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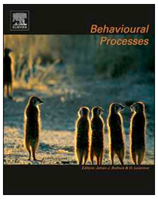

Comparative spatial memory and cue use: The contributions of Marcia L. Spetch to the study of small-scale spatial cognition

Eric L.G. Legge

Department of Psychology, MacEwan University, 10700 – 104 Avenue, City Centre Campus, Edmonton, AB, T5J 4S2, Canada

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ABSTRACT

Dr. Marcia Spetch is a Canadian experimental psychologist who specializes in the study of comparative cognition. Her research over the past four decades has covered many diverse topics, but focused primarily on the comparative study of small-scale spatial cognition, navigation, decision making, and risky choice. Over the course of her career Dr. Spetch has had a profound influence on the study of these topics, and for her work she was named a Fellow of the Association for Psychological Science in 2012, and a Fellow of the Royal Society of Canada in 2017. In this review, I provide a biographical sketch of Dr. Spetch's academic career, and revisit her contributions to the study of small-scale spatial cognition in two broad areas: the use of environmental geometric cues, and how animals cope with cue conflict. The goal of this review is to highlight the contributions of Dr. Spetch, her students, and her collaborators to the field of comparative cognition and the study of small-scale spatial cognition. As such, this review stands to serve as a tribute and testament to Dr. Spetch's scientific legacy.

1. Biographical Sketch

Marcia L. Spetch was born and raised in Burnaby, British Columbia, Canada. In 1972, she began her post-secondary education at the nearby University of British Columbia (UBC) studying psychology. There, Spetch became interested in the study of animal learning and memory, a topic that would define much of her research throughout her career. Specifically, during the third year of her program, Spetch took a statistics class taught by Donald Wilkie where she learned of his research in the area of animal learning. Intrigued, that summer she began working as a research assistant in Wilkie's lab focusing on operant conditioning. She continued her research in Wilkie's lab during her fourth and final year at UBC as part of an independent research course, and graduated with her BA in 1977.

At this point, Spetch was thoroughly engrossed with the study of animal learning, and immediately entered into the Masters of Arts program at UBC under Wilkie's supervision. During this time, Spetch was heavily involved in the study of discrimination learning and short-term memory in animals, publishing numerous papers in journals such as *Animal Learning and Behavior, Psychological Record*, *Learning and Motivation*, and the *Journal of the Experimental Analysis of Behavior* (see further: Wilkie and Spetch, 1978, 1980, 1981; Wilkie et al., 1981b; Spetch et al., 1981). Her research led her to obtain her MA and PhD in Biopsychology in 1979 and 1981, respectively.

After completing her PhD, Spetch accepted a Postdoctoral Fellowship under the supervision of Edmund Fantino at the University of California at San Diego in California (UCSD), where she studied sub-optimal choice, the delay reduction hypothesis, and choice behavior from 1981-1983. During her time at UCSD, Spetch worked with people such as Roger Dunn (also a student of Fantino's at the time) and Ben Williams in the study of operant conditioning (e.g. Spetch and Dunn, 1987; Dunn and Spetch, 1990), as well as Dallas Treit and Anthony Deutsch on consummatory behavior in rats (e.g., Treit et al., 1983, 1984).

In 1983, Spetch moved to Halifax, Nova Scotia, Canada, to begin a position as an Assistant Professor of Psychology at Dalhousie University. Now with her own lab, Spetch was free to pursue her own research agenda: the study of comparative spatial cognition. This new focal area of research, which would remain one of her major topics of study for the rest of her career, was a dramatic divergence from many of the topics she pursued as a graduate student and post-doctoral fellow. In an interview with Spetch, she suggested that the study of spatial cognition, particularly with pigeons, had been an area she became enamored with as undergraduate student UBC. She stated that her interest in the area came from two events in particular: a study that she worked on in Wilkie's lab on memory capacity for spatial information in ring doves (Wilkie et al., 1981a), and a talk she attended in the 3rd year of her BA by William (Bill) Keeton on homing pigeon behavior (M. Spetch, personal communication).

It is also likely that, as discussed in Cheng et al. (2006), Spetch's

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E-mail address: eric.legge@macewan.ca.

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research was influenced by comparative work testing pigeons in radial maze tasks taking place at the same time. In some of this research (e.g., Bond et al., 1981; Olson and Maki, 1983) pigeons were shown to have much poorer spatial working memory than rats. In contrast however, Roberts and Van Veldhuizen (1985) were able to gradually train pigeons to perform almost as well as rats in a radial maze, thus leading them to suggest that pigeons' poor working memory performance in past research was because a radial maze is not representative of pigeons' natural foraging ecology. Following on this, in one of Spetch's first studies of spatial memory in her new lab, Spetch and Edwards (1986) tested pigeons in a few different radial maze configurations, each designed to mimic the environment in which pigeons' typically forage more closely than a traditional radial maze containing alleyways (e.g., feeders placed on the ground in a radial pattern without barriers between them; elevated feeders to which pigeons could fly). Spetch and Edwards found that in their radial maze tasks, pigeons displayed very accurate spatial working memory performance and thus concluded that the tasks used to assess spatial memory in animals should be designed to closely match their natural foraging habitat, something that is now a central consideration for comparative psychologists when designing new testing apparatuses.

Following on the success of her 1986 work with Edwards, Spetch continued to study comparative spatial memory and cognition in pigeons, and collaborated heavily with other researchers at Dalhousie such as Bruce Moore and Werner Honig (e.g., Honig and Spetch, 1988; Spetch and Honig, 1988; Spetch et al., 1990). Indeed, Spetch's collaboration with Moore quickly led a visiting researcher position as part of the Laboratory of Ornithology at Cornell University in Ithaca, NY during the summers from 1985 to 1989, where she studied pigeon homing behavior in the field with Moore and Robert Madden.

Spetch remained at Dalhousie until 1987, when she moved to the University of Alberta as an Associate Professor of Psychology. She would remain at the University of Alberta for the rest of her career, earning the title of Professor in 1994, and retiring as Professor Emerita in 2018. During her time at the University of Alberta, Spetch's research continued to focus primarily on comparative spatial cognition (discussed in detail in this review), with a secondary focus on the study of gambling and decision making (e.g., Ludvig et al., 2014; Madan et al., 2015). Additionally, during her career, Spetch has collaborated heavily with researchers across the globe on a wide range of other topics such as object recognition (e.g., Spetch et al., 2001; Spetch and Friedman, 2003), peak shift (e.g., Cheng et al., 1997; Spetch and Cheng, 1998), timing (e.g., Ludvig et al., 2011; McMillan et al., 2016), neural networks (e.g., Dawson et al., 2010, 2009), perception (e.g., Kelly et al., 2001; Nankoo et al., 2012), reward memory (Madan and Spetch, 2012) and interactive storytelling in video games (e.g., Thue et al., 2008, 2009).

Of particular relevance to the topics discussed in this paper are Spetch's longstanding and ongoing collaborative relationships with Ken Cheng and Debbie Kelly. Cheng, currently a Professor in the Department of Biological Sciences at Macquarie University in Sydney, Australia has likely been Spetch's longest and closest collaborator. Since publishing their first paper together in 1992 (Spetch et al., 1992), Spetch and Cheng's work has focused primarily on the study of landmark learning and use in animals. Later in this manuscript, particularly in the section on resolving cue conflict, I will revisit some of Cheng and Spetch's collaborative work in more detail, and showcase the impact it has had on the field.

Kelly, on the other hand, was once a graduate student of Spetch's, where she studied geometric cue use in pigeon and human spatial memory. Since earning her PhD in Spetch's lab, Kelly has become a prolific researcher in her own right, and is currently a Professor and Canada Research Chair in Comparative Cognition at the University of Manitoba. As the reader will see in the section on using environmental geometry below, Kelly and Spetch's collaborative work has had a major impact on our understanding of the topic of geometric cue use in human and non-human animals.

Together, the collaborative relationship between Spetch et al. cumulated in a paper written together with Verner Bingman on small-scale spatial cognition in pigeons. This work, which is a seminal reflection on how the study small-scale spatial cognition has evolved over the last 30+ years, exemplifies the deep collaborative ties between Spetch, Cheng, and Kelly, as well as the impact their collaborations have had on research in the field (see further Cheng et al., 2006). As such, it complements this paper well, and is recommended to interested readers.

While Spetch's research and collaborative work have certainly contributed to the development of the field of comparative cognition, her service contributions have perhaps played an even larger role. In particular, Spetch was one of four scientists (the others being Ronald Weisman, Mark Bouton, and Edward Wasserman) studying comparative cognition in the 1980s that help found the International Conference on Comparative Cognition, to my knowledge the first dedicated conference to the study of comparative cognition in North America (the first meeting was in 1994; Weisman et al., 2015). In addition, Spetch was one of the founding members of the Comparative Cognition Society (CCS; established in 1999), the present-day primary scientific society dedicated to the study of comparative cognition. Finally, between 2008 and 2010, Spetch served as the president of the CCS, helping guide the organization over her two-year term of service (Comparative Cognition Society, 2018).

