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FEATURED ARTICLE ESSAY

Is the SNARC a Boojum?

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For the past half-century, psychologists have examined how humans make use of spatial representations when making judgments about numerical properties of sets of items. This line of work was initiated by Frank Restle (1970), who asked college students at Indiana University to choose the larger number, either the sum of $A + B$ or C , as rapidly as possible. Restle found that the timing of people's choices fit an analog model of numerical judgment that had been proposed a few years earlier (Moyer & Landauer, 1967) and that people seemed to judge the magnitude of numbers by their position on a mental number line. Restle explained it in the following way:

If a typical problem is of the form $A + B$ vs. C , where $A < B$, the hypothesis is that S places A , B , and C on the number line, matching the distance from the origin (OA) to the magnitude of A , etc. He then must transport the smaller distance OA and concatenate it to OB , thereby locating a point X corresponding to this sum. Decision then requires that point X be compared with the comparison number (C); the comparison can be made with respect to their locations on the number line. (Restle, 1970, p. 277).

For example, if you are asked "Which is larger, $1 + 2$ or 4 ?", to reach a decision, you first locate 1 along a number line originating at 0 , then do the same for 2 , then concatenate those two distances, and in the last step, compare the concatenated distance with the distance of 4 along that same line.

Much additional work followed Restle's provocative study, and now we know that people are generally quicker to choose a smaller quantity more quickly if it is displayed on a particular side of a spatial array (say, the left side for most readers of English) and conversely choose a large quantity more quickly if it is displayed on the other side of the array. The hypothetical number line is now called the "mental number line," and the effect on latency to respond to questions about numbers that results from use of the mental number line has been labeled the "Spatial Numerical Association of Response Codes" or SNARC for short. The mental number line usually runs in the direction that one reads, but there is variation in its direction (small to large, left to right, or right to left) even within the same reading culture. Psychologists have not yet resolved when a mental number line first appears in children, and they are still exploring contextual effects, such as the effects

of thinking about numbers on a clock face. They are also exploring neurological correlates and relations with specific memorial processes, such as long-term memory and working memory.

Nonhuman animals' (possible) numerical abilities have fascinated people since before psychology existed as a discrete branch of science. At the turn of the 20th century, the public's interest in this topic was heightened by the performances of the famous "counting horse," Clever Hans, that appeared to count by stroking its hoof on the ground the appropriate number of times to "answer" a request to count to N . However, Oskar Pfungst (1911) showed convincingly that the horse was using movements of its human questioner to guide its actions, and psychologists remained appropriately skeptical about nonhuman animals' numerical abilities thereafter. Nevertheless, numerical cognition remained an important area of comparative research, as evidenced by Davis and Perusse's (1988) influential review of the area more than 30 years ago, and much additional experimental work since then (Agrillo & Beran, 2013). Agrillo and Beran (2013) suggested

that an inter-disciplinary approach including cognitive (non-verbal numerical judgments in adults), developmental (newborns and infants) and comparative psychology will represent the very frontier of numerical cognition studies, enabling us to understand both the evolutionary foundations of our numerical abilities and the exact mechanisms underlying quantity discrimination in the absence of language. (p. 1).

This issue's Featured Article (Beran, French, Smith, & Parrish, 2019) is an excellent example of comparative study of this topic.

From an evolutionary perspective, the use of a mental number line and the proposed mechanisms supporting SNARC should be shared to some degree with other species sharing underlying numerical cognition and associated neural processes with humans. Accordingly, since the early 2000s, comparative psychologists interested in numerical cognition began to explore whether nonhuman animals show evidence of a mental number line in the same situations as humans do. Many studies used a computer-presented binary visual judgment task (e.g., to touch the smaller of two dot arrays on a computer monitor). These studies provided some support for a SNARC effect. However, one of the strongest claims for a SNARC effect in nonhuman animals derives from a study with 3-day-old chicks (Rugani, Vallortigara, Priftis, & Regolin, 2015). First, chicks were trained to walk behind a central panel displaying five dots to find food. Then they were given a choice to search behind two panels displaying two or eight dots, or in a second experiment, after training with 20 dots, to search behind panels displaying eight dots or 32 dots. When two panels were

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Life History Correlates of Human (*Homo sapiens*) Ejaculate Quality

