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## FEATURED ARTICLE ESSAY

Dogs (*Canis familiaris*) Ignore GravityDorothy Munkenbeck Fragaszy  
University of Georgia

At the dawn of comparative psychology as a science, C. Lloyd Morgan (1903, p. 241) described how his terrier puppy learned to pick up and carry a knobbed stick over the course of a few hours of playing “fetch” with his master. The dog began by picking up the stick in its mouth near the middle, as it had carried other sticks many times before, but the knobby stick was unbalanced and awkward to carry in this way. The dog gradually started to pick up the stick nearer to the heavier, knobby end, rather than in the middle. Morgan suggested that the dog’s behavior could be explained as learning from sensory experience of the forces (such as gravity) acting on his body when he handled the stick. He argued that the dog’s behavior did not reflect perception of the “space/force relations” of the object per se (Morgan, 1903, pp. 241–243). In more contemporary terms, the dog was not attentive to gravity acting on the stick, but rather to the torque produced by the stick in its mouth.

A century later, a series of clever studies with human children initiated by Bruce Hood (1995) examined whether young children expect that objects move in accordance with gravity. Hood presented children 2 to 4 years old with a search problem: He dropped a ball into a tube and asked the children to retrieve the ball. The task was presented in several variations: Sometimes the tube was curved, sometimes two or more tubes were present, sometimes the tubes were opaque, and sometimes they were transparent. Overall, children in this age range looked for the ball in a place directly below where it was dropped, regardless of the arrangement of the tubes, unless the tubes were transparent and the children could see the ball rolling down one of the tubes. Hood and colleagues described the children’s biased search behavior as reflecting a “naïve theory” of gravity—an expectation that dropped objects follow a straight trajectory downward—and proposed that the bias is resistant to counterevidence—that is, it persists across repeated trials in spite of failing to find the ball when searching directly below the point where it was dropped (Hood, 1995, 1998; Hood, Wilson, & Dyson, 2006).

Since Hood’s (1995) seminal study, many variations of this “gravity tube task” have been presented to children—and to non-human primates by comparative psychologists—to probe these populations’ reasoning about the movement of objects released above a surface. This effort is part of the larger comparative

psychological enterprise seeking evidence of continuity in cognitive processes across species. Although the evidence in support of a gravity bias is strong for young children, the evidence for the same phenomenon in adult nonhuman primates is decidedly mixed. The strongest positive evidence concerns chimpanzees. For example, chimpanzees showed a gravity bias when they had to predict where a reward would appear before it was dropped into one of two crossed tubes (Tomonaga, Imura, Mizuno, & Tanaka, 2007). One study presented a gravity tube task to a nonprimate taxon, domestic dogs (*Canis familiaris*; Osthaus, Slater, & Lea, 2003). Osthaus et al.’s (2003) findings provide, according to Tecwyn and Buchsbaum (2018), suggestive but nonsignificant evidence for a possible initial gravity bias in Trial 1, but no evidence for a persistent gravity bias across trials. Nevertheless, this study has been cited several times in support of the idea that dogs display a (persistent) gravity bias when searching for a dropped item in “gravity tube tasks” (Bascandziev & Harris, 2010; Cacchione & Call, 2010; Joh, Jaswal, & Keen, 2011; Kunder, De Los Reyes, Taglang, Baruch, & German, 2010; Range, Möslinger, & Virányi, 2012; Tomonaga et al., 2007) as do human children and (some) nonhuman primates. A shared “gravity bias” would be important support for the hypothesis of continuity in physical cognition across mammals.

Tecwyn and Buchsbaum (2018) in this issue challenge the idea that dogs display a persistent gravity bias. In four experiments, they probed where dogs search for a ball after it is dropped into a tube. First, they replicated diagonal tube task experiments previously conducted with apes (Cacchione & Call, 2010) to investigate how auditory and visual information about the tubes influenced the dogs’ search. Next, they examined how dogs’ search shifted when the middle location was no longer an option. Third, they probed whether dogs’ search could be explained by proximity between the reward’s release point and the search locations (a condition depicted in Figure 1). Finally, they presented tasks in which any of the biases that might have guided them in the previous experiments (namely, gravity, middle position, or proximity to the point where the ball was dropped) could not guide their search. Searching accurately in this situation, but not in the first three experiments, would suggest that dogs expected a solid object dropping down a solid tube to emerge at the tube’s lower end, but were unable to inhibit searching at some other location on the basis of some bias. In all experiments they examined how dogs performed in Trial 1 and how performance changed across repeated trials.