In addition to these major direct contributions, Spech also helped develop and serve the discipline in other ways throughout her career. For example, Spetch has held a number of critical research and professional postings that have futured the field of comparative cognition. Some positions that Spetch has held in this regard include serving as: a Psychology Grant Selection Committee Member for the Natural Sciences and Engineer Research Council of Canada (1996–1999), and as an Editor, or on an editorial board, for a number of major publications in the discipline. Some of the positions she has held in this capacity include: Associate Editor of *Animal Learning and Behavior* (1997–2000), Consulting Editor of *Learning and Behavior* (2003–2007), and the *Journal of Experimental Psychology: Animal Behavior Processes* (1993–2009; 2011–2013), Review Editor for *Frontiers in Comparative Psychology* (2010-present), *Co-Editor for Comparative Cognition and Behavior Reviews* (2014–2020), and serving on the editorial board of journals such as *Animal Cognition* (2014–2017), *Comparative Cognition and Behavior Reviews* (2012–2013), *Learning and Behavior* (2015-present), and the *Journal of the Experimental Analysis of Behavior* (2016-present).

Overall, Spetch has had a profound influence on the study of comparative cognition, particularly with respect to small scale spatial cognition. Reflecting this, Spetch currently has in excess of 150 publications, an h-index of 33, and a citation count of over 3500 (Scopus, 2018), and has held a number of major grants from the Natural Sciences and Engineering Council of Canada and the Alberta Gambling Research Institute. For her contributions to the study of comparative cognition and decision making, Spetch was named a Fellow of the Association for Psychological Science in 2012, and a Fellow of the Royal Society of Canada in 2017. While now retired, Spetch continues to maintain her own research program studying small scale spatial cognition and decision making, and collaborates frequently with researchers across the globe.

This biographical review is designed to highlight Spetch's scientific legacy with respect to her work on the study of small-scale spatial cognition. The goal of this review is to revisit and highlight the work of Spetch and her collaborators in these areas, and serve as a testament to her scientific legacy.

2. The study of spatial cogniton

2.1. Transformational approach

Many studies of human and non-human spatial cognition use the transformational approach, originally reported by Tinbergen (1972), to study place-finding behaviour. Tinbergen employed the transformational approach to investigate how digger wasps (*Philanthus triangulum*) could relocate the entrance to their nest, a small hole in the ground, after leaving to obtain food for its larvae within. To do this, Tinbergen would observe wasps making their nest. While the wasps were inside, Tinbergen would place a ring of pinecones around the nest entrance. When wasps would leave to search for food, Tinbergen observed they would spend some time flying over the nest entrance before leaving, possibly to memorize terrestrial features near the nest to help relocate the nest entrance upon their return. To test this, Tinbergen would move the ring of pinecones a short distance away from its original location while wasps were away (thus "transforming" the search space), and observed their search behaviour when they returned. Tinbergen found that upon the wasps' return, they would search in the center of the ring of pinecones in its new location, rather than search for the nest in its correct position in space. This study demonstrates that digger wasps rely on visual cues near their nest to identify its location on their return flight, and do not store the nest's absolute position in space relative to some internal positional system. This transformational (or displacement) approach has been used heavily since Tinbergen's original work, with many species and taxa, including birds (e.g., pigeons, *Columba livia*: Spetch et al., 1992; Clark's nutcrackers, *Nucifraga columbiana*: Kelly et al., 2010; hummingbirds, *Selasphorus rufus*: Pritchard et al., 2016), rodents (e.g., rats, *Rattus norvegicus*: Benhamou and Poucet, 1998; hamsters, *Mesocricetus auratus*: Etienne et al., 1990; gerbils, *Meriones unguiculatus*: Collett, 1987), and insects (ants, *Melophorus bagoti*: Legge et al., 2010; bees, *Apis mellifera*: Cartwright and Collett, 1983; beetles, *Scarabaeus satyrus*: Dacke et al., 2013). For a comprehensive review and discussion of transformational approach, see Cheng and Spetch (1998).

In contemporary laboratory studies, the transformational approach is typically implemented in either open-field (a navigable real-world space) or computer-based tasks. In both of these, the person or animal is initially trained to find a goal relative to one or more landmarks arrayed in the search space. Typically, the landmarks are moved on each trial, but the goal location, and each landmark's position relative to one another, remain fixed. This type of manipulation allows the animal to learn the position of the goal relative to the landmarks, but ensures that stable environmental cues such as the walls of a testing room are uninformative. In such tests, search behaviour is recorded and typically becomes more accurate as the number of successful trials increase. After the subject has reached some pre-determined accuracy criteria, they are moved to one or more testing phases where the goal is no longer present (to prevent potential confounds such as olfactory cues), and the landmarks are manipulated. For a single landmark, this could mean changing the featural properties, such as its size, color, or shape. For an array of landmarks, it could involve removing one of the landmarks, or altering the position of a landmark relative to the rest by moving it (the latter being known as a conflict test because the spatial information provided by the displaced landmark now conflicts with the information provided by the landmarks that were not displaced). After the manipulation, search behaviour of the subject is recorded and compared to test trials where the landmark or array was not manipulated, but where the goal was still removed (known as probe or control tests). By comparing factors such as search accuracy between the manipulated and unmanipulated conditions, researchers can determine how important the manipulated features or cues were for accurate goal localization.

In her work, Spetch often employed the transformational approach to test hypotheses related to human and non-human animals' encoding and use of spatial cues. To this end, this biographical review will focus on two broad areas of inquiry from Spetch's lab that employ the transformational approach: i) the use of environmental geometric cues for goal localization and re-orientation, and ii) the study of how animals cope with cue conflict when searching for a goal. Note that this review is not meant to be exhaustive, and is instead designed to highlight Spetch's scientific contributions in these areas. For more exhaustive reviews, see Cheng et al. (2013); Kelly and Spetch (2012), or Cheng and Newcombe (2005) for use of environmental geometry, and Cheng et al. (2007), Spetch and Kelly (2006); Cheng et al. (2006), or Cheng and Spetch (1998) for the resolution of cue conflict.

3. Using environmental geometry

In 1986, Cheng published his now seminal work demonstrating that rats could use environmental geometry to reorient and locate a goal. Specifically, Cheng (1986) placed rats in a rectangular arena with unique visual cues to distinguish each corner. Food was placed in one corner of the arena, and after rats had consumed approximately half of it were removed and disoriented before being placed in an identical enclosure with the food hidden in the same corner as the original arena. Cheng reported that rats would often make rotational errors when searching for the food in the new enclosure, searching in a corner diagonally opposite the one that contained food even if there were distinctive features in each corner of the apparatus. This result led Cheng to hypothesize that animals such as rats encode environmental geometry automatically, and that such information is preferentially relied upon for reorientation.

Cheng's work has since spurred a vast amount of follow up research across a wide range of species, to which Spetch and colleagues have been important contributors. It is to Spetch et al.'s contributions in this area that we turn to next.

3.1. Similarity between two- and three-dimensional environments

One of the challenges of conducting research on geometric cue use is the requirement that enclosures be built to such a size that subjects can freely navigate within the space. For test trials where the shape or size of the apparatus is manipulated, additional enclosures must be built, or existing enclosures designed in such a way that they are easily manipulated. These space constraints, construction challenges, and their added expense may make it difficult for researchers to conduct multiple studies simultaneously, and limit the type and degree of manipulations made during testing. One potential solution to this problem is the use of digital, two-dimensional (2-D) environments created on a computer monitor, or immersive three-dimensional (3-D) environments using head-mounted displays for humans. However, to use digital environments, one must be sure that animals treat such environments as similar to their real-space counterparts. Spetch and colleagues in the mid-90 s demonstrated that humans and pigeons tend to use landmarks to search for a goal in similar ways in real-space and 2-D digital environments (Spetch et al., 1996, 1997). Such findings therefore raised the question of whether human and non-human animals would also encode geometric information derived from digital 2-D and real-space environments in a similar manner.

To test this, Kelly and Spetch conducted a series of experiments with humans (2004a) and pigeons (2004b) using 2-D schematic environments presented on a computer monitor (humans) or a touch screen (pigeons). They found that, similar to real-space environments (pigeons: Kelly et al., 1998; adult humans: Hermer and Spelke, 1994, 1996), both humans and pigeons could use featural or geometric cues in the environment to locate a goal, even when both cue types were presented simultaneously during training. However, subjects that were trained solely with environmental geometry had difficulty learning to use geometric cues to locate the goal, something not seen when geometric cues were presented in conjunction with featural information.[1] This difficulty was not seen when using real-space environments (pigeons: Kelly et al., 1998; adult humans: Hermer and Spelke, 1994, 1996), and may have been due to the novel top-down view of the schematic environments, as similar results have been found with tests of children who were given models of rectangular environments on a tabletop (Gouteux et al., 2001). Overall, the results of Kelly and Spetch (2004a,b) show that there are slight differences between learning geometric information in a 2-D schematic environment compared to a real-space environment, however, these differences are generally minor and likely due to the top-down schematic nature of the digital space.

The comparative work of Kelly and Spetch (2004a,b) has had a major impact on the methods employed to study geometric cue use by paving the way for other researchers to use digital environments to test their hypotheses in the area. As such, using 2-D and 3-D platforms for testing geometric encoding is now standard practice, particularly with humans. Examples of such work can be seen in manuscripts such as Sturz et al. (2018); Mou et al. (2014), and Kelly and Bischof (2008) among others (see Kelly and Spetch, 2012 for a review; however, see Kimura et al., 2017 for findings that suggest subtle differences between real-space and virtual reorientation using environmental geometry). Additionally, the ability to test encoding and use of geometric information using 2-D and 3-D environments has allowed researchers to conduct noninvasive neuroimaging studies on the topic (e.g., Sutton et al., 2010, 2012), which otherwise would not be possible due to how these devices restrict movement.

3.2. The role of experience

In spatial localization tasks, experiential factors such as the order in which landmark-to-goal relations are acquired and how reliable a cue is for predicting the location of a goal can have a profound influence spatial cue use (Reichert and Kelly, 2015; Lyons et al., 2014). Such experiential influences also extend to the use of environmental geometry for reorientation and goal localization, a topic that Spetch et al. have investigated heavily.