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Life history strategies reflect resource allocation decisions, which manifest as physiological, psychological, and behavioral traits. We investigated whether human ejaculate quality is associated with indicators of relatively fast (greater resource allocation to mating effort) or slow (greater resource allocation to parenting effort) life history strategies in a test of two competing hypotheses: (a) The *phenotype-linked fertility hypothesis*, which predicts that men pursuing a relatively fast life history strategy will produce higher quality ejaculates, and (b) the *cuckoldry-risk hypothesis*, which predicts that men pursuing a relatively slow life history strategy will produce higher quality ejaculates. Men ($n = 41$) completed a self-report measure assessing life history strategy and provided two masturbatory ejaculate samples. Results provide preliminary support for the cuckoldry-risk hypothesis: Men pursuing a relatively slow life history strategy produced higher quality ejaculates. Ejaculate quality may therefore reflect resource allocation decisions for greater parenting effort, as opposed to greater mating effort. The findings contribute informative data on correlations between physiological and phenotypic indicators of human life history strategies.

Keywords: life history theory, ejaculate quality, humans, phenotype-linked fertility, cuckoldry-risk

Life history theory addresses organisms' resource allocation decisions for conflicting life tasks over the life span (Del Giudice, Gangestad, & Kaplan, 2015). There are three fundamental life history trade-offs to which humans must allocate their resources (Kaplan & Gangestad, 2005). The trade-off between present versus future reproduction entails allocating resources to (a) early reproduction at the cost of continued bodily growth and maintenance, or (b) continued growth and development at the cost of delaying reproduction. The trade-off between quantity versus quality of offspring entails allocating resources to (a) producing a greater quantity of offspring, which increases the chances that one or more of these offspring will survive to reproductive age, but at the cost of decreased investment per offspring, or (b) producing higher quality offspring by investing more in each offspring, but at the cost of producing fewer offspring. The trade-off between mating effort versus parenting effort entails allocating resources to (a) high mating effort to increase offspring quantity or (b) high parenting effort to increase offspring quality. These resource allocation strategies require trade-offs because individuals have limited resources to allocate to such tasks. Such strategic resource allocation "decisions" are made throughout the life span.

Resource allocation decisions manifest as phenotypic traits—including physiological, psychological, and behavioral traits

(Braendle, Heyland, & Flatt, 2011; Del Giudice et al., 2015). Phenotypic variation therefore reflects resource allocation strategies, or *life history strategies*, by which individuals attempt to optimize resource expenditure (Del Giudice & Belsky, 2011). Human life history strategies can be conceptualized on a *slow-fast continuum* (Promislow & Harvey, 1990) whereby life history strategies reflect coordinated patterns of phenotypic traits. Relatively fast life history strategies are characterized by greater allocation of resources to mating effort to increase offspring *quantity*. Relatively slow life history strategies are characterized by greater allocation of resources to parenting effort to increase offspring *quality* (Kaplan & Gangestad, 2005).

Within a life history framework, empirical work applying life history theory to humans focuses largely on identification of physiological, psychological, and behavioral traits that comprise relatively fast or slow life history strategies (Figueredo et al., 2005, 2006). For example, previous work has mapped personality traits—both normative (Figueredo, Vásquez, Brumbach, & Schneider, 2007) and pathological traits (Del Giudice, 2016)—onto the life history strategy continuum. Other suites of traits have also been identified to map onto life history strategies, such as a "covitality" component representing health and well-being (Figueredo et al., 2007), and physiological correlates including androgens, estradiol, and testosterone (Del Giudice & Angeleri, 2016; Eisenegger, Haushofer, & Fehr, 2011; Pollet, van der Meij, Cobey, & Buunk, 2011). Mapping individual differences on the slow-fast continuum of life history strategies has improved our understanding of adaptive phenotypic variation within humans.

Ejaculate quality may also be associated with phenotypic indicators of life history strategies. Human ejaculate quality has been shown in some studies to be correlated with men's trait attractiveness (see Jeffery, Pham, Shackelford, & Fink, 2016, for a review).

