



Using an Ambiguous Cue Paradigm to Assess Cognitive Bias in Gorillas (*Gorilla gorilla gorilla*) during a Forage Manipulation

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Abstract - In nonhumans, ‘optimism’ is often defined as responding to an ambiguous item in the same manner as to items previously associated with reward (or lack of punishment), and “pessimism” is defined as responding to an ambiguous item in the same manner as to items previously associated with a lack of reward (or with punishment). We measured the degree of “optimism” and “pessimism” in three captive male western lowland gorillas (*Gorilla gorilla gorilla*) during four consecutive two-week periods in which the amount of available forage material (mulberry, *Moraceae* or alfalfa, *Medicago sativa*) was manipulated. We assessed cognitive bias using an ambiguous cue paradigm for the first time. Pairs of two-dimensional shapes were presented on a touch-screen computer in a forced choice task in which one shape was always reinforced (P), one was never reinforced (N), and one was reinforced half the time, making it ambiguous (A). The gorillas were presented with an equivalent number of PA and NA pairs prior to testing, which also included probe trials of ambiguous items paired with novel items. During the limited forage phase, the gorillas, as a group, selected the ambiguous stimulus (indicating optimism) at a level greater than chance; tests for all other phases were non-significant. The gorillas displayed individual differences in learning PA and NA trials and in their choice of ambiguous items on test trials. Idiosyncratic preferences for particular stimuli suggest that the ambiguous cue paradigm may not be ideal for assessing cognitive bias in nonhumans.

Keywords – Cognitive bias, Ambiguous cue paradigm, Gorilla, Forage, Cognitive enrichment, Welfare

Animal models are commonly used by researchers to aid in the identification of factors that may contribute to the onset and maintenance of mood disorders, such as depression and anxiety (Katz & Chauvin, 2016), as well as the assessment of possible treatments (Overstreet, 1993). As in humans, a history of trauma or abuse increases the likelihood of developing persistent mood disorders (i.e., depression) in adulthood (Chapman et al., 2004; Günther, Dannlowski, Kersting, & Suslow, 2015; Widom, DuMont, & Czaja, 2007). A history of neglect was also found to impact persistent mood later in life in animals such as domestic goats, as assessed in the form of judgment biases defined below (Briefer & McElligott, 2013). On the flip-side, positive biases may be associated with life satisfaction and resiliency (Kleim, Thörn, & Ehlert, 2014). In nonhumans, persistent mood states cannot be assessed directly. Instead, researchers must infer mood states from various behavioral and physiological indicators. For instance, researchers often measure

animals' responses to situations that are assumed capable of inducing particularly strong emotional responses (e.g., looking for signs of depression or anxiety in poor welfare conditions or for signs of positive emotion in good welfare conditions; Mendl, Burman, & Paul, 2010).

One popular method of assessing mood in nonhumans is via cognitive bias tasks. Cognitive bias, otherwise known as affective or judgment bias, can be defined as a bias in the judgment of ambiguous or neutral stimuli and is often associated with mood or emotional states in both humans and nonhumans (Hallion & Ruscio, 2011). Cognitive bias assessments are especially useful when it comes to the study of nonhuman species as they can be used as a measure of positive welfare (a phenomenon that can be difficult to measure directly). In these cases, researchers implement changes that would be expected to produce positive responses and then assess the degree to which those changes influence the animals' judgements of ambiguous or novel stimuli. For instance, it has been found that larger or enriched environments result in positive cognitive biases (often referred to as optimism) in a variety of species including pigs (*Sus scrofa domestica*; Douglas, Bateson, Walsh, Bédoué, & Edwards, 2012), European starlings (*Sturnus vulgaris*; Matheson, Asher, & Bateson, 2008), and rats (*Rattus norvegicus*; Brydges, Leach, Nicol, Wright, & Bateson, 2011).

Researchers have also found that dogs that display separation-behaviors consistent with anxiety (i.e., separation anxiety) also display pessimism when tested on a cognitive bias task (Mendl, Brooks et al., 2010). Similarly, captive tufted capuchins that displayed stereotypic head twirling behavior (abnormal behavior that is associated with compromised well-being) also performed pessimistically on a cognitive bias task (Pomerantz, Terkel, & Suomi, 2012). Assessments of mood or affective states will allow caretakers to determine stimuli and environmental factors that impact mood states positively or negatively, and, thus, can be used to inform and improve animal welfare.