In one of the earliest investigations into the effects of experiential factors on geometric cue use from Spetch's lab, Kelly et al. (1998) conducted a series of experiments that presented pigeons (*Columba* livia) with featural cues in conjunction with environmental geometric cues to locate a hidden goal. Kelly et al. found that pigeons could use featural information to locate a goal, even when coupled with reliable geometric information, regardless of whether the features were two-dimensional images or three-dimensional objects (see Fig. 1, panel a). As well, Kelly et al. found that how pigeons were trained had a significant impact on their later cue preference. On conflict tests where featural and geometric information indicated different possible goal locations, pigeons trained with featural and geometric information together (Feature Group) primary relied on featural information to search for the goal (Fig. 1, panel b). However, pigeons trained with only geometric information (Geometry Group) displayed no clear preference for featural information over geometric information (Fig. 1, panel c). Thus, the types of information pigeons had access to when learning to reorient in the apparatus had a significant effect on their later cue preference.

The findings from Kelly et al. (1998) suggest that experiential factors such as the order in which features are presented to animals in a geometry-task can have a meaningful impact on animals' later cue preference. These results would later inform the research of a number of other researchers who investigated topics such how enclosure size or sex could affect the encoding of geometric information in children (e.g., Learmonth et al., 2008; Lourenco et al., 2011). However, most relevant for the current discussion is that Kelly et al.'s (1998) findings raise the possibility that preference for geometric information may be influenced by factors such as the presence of unique featural information in the environment early in the learning process. Such a finding would suggest that in some cases geometric and featural information may interact, and thereby raises the potential for cue competition. If evidence of cue competition were found, it would create problems for the prevailing theory of geometric cue learning of the time, the notion that geometry is learned via an encapsulated module, separate from systems that encode non-geometric information (the geometric module theory). As such, the work of Kelly et al. would be one of the major motivating factors behind later research investigating cue competition between geometric and featural information discussed below.

3.3. Features overshadow geometry

As previously discussed, many animals have been shown to encode both featural and geometric cues for re-orientation and goal localization in enclosed environments (for a review, see Cheng et al., 2013). Typically, simultaneously learning multiple spatial cues leads to cue competition effects such as overshadowing (Spetch, 1995) or blocking (Rodrigo et al., 1997). However, this does not appear to be the case in most situations where featural and geometric cues are presented simultaneously (e.g., Kelly et al., 1998; Kelly and Spetch, 2004a,b; Hermer and Spelke, 1996). Gray et al. (2005) noted at the time that most animals studied were raised in, and had a great deal of experience with, environments with regular geometry such as wire cages or enclosed rooms with right-angled corners. As such, Gray et al. speculated that it is perhaps this extensive experience with informative geometric cues that leads animals to encode geometric and featural information simultaneously without typical cue competition effects. To test this, Gray et al. captured and tested wild Mountain chickadees (*Poecile gambeli*) who inhabit a forested mountain environment with limited regular geometry (i.e., right-angled corners), and thus provided an ideal test subject for their hypothesis. Gray et al. found that the chickadees trained with only geometric cues (geometry only condition), or with geometric cues and a distinctly coloured wall opposite to the goal (far feature condition) readily encoded environmental geometry. As such, on tests where only geometric cues were available due to the removal of the colored wall, both groups split their searches between the correct and rotationally equivalent corners (see Fig. 2). Surprisingly, however, on the same geometry-only test trials, birds trained with geometric cues and a distinctly coloured wall adjacent to the goal (near feature condition) split their searches evenly across the featurally correct, geometrically correct, and rotationally equivalent corners of the apparatus, thus suggesting they were unable to use environmental geometry to solve the task (see Fig. 2). Because these birds did not have any difficulty locating the correct corner when the feature was present, this finding suggests that the presence of a nearby unique feature during training overshadowed the encoding the geometric information for locating the goal. This was the first demonstration of features overshadowing the encoding of geometric information, and as such, had important implications for our theoretical understanding of how geometry was encoded at the time (see Kelly and Spetch, 2012 for an in-depth discussion).

In a follow-up study, Batty et al. (2009) sought to expand on the work of Gray et al. (2005) and determine if the findings were due to early experience or species factors. To test this, Batty et al. trained and tested wild-caught mountain chickadees, wild-caught black capped chickadees (*Poecile atricapillus*), and hand-reared black-capped chickadees in a similar task to that of Gray et al. (2005). Batty and colleagues found that both the wild-caught and hand-reared black-capped chickadees were able to use geometric information to reorient in all conditions, including the near-feature condition that produced an overshadowing effect with mountain chickadees in Gray et al. (2005). This

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[1] It is possible subjects found it easier to encode geometric information when features were present, rather than absent, as features have been shown to enhance the encoding of geometric information in some situations (Kelly, 2010).

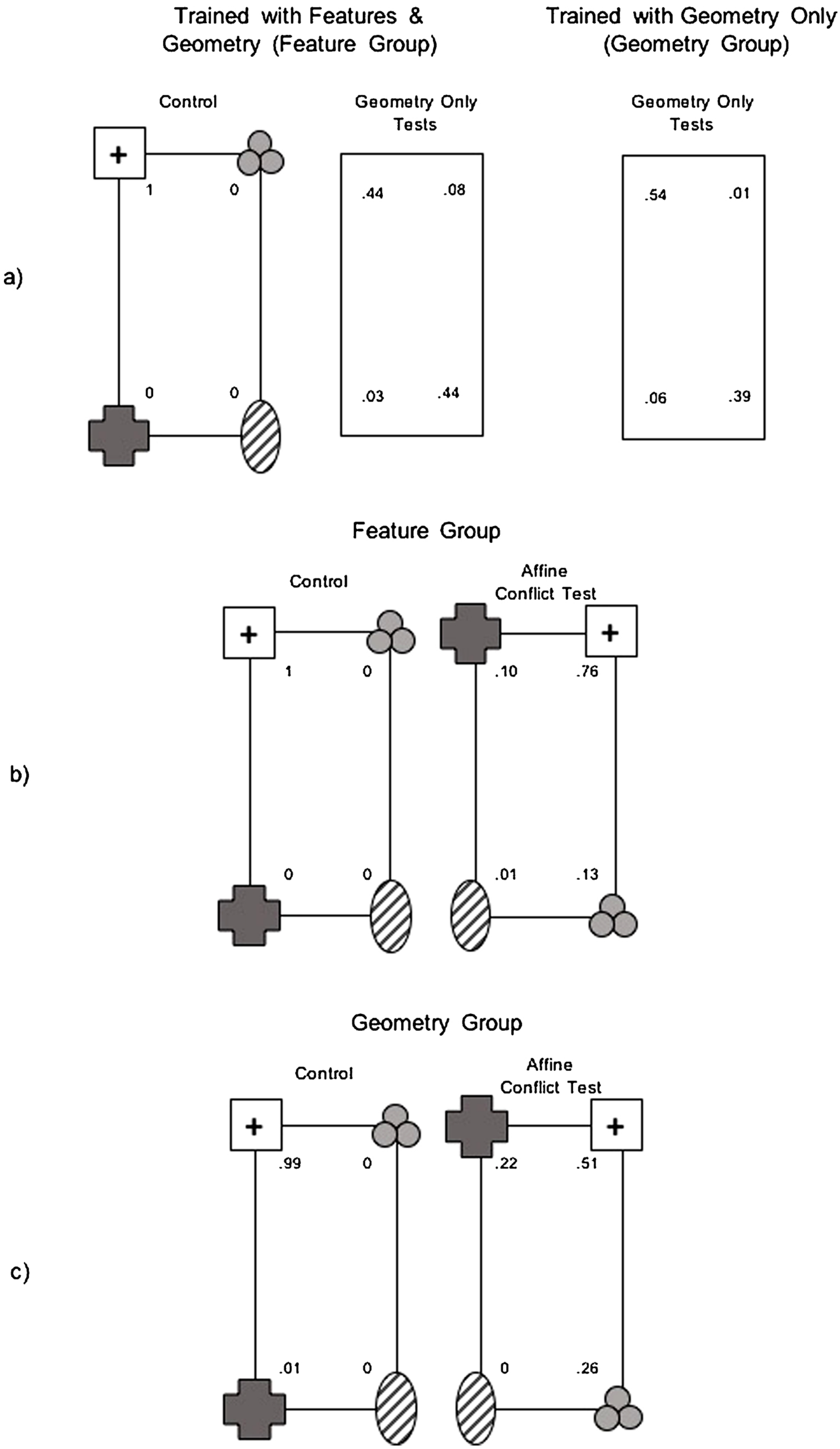

Fig. 1. Proportion of choices to each corner during test trials. The correct corner is standardized to be the top-left corner in each image, although was counterbalanced across birds in the experiment. a) For the feature group, control trials were those where the features and geometric cues were presented in the same relation to one another as in training, and geometry only trials were those where either all features were removed or identical. For the geometry group, geometry only tests were the same as presented during training. b–c) Results of control and affine transformation conflict tests for the feature only group (panel b), and the geometry only group (panel c). Adapted with permission from Figs. 2 and 4 in Kelly et al. (1998). “Pigeons' (Columba livia) encoding of geometric and featural properties of a spatial environment”. *Journal of Comparative Psychology, 112*(3), p.262–264.