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Monkeys (*Sapajus apella* and *Macaca tonkeana*) and Great Apes (*Gorilla gorilla*, *Pongo abelii*, *Pan paniscus*, and *Pan troglodytes*) Play for the Highest Bid

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Many studies investigate the decisions made by animals by focusing on their attitudes toward risk, that is, risk-seeking, risk neutrality, or risk aversion. However, little attention has been paid to the extent to which individuals understand the different odds of outcomes. In a previous gambling task involving 18 different lotteries (Pelé, Broihanne, Thierry, Call, & Dufour, 2014), nonhuman primates used probabilities of gains and losses to make their decision. Although the use of complex mathematical calculation for decision-making seemed unlikely, we applied a gradual decrease in the chances to win throughout the experiment. This probably facilitated the extraction of information about odds. Here, we investigated whether individuals would still make efficient decisions if this facilitating factor was removed. To do so, we randomized the order of presentation of the 18 lotteries. Individuals from 4 ape and 2 monkey species were tested. Only capuchin monkeys differed from others, gambling even when there was nothing to win. Randomizing the lottery presentation order leads all species to predominantly use a *maximax* heuristic. Individuals gamble as soon as there is at least one chance to win more than they already possess, whatever the risk. Most species also gambled more as the frequency of larger rewards increased. These results suggest optimistic behavior. The *maximax* heuristic is sometimes observed in human managerial and financial decision-making, where risk is ignored for potential gains, however low they may be. This suggests a shared and strong propensity in primates to rely on heuristics whenever complexity in evaluation of outcome odds arises.

Keywords: risk preferences, heuristics, decision-making, gambling, primates

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Measuring Personality in the Field: An *In Situ* Comparison of Personality Quantification Methods in Wild Barbary Macaques (*Macaca sylvanus*)

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Three popular approaches exist for quantifying personality in animals: behavioral coding in unconstrained and experimental settings and trait assessment. Both behavioral coding in an unconstrained setting and trait assessment aim to identify an overview of personality structure by reducing the behavioral repertoire of a species into broad personality dimensions, whereas experimental assays quantify personality as reactive tendencies to particular stimuli. Criticisms of these methods include that they generate personality dimensions with low levels of cross-study or cross-species comparability (behavioral coding in unconstrained and experimental settings) or that the personality dimensions generated are not ecologically valid, that is, not reflecting naturally occurring behavior (trait assessment and experimental assays). Which method is best for comparative research is currently debated, and there is presently a paucity of personality research conducted in wild subjects. In our study, all three described methods are used to quantify personality in a wild animal subject, the Barbary macaque (*Macaca sylvanus*). Our results show that the structures generated by unconstrained behavioral coding and trait assessment were not equivalent. Personality dimensions derived from both trait assessments and experimental assays demonstrated low levels of ecological validity, with very limited correlation with behaviors observed in nonmanipulated circumstances. Our results reflect the methodological differences between these quantification methods. Based on these findings and the practical considerations of wild animal research, we suggest future comparative studies of quantification methods within similar methodological frameworks to best identify methods viable for future comparisons of personality structures in wild animals.

Keywords: animal personality, quantification methods, comparative research

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Intraindividual consistency and interindividual variation in behavior (“personality”; Réale, Reader, Sol, McDougall, & Dingemanse, 2007) have been found in a broad range of animal taxa (Freeman & Gosling, 2010; Réale et al., 2007; Sih, Bell, &

Johnson, 2004). The apparent ubiquity of personality in animals presents comparative opportunities to explore the evolutionary history of personality within and between different taxa (Adams et al., 2015; Gosling, 2008). Nonhuman animal (hereafter animal)

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Perception of Degraded Speech by Chinchillas (*Chinchilla laniger*): Word-Level Stimulus Generalization

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One characteristic of human speech perception is a remarkable ability to recognize speech when the speech signal is highly degraded. It has been argued that this ability to perceive highly degraded speech reflects speech-specific mechanisms. The present study tested this hypothesis by measuring the ability of chinchillas to recognize noise-vocoded (NV) versions of naturally spoken monosyllabic words using operant conditioning in a stimulus generalization paradigm. Chinchillas do not generalize the vocoded words to be perceptually equivalent to the naturally spoken words. The responses from chinchillas to the vocoded words fall well below their responses to the naturally spoken words. In this case, pitch cues rather than speech cues may be controlling the behavioral responses. To reduce pitch cues, chinchillas were retrained using 64-channel NV words. The responses from chinchillas to the vocoded test words were now similar to those of the 64-channel versions and were similar to those obtained from human listeners. However, responses obtained from chinchillas to time-reversed versions were high and similar to responses obtained to time-normal versions suggesting that the cue controlling behavioral responses was the phonetic structure of the words. These results show that chinchillas used different acoustic cues than human listeners. The ability of chinchillas to recognize NV words as being perceptually equivalent to the naturally spoken versions is inferior compared to that of human listeners. The findings suggest that the ability of human listeners to recognize highly degraded speech is unlikely to be based solely on the general auditory and perceptual mechanisms that are common among mammals.