In humans, cognitive bias tasks often make use of various verbal exercises, asking participants to interpret ambiguous statements (e.g., Hallion & Ruscio, 2011). Despite the challenges of assessing affective states in nonhumans, there are a variety of non-verbal methods that have been developed to tap into cognitive biases. One of the most common of these is the go/no-go task originated by Harding, Paul and Mendl (2004) in which animals are trained to make a response to one cue (a color, tone etc.) and withhold a response when presented with a different cue (see also Bateson, Desire, Gartside, & Wright, 2011; Douglas et al., 2012; Matheson et al., 2008). The two cues often represent different end points of a continuum, such as color or space. After mastering the discrimination, the subject is then presented with ambiguous cues, which are either intermediate between the two trained cues or represent a blend or combination of the trained cues. If subjects respond to the ambiguous cue as if it is the positive (go) cue, they are displaying positive bias (optimism), whereas if they respond as if it is the negative (no-go) cue, they are displaying negative bias (pessimism).

Due to the nature of this paradigm, it is possible that some of the intermediate stimuli may be perceived as being less ambiguous than others. For example, if an animal was trained to discriminate between two auditory tones (one high pitched and one low), the most ambiguous tone would be one that is exactly intermediate between the two trained tones. Alternative intermediate pitches that may be lower than this true "middle" stimulus would be more similar to the lower tone than to the higher tone and therefore less ambiguous. Studies have used color (in which the intermediate cue is a blend of the trained colors, (Burman et al., 2011), sound (Douglas et al., 2012), scent (Bateson et al., 2011), line length (Bethell, Holmes, MacLarnon, & Semple, 2012), and spatial location (Briefer et al., 2014). Whereas responses to these skewed intermediate cues may be informative with regard to cognitive bias, it is possible that responses may also reflect a general discriminatory ability such that responses to the most intermediate case are simply intermediate themselves. This concern is somewhat allayed when an animal's responses to the intermediate stimulus are biased in one direction, but one cannot assure such results a priori. A problem arises when responses are completely consistent with a perceptual judgment such that responses show a linear relationship to the trained stimuli, with responses to the intermediate stimulus being perfectly intermediate as well. In such cases, it would not be possible to determine whether an animal's affective state was in fact neutral, or whether its responses indicated only its ability to make the perceptual judgment. Across many studies, there seem to be differences in how animals respond to probe cues that are closest to

the reward cue (P+), intermediate between the trained cues, and closest to the unrewarded/punished cue (P-) (Bethell et al., 2012). For instance, some studies (Bateson & Matheson, 2007; Doyle et al., 2011) have interpreted a reduction in responding to P+ as an indication of depression whereas other studies (Burman, Parker, Paul, & Mendl, 2008; Mendl, Burman et al., 2010) interpreted a reduction in responding to P- (Burman et al., 2008) as indicating anxiety. Additionally, other studies (Brilot, Asher, & Bateson, 2010; Mendl, Brooks et al., 2010) interpret reduced responding to the intermediate probe as pessimism. Clearly, there are important differences in both the ways that animals respond to probe trials and in how those responses are interpreted. Bethell et al. (2012) suggest that one reason for these differences, and consequently, the reason that it can be so hard to compare findings across studies, is the fact that the salience of the preceding positive or negative event for each studies subjects may differ.