result, coupled with the finding that half of the wild-caught mountain chickadees still demonstrated an overshadowing effect in the near-feature condition even with the procedural changes of Batty et al. (2009), suggested that a species-specific factor led mountain chickadees to be more prone to cue completion effects in tasks requiring geometric cue use. While it is not clear what this species factor could be, the authors speculated that differences in how the two species make their nests and forage could be responsible. Taken together, the results of both Gray et al. (2005) and Batty et al. (2009) suggest that using environmental geometry to reorient is a less preferred strategy for

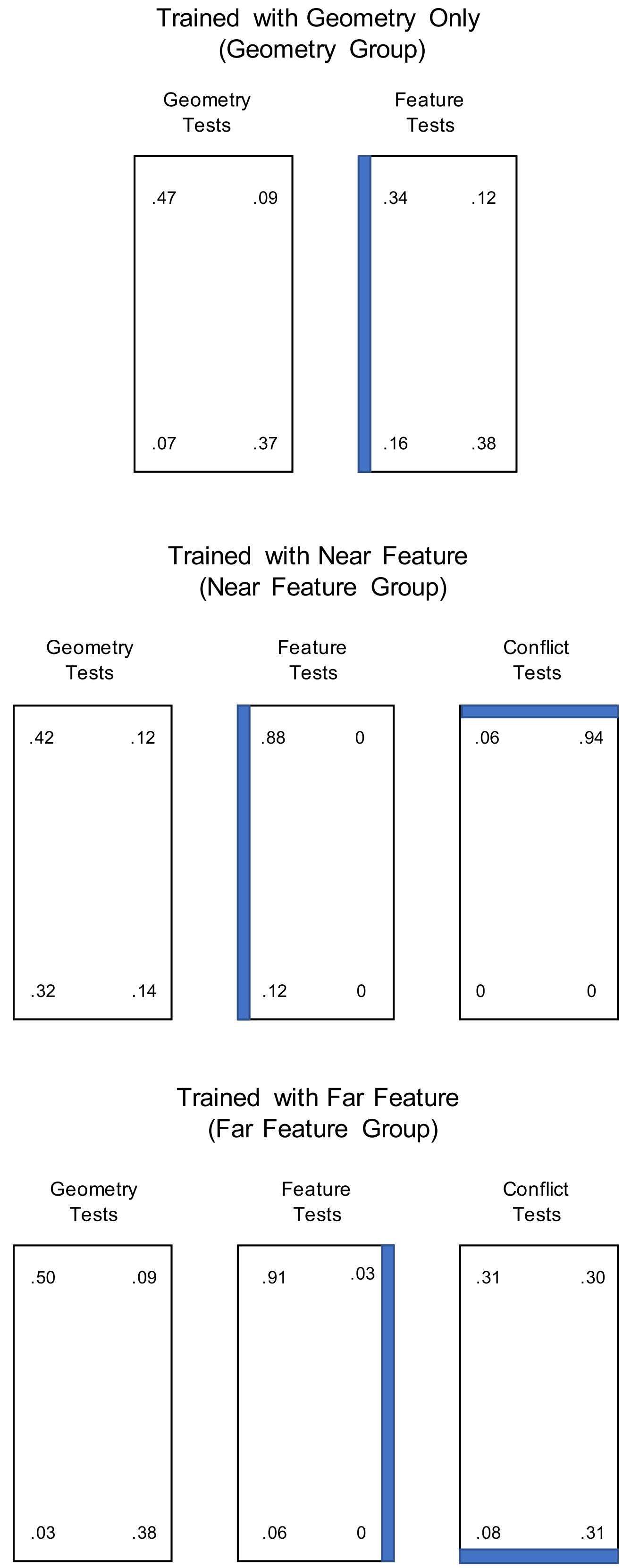

Fig. 2. Proportion of choices to each corner during test trials. The correct corner is standardized to be the top-left corner in each image, although it was counterbalanced across birds in the experiment. Additionally, while the images here only show the trained feature as a long wall, in Gray et al.'s (2005) experiment, the feature wall was on the short wall for half of the subjects. In all panels, the left-most image displays results from tests where features were removed (geometry tests). The middle image displays results from feature tests where a colored wall was presented as part of the apparatus (as it was displayed in training for the near- and far-feature groups). The right-most images display the results of conflict tests for birds that were trained with a feature. Conflict tests were not conducted for birds trained without a feature (geometry group, topmost panel). Adapted with permission from Figs. 1 and 2 in Gray et al. (2005). "Spatial encoding in mountain chickadees: features overshadow geometry". *Biology Letters, 1*(3), p.315–316.

mountain chickadees than for black-capped chickadees, and this may explain why they are more susceptible to cue-competition effects.

The work of Gray et al. (2005) and Batty et al. (2009) has spurred a great deal of research into the study of cue competition between geometric and featural information. For example, Pearce et al. (2006) showed that featural cues could overshadow geometric cues with rats in a water maze task. And, if rats were pre-trained to respond to featural information in such a task, this prior learning blocked rats later ability to learn the location of the goal when both featural and geometric cues were present. Kosaki et al. (2013) further demonstrated that overshadowing of geometric information by featural cues in rats depends heavily on stimulus saliency and the relatively reliability of those cues in predicting the goal location. And conversely, Kelly (2010) has reported that the presence of features can enhance the encoding of environmental geometry in some situations.

Taken together, these findings are difficult to reconcile with the prevailing theory of geometric cue use of the time, the idea that animals have a geometric module that encodes geometric information separately and automatically, without influence from other sources of information. If this was the case, then experience with or the presence of a feature should not influence the acquisition of geometric information (see Twyman and Newcombe, 2010; Cheng, 2008 for a more in-depth discussion of potential issues with the notion of a geometric module). However, as this research demonstrates, prior experience with geometric information and/or species factors can have a dramatic effect on the acquisition of geometric information. As such, these findings have played a role in the development of alterative theories of geometry learning and use, such as the Miller-Shettleworth associative model (Miller and Shettleworth, 2007, 2008), the Adaptive-combination model (Ratliff and Newcombe, 2008), and the View-Based Matching hypothesis (Stürzl et al., 2008; Cheung et al., 2008), among others.

3.4. *Rearing*

One question that arises from the work of Gray et al. (2005) and Batty et al. (2009) is whether an animal requires early experience with regular environmental geometry to use it effectively for reorientation and goal localization. To test this, Brown et al. (2007) reared Convict cichlid fish (*Archocentrus nigrofasciatus*) in either a rectangular or circular tank, the latter being devoid of distinctive environmental geometric information that could be used to localize a goal, before being trained and tested to locate a goal in a rectangular environment. In training, fish were randomly assigned to either a geometry or feature training group and trained to swim to a specific corner of the tank. In the feature training group, one wall of the tank was coloured blue, thus providing featural and geometric information to help locate the correct corner. In the geometric training group, the feature was not present, leaving fish with only geometric information to locate the goal. Brown et al. found that fish reared in both the rectangular and circular environments could learn to use geometric information with training, thus suggesting that fish do not require early exposure to angular geometry to encode and use it later in life.

However, rearing condition had an effect on the speed with which fish could learn to use the environmental feature to locate the goal, as well as cue preference in cue conflict situations. Specifically, fish reared in the circular environment were able to learn the feature task more quickly than those reared in the rectangular environment, suggesting that early exposure to geometry interfered with the ability of fish to use featural information to locate the goal. When featural and geometric cues were placed in conflict, fish reared in the circular environment relied on featural information to solve the task, whereas fish reared in the rectangular environment split their responses between using featural and geometric information. Thus, the work of Brown et al. (2007) suggests that early exposure to geometry is not necessary for an animal to use such information later in life, but such experience increases the saliency of geometric information.

The work of Brown et al. has led others to question the role of early experience plays in animals' ability to encode and use geometric information. Particularly, some of Brown et al.'s (2007s) findings, such as the fact fish reared without rectangular geometry preferred featureal cues to geometric cues in conflict tests, are difficult to reconcile with the notion that geometric information is acquired automatically and used preferentially via an inborn core-knowledge system (i.e., geometric module). As such, Brown et al.'s work has spurred follow-up rearing studies with mice (Twyman et al., 2013), chicks (Chiandetti and Vallortigara, 2008, 2010; Chiandetti et al., 2015), and other fish species (Sovrano and Chiandetti, 2017). Interestingly, work with other species has not provided a clear pattern of results in this regard, as Twyman et al.'s (2013) work showed that young mice reared in circular environments, unlike those reared in rectangular environments, did not spontaneously encode geometric information in environments where a feature could be used to locate the goal (i.e., presence of features overshadowed geometry). However, in work with chicks and other fish species using similar rearing methods found no evidence of overshadowing in such tests (Sovrano and Chiandetti, 2017; Chiandetti et al., 2015; Chiandetti and Vallortigara, 2008, 2010). As such, there may be species specific factors at play, which will require additional, carefully controlled research to identify.

3.5. *What geometric features are critical for orientation*

Over the past 15 years, many researchers, including Spetch et al., have begun investigating what specific properties are extracted from an environment's geometry to be used for reorientation and goal localization. Below, I discuss two such areas where Spetch et al. have been active.