Keywords: chinchilla, speech perception, noise-vocoder, stimulus generalization

Humans possess a remarkable ability to recognize and understand speech when the speech signal is highly degraded, and the existence of specialized speech mechanisms could account for this ability (e.g., Remez, Rubin, Berns, Pardo, & Lang, 1994; Remez, Rubin, Pisoni, & Carrell, 1981). However, the ability to recognize degraded speech alone provides insufficient evidence for the existence of specialized speech mechanisms. To argue for the existence of speech-specific mechanisms, it is necessary to demonstrate an inability to perceive degraded speech based solely on general auditory processing mechanisms (Fitch, 2011). A comparison of speech perception in humans to speech perception based solely on general auditory processing mechanisms in nonhuman mammals provides constructive insights into understanding the adaptations that may be enhanced or specialized for speech processing in humans. Only a few studies have examined the perception of degraded speech by nonhuman mammals (Heimbauer,

Beran, & Owren, 2011; Ranasinghe, Vrana, Matney, & Kilgard, 2012; Shofner, 2014). Of particular interest here, is the study of Heimbauer et al. (2011), in which they report on noise-vocoded (NV) word recognition in Panzee, a linguistically trained chimpanzee. Noise-vocoding is a common method for degrading speech sounds used in human perceptual studies, in part, because of the relationship between vocoding and the processing in cochlear implants.

Heimbauer et al. (2011) showed a parallel in NV word recognition performance for the same set of words between Panzee and a group of human listeners, suggesting that the mechanisms underlying degraded speech perception may have been present in the common ancestor of humans and chimpanzees. One conclusion of their article is that linguistic experience plays a critical role in speech perception in humans and Panzee. Although the role of linguistic experience may seem important intuitively, its importance for degraded speech perception is challenging to test directly. Specifically, it is critical to measure degraded word recognition performance in the absence of linguistic experience, but the absence of linguistic experience is difficult to achieve. For example, one approach might be to study vocoded word recognition in human listeners using nonsense words. However, Remez et al. (1981) demonstrated that when listeners were presented with sentences based on sine-wave speech, they did not recognize the sounds as speech, but when listeners were simply told the sound they were hearing was computer-generated speech, listeners could then recognize and understand a substantial number of words in the highly degraded, sine wave sentences. Thus, if listeners are

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Do Capuchins (*Sapajus apella*) Know How Well They Will Remember? Analysis of Delay Length-Dependency With Memory Strategies

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Flexibly changing information processing based on required cognitive resources allows adaptation in terms of cognitive parsimony. Several species have been shown to use temporal durations between memory acquisition and retrieval as a cue for memory-controlling and to engage selectively in active memorization in situations involving lower cognitive cost. However, few studies have addressed whether signaling delay length at different stages of memory affects memorization differently. In the present study with tufted capuchin monkeys (*Sapajus apella*), we added visual cues signaling upcoming delay length to a delayed matching-to-sample task, so that the monkeys were informed about how long information should be maintained at different points during *with-sample* or *after-sample* conditions. We investigated whether the monkeys changed their information processing depending on their expectation of the upcoming delay length and on whether encoding was controllable (4 s vs. 16 s, Experiment 1). The results indicate that two monkeys showed different patterns depending on whether encoding was controllable, whereas the third monkey never changed her strategy. The following experiment using shorter delays showed that one monkey showed a similar pattern across experiments, providing robust evidence for cognitive flexibility in accordance with relative task difficulty (1 s vs. 8 s, Experiment 2). Overall, our results suggest that capuchins adopt two kinds of strategies depending on the experimental context, that is, expending fewer resources on relatively difficult trials and/or maintaining their processing style irrespective of delays. Their strategies aiming at saving cognitive costs may reflect a psychological function to control memory formation either prospectively or retrospectively.

Keywords: tufted capuchin monkeys, directed forgetting, delayed matching-to-sample task, memory control

Cognitive resources are limited and therefore should be used selectively to memorize important or necessary information and to ignore or forget useless information. Sometimes, ostensive cues signal informational value (Csibra & Gergely, 2009); however, even in the absence of such cues, we can make a judgment on what is unnecessary information. For example, important information is likely to have been retrieved frequently in the past, compared with less important information, which is also more likely to have last

been retrieved long ago (Anderson & Schooler, 1991). Moreover, a study showed that rats (*Rattus norvegicus*) could judge flexibly what to remember to minimize the amount of information to be memorized, according to a situational change in which the relative merit of retrospective and prospective coding changed (Cook, Brown, & Riley, 1985). This selection of coding strategies is considered adaptive to cope with the environment at the least cognitive cost.

