013
Accepted December 17, 2013