3.5.1. *Size of angles and relative wall length*

In 2004, Tommasi and Polli, showed that domestic chicks (*Gallus gallus*) could use both relative wall lengths and the size of the angle formed by the intersection of walls at a given corner (angular amplitude) to reorient. Building on this work, Spetch et al. examined whether adult humans (Lubyk et al., 2012) and pigeons (Lubyk and Spetch, 2012) could also use these cues to reorient in virtual (for humans) and real-space (for pigeons) environments. Similar to Tommasi and Polli (2004), subjects in both Lubyk et al. (2012), and Lubyk and Spetch (2012) were trained to locate a goal in a featureless parallelogram enclosure. For half the subjects, the reinforced corner had an acute angular amplitude, whereas for the remaining subjects, it was obtuse. After training subjects such that they could reliably select the correct corner or its rotational equivalent, they were tested with environments that removed relative wall-length but maintained angular amplitude (a rhombus), made angular information uninformative but maintained relative wall length (a rectangle), or placed both relative wall length and angular information in conflict (a reverse parallelogram). Results from both studies demonstrated that adult humans and pigeons could use relative wall-length and angular information alone to locate the correct corner or its rotational equivalent significantly above what would be expected by chance (see Fig. 3). On tests in which angular information was placed in conflict with relative-wall length (a reverse parallelogram enclosure), pigeons and adults preferred to use angular information to resolve the conflict (see Fig. 3). Unlike the chicks in Tommasi and Polli's (2004) research, however, adults and pigeons' response patterns did not change as a function of the angle of the correct corner in training, suggesting that both pigeons and humans perceived angular amplitude as the more salient feature, regardless of how large it was (see Fig. 3).

Most research on geometric cue use has used enclosed environments which provide information from continuous surfaces (i.e., relative wall length) and angular information to aid reorientation. However, the results of Lubyk et al. (2012) and Lubyk and Spetch (2012) above suggest that animals may only require angular information for reorientation. To test this, Lubyk et al. (2013) trained pigeons in an open field environment, and adult humans in an immersive 3-D environment, to locate a specific corner in a diamond shaped array of landmarks or enclosure. Lubyk et al. also included a salient feature in the enclosure or array to determine whether encoding of angular information would be inhibited or enhanced by the presence of an additional cue. Results revealed first that both adult humans and pigeons could learn to use the angular information derived from both the enclosure and landmark array to locate the correct corner, or its rotational equivalent, at levels significantly above chance. Second, the presence of a salient feature during training did not interfere with the encoding of the angular information in either the enclosure or array. Third, in conflict tests where featural cues were placed in conflict with angular information, a complex pattern of results emerged. For adult humans, female participants weighted featural information more heavily than angular information, whereas male participants did not show any difference in cue weighting. This sex difference did not depend on the environment in which participants were trained, and is consistent with past literature (Kelly and Bischof, 2005). For pigeons, those that were trained with an acute corner displayed heavier weighting of angular information than featural information, whereas those trained with an obtuse angled corner did not display any difference in cue weighting. This finding, which is consistent with the findings of Tommasi and Polli (2004) with chicks, did not depend on whether the pigeons were trained in the array or enclosed environment. Taken together, these findings suggest that for both pigeons and humans, similar processes underlie the use of angular information for reorientation in enclosed environments and landmark arrays, and as such, continuous surfaces are not necessary for reorientation when distinctive local angular information is available as a part of an environment's geometric composition.

3.5.2. *Height cues*

In most research studying the use of geometric information for reorientation, animals are trained and tested in environments that provide distinct horizontal geometric cues (relative wall length and angles) that can be used to reorient. Such environments are purposefully constructed so that vertical cues such as wall height or floor slope are constant. While past research has demonstrated that vertical cues can be used to aid goal localization (Henderson et al., 2001; Holbrook and de Perera, 2009; Grobéty, and Schenk, 1992), only recently have vertical cues such as the slope of the floor (human children: Holmes et al., 2015; pigeons: Nardi and Bingman, 2009) or height of the ceiling (human children: Hu et al., 2015) been shown to be used in conjunction with environmental geometry to aid reorientation. Building on this work, Du and colleagues in Spetch's lab have investigated whether pigeons (Du et al., 2016a) and adult humans (Du et al., 2016b) can use vertical cues provided by the height of walls in an enclosure for reorientation.

In Du et al. (2016a), trained pigeons in two experiments to locate food in one corner of a rectangular enclosure where the long walls were half the height of short walls. Thus, in addition to the horizontal environmental cues within the environment, such as relative wall length, the height difference between walls provided a stable vertical feature. Du et al. found that pigeons were able to reorient using vertical cues derived from the height difference between the walls of the enclosure.

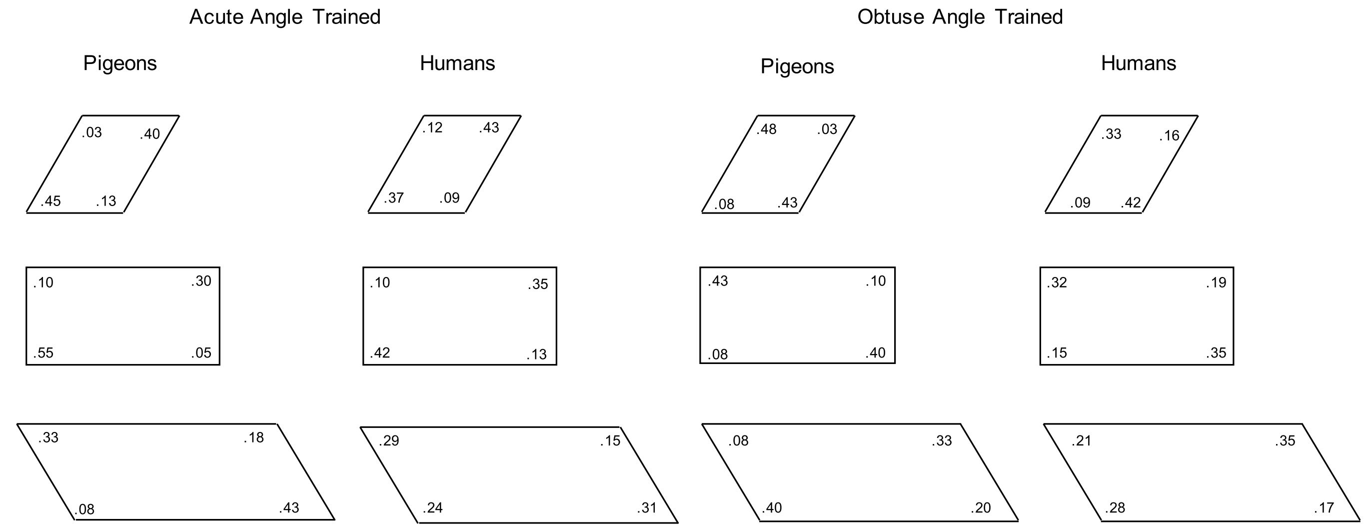

Fig. 3. Proportion of choices to each corner for acute-corner (*left two panels*) and obtuse-corner trained (*right-two panels*) human and pigeon subjects in the rhombus (*top row*), rectangular (*middle row*), and reverse parallelogram (*bottom row*) test enclosures. Adapted with permission from Fig. 3 in Lubyk et al. (2012). "Geometric orientation by humans: angles weigh in." *Psychonomic Bulletin and Review, 19*(3), p. 440, and Figs. 2 and 4 in Lubyk and Spetch (2012). "Finding the best angle: Pigeons (*Columba livia*) weight angular information more heavily than relative wall length in an open-field geometry task." *Animal Cognition, 15*(3), p.310–311.

However, on conflict tests in which vertical and horizontal cues were placed in conflict, pigeons preferred horizontal cues for reorientation.

In work by Du et al. (2016b), adult humans were tested in immersive 3D environments with a similar research design to that of Du et al. (2016a). In contrast to pigeons (Du et al., 2016a) and children (Hu et al., 2015), adults were able to use both vertical and horizontal cues for reorientation, and did not show a preference for one cue type over another in conflict tests. In Hu et al.'s work specifically, children preferred horizontal cues to vertical cues, although the vertical cues came from a slanted ceiling instead of relative wall heights. Thus, it is possible that the difference in Du et al.'s (2016a,b) findings are due to either developmental or procedural differences, which will require additional research to disentangle. In sum, work by Du et al. (2016b), and Du et al. (2016a) demonstrate that both adult humans and pigeons can use vertical cues derived from wall height to reorient.

In conclusion, Spetch et al. have made significant contributions to our understanding of how environmental geometric information is used for goal localization and reorientation. Specifically, as discussed above, research by Spetch et al. has demonstrated that: pigeons and humans use geometric information extracted from 2-D schematic environments in a similar manner as geometric information extracted from real-space environments (Kelly and Spetch, 2004a,b); the order in which featural or geometric information is learned can significantly affect later cue preference (Kelly et al., 1998); for mountain chickadees (but not black-capped chickadees), features overshadow learning about environmental geometry (Gray et al., 2005; Batty et al., 2009); early exposure to regular environmental geometry is not necessary for an animal to use such information later in life, but does increase the saliency of geometric information (Brown et al., 2007); angular amplitude is a more salient geometric feature than relative wall length for reorientation (Lubyk et al., 2012; Lubyk and Spetch, 2012); and both pigeons and adult humans can use vertical cues derived from wall height to reorient, although for pigeons, such cues are less preferred than horizontal geometric cues such as angular amplitude (Du et al., 2016a, b). As this list clearly indicates, without the work of Spetch et al., our understanding of how animals use geometric information for reorientation and goal localization not be nearly as rich and robust as it is today.

4. Resolving cue conflict

Next, this review will revisit another area of research on comparative spatial cognition in which Spetch has had a profound influence: the study of how animals resolve cue conflict. Cue conflict occurs when animals encode spatial information from more than one cue, and due to changes in the environment, one or more of the cues are displaced. Therefore, the learned relationship between each cue and the goal conflict by suggesting different search locations. For example, imagine a pigeon has stored the location of its nest using both a nearby tree and boulder as landmarks. The pigeon has therefore encoded a vector from each landmark to its nest to help find it. If one cue was suddenly removed, such as the tree falling down, then this redundant encoding of spatial information would allow the pigeon to still locate its goal by relying on the remaining cue. Such redundancy, while generally useful, can sometimes create problems when a cue is displaced instead of lost. If, for example, the tree remained standing, but the boulder was moved 5-meteres North-East, the vector from the tree and the boulder now provide cue conflict by indicating different possible goal locations.