Memory fades over time (Blough, 1959; Hunter, 1913). Fading represents an automatic loss of memory traces but can also include an active process that occurs as a function of time. This idea is supported by the directed forgetting paradigm, in which a stimulus is followed by a visual cue signaling the presence or absence of a memory test: the remember-cue (hereafter, R-cue) and forget-cue (hereafter, F-cue), respectively. After the contingency between each cue and the presence/absence of the test has been learned, probe trials in which memory for an F-cued sample is tested are occasionally inserted. Studies have shown that accuracy following the R-cue is significantly higher than those following the F-cue (pigeons [*Columba livia*]: Maki & Hegvik, 1980; squirrel monkeys [*Saimiri sciureus*]: Roberts, Mazmanian, & Kraemer, 1984). However, these kinds of paradigms are vulnerable to alternative explanations that forgetting was driven by non-memory-related factors such as reduced attentiveness or motivational state in F-cued trials (Grant, 1981; Zentall, Roper, & Sherburne, 1995). Other studies (Roper, Kaiser, & Zentall 1995) called for caution and emphasized

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Multiple Parasitism Reduces Egg Rejection in the Host (*Acrocephalus arundinaceus*) of a Mimetic Avian Brood Parasite (*Cuculus canorus*)

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A host that has been targeted by an avian brood parasite can recover most of its potential fitness loss by ejecting the foreign egg(s) from its nest. The propensity for some hosts to engage in egg rejection behavior has put selective pressure on their parasites to evolve mimetic eggshells resembling the host's own shell colors and maculation. In turn, hosts have counterevolved increasingly more sophisticated detection methods such as narrowing visual egg acceptance thresholds or using social cues to recognize parasitism. However, multiple cognitive mechanisms acting simultaneously could theoretically interfere with one another and ultimately decrease egg rejection accuracy, especially if these heuristics yield differing targets for rejection. By painting hosts own eggs, we studied a host species of the common cuckoo *Cuculus canorus*, the great reed warbler *Acrocephalus arundinaceus*, and tested its responses to the presence of "foreign" eggs of varying quantity, colors, and uniformity. Using reflectance spectra of egg background coloration and avian perceptual modeling, we then estimated the sensory thresholds triggering egg rejection by this host for each treatment. As previously reported, rejection rates were positively related to the perceptual distance between own and foreign eggs in the nests in all treatments. However, rejection thresholds were more permissive (error prone) both with greater proportions of foreign eggs per clutch and/or when the suite of foreign eggs was perceptually more variable within the nest. These results suggest that parasites, through multiple parasitism, can partially overcome the evolution of hosts' recognition of mimetic parasite eggs.

Keywords: acceptance thresholds, coevolution, host–parasite interactions, sensory modeling

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Testes Size, Vaginal Complexity, and Behavior in Toothed Whales (Odontocetes): Arms Race or Tradeoff Model for Dusky Dolphins (*Lagenorhynchus obscurus*), Harbor Porpoises (*Phocoena phocoena*), and Bottlenose Dolphins (*Tursiops* spp.)?

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Sexual selection influences both genital diversity and mating behaviors, yet the integrated coevolution of pre- (behavioral) and postcopulatory (anatomical) traits in both sexes has received little attention. Traits could potentially evolve through an arms race model of escalations in male persistence and female resistance, and/or through a tradeoff model of inverse correlations between investments in pre- and postcopulatory traits. Pre- and postcopulatory traits of dusky dolphins (*Lagenorhynchus obscurus*) were compared with bottlenose dolphins (*Tursiops* spp.) and harbor porpoises (*Phocoena phocoena*). Relative testes size and vaginal complexity were measured from dissected specimens. Behavioral traits were analyzed from video recordings of individuals in free-ranging populations. Female precopulatory and male postcopulatory traits were associated, whereas female and male postcopulatory traits or female pre- and postcopulatory traits were not associated. Dusky dolphins differed substantially in several behavioral traits including longer durations of mating group interactions, lower rates of copulation attempts, more males per group, and higher female behavioral resistance. To explore complex processes of integrative coevolution, we recommend future research incorporate pre- and postcopulatory traits and focus on alternative measures of female resistance and male persistence.