The thorough nature of their experimental project paid off in clear findings: Dogs as a group were generally unable to solve the

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# What Factors Really Influence Domestic Dogs' (*Canis familiaris*) Search for an Item Dropped Down a Diagonal Tube? The Tubes Task Revisited

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It has been suggested that domestic dogs—like young human children—have a “gravity bias”; they expect an unsupported object to fall straight down, regardless of any obstacles that redirect or halt its path. In the diagonal tube task, this bias is revealed by a persistent tendency to search the incorrect location directly beneath the top of the tube the item is dropped into, rather than the correct location attached to the bottom of the tube. We presented dogs ( $N = 112$ ) with seven different versions of the diagonal tube task, to examine what factors influence their search behavior for an object dropped down a diagonal tube, and investigate their physical reasoning skills more generally. Contrary to previous claims, we found no evidence for dogs exhibiting a persistent, or even a Trial 1, gravity bias. However, dogs were also unable to search correctly for the reward, even when it could be heard rolling through the tube, though they succeeded when the tube was transparent (Experiments 1a–c). Experiment 2 suggested that dogs might search on the basis of proximity, but Experiments 3a–b ruled this out and showed that they prefer to commence searching at the center of the apparatus. Finally, when potential sources of bias were eliminated from the task (Experiment 4), dogs' performance was improved, but still not above chance, suggesting that they are unable to reason about the tube's physical–causal mechanism. We conclude that, on current evidence, the gravity bias might be unique to some primate species.

**Keywords:** comparative cognition, domestic dog, gravity bias, physical reasoning, tubes task

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As human adults we possess sophisticated knowledge about the physical world. We know, for example, that objects continue to exist even when they move out of sight, that a solid object cannot pass through another solid object, and that gravity causes unsupported objects to fall (Baillargeon, 2002). Understanding how inanimate objects behave and interact with one another is also important for young humans, as well as being ecologically relevant

for many nonhuman species. For example, it is extremely useful to be able to track and relocate objects that move out of sight, and all terrestrial species experience evidence of the effect of gravity on falling objects, so it is feasible that similar physical reasoning mechanisms might be widely shared among species. The developmental and evolutionary origins of our rich physical reasoning abilities have thus long been of interest to researchers in the fields of cognitive development and comparative cognition. Do young children and nonhuman animals (hereafter, animals) reason about objects in the same way as human adults, or are there fundamental differences?

The tubes task (Hood, 1995) has been used widely in the fields of cognitive development and comparative cognition to investigate children's and animals' physical reasoning abilities—specifically, how different-aged children and different species reason about the way objects behave under the influence of gravity (see Tecwyn & Buchsbaum, 2018, for a review). The version of the task typically used with children consists of three intertwined opaque tubes positioned vertically in a frame, each attached to a nonaligned cup at the base of the apparatus (Baker, Gjersoe, Sibielska-Woch, Leslie, & Hood, 2011; Bascandzjev & Harris, 2010; Freeman, Hood, & Meehan, 2004; Hood, Wilson, & Dyson, 2006; Jaswal, 2010; Joh & Spivey, 2012). The task as typically used with animals is a simplified version of this and involves just a single diagonally configured tube (Figure 1). We will refer to this simplified version as the “diagonal tube task,” and given the comparative focus of the current study, the majority of this introduction will focus on how individuals perform in this version of the task.

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# Behavioral Conservatism is Linked to Complexity of Behavior in Chimpanzees (*Pan troglodytes*): Implications for Cognition and Cumulative Culture

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Cumulative culture is rare, if not altogether absent in nonhuman species. At the foundation of cumulative learning is the ability to modify, relinquish, or build upon previous behaviors flexibly to make them more productive or efficient. Within the primate literature, a failure to optimize solutions in this way is often proposed to derive from low-fidelity copying of witnessed behaviors, suboptimal social learning heuristics, or a lack of relevant sociocognitive adaptations. However, humans can also be markedly inflexible in their behaviors, perseverating with, or becoming fixated on, outdated or inappropriate responses. Humans show differential patterns of flexibility as a function of cognitive load, exhibiting difficulties with inhibiting suboptimal behaviors when there are high demands on working memory. We present a series of studies on captive chimpanzees that indicate that behavioral conservatism in apes may be underlain by similar constraints: Chimpanzees showed relatively little conservatism when behavioral optimization involved the inhibition of a well-established but simple solution, or the addition of a simple modification to a well-established but complex solution. In contrast, when behavioral optimization involved the inhibition of a well-established but complex solution, chimpanzees showed evidence of conservatism. We propose that conservatism is linked to behavioral complexity, potentially mediated by cognitive resource availability, and may be an important factor in the evolution of cumulative culture.

**Keywords:** behavioral flexibility, cumulative culture, chimpanzee, executive functions, decision-making

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Sarah J. Davis and Andrew Whiten conceived the experiments. Sarah J. Davis conducted the experiments and analyzed the results. Sarah J. Davis

and Andrew Whiten wrote the manuscript. Steven J. Schapiro, Susan P. Lambeth, and Lara A. Wood provided essential logistical support. All authors reviewed the manuscript.

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# Baboon (*Papio anubis*) Chimeric Face Processing by Human (*Homo sapiens*) Judges: Influence of Stimuli Complexity on the Perception of Oro-Facial Asymmetries

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Two methodologies have traditionally been used to measure hemispheric specialization for perception and expression of emotions in human and nonhuman primates. The first refers to objective measures, that is, measures of area and length of facial features, and the second concerns subjective “measures,” that is, assessment of chimeric faces by human judges. We proposed a refined approach to the subjective assessment of hemispheric specializations, which aims at delimiting methodological issues in the study of orofacial asymmetries. The study focused on a baboon threat orofacial expression, which has led to discordant results according to the methodology used (Wallez & Vauclair, 2011, 2013). We presented human participants with two sets of chimeric stimuli varying the regions of the face likely to be processed. The whole face set was composed of classical chimeric faces, and the upper face set was made of chimeric faces for which the lower part was blurred. The purpose of this new procedure was to shed light on the perception process of baboon faces by human participants during a free-viewing chimeric task. Results showed a concomitant influence of the chimera structure depending on the order of the presentation of the set, revealing a training effect in our human judges. These factors combined together allowed the appearance of an overall left–left chimeric choice by human judges (i.e., which indicates a right hemisphere involvement in baboon threat expression). These findings bring novel insights into the study of orofacial asymmetries in nonhuman primates by human judgments.