In the previous sections of this paper, we have discussed cue conflict extensively with discrete choice tasks that test geometric cue use. However, cue conflict often occurs in natural settings between landmarks where the search space is continuous. Understanding how animals resolve cue conflict in such situations is a major area of investigation with a rich theoretical background. In general, research has shown that animals use a variety of methods (sometimes referred to as strategies) to resolve cue conflict, with the exact method employed depending on factors such as the degree of conflict between two cues (Legge et al., 2016). Here I will review some of the methods animals use to resolve cue conflict while drawing special attention to the work of Spetch and colleagues, who have published heavily in this area. Again, this is not meant to be an exhaustive review, but instead is designed to highlight Spetch's scientific legacy. For more comprehensive reviews, see Cheng et al. (2007); Spetch and Kelly, (2006); Cheng et al. (2006), or Cheng and Spetch (1998).

4.1. Hierarchical cue use

Hierarchical strategies (also known as winner-take-all or take-the-best strategies, Gigerenzer and Brighton, 2009; Wills et al., 2009; Morgan et al., 1998) are those in which animals rank order cues, such that one cue, or cue type, is preferred to others that are available. When faced with cue conflict, the animal will use the preferred cue to the exclusion of others. Critically, however, hierarchical strategies are not a case of the animal only learning the relation of a goal relative to the preferred cue; the goal is encoded relative to multiple cues, but when conflict arises, only information from the preferred cue is used. Thus, if the preferred cue type is lost, the animal can still locate the goal. Unfortunately, however, using a hierarchical strategy means that an animal must disregard potentially relevant information from nearby, nonpreferred cues, which may lead the animal to search in an incorrect location if the preferred cue is displaced.

Many animals have been shown to use hierarchical strategies for coping with cue conflict in discrete choice tasks. One seminal example comes from work by Spetch and Edwards (1988) in an open-field laboratory task. In their study, Spetch and Edwards created landmark arrays made out of identical discarded milk-cartons which pigeons had to search to find a hidden food reward. In training, the cartons placed in the same room location and position relative to one another. Thus, across trials pigeons could learn the location of the baited carton (the goal) either by using the position of the hidden food relative to the walls and corners of the room (global cues), or using the position of the baited carton relative to other items in the array (local cues). On test trials, Spetch and Edwards would remove a carton or alter the position of the array to see whether pigeons could use local or global cues alone to locate the goal, and if so, which cue they would prefer when the two cues were placed in conflict (see Fig. 4).

Spetch and Edwards (1988) found that on tests where only local or global information was available, pigeons selected the carton that was correct according to the available cue significantly more than would be expected by chance. Thus, pigeons had encoded the goal location relative to both the local (configural) and global (room position) spatial information during training. On conflict tests, most pigeons preferred to use the local position to resolve the cue conflict, although there were some individual differences in cue preference. These results suggest pigeons relied on a hierarchical strategy for resolving cue conflict, preferring local cues to global cues when conflict arose, but being able to use either source if one type of information was removed.

As noted by Cheng et al. (2006), Spetch and Edwards' (1988) paper was one of two studies that began the lab-based study of landmark use in pigeons (the other being Cheng, 1988), an area which has since become a very active area of research (see Cheng et al., 2006 for a comprehensive review of the study of small-scale spatial cognition in pigeons). Additionally, the question of how other animals prioritize local and global spatial information when conflict arises has led to a number of other comparative investigations. Interestingly and in contrast to Spetch and Edwards' (1988) pigeons, most species studied have shown a preference for global cues over local cues when faced with cue conflict (domestic dogs, *Canis familiaris*: Fiset, 2007; black-capped chickadees, *Parus atricapillus*: Brodbeck, 1994; Clark's nutcrackers, *Nucifraga columbiana*: Gould-Beierle and Kamil, 1996; Rufous hummingbirds, *Selasphorus rufus*: Hurly and Healy, 1996; Bumblebees, *Bombus impatiens*: Church and Plowright, 2006; and Columbian ground squirrels, *Urocitellus columbianu*: Vlasak, 2006a,b, among others).

Since Spetch and Edwards (1988), research on spatial cue preference in situations of conflict has shown that it can be influenced by stimulus factors such as enclosure size and density of stimuli (Learmonth et al., 2002; Vallortigara et al., 2005; Sovrano et al., 2005; Neiworth et al., 2006). It is therefore possible that the stable horizontal orientation of the array used in Spetch and Edwards (1988) predisposed pigeons to prefer local cues to global cues to resolve cue conflict. To test this, a follow-up study was conducted by Legge et al. (2009) in Spetch's lab. Legge et al.'s training procedure differed from Spetch and Edwards in that they trained pigeons to peck a central square in a three-square array that was presented on a touch-screen in an operant chamber. Pecks to the central square of the array were reinforced, and during training the number and position of the squares on the screen did not change. As such, pigeons could learn which square to select using either local cues based on the configuration of the array (i.e., select the middle square), global cues based on the position of the reinforced square relative to the edges of the touchscreen, or both. As well, Legge et al. manipulated the orientation of the array during training across three experiments such that the arrays were vertically oriented (Experiment 1), horizontally oriented (Experiment 2), or vertically, horizontally, and diagonally oriented (Experiment 3). Results of these experiments demonstrated that the orientation of the array was a major factor in the type of cue pigeons would prefer when faced with conflict. Specifically, when arrays were horizontally oriented during training (Experiment 2), most pigeons preferred local cues to global cues, a finding in line with that of Spetch and Edwards (1988). However, when arrays were vertically oriented (Experiment 1), or presented in multiple orientations during training (Experiment 3), most pigeons preferred global cues. This difference in cue preference may reflect the operation of gravity-defined axis (Kelly and Spetch, 2004a,b), increasing the saliency of global information when pigeons were trained with arrays that were vertically oriented. While this suggestion merits further investigation, the work of Legge et al. demonstrates that pigeons' cue preference is flexible and dependent on environmental factors.

In sum, early work by Spetch and Edwards (1988) on pigeon spatial cue preference in conflict situations was influential in promoting similar comparative tests in human and non-human animals. Additionally, the work of Spetch and Edwards was noteworthy in that it was one of the first comprehensive laboratory studies of pigeon landmark use (Cheng et al., 2006), which is now one of the more frequently used animal models for studying spatial cognition. Finally, work of Spetch and colleagues which have followed up on the work of Spetch and Edwards, such as that of Legge et al. (2009), have helped support the notion that pigeon cue preference is flexible and dependent on factors such as the orientation of arrays of visual stimuli. The study of such factors, and how they may affect hierarchical processing of visual stimuli, continues to be an area of investigation, and in which work such as Legge et al. (2009) continue to be informative (e.g., Truppa et al., 2010; Wasserman et al., 2014; Chiandetti et al., 2014).

4.2. Absolute vs. relational strategies

Occasionally, animals may find themselves in a situation where they have to encode the position of a goal relative to multiple landmarks that are difficult to differentiate. In such situations, a hierarchical strategy cannot be employed, as one cue cannot be isolated from the rest for preferential use. Instead, an animal may use a relational or absolute search strategy to resolve cue conflict. A relational (or relative) strategy is one where the position of the goal is encoded relative to its position within the array (i.e., in the middle). An absolute strategy is one where the absolute position of the goal is encoded relative to each cue within the array with the array's configuration serving as the basis for the landmark-to-goal vectors. To exemplify both strategies, consider a situation where two identical landmarks are positioned 5-meteres away from one another with the goal located centrally between the two cues (see Fig. 5, panel a). The animal could encode the goal's position relative to both landmarks in the array (i.e., the goal is half-way between the two landmarks), or as an absolute vector from each landmark (i.e., the goal is 2.5 m to the right of the landmark on the left, and 2.5 m to the left of the landmark on the right). If the array was then expanded, the relative and absolute strategies would predict quite different goal locations (see Fig. 5, panel b).