In order to ensure that responses to the ambiguous stimuli reflect affective states rather than an animal's discriminatory ability, it may be useful to develop a method of assessing cognitive bias that avoids intermediate stimuli and instead makes use of stimuli that obtain an ambiguous status through their association (or lack thereof) with reward. In the current study, we adapted the ambiguous cue paradigm (Fletcher & Woodruff, 1966; Vasconcelos & Monteiro, 2014), which allowed for the creation of multiple, equally ambiguous probe stimuli. In this paradigm, animals are trained to discriminate between the conditions under which three distinct stimuli have unique reward associations. The three visual stimuli are arranged into two stimulus pairs (PA and NA). One stimulus is arbitrarily designated as the positive cue (P), which is always rewarded when selected, another is designated as the negative cue (N), which is never rewarded when selected, and the last is designated as the ambiguous cue (A), which is either rewarded (when paired with N) or not rewarded when selected (when paired with P). Subjects can either reach a criterion level of performance on both types of trial, or be exposed to the same number of both types of trial for a sufficient length of time to discriminate between their reward outcomes. A is then presented alongside novel stimuli in probe pairings, which are inserted amidst the previously trained pairs (NA and PA). How subjects respond to the novel-ambiguous pairing (and specifically to A) lends insight into their cognitive biases. For example, a subject that selects A over the novel stimuli is exhibiting optimism because selecting A indicates the expectation of a reward. Conversely, choosing the novel cue demonstrates pessimism - an expectation that selecting A would result in no reward. Choices are assumed to be more strongly controlled by the ambiguous reinforcement history of the familiar ambiguous item rather than by the novel item that has no reinforcement history. This assumption is based on the notion that animals have prior information regarding only one of the two stimuli. However, it is possible that preferences for, or aversions to, novelty may also drive responding. This is a testable hypothesis that could be assessed by pairing novel stimuli with the positive and negative stimuli, in addition to the ambiguous stimulus, at testing. Whereas some species, humans included, have been found to exhibit a preference for novelty, as demonstrated on attentional bias tasks, it is possible that other factors may also influence preferences. In human infants, researchers have found that inherent preferences for novelty can be reversed if the familiar object has been paired with a primary reinforcer (Najm-Briscoe, Thomas, & Overton, 2000). This result suggests that even if the gorillas in this study had preferences for novelty at the start of this experiment, through their experiences in the training phase, they should have learned to associate the familiar (ambiguous) stimulus with food rewards. This prior association may have been able to override a novelty preference.

Traditionally, the ambiguous cue paradigm has been used as a tool for assessing the mechanics of learning. For example, the interfering cue hypothesis proposes differential acquisition of the NA and PA discriminations due to interference with the PA pairings (Vasconcelos & Monteiro, 2014). Specifically, it should take animals longer to learn the PA pairing as both cues are rewarded at least some of the time (P is always reinforced while A is partially reinforced), whereas they should learn the NA pairings faster because there is no interference (N is never reinforced). This hypothesis has been supported by work with European starlings (Vasconcelos & Monteiro, 2014). However, work with rhesus macaques (Fletcher & Woodruff, 1966), has demonstrated the opposite pattern, which indicates that they were attending to information about non-reinforcement. This is because both cues are not rewarded at least some of the time on NA pairings (N is never reinforced while A is unreinforced half of the time), whereas there is no interference on the PA pairings (P is always reinforced). Differential learning of these pairs can thus inform the researcher as to

the type of information prioritized by the animal when learning the discriminations. Attending to reinforcement versus lack of reinforcement might also be considered an indication of optimism versus pessimism in itself.

Development of a novel and useful cognitive bias test will be beneficial because such a test can be used to investigate the effects of environmental changes, such as presence or absence of enrichment, on affective states (Bateson & Matheson, 2007; Burman et al., 2011; Douglas et al., 2012; Matheson et al., 2008). Investigating the effects of varying enrichment opportunities on behavior and affect is important if animal caretakers wish to understand how best to promote emotional well-being in the animals they manage.

Browse (leafy and fibrous plant material) is a common enrichment item for animals, like western lowland gorillas, which spend a significant amount of their time (67% of the day) foraging and grazing in the wild (Masi, Cipolletta, & Robbins, 2009). This experiment was conducted to coincide with and complement a study to monitor the effects of varying the availability of forage material on behavioral and endocrine responses in a bachelor group of gorillas at the Detroit Zoo (Fuller, Vonk, McGuire, Murray, & Allard, 2015). We attempted to measure the degree of “optimism” or “pessimism” after four two-week periods in which the amount of forage material available to three adult male gorillas was manipulated. The study phases were: an initial baseline phase in which the gorillas received alfalfa twice per week and mulberry branches twice per week (the traditional amount of forage material provided by the zoo), a second phase in which the amount of forage material was reduced (only alfalfa given twice a week), a third phase of elevated amounts of forage material (alfalfa twice a week and mulberry branches five days per week) and lastly, a final baseline phase that was identical to the first. We predicted that gorillas would show the most optimism at the end of the elevated forage phase and the least optimism during the reduced forage phase.