**Keywords:** hemispheric specialization, stimuli complexity, orofacial asymmetry, training effect, olive baboons

Faces are one of the most important and salient classes of stimuli involved in communication of all primates. During social interactions, they provide important information about other individuals’ intrinsic features such as identity, sex, age, or emotional state (Ekman, 1992; Tranel, Damasio, & Damasio, 1988). Since Darwin (1872/2002), it is well-established that humans and animals share several basic emotions associated with common motor patterns. According to neurobiologists and psychologists, emotions are considered as an adaptive phenomenon that induces multiple modifications in the physiological system, including the somatic and neuronal components in response to a stimulus (Damasio, 1995; Scherer, 2000). From an evolutionary standpoint,

it is worth noting that the emotional state is made visible externally by social animals, including humans, which raises important questions about the functions of emotional expression in our lineage. Several authors have described clear counterparts between the facial repertoire of nonhuman primates and that of humans (Chevalier-Skolnikoff, 1973; Preuschoft, 2000), and recent research on facial musculature has pointed out extensive homologies between humans, chimpanzees (Burrows, Waller, Parr, & Bonar, 2006), and macaques (Burrows, Waller, & Parr, 2009; Waller, Parr, Gothard, Burrows, & Fuglevand, 2008). Moreover, most primate facial expressions seem to be asymmetrical, suggesting that hemispheric specialization might have been specifically selected for (for reviews, see Hopkins & Fernández-Carriba, 2002; Hopkins & Vauclair, 2012).

Orofacial asymmetries are considered as a suitable index to examine the neurological basis of behavior expressed by faces, such as language and emotional expression. Graves and Landis (1990) described that the right side of the mouth opens wider or moves faster than the left side during speech, implicating greater involvement of the left hemisphere, whereas the left side of the mouth (i.e., right hemisphere dominance) is more activated during smiling. It has long been established that the left hemisphere is more involved in language processing, particularly during production (Broca, 1865; Wernicke, 1874). By contrast, the comprehension of the cerebral mechanisms underlying emotional processing

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# Increased Egg–Nest Visual Contrast Does Not Induce Egg Ejection in the Eastern Phoebe (*Sayornis phoebe*), an Acceptor Host of the Brood Parasitic Brown-Headed Cowbird (*Molothrus ater*)

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Hosts of obligate brood parasitic birds can offset the costs of parasitism by rejecting foreign eggs. Like the vast majority of brown-headed cowbird (*Molothrus ater*) hosts, the eastern phoebe (*Sayornis phoebe*) paradoxically incurs substantial fitness costs by accepting cowbird parasitism. We investigated whether acceptance of brown-headed cowbird eggs may be mediated via lack of recognition due to crypsis in eastern phoebe nests, and whether egg-rejection behavior could be induced by manipulating egg–nest visual contrast as a means of facilitating parasitic egg detection in an artificial parasitism experiment. We found that brown-headed cowbird eggs have significantly lower achromatic, but not chromatic, visual contrast against the natural nest lining relative to phoebe eggs, suggesting that cowbird eggs may be cryptic in the low ambient light environments of natural or artificial covered ledges where eastern phoebes tend to nest. We also found that despite successfully increasing egg–nest visual contrast in our treatment, eastern phoebes did not reject model parasitic eggs. Our findings are consistent with previous work showing that increased egg–nest visual contrasts do not increase parasitic egg discriminability and rejection in hosts of avian brood parasites. Because sensory modeling showed that eastern phoebes were predicted to be able to visually perceive natural and experimental parasitism events, these hosts are suggested to lack the cognitive flexibility necessary to reject dissimilar eggs in their nests. Future work should determine whether this and other acceptor species can be made to reject parasitism by using a more diverse array of artificial egg stimuli.