Early work in investigating how animals resolve cue conflict with arrays of identical landmarks were conducted with honeybees (*Apis mellifera*, Cartwright and Collett, 1983) and gerbils (*Meriones unguiculatus*, Collett et al., 1986). Cartwright and Collett (1983) found that honeybees encoded the position of a goal using a relational strategy, whereas Collett et al. (1986) found that gerbils encoded spatial information using an absolute strategy. As such, it is possible that there may be species differences in how animals encode the position of

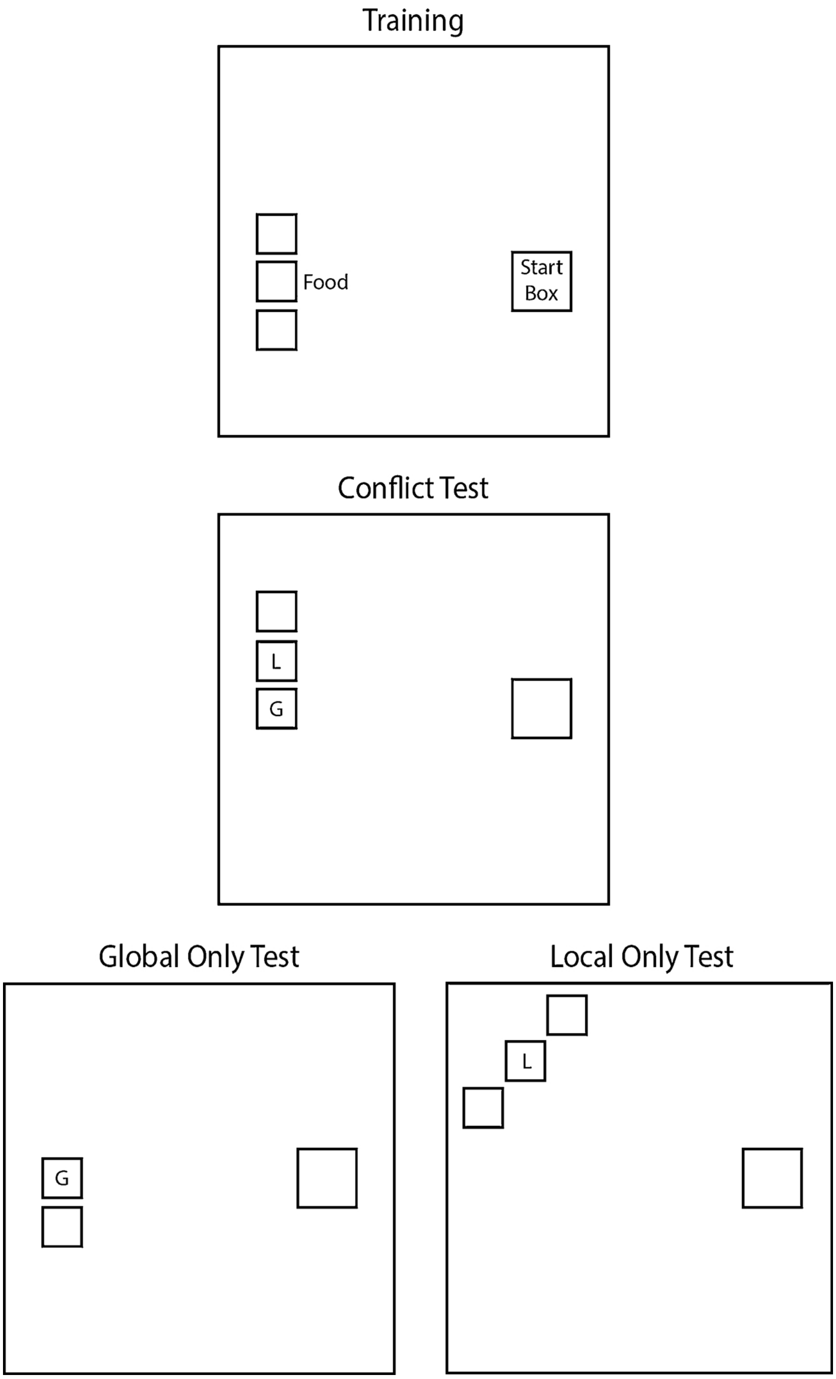

Fig. 4. Diagram of training and testing trials from Spetch and Edwards (1988). Squares marked with "L" denote the box that is correct according to local cues (the box's position in the array). Squares marked with "G" denote the box that is correct according to global cues (the box's position relative to room cues). Adapted with permission from Fig. 1 in Spetch and Edwards (1988). "Pigeons', *Columba livia*, use of global and local cues for spatial memory." *Animal Behavior, 36(1),* p.294.

a goal relative to an array of identical landmarks.[2]

Building on this work, Spetch and colleagues investigated whether adult humans and pigeons would use relational or absolute search strategies to resolve cue conflict when trained to locate a goal within an array of identical landmarks on a touch screen (Spetch et al., 1996) or in an open-field environment (Spetch et al., 1997). Regardless of whether subjects were trained with a touch screen or in an open field, conflict tests where the landmark array was expanded or contracted revealed that adult humans relied on a relational search strategy while pigeons relied on an absolute search strategy. As the training and testing procedures were similar in both experiments, these results suggest a species difference.

More recent investigations have shown that most non-human animals use an absolute search strategy to resolve cue conflict when landmarks within an array cannot be differentiated. For example, in work by MacDonald et al. (2004), marmoset monkeys (*Callithrix jacchus cacchus*), human adults, and human children (ages 5–9) were trained to search for a hidden goal in the center of an array of four identical landmarks arranged in a square. While all subjects could learn to locate

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[2] It should be noted that there were a number of procedural differences between Cartwright and Collett's (1983) and Collett et al.'s (1986) studies that could also have led to the difference in the strategy observed.

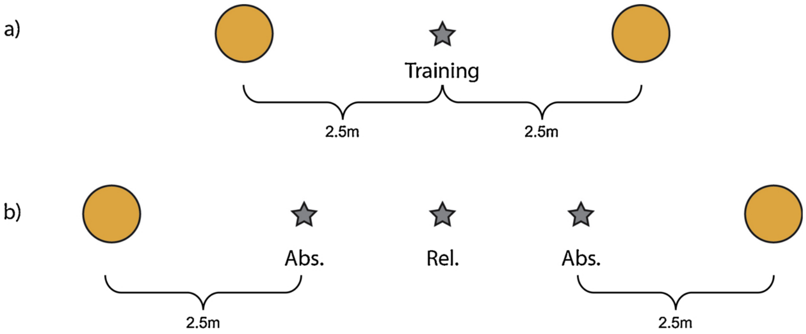

Fig. 5. *a)* Example of an array of two landmarks with the goal location presented equidistant from each landmark in the horizontal plane. *b)* Example of an expansion test. If the animal used a relative search strategy, it would search in a location that maintains the relative position of the goal to the two landmarks (in this case, in the center of the array). If the animal used an absolute search strategy, it would search in a location that maintains the distance and direction of the goal location from each landmark from training.

the goal during training, only adult humans used the relative relationship between the landmarks to search for the goal when the array was expanded. Marmosets and human children tended to use an absolute search strategy. Other species such as capuchin monkeys, (*Cebus apella*, Poti et al., 2005), bonobos (*Pan paniscus*, Poti et al., 2010), orangutans (*Pongo abelii*, Marsh et al., 2011), Clark's Nutcrackers (*Nucifraga Columbiana*, Kelly et al., 2008), and bats (*Glossophaga soricina*, Winter et al., 2005) have also been shown to primarily rely on absolute search strategies to locate a goal when experiencing cue conflict in an array of identical landmarks. However, as noted by Kelly et al. (2008), such a tendency may be due to most studies using only a single exemplar (i.e., a single array) during training. In studies where birds were trained with multiple exemplars, relational strategies were readily learned (e.g., Clark's Nutcrackers: Kamil and Jones, 1997; pigeons: Spetch et al., 2003). Such encoding flexibility is also supported by research with human children where factors such as age, context, and task instructions have been shown to influence whether relational or absolute search strategies are used (see further: Batty et al., 2010; Marsh et al., 2011; Ankowski et al., 2012; Waismeyer and Jacobs, 2013). Overall, more research is needed in this area to determine the extent to which strategy adoption is flexible, particularly with non-human animals.

In summary, the comparative work of Spetch et al. (Spetch et al., 1996, 1997) on whether adult humans and pigeons encode landmark arrays in an absolute or relational fashion revealed a species difference: humans tended to encode landmark-to-goal relations in a relational fashion, while pigeons relied on an absolute encoding strategy. Spetch and colleagues' work has led researchers to test how other species encode and use multiple landmarks for goal localization, and has played a role in motivating later research into the malleability of cue preference due to factors such as training experience (Sutton, 2002) and the presence of salient orienting cues (Sturz and Katz, 2009).

4.3. Integrative strategies

In addition to hierarchical and absolute/relational strategies, animals may also employ integrative strategies to cope with cue conflict. Integrative strategies require animals to combine information from multiple sources, including those that are displaced, to identify a "best guess" location that is close enough to the true goal for success (Cheng et al., 2007). Because an integrative strategy requires animals to use information from many sources, they have the potential to provide a more accurate estimate of a goal's location than strategies that rely on only a single cue to predict where the goal would be.

Previous research in which adult humans (Spetch et al., 1996, 1997) and honeybees (Cartwright and Collett, 1983) have been shown to use a relational strategy to resolve cue conflict suggests that these animals can integrate vectors from multiple sources. It is unclear from these studies, however, how animals integrate the dictates of each cue. Recently, researchers such as Cheng et al. (2007) have suggested that animals may use a Bayesian strategy, whereby the vectors provided by each cue are weighted according to their relative reliability.[3] Adult humans, for example, have been shown to use Bayesian integration for multiple sources of perceptual information within (Jacobs, 1999; Jacobs and Fine, 1999; Oruç et al., 2003) and across modalities (Deneve and Pouget, 2004; Alais and Burr, 2004; Ernst and Banks, 2002), as well as for localizing a goal using visual and auditory cues (Battaglia et al., 2003). Until recently, however, direct investigations of whether, and if so how, human and non-human animals integrate multiple sources of visual-spatial information for goal localization were missing. Towards this end, recent work by Spetch et al. have focused on understanding how different species, namely pigeons, adult humans, and desert ants, resolve spatial cue conflict through integrative strategies.

In a recent study from Spetch's lab, Legge et al. (2016) set out to test how pigeons use multiple spatial cues for goal localization when faced with varying degrees of cue conflict. Pigeons were trained to locate a hidden goal relative to two distinct landmarks in an open-field environment. On test trials, one of the landmarks was removed (single-cue tests), or the landmark array was expanded in the parallel or orthogonal dimension relative to the largest landmark (conflict tests). Legge et al. found that when the array was expanded only a little, thus creating a relatively small degree of cue conflict, pigeons used an integrative strategy to search for the goal. However, when the array was expanded a great deal, thus creating a large degree of cue conflict, pigeons instead treated each landmark as a separate source of information and searched relative to each cue independently (i.e., they no longer treated the two landmarks as part of an array). Of particular interest was when pigeons used an integrative strategy to search for the goal, model comparisons revealed that the pigeon's search distribution was consistent with what would be expected if pigeons were weighting cues according to their reliability. Such results are congruent with recent theoretical discussions based on Bayesian inference of how animals cope with cue conflict and integrate spatial information (Cheng et al., 2007; Körding et al., 2007; Pfuhl et al., 2011).