Method

Subjects

Three captive adult male western lowland gorillas (Chip, 19 years old; Pende, 18 years old; and Kongo, 17 years old) were tested. These gorillas were housed together in a bachelor group at the Detroit Zoo (an institution accredited by the Association of Zoos and Aquariums) and had previous training using a touch screen computer in a quantity estimation task (Vonk et al., 2014) as well as on preference assessment tasks (unpublished data). During data collection for this project, the gorillas also received training using the touch-screen computer for an unrelated conditional discrimination task. Research took place in an indoor area not accessible to zoo visitors three mornings each week when the gorillas were separated for their morning meal. The gorillas were separated twice a day (once before the zoo opened and once after hours) for feeding, and received browse, alfalfa, and additional food items once a day while in their usual habitat. Training and testing with these animals complied with the IACUC of Oakland University, and the activities were presented as a form of cognitive enrichment.

Materials

A durable Panasonic Toughbook Laptop CF19 computer and 1900 VarTech Armorall capacitive touch-screen monitor welded inside a rolling LCD panel cart encased with top and sides comprised the experimental apparatus. The apparatus was positioned so that it was flush with the mesh of the gorilla enclosure using a 1.2 m by 1.2 m plywood ramp. Food items (consisting of assorted fruits, vegetables, and primate chow) from their morning diet were used as rewards. When rewarding the gorillas for a correct choice, small pieces of food were delivered to the gorilla using a PVC chute attached to either side of the apparatus (see Figure 1).



Figure 1. Experimental apparatus, front and back.

The experiments were programmed using Inquisit Version 3 for Windows. Two stimuli were presented simultaneously centered to the left and right of the center of the screen (see Figure 2). Arbitrary shape symbols were utilized in this study because the symbols used in the assessments needed to be devoid of any prior meanings or associations for the gorillas (otherwise their responses may have been biased). In addition, there is no clear evidence that gorillas represent two-dimensional stimuli as being meaningful real life objects (Parron & Call, 2008) so we used simple stimuli that varied on only two dimensions (shape and color) to reduce the complexity of the task. The gorillas had already been trained on this basic task using natural stimuli and static and moving dots representing different quantities (Vonk et al., 2014). In the example shown in Figure 2, the PA pair consists of a red square (incorrect) and an orange triangle (correct). The NA pair consists of a blue circle (incorrect) and the red square (correct). The red square is present in both the PA and NA pairings, yet is consistently the correct choice in the NA pair and the incorrect choice in the PA pair. Thus, it is an ambiguous symbol.

Each phase of the study was assigned a unique set of trained stimuli (A, N, and P) as well as two unique novel stimuli used on probe trials, resulting in a total of 20 distinct stimuli (12 trained and 8 novel) that the gorillas were exposed to across the four phases of testing. There were no overlapping shapes or colors used across the four phases. These stimuli consisted of shapes on a white background, 400 x 600 pixels in size, and were distinct in both shape and color (see Figure 3 for examples).

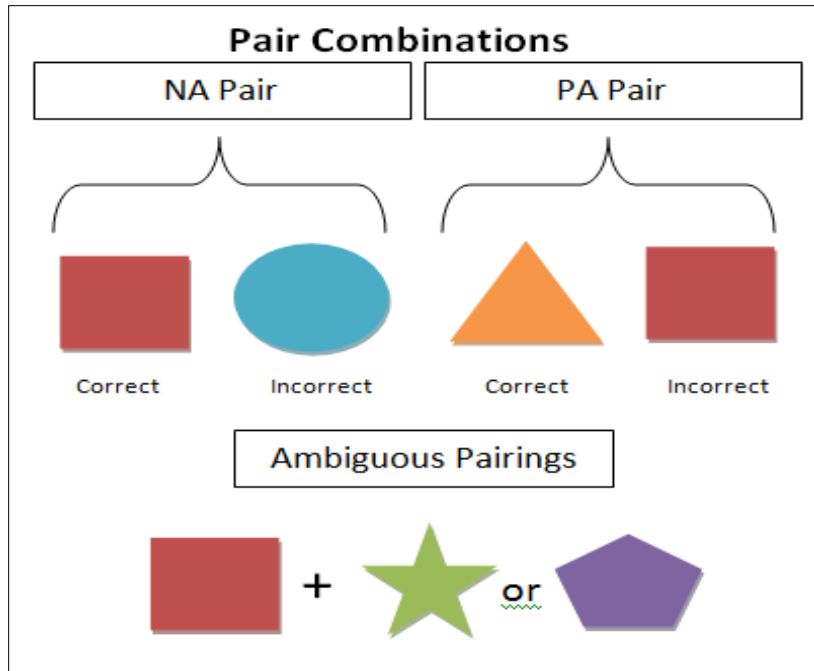


Figure 2. Example cue combinations.