**Keywords:** brood parasitism, visual modeling, visual ecology, egg rejection

Obligate brood parasitism in birds is rare, comprising just 1% of all extant avian species (Davies, 2000), arising through at least seven independent origins (Payne & Sorenson, 2005). Species within these obligately parasitic lineages build no nests, and instead lay eggs into the nests of other species, thereby passing the costs of parental care onto their hosts (Davies, 2000; Hauber, 2003b, 2003c; Hoover, 2003; Lorenzana & Sealy, 2001). The cost of raising genetically unrelated offspring favors the evolution of host responses to detect and reject parasitism, including parasitic

egg (Langmore et al., 2005; Moskát, 2005) and nestling (Langmore, Hunt, & Kilner, 2003; Sato, Tokue, Noske, Mikami, & Ueda, 2010) ejection, nest abandonment (Avilés, Rutila, & Møller, 2005; Peer & Sealy, 2004; Servedio & Hauber, 2006), and nest vigilance (Welbergen & Davies, 2009). The ensuing coevolution of host egg mimicry by parasites and enhanced egg detection by hosts (Davies, 2011; Davies & Brooke, 1989; Stoddard & Hauber, 2017; Stoddard & Stevens, 2010, 2011) have made brood parasite–host interactions textbook examples of coevolutionary arms races (Davies, 2000, 2011; Stoddard, Kilner, & Town, 2014). The best-described system remains the Eurasian common cuckoo *Cuculus canorus*–host system, in which host-races of parasites have evolved striking egg mimicry while hosts coevolved increasingly sensitive visual discrimination of parasitic eggs (Davies, 2000; Stoddard & Stevens, 2010).

Recent efforts to quantify the visual cues used by host species in parasitic egg discrimination have increasingly used avian perceptual models, which assess egg color and brightness as processed via the avian visual system (Gomez, 2006; Vorobyev & Osorio, 1998). Such approaches have increased explanatory power over those relying exclusively on human visual perception because we possess different visual sensory physiology than birds (Aidala et al., 2012; Hart, 2001; Hunt, Carvalho, Cowing, & Davies, 2009;

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# Visual Attention, Indicative Gestures, and Calls Accompanying Gestural Communication Are Associated With Sociality in Wild Chimpanzees (*Pan troglodytes schweinfurthii*)

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The challenges of life in complex social groups may select for complex communication to regulate interactions among conspecifics. Whereas the association between social living and vocalizations has been explored in nonhuman primates, great apes also have a rich repertoire of gestures, and how the complexity of gestural communication relates to sociality is still unclear. We used social network analysis to examine the relationship between the duration of time pairs of chimpanzees spent in proximity (within 10 m) and the rates of gestural communication accompanied by visual attention of the signaler, one-to-one calls, indicative gestures (collectively self-relevance cues), and synchronized pant-hoot calls. Pairs of chimpanzees that spent a longer duration of time in proximity had a higher rate of visual gestures accompanied by these behaviors. Further, individual chimpanzees that had a greater number of proximity bonds had a larger social network maintained through gestures accompanied by synchronized pant-hoot calls. In contrast, gestures unaccompanied by these behaviors were not positively associated with either proximity bonds in pairs of chimpanzees or individual differences in sociality. These results suggest that self-relevance cues and synchronized pant-hoot calls accompanying gestures may increase the efficiency of gestural communication in social bonding and that multimodal communication may have played a key role in language evolution.

**Keywords:** chimpanzees, gestural communication, self-relevance cue, social network, synchronized call

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The association between sociality and communication has long been of interest both in understanding complex sociality in nonhuman animals and also in developing theories of how language evolved in humans (Arbib, Liebal, & Pika, 2008; Corballis, 2009; Dunbar, 2012; Freeberg, Dunbar, & Ord, 2012; Pollick & de Waal, 2007). Individuals maintaining complex social relationships may require more complex communication to regulate interactions with group members (Freeberg et al., 2012). Complex social relationships have been defined as *those in which individuals frequently interact in many different contexts, and often repeatedly interact*

*over time*, and complex communicative systems have been defined as *those that contain a large number of structurally and functionally distinct elements (e.g., large display repertoire sizes) or possess a high amount of bits of information* (Freeberg et al., 2012; Langergraber, Mitani, & Vigilant, 2009; Mitani, 2009; Silk, 2007; Silk et al., 2010b). Although in primates individuals can maintain social relationships and communicate with partners who do not reciprocate their investment into the social relationship, reciprocated social relationships are a key feature of complex sociality (Foerster et al., 2015; Mitani, 2009). Language does not leave a direct fossil trace, and therefore studies of communication and sociality in nonhuman primates can provide insights into factors that have shaped the evolution of language in humans (Byrne et al., 2017; Fitch, 2010; Pollick & de Waal, 2007; S. G. B. Roberts & Roberts, 2016; Seyfarth & Cheney, 2014). In this study, we explore the association between the complexity of sociality, defined as the presence or absence of reciprocated proximity ties, and gestural communication of wild chimpanzees to provide insight into the origins of language.

Many theories of language evolution propose that nonhuman primate vocalizations provided the starting point for the development of more complex vocal communication seen in humans (Crockford, Wittig, Mundry, & Zuberbühler, 2012; Enard et al., 2002; Engh, Hoffmeier, Cheney, & Seyfarth, 2006; Fitch, 2010; Fitch, de Boer, Mathur, & Ghazanfar, 2016; Schel, Townsend, Machanda, Zuberbühler, & Slocombe, 2013; Seyfarth & Cheney,

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Both the authors equally contributed to this work.