In other work investigating cue integration from Spetch's lab, Du et al. (2017) recently trained human participants to search for a hidden goal on a horizontal line between two distinct landmarks on a computer screen. The landmarks were presented such that one landmark was always closer to the goal than another, and the relative distance between the landmarks was held constant across training trials. In their first experiment, Du et al. trained participants to locate the goal by varying how the landmarks were presented. On some trials, landmarks were presented alone, whereas in others, they were presented together. On test trials, the two landmarks were presented together and the array expanded, thus creating cue conflict. Similar to Legge et al. (2016), the amount of array expansion varied across trials, allowing the authors to

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[3] Fitting for this review, Cheng et al. (2007) reanalyzed old pigeon search data from Spetch and Mondloch (1993) to show that on transformation tests, a Bayesian model did a good job explaining the pattern of responses from Spetch's pigeons on test trials.

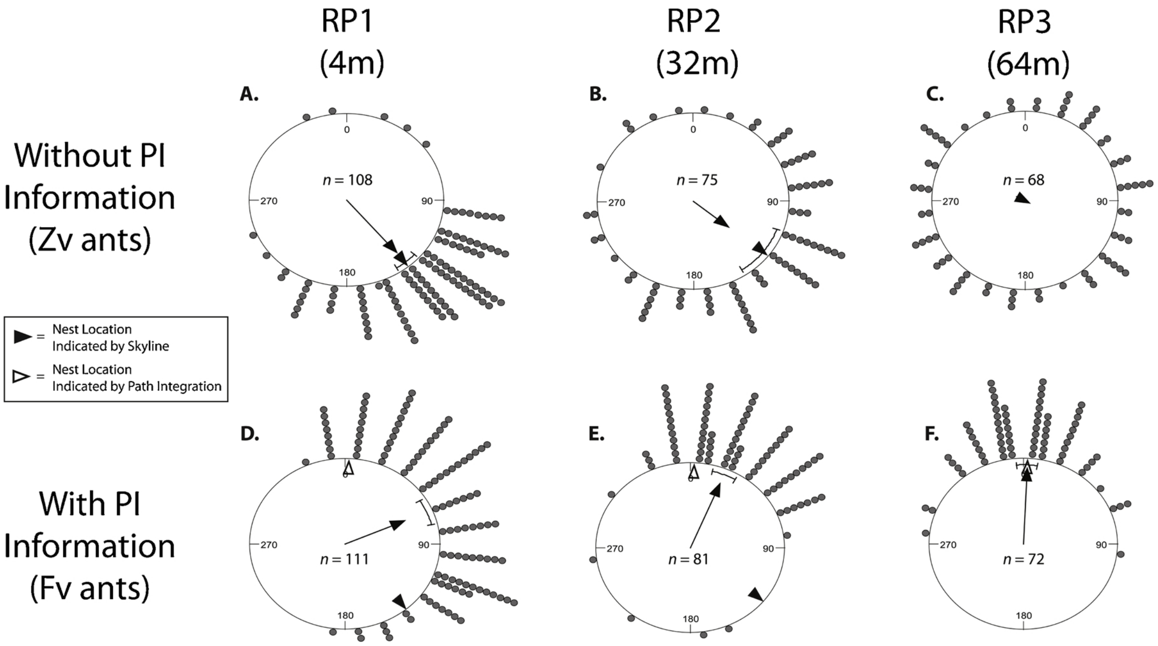

Fig. 6. Ant directional bearings for each test from Legge et al. (2014) described in the main text. Grey circles indicate an ant's directional bearings after crossing a marked line 30 cm from the point of release. Open triangular markers indicate the nest direction according to ants' path integration system. Closed black triangular markers indicate the nest direction according to the surrounding visual panorama. Note that there are no open triangular markers in panels (A)-(C), as all ants tested were zero-vector, and did not have access to path integration information. Note also that there are no closed triangular markers in panels (F) and (C), as ants could not use view-based navigational cues to orient themselves at this release point. When ants were significantly oriented, the 95% confidence interval of the mean is displayed as a curved marker on the inside of the circular plot. Reproduced with permission from Fig. 4 in Legge et al. (2014). "Combining sky and earth: desert ants (*Melophorus bagoti*) show weighted integration of celestial and terrestrial cues." *Journal of Experimental Biology, 217*(23), p.4162.

test how search behaviour would change as a function of the degree of cue conflict present on a given trial. Du et al. (2017) found that participants used an integrative strategy to search for the goal on expansion tests, and that the cue that was closer to the goal was weighted more heavily than the cue that was further from the goal.

In a second experiment, Du et al. were interested in determining whether the conditions in which people were trained would influence their search behaviour. As such, they trained participants with the cues presented together or separately. On test trials where both cues were presented together and the array was expanded, participants trained with each cue individually did not show evidence of integration, while those trained with both cues together did. While more research is required, the authors speculate that the lack of integration in the groups where participants were trained with individually presented cues may have predisposed them to assume the two cues were spatially unrelated (i.e., that they were representative of two completely separate search tasks). Overall, the work of Du et al. demonstrated that adult humans can integrate the dictates of two landmarks to localize a goal if the landmarks are presented together in training, although such integration does not occur if participants are trained with multiple cues individually before they are presented together.

Finally, research by Spetch and colleagues have also investigated cue integration in natural settings using an invertebrate model, specifically the Central Australian red honey desert ant, *Melophorus bagoti*. *M. bagoti* is an intriguing study species for such work, as it has been shown to have a robust navigational toolkit, including the ability to path integrate (Narendra, 2007a, b), and to use the landmarks derived from the panoramic skyline (Graham and Cheng, 2009; Wystrach et al., 2011, 2012) for navigating back to its nest after a foraging trip. In one experiment by Legge et al. (2014), ants were trained to forage at a feeder located 10 m away from their nest. As foraging ants made multiple trips from the nest to the feeder to collect food each day, they gained experience with the surrounding visual panorama along the path that they were forced to travel. On test trials, ants were transported to one of three release sites (located 4 m, 32 m, or 64 m from the nest) which provided varying degrees of similarity between the stored visual panorama near the nest, and the current visual panorama at the release site. The release sites thereby allowed the researchers to "degrade" the reliability of visual panorama for test trials, as there was a close match between the visual panorama at 4 m and the nest, a moderate degree of visual match at the 32 m release site, and almost no match at the 64 m release site.

Conflict tests that pitted navigational information from ants' path integration system with that of the visual panorama at the release site (full-vector ants released at the 4 m and 32 m release points, see Fig. 6, panels a and b) showed they integrated the dictates of each informational source by selecting a homebound direction of travel between the directions specified by each system. Additionally, ants' direction of travel suggested they weighted the information provided by each cue according to its reliability. Ants released at the 32 m site weighted the vector from their path integrator more heavily than the vector from the panorama, whereas ants released at the 4 m release site weighted the vectors specified by their path integrator and the visual panorama almost equally.

The results of this study suggest that ants may integrate the dictates of multiple cues using a form of Bayesian integration, which would be in line with follow up research by Legge et al. (2016) with pigeons. However, recent research by Wystrach et al. (2015), calls into question the Bayesian interpretation of Legge et al. (2014), as their work with *Cataglyphis velox* suggests these ants do not compute and use the directional certainty of their path integration system to integrate a Bayesian optimal homebound vector with available visual information. Instead, it appears that ants may rely on a simpler mechanism such as using the length of their computed homebound path integration vector as a proxy for cue reliability. Such work highlights the need for additional controlled and nuanced research in this area, which surely the groundwork laid by Spetch and colleagues on the integration of spatial information in humans, desert ants, and pigeons will surely play a role (which is already beginning if very recent work by Hoinville and Wehner, 2018, is any indication).

5. Conclusion

As can be seen from this review and tribute, Marcia Spetch has had a profound influence on the development of the field of comparative cognition and the comparative study of small-scale spatial cognition. In the development of the field of Comparative Cognition, Spetch was one of the founding members of the Comparative Cognition Society, and integral to the establishment of the International Conference on Comparative Cognition. With respect to the study of spatial cognition, not only has Spetch's direct contributions given us a much richer and clearer understanding of how human and non-human animals use spatial information for reorientation and goal localization, but her work has also informed the work of many other scientists whom have built upon her work. Finally, Spetch's strong collaborative ties, particularly with Debbie Kelly and Ken Cheng, have led to a cohesiveness within the study of comparative spatial cognition, particularly with pigeons, which would likely have not been possible without her. The effect these collaborative ties have had on the topic of small-scale spatial cognition in pigeons can easily be seen by reading Cheng et al.'s (2006) review paper.

Although Spetch formally retired in 2018 as a Professor Emerita at the University of Alberta, she continues her research on small scale spatial cognition, with a particular focus on field work with the group foraging desert ant *Veromessor pergandei* (Plowes et al., 2018) and the study of human memory and decision making (McDevitt et al., 2018; Ludvig et al., 2018). As should be clear from this review, Spetch's research and service has had an unmistakable and lasting impact on the field of comparative cognition, which will continue to be felt for many years to come.

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