Keywords: tradeoff, arms race, coevolution, mating behavior, reproductive morphology

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Mesnick, Marc Webber, provided helpful suggestions or feedback on the manuscript. Sarah Piwetz, Jessica Hillhouse, and Jody Weir kindly categorized behaviors in Tables 1 and 2 as high or low intensity. We thank the New Zealand Common Dolphin Project (especially Karen Stockin and Catherine Lea), Texas Marine Mammal Stranding Network (especially Heidi Whitehead and Sarah Piwetz), The Marine Mammal Center (especially Frances Gulland and Lauren Rust), and the National Oceanic and Atmospheric Administration (NOAA Fisheries, especially Erin Fougères) for providing reproductive tracts.

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The excised female reproductive tracts were collected under a National Marine Fisheries Service (NMFS) salvage permits and an institutional Convention on International Trade in Endangered Species of Wild Fauna and Flora permit (CITES Mammal Import Permit: 15US774223/9; MMPA/ESA research permit: 14097). No research permits were required to follow and video-record cetaceans, although authority was provided by the New Zealand Department of Conservation, U.S. National Oceanic and Atmospheric Administration (permits LOC 15477 and 20386), Red Sea Governor of Egypt, and supported by the Technische Universität Berlin Campus El Gouna.

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Sloth Bears (*Melursus ursinus*) Fail to Spontaneously Solve a Novel Problem Even if Social Cues and Relevant Experience Are Provided

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The ability to solve novel problems is crucial for the survival and fitness of individuals living in dynamic environments. Studies of problem-solving date back to the beginning of the past century, but our knowledge is nonetheless still limited to very few taxa. In this study, we aimed to test a species of the order Carnivora, sloth bears (*Melursus ursinus*), on the ability to solve a novel foraging task. Bears were individually presented with honey spread on the wall and a familiar bucket, and, depending on the condition, they had to move the bucket and climb on it to access the honey. In follow-up conditions, they also repeatedly received cues to help them solve the task: before being tested, they either observed a human experimenter solving the problem or received direct relevant experience about how to solve the task. Despite high motivation, and in contrast to our predictions, none of the tested bears used the bucket to access out-of-reach food, even when social information and direct relevant experience were provided. These findings suggest that bears in this task may have failed to cognitively represent the problem and recognize the relevant aspects that would have led to its solution.

Keywords: problem-solving, carnivores, tool use, social learning, innovation

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In animals, the ability to spontaneously solve problems plays a crucial role in successfully coping with novel socioecological challenges, exploiting new resources, invading new niches, or finding new social strategies, with a critical effect on the survival and fitness of individuals in complex dynamic environments (Lee, 1991; Lefebvre, Whittle, Lascaris, & Finkelstein, 1997; Nicolakakis, Sol, & Lefebvre, 2003; Ramsey, Bastian, & van Schaik, 2007; Reader & Laland, 2003; Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005a, Sol, Lefebvre, & Rodríguez-Teijeiro,

2005b). A first approach to the study of problem-solving in animals dates back to Köhler (1926). In one of his seminal studies, chimpanzees (*Pan troglodytes*) had to either stack boxes to reach a banana hanging out of reach or combine short sticks to reach for food. From the first trials, chimpanzees proficiently used tools to solve the novel tasks, and these results were interpreted as chimpanzees showing “insight,” in that they successfully obtained food without having to use trial-and-error strategies (Epstein, Kirshnit, Lanza, & Rubin, 1984; Thorpe, 1963; but see Shettleworth, 2010).

Since Köhler’s (1926) studies, a variety of approaches have been used to study problem-solving and several related aspects, including the effect of social learning on problem-solving, or the social transmission of innovations (Aplin, Farine, et al., 2015; Aplin, Sheldon, & Morand-Ferron, 2013; Hoppitt & Laland, 2013). So far, most studies of problem-solving have been conducted on primates (Day, Coe, Kendal, & Laland, 2003; Dean, Hoppitt, Laland, & Kendal, 2011; Hrubesch, Preuschoft, & van Schaik, 2009; Laidre, 2008; Manrique, Völter, & Call, 2013; Visalberghi, Frigaszy, & Savage-Rumbaugh, 1995) and birds (Bond, Kamil, & Balda, 2007; Boogert, Monceau, & Lefebvre, 2010; Boogert, Reader, Hoppitt, & Laland, 2008; de Mendonça-Furtado & Ottoni, 2008; Epstein et al., 1984; Gajdon, Fijn, & Huber, 2004; Morand-Ferron, Cole, Rawles, & Quinn, 2011; Morand-Ferron, Lefebvre, Reader, Sol, & Elvin, 2004; Morand-Ferron & Quinn, 2011; Tebbich, Seed, Emery, & Clayton, 2007;