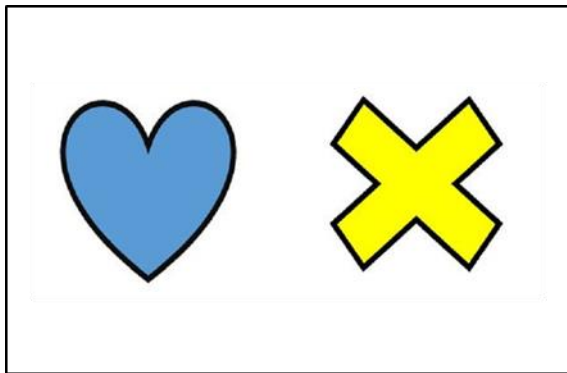


Figure 3. An example trial. One stimulus is always rewarded or non-rewarded and the other is ambiguous.

Procedure

Each gorilla received training three mornings per week between 7:00 AM – 9:00AM. Each day they received approximately 20 – 30 mins of training during which they received approximately six to eight 8 – 12 trial sessions. Correct responses were followed by a melodic tone, a blank screen, and a small food reward. Incorrect responses were followed by a buzzer tone, a blank screen, and no food reward. There were no time-outs given for incorrect responses. Therefore, the inter-trial intervals for both correct and incorrect trials were approximately 750 ms. However, the gorillas were not under any time pressure to respond. Previous training with the gorillas had indicated that they became less frustrated with short intervals between trials.

Training

The gorillas were presented with a two-alternative-forced-choice task in which one cue was always the correct choice. For each phase of the forage study, we trained the gorillas on a different cue set in case there were innate preferences for certain symbols that may have influenced their choices, and because the ambiguous stimulus can be paired only infrequently with novel stimuli before it is no longer ambiguous in such contexts. The designation of the specific stimuli (A, P, or N) was counterbalanced across the gorillas such that each symbol was used in each role during each phase.

Before the forage manipulation began, training sessions consisted of randomized intermixed NA and PA trials (eight trial sessions, four of each pairing). However, after 18 sessions, it became clear that the gorillas were not making progress and the decision was made to divide the NA and PA pairs into segregated sessions to facilitate learning. Thus, these sessions consisted of 10 trials of only NA or PA pairs (one type of pairing per session). Each morning, the gorillas would receive approximately three to four sessions of each type in blocks of one type of session. Training would last for the duration of the forage manipulation phase, at the conclusion of which they received four test sessions across the last two test days of the phase. Due to the time constraints of the forage manipulation aspect of the project, the gorillas were trained for the two-week period each time instead of training to a set performance criterion. This approach is consistent with other studies using the ambiguous cue paradigm (Boyer & Polidora, 1972).

Testing

After completing the training phase, gorillas participated in four test sessions in which they encountered the original ambiguous stimulus paired with one of two novel stimuli (see Figure 3) on two probe trials within the session. Each gorilla participated in four testing sessions across two days. Each test session consisted of 12 trials made up of five PA pairs, five NA pairs, and two ambiguous pair trials. In these ambiguous cue trials each neutral marker was presented once with the A stimulus using non-differential reinforcement such that the gorilla was given a food reward regardless of which stimulus he selected. The PA and NA trials occurred in random order, but the probes always occurred on trials 5 and 8. Each stimulus in every set was assigned a different role (A, P, or N) for each gorilla. In this phase we attempted to determine whether the gorillas perceived the ambiguous stimulus as positive or negative, based on selections of the ambiguous stimulus on probe trials, which would indicate their optimism or pessimism.

If the gorillas selected the ambiguous stimulus on the probe trials, this would indicate a positive cognitive bias as they would be demonstrating optimism regarding the outcome of selecting the ambiguous stimulus. Conversely, if they failed to select the ambiguous stimulus (instead selecting the novel cue) this would indicate a negative cognitive bias as they would be demonstrating pessimism. We predicted that the gorillas would demonstrate the greatest positive cognitive bias during the elevated forage phase, when they had access