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# Artificial Visual Stimuli for Animal Experiments: An Experimental Evaluation in a Prey Capture Context With Common Marmosets (*Callithrix jacchus*)

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Experimenters often use images of real objects to simulate interactions between animal subjects or visual stimuli on a touchscreen to test animal cognition. However, the degree to which nonhuman animals recognize 2-D images as representing the corresponding real objects remains debated. The common marmoset monkey (*Callithrix jacchus*) has been described as a species that spontaneously shows natural behaviors to 2-D images, for example, grasping behaviors to insects and fear responses to snakes. In this study, we tested 10 monkeys with their favorite food item (crickets), 2-D images (a photo and videos of a cricket), and a 3-D plastic model to reevaluate marmoset's spontaneous responses to 2-D images and to explore which artificial visual stimuli can motivate spontaneous interactions. The monkeys showed grasping behavior to the real cricket and the 3-D plastic model, but to none of the 2-D images. Our experiment suggests that depth information is the most important factor eliciting predatory behavior from the marmosets, and, therefore, a stimulus produced by a 3-D printer could be a good alternative when a spontaneous interaction or a convincing stimulus is required. Furthermore, this work serves as a cautionary tale for those using 2-D image presentations with marmosets, and perhaps other animal species.

**Keywords:** common marmoset monkey, visual perception, depth perception, image recognition

Spontaneous recognition of real objects from 2-D images seems to be a straightforward task to most people. However, it is not always an easy task depending on their age, past experiences, and characteristics of images. People who have never experienced pictures showed difficulties in recognizing objects in black-and-white photographs. (Deregowski, Muldrow, & Muldrow, 1972; Miller, 1973) Young children who were 15 months old or 18 months old successfully extended newly learned labels from pictures to objects and from objects to pictures. The performance of 15-month-old children was decreased when the pictures were less realistic drawings. (Ganea, Pickard, & DeLoache, 2008) These children were mainly White, middle-class, and living in eastern United States, which suggests that they were probably experienced with pictures. In the study of DeLoache, Pierroutsakos, Uttal, Rosengren, and Gottlieb (1998), 9-month-old children from both the United States and a rural village in Africa tried to grasp

photographs of toys. However, an infant's grasping motion to a mounted photograph on a cardboard page does not necessarily mean recognition of a toy from the photograph. Infants often show manual exploration, including grasping to any object within their reach, regardless of recognition. In another study, DeLoache and Burns (1994), two age groups of children were asked to retrieve a hidden toy after an experimenter showed the hidden location using a photograph. Although 24-month-old children failed, 30-month-old children succeeded to retrieve the hidden toys.

The degree to which nonhuman animals recognize 2-D images (photographs, videos, etc.) as the corresponding real objects remains debated. Nonhuman primates showed recognition of real objects (food items) in pictures to a certain degree in an experiment (Judge, Kurdziel, Wright, & Bohrman, 2012), whereas another experiment showed a failure of learning from video clips (J. R. Anderson, Kuroshima, & Fujita, 2017). A number of studies showing different results were reviewed in the studies by Bovet and Vauclair (2000) and D'earth (1998). Because of differences in eye orientation, color vision, acuity, and potential reliance on movement to draw attention, it cannot simply be assumed that a nonhuman species perceives images in a way similar to humans. Fleishman and Endler (2000) provided caveats concerning the use of video stimuli due to animal species' different perceptual systems. Although subjective experiences are experimentally inaccessible, one way to approach this problem is to use natural behaviors that are reliably elicited by a given visual object, and then test to see if images/videos elicit similar responses.

The common marmoset monkey is a small (250–500 g), non-endangered New World primate, which has been used for a wide

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# Capuchin Monkeys (*Cebus [Sapajus] apella*) Show Planning in a Manual Maze Task

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The capacity for planning in nonhuman species has long been an interest of many comparative and cognitive psychologists. There is now considerable evidence that at least great apes show both motor planning and planning for future needs in various contexts and modalities. Few studies, however, have investigated planning ability in a monkey species, and most of these exceptions have used computerized procedures. To gain a broader view, in the current study, we tested capuchin monkeys' capacity for motor planning using the "paddle-box" apparatus, a manual maze task originally designed for testing planning skills in apes (Tecwyn, Thorpe, & Chappell, 2013). This consisted of a box containing different levels of paddles that subjects rotated to drop food into a tube that delivered it to the subject. To evaluate subjects' degree of skill in the task, the initial locations of the food and the final goal (i.e., the "paths" the food could take) were chosen according to the probability of retrieving the reward, starting with those that gave the highest probability of success and moving sequentially to those with the lowest probability. Most subjects solved all levels of difficulty in the task, and capuchin monkeys succeeded as a group in a generalization test with novel paths. These findings demonstrate that some monkeys, like apes, show planning in different contexts and modalities.

**Keywords:** cognition, planning, maze task, paddle-box task, *Cebus [Sapajus] apella*

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Anticipating which actions will allow us to reach a goal is part of our daily routine. However, we are not alone in this; like us, other animals plan. Planning covers a wide range of behaviors, but each of these generally belongs to one of two categories. First, animals can plan for future events, that is, planning oriented

toward *future* needs (e.g., saving tools or food for later use; Kabadayi & Osvath, 2017; Mulcahy & Call, 2006; Osvath & Osvath, 2008; Raby, Alexis, Dickinson, & Clayton, 2007). Second, and of particular interest for this study, planning can occur when solving problems that require performing a series of physical actions to obtain some goal at the end, that is, planning oriented toward *current* needs (e.g., serializing nesting cups or solving mazes/puzzles; Frigaszy, Johnson-Pynn, Hirsh, & Brakke, 2003; Johnson-Pynn & Frigaszy, 2001; Johnson-Pynn, Frigaszy, Hirsh, Brakke, & Greenfield, 1999; Tecwyn, Thorpe, & Chappell, 2012). In the current study, we focused on the latter, by testing the ability of brown capuchin monkeys (*Cebus [Sapajus] apella*) to plan motor actions in a novel puzzle situation.