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Probabilistic Inferential Decision-Making Under Time Pressure in Rhesus Macaques (*Macaca mulatta*)

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Decisions often involve the consideration of multiple cues, each of which may inform selection on the basis of learned probabilities. Our ability to use probabilistic inference for decisions is bounded by uncertainty and constraints such as time pressure. Previous work showed that when humans choose between visual objects in a multiple-cue, probabilistic task, they cope with time pressure by discounting the least informative cues, an example of satisficing or “good enough” decision-making. We tested two rhesus macaques (*Macaca mulatta*) on a similar task to assess their capacity for probabilistic inference and satisficing in comparison with humans. In each trial, a monkey viewed two compound stimuli consisting of four cue dimensions. Each dimension (e.g., color) had two possible states (e.g., red or blue) with different probabilistic weights. Selecting the stimulus with highest total weight yielded higher odds of receiving reward. Both monkeys learned the assigned weights at high accuracy. Under time pressure, both monkeys were less accurate as a result of decreased use of cue information. One monkey adopted the same satisficing strategy used by humans, ignoring the least informative cue dimension. Both monkeys, however, exhibited a strategy not reported for humans, a “group-the-best” strategy in which the top two cues were used similarly despite their different assigned weights. The results validate macaques as an animal model of probabilistic decision-making, establishing their capacity to discriminate between objects using at least four visual dimensions simultaneously. The time pressure data suggest caution, however, in using macaques as models of human satisficing.

Keywords: rhesus macaque, decisions, probabilistic inference, satisficing

Everyday decision-making may require the use of multiple, simultaneous cues with different diagnostic values. A person or animal choosing between pieces of fruit, for example, may assess their ripeness, symmetry, and abrasions, that is, the dimensions of color, shape, and texture. Probabilistically, color may be a better indicator of palatability than shape, which may in turn be more

important than texture. In the human cognitive literature, learning the statistical properties of such cues is termed *probabilistic inference* (for reviews, see Fiser, Berkes, Orbán, & Lengyel, 2010 and Ma, 2012).

The ability to make decisions based on probabilistic inference of multiple, simultaneous cues, such as in our fruit example, has been

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When Walking in an Outside Area, Shelter Dogs (*Canis familiaris*) Synchronize Activity With Their Caregivers but Do Not Remain as Close to Them as Do Pet Dogs

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When taken for walks, pet dogs synchronize their walking with that of their owners. The aim of this study was to ascertain whether shelter dogs do the same with their caregivers. We documented the behavior of 30 shelter dogs when they were taken outside in their regular walking area by their principal caregivers. The caregivers were instructed to behave in three ways: stay still, walk normally, and walk fast. The shelter dogs synchronized their locomotor activity with their caregiver less strongly than did pet dogs in a previous study. Shelter dogs also maintained greater distances to their caregivers than pet dogs with their owners. The present study predicts that the strength of the social bond between the caregiver and the dog explains most of the findings, which are similar to those found between adult human interacting partners. Further research could disentangle what aspects of experience contribute to the differences between pet dogs and shelter dogs in behavioral synchronization with a familiar human.

Keywords: dog–human synchronization, dog–human affiliation, locomotor synchrony, interspecific synchronization, shelter dogs

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Behavioral synchronization can generally be defined as doing the same thing at the same time and in the same place as other individuals (Louwerse, Dale, Bard, & Jeuniaux, 2012). There are several subtypes of behavioral synchronization, such as temporal synchrony (switching activity at the same time; Dostálková & Špinka, 2007), activity synchrony (exhibiting the same behavior at the same time, also called behavioral similarity, mimicry, allomimicry or behavioral matching; Chartrand & Bargh, 1999; Chartrand & Lakin, 2013; Gautrais, Michelena, Sibbald, Bon, & Deneubourg, 2007), and location synchrony (being in the same place at

the same time; Bertram, 1980; King & Cowlshaw, 2009). Behavioral synchronization can be observed in simple situations such as walking side by side (in humans: van Ulzen, Lamoth, Daffertshofer, Semin, & Beek, 2008; in dogs: Duranton, Bedossa, & Gaunet, 2017b, 2018) and in more complex ones implying a third party such as social referencing when a dog adjusts to the social cues provided by the partner (Duranton, Bedossa, & Gaunet, 2016; Merola, Prato-Previde, & Marshall-Pescini, 2012).