Motor planning has long been studied in our closest phylogenetic relatives, the great apes (Döhl, 1968; Rensch & Döhl, 1968). There is now considerable evidence that chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*) and orangutans (*Pongo spp.*) show motor planning in various contexts and modalities (e.g., joystick-based computerized maze tasks: Beran, Parrish, Futch, Evans, & Perdue, 2015; Frigaszy et al., 2003, 2009; touchscreen-based computerized maze task: Iversen & Matsuzawa, 2001; manual paddle-maze task: Tecwyn et al., 2013; for a comparison with human children in the same task, see Tecwyn, Thorpe, & Chappell, 2014; manual finger-maze task: Völter & Call, 2014a; for a tool-use version, see Völter & Call, 2014b; puzzle-tube task: Tecwyn et al., 2012). Few studies, however, have investigated this ability in a monkey species, and most of these exceptions have tested capuchin monkeys using computerized procedures (Beran et al., 2015; Frigaszy et al., 2003, 2009; Pan et al., 2011).

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## The Structure of Ape (*Hominoidea*) Intelligence

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We used contemporary psychometric theory of intelligence and confirmatory factor analysis to reanalyze data obtained on samples of nonhuman primates administered the Primate Cognition Test Battery. Our main goals were to interpret stability of the Primate Cognition Test Battery tasks and factors over time and to determine whether the cognitive factors that emerge from confirmatory factor analysis for apes can be interpreted from the perspective of a major theory of human intelligence, namely, the Cattell–Horn–Carroll model. We also analyzed data for 2½-year-old children on Wechsler’s preschool test to afford a comparison between ape and child cognitive factors. Results indicated that multiple cognitive abilities provide the best factor solutions for both apes and children, and that the ape factors can be meaningfully interpreted from Cattell–Horn–Carroll theory.

*Keywords:* Primate Cognition Test Battery, Cattell–Horn–Carroll theory, Wechsler Preschool and Primary Scale of Intelligence-IV, nonhuman primate, psychometric

In humans, *g* or a general intelligence factor (Spearman, 1904, 1927) has enjoyed a lengthy, and often controversial, research history (Jensen, 1998). Although currently most human intelligence researchers and clinicians favor multiple abilities theories of cognitive development, *g* theory has yet to fall completely out of favor (Canivez, 2013; Canivez, Watkins, & Dombrowski, 2017).

The measurement of human intelligence began with Sir Francis Galton’s (1869, 1883) perception/sensation approach and Alfred Binet’s ingenious cognitive methodology (Binet & Simon, 1904), followed closely by Spearman’s (1904, 1927) general intelligence or *g* theory. Soon after, David Wechsler (1939) moved beyond *g* when measuring human intelligence, introducing the verbal–performance (nonverbal) dichotomy as well as profiles of specific

abilities; Wechsler’s tests and clinical approach to children’s and adults’ assessment continue worldwide to the present day (Kaufman, Raiford, & Coalson, 2016). The field of IQ testing has witnessed the development of theory-based tests (Kaufman & Kaufman, 1983; Woodcock, McGrew, & Mather, 2001) that have been constructed with sophisticated psychometrics such as Rasch latent-trait models, confirmatory factor analysis (CFA), and structural equation modeling, and it has weathered numerous genetic controversies (Herrnstein & Murray, 1994; Rushton, 1997). Contemporary IQ testing has blossomed in the wake of dynamic, well-researched multiability theories that combine the notion of a general overall intelligence with smaller, specific intellectual abilities (Carroll, 1993; Horn & Cattell, 1966; Schneider & McGrew, 2012, in press).

This brief history of human intelligence stands in direct contrast to the history of nonhuman animal intelligence. Whereas human intelligence researchers started with the construct of *g* and worked outward toward smaller, multiple intelligences, nonhuman animal researchers have traditionally taken the opposite route—intelligence was seen from an evolutionary perspective and viewed as modular, dealing with specific skills and abilities (Balda, Kamil, & Bednekoff, 1996; Bond, Kamil, & Balda, 2003; MacLean et al., 2012). Pioneers in human intelligence testing, such as Binet, developed tasks that were cognitive (rather than social) in nature, that were intended to measure aspects of *g* or global capacity, and that could be administered in a laboratory or clinical setting. By contrast, the evolutionary approach taken by researchers of nonhuman animal intelligence viewed the mind as comprising domain-specific processes that were targeted to solve problems within their natural habitat—for example, related to foraging patterns and group living. This emphasis on the evolution of nonhuman animal intelligence led to insightful studies of differences among species

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# Zebra Finches (*Taeniopygia guttata*) Can Categorize Vowel-Like Sounds on Both the Fundamental Frequency (“Pitch”) and Spectral Envelope

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Humans can categorize vowels based on spectral quality (vowel identity) or pitch (speaker sex). Songbirds show similarities to humans with respect to speech sound discrimination and categorization, but it is unclear whether they can categorize harmonically structured vowel-like sounds on either spectrum or pitch, while ignoring the other parameter. We trained zebra finches in two experimental conditions to discriminate two sets of harmonic vowel-like sounds that could be distinguished either by spectrum or fundamental frequency (pitch). After the birds reached learning criterion, they were tested on new sounds that were either noise-vocoded versions of the trained sounds (sharing the spectral envelope with the trained sounds but lacking fine spectral detail from which pitch could be extracted) or sounds lacking the amplified harmonics (sharing only pitch with the trained sounds). Zebra finches showed no difference in the number of trials needed to learn each stimulus–response mapping. Birds trained on harmonic spectrum generalized their discrimination to vocoded sounds, and birds trained on pitch generalized their discrimination to harmonic sounds with a flat spectrum. These results demonstrate that, depending on the training requirements, birds can extract either fundamental frequency or spectral envelope of vowel-like sounds and use these parameters to categorize new sounds.

**Keywords:** pitch perception, categorization, harmonic sounds, songbird, spectral envelope

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Driven by an interest in speech sound perception and its evolution, multiple studies investigated to what extent nonhuman animals (hereafter: animals) are able to discriminate and categorize speech sounds. In particular, the discrimination and/or categorization of vowel-like sounds has been examined and shown for a range of species, such as ferrets (Bizley, Walker, King, & Schnupp, 2013; Town, Atilgan, Wood, & Bizley, 2015), cats (Dewson, 1964), budgerigars (Dooling & Brown, 1990), European starlings (Kluender, Lotto, Holt, & Bloedel, 1998), and zebra finches (Kriengwatana, Escudero, Kerkhoven, & ten Cate, 2015; Kriengwatana, Escudero, & ten Cate, 2015; Ohms,

Escudero, Lammers, & ten Cate, 2012; Ohms, Gill, Van Heijningen, Beckers, & ten Cate, 2010).

Essential for speech perception is the ability to categorize speech sounds (Goudbeek, Swingley, & Kluender, 2007; Goudbeek, Swingley, & Smits, 2009; Holt & Lotto, 2006, 2010). Humans can categorize the same speech sound on different dimensions, for example, vowel and speaker identity or speaker sex. Speaker sex categorization is mostly driven by sex differences in pitch, which are related to differences in fundamental frequency ( $f_0$ ; the human analogue of pitch) and its harmonic spectrum. In contrast, vowel categorization is driven by differences in timbre, called “formants” for speech sounds, characterized by different amplitude peaks in the harmonic spectrum (Fuller et al., 2014; Holt & Lotto, 2010). Songbirds are also able to discriminate between speech sounds (Kluender et al., 1998; Ohms et al., 2010, 2012) and speakers (Dooling, 1992), suggesting they can identify the most important parameters that humans use, that is, pitch and spectral envelope, to categorize vowel-like sounds.

Despite these similarities, pitch processing is often assumed to differ between humans and birds. In tone sequences and music, humans are known to perceive relative pitch: We attend to the relationship or intervals between successive sound elements to recognize and discriminate sound sequences (Bregman, Patel, & Gentner, 2012). This ability has also been shown by several mammal species, including Japanese (Izumi, 2001) and macaque

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# Naïve 3-Day-Old Domestic Chicks (*Gallus gallus*) Are Attracted to Discrete Acoustic Patterns Characterizing Natural Vocalizations

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Nonsongbirds can produce rhythmical sounds that, at times, have been shown to be meaningful in their communication. This raises the possibility that rhythm is a separate ability that might have evolved earlier than song. We asked whether nearly completely naïve domestic chicks perceive rhythm and respond in specific ways to different rhythmic patterns. To do so, specific constituent parameters of rhythmicity were used based on the sound of a natural mother hen's cluck. The sound samples created ranged from a continuous sound to articulated rhythmic patterns of alternating strong and weak events. Chicks' reactivity to the patterns was tested over a series of sound exposure experiments by their propensity to operate a running wheel toward the acoustic source, a paradigm simulating chicks' natural affiliative response to the hen's call. Results showed that motor activity increased markedly when acoustic events were discrete (compared with continuous), and significantly when accent structure was faster (compared with slower rates). Similar to human infants, chicks showed a significant preference for pulsed over continuous patterns. Chicks also ran harder toward calls with fast strong pulsating events, suggesting that different arrangements of events in time can be differently arousing, but independently of whether the events were presented in a regular or nonregular fashion.

*Keywords:* rhythm, pattern, tempo, domestic chick, music

Music perception and rhythmical appreciation had long been regarded as abilities unique to humans (Hodges, 2000). This assumption was successfully questioned once the parameters of music had been broken down into specific constituent parts, as it emerged for instance from studies of animal welfare providing evidence of the positive physiological effects of music playback (Alworth & Buerkle, 2013; Dávila, Campo, Gil, Prieto, & Torres, 2011; Gvoryahu, Cunningham, & Van Tienhoven, 1989). The

most convincing clue comes from studies showing that several species (Kaplan, 2009; Rouse, Cook, Large, & Reichmuth, 2016) are able to discriminate between specific parameters of music. An important issue in the comparative investigation of specific music parameters is whether discrimination of rhythm requires a song control system or could be computed even by nonsongbirds (Chiandetti & Vallortigara, 2011; Hoeschele, Merchant, Kikuchi, Hattori, & ten Cate, 2015).

One of the rhythm-related abilities is the capability of rhythmic entrainment, that is, the motor or voice synchronization to an external pulse, that has been recently observed also in nonhuman animals although evidence is still quite sparse (Merker, Madison, & Eckerdal, 2009; Ravignani, Bowling, & Fitch, 2014; Wilson & Cook, 2016). Although a good deal of research has yet to be done on entrainment of rhythm in birds (and other animals species would need to be tested), we were here specifically interested in investigating the issue of spontaneous rhythm perception, and whether it is of any behavioral relevance to an avian species. For instance, a recent study describes a spontaneous use of rhythm perception to identify other members of the colony and their social status in northern elephant seals (*Mirounga angustirostris*). These seals were shown to naturally encode, remember, and recognize other individuals on the basis of the rhythm and the tone of their calls (Mathevon, Casey, Reichmuth, & Charrier, 2017). This is the first example of a spontaneous use of rhythm, despite the fact that pervasiveness of rhythm is apparent from the simplest inverte-

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# Object Permanence in the Pigeon (*Columba livia*): Insertion of a Delay Prior to Choice Facilitates Visible- and Invisible-Displacement Accuracy

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Object permanence, often viewed as a measure of human cognitive development, has also been used to assess animals' cognitive abilities. Tests of object permanence have distinguished between visible displacement, in which an object may be placed into one of two (or more) containers to be retrieved, and invisible displacement, in which after the object is placed into the container, the container is moved before retrieval is attempted. We tested pigeons' accuracy on both visible and invisible displacement using a rotational beam with a container at either end. In Experiment 1, the pigeons showed some evidence of object permanence on an initial visible displacement test, but they did not maintain accurate choice. With training, their accuracy improved but only to about 70% correct. When tested on a 90° invisible displacement (rotation), accuracy transferred but once again dropped with further training. In Experiment 2, a 5-s delay was inserted between container baiting and choice. Once again, the pigeons showed some evidence of object permanence on an initial visible displacement test, although on the first test session, choice accuracy was not much better than in Experiment 1. With training, choice accuracy improved greatly. Furthermore, pigeons showed good transfer when they were tested on the 90° invisible displacement. Finally, and importantly, they also transferred well to a 180° invisible displacement, a displacement on which dogs failed. The results of these experiments suggest that under the right conditions, pigeons can show a moderate degree of object permanence.

*Keywords:* object permanence, visible displacement, invisible displacement, delayed choice, pigeons

According to Piaget (1954), object permanence is a cognitive capacity whose function is to attribute continued existence to objects that have disappeared. Object permanence implies that an organism can represent an object that cannot be directly perceived in the environment.

Procedures that have been used to demonstrate object permanence have varied. In the visible displacement<sup>1</sup> task, an object that has been placed in front of an organism is then hidden behind a screen (or occluder). The organism is then tested to determine if it will look behind the screen. Children generally succeed at this task by the age of 12 months (Piaget, 1954). For a more experimental measure, two occluders may be provided so that an incorrect response can be objectively determined.

In the more advanced invisible displacement task, the object is placed in a container (the displacement device) that is then placed inside a container or behind an occluder. The object is then invisibly transferred out of the displacement device behind the occluder. The displacement device (now empty) is shown to the

child. Once children reach the age of about 2 years, they successfully search behind the occluder that the displacement device last visited (Kramer, Hill, & Cohen, 1975; Piaget, 1954).

Object permanence has also been studied in children (Baillargeon, Spelke, & Wasserman, 1985) and dogs (Pattison, Miller, Rayburn-Reeves, & Zentall, 2010) using a gaze duration measure with "possible" and "impossible" events. An object was placed behind a solid screen that was originally flat in the horizontal plane and then rotated in the depth plane through an arc front to back. In the possible event, the screen stopped when it reached the occluded object; in the impossible event, the screen appeared to move through the space occupied by the object. Both children and dogs looked reliably longer at the impossible than at the possible event. This finding suggests that both children and dogs understand that the object continued to exist at its same location, and they expected the screen to stop against the occluded object.

Another procedure that has been used with human infants involves the operant sucking response (Bower, 1967). Infants were trained to suck in the presence of a target. When the target faded away or suddenly disappeared they stopped sucking. But when the target slowly moved behind a screen, significant sucking contin-

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<sup>1</sup> The term visible displacement has been used to describe the object permanence experiment in which an object is placed in one of two or more containers and the subject can choose one of the containers in which to search for the object (Jaakkola, 2014). The term has also been used in the A-not-B task to describe the shift from placement of an object in container A for a number of trials and then the visible transfer of the object to container B on a test trial (Thelen et al., 2001). In the present research, the term will be used as it is used in object permanence research.