Behavioral synchronization is broadly observed in mammals and is supposed to have various adaptive values, such as reducing predation pressure and increasing group members' survival (Duranton & Gaunet, 2016a). One value that is of interest for the present work is its role in social bonds: Behavioral synchronization is acknowledged to increase social cohesion by increasing affiliation between individuals (Chartrand & Lakin, 2013), by allowing better social learning between individuals (Fragaszy et al., 2017), and better empathy (in humans: Koehne, Schmidt, & Dziobek, 2016; in nonhuman primates: Mancini, Ferrari, & Palagi, 2013). Conversely, the more affiliated two individuals are, the more behavioral synchronization they display (see Duranton & Gaunet, 2016a for a review). For example, the more two cetaceans are affiliated, the more synchronized pair-swimming behaviors they display (e.g., wild bottlenose dolphins: Sakai, Morisaka, Kogi, Hishii, & Kohshima, 2010; long-finned pilot whales: Senigaglia, de Stephanis, Verborgh, & Lusseau, 2012). In humans, rapport and liking are linked to a higher level of behavioral synchronization

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Lowland Gorillas (*Gorilla gorilla gorilla*) Failed to Respond to Others' Yawn: Experimental and Naturalistic Evidence

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Yawn contagion, possibly a form of emotional contagion, occurs when a subject yawns in response to others' yawns. Yawn contagion has been reported in humans, chimpanzees, bonobos, geladas, wolves, and dogs. In these species, individuals form strong, long-term relationships and yawn contagion is highest between closely bonded individuals. This study focuses on the possible expression of yawn contagion in western lowland gorillas (*Gorilla gorilla gorilla*). Gorillas share with geladas a similar basic social structure (one dominant male and several adult females with offspring) and differ from bonobos and chimpanzees, which live in multimale–multifemale societies. Gorillas stand out because they are spatially aggregated but show especially low levels of social affiliation. If the expression of yawn contagion is linked to the investment of animals in establishing long-term social relationships, the phenomenon should not be detected in gorillas (*social relationship hypothesis*). For the first time, we applied to the same subjects the naturalistic approach typically used in ethology (all occurrences behavioral sampling) and the experimental approach typically used in psychology (response to video stimuli). During the video demonstration (avatar yawn/control; unfamiliar gorilla yawn/control), we checked for the attentional state of the subjects. Anxiety-related self-directed behaviors were recorded in all conditions and settings. We failed to detect yawn contagion in both naturalistic and experimental settings, with yawning being possibly associated with anxiety during video shows (revealed by the increased frequency of self-directed behaviors). In conclusion, yawn contagion may be a socially modulated phenomenon that remains largely unexpressed when individuals share weak social affiliation.

Keywords: contagion, *Gorilla gorilla gorilla*, anxiety, weak social engagement

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This article does not contain any studies with human participants performed by any of the authors. This study was approved by University of Pisa (Animal Care and Use Board). Because the study was purely observational, the committee waived the need for a permit. The study was conducted with no manipulation of animals. Gorillas were observed in their home enclosures, including the video presentation. Data were collected on the animals that spontaneously approached the tablet. The animals were never deprived of water and food at any stage and were never isolated from their social group. All animal experiments were carried out in accordance with the U.K. Animals (Scientific Procedures) Act, 1986 and associated guidelines, EU Directive 2010/63/EU for animal experiments.

The data used for this study are provided as electronic supplementary material. The statistical tools EASYFIT and SPSS used in this study are proprietary software. However, trials (limited time/limited functionality) can be found online on the producer's websites (EASYFIT: www.mathwave.com;

SPSS: <https://www-01.ibm.com>), along with the freeware Resampling Procedures 1.3 package by David C. Howell (<https://www.uvm.edu/~dhowell/StatPages/ResamplingWithR/ResamplingR.html>).

Elisabetta Palagi conceived the study. Elisabetta Palagi and Giada Cordoni designed the study. Elisabetta Palagi, Ivan Norscia, and Giada Cordoni performed the video experiments. Elisabetta Palagi, Ivan Norscia, and Giada Cordoni analyzed videos and data. Elisabetta Palagi, Ivan Norscia, and Giada Cordoni wrote the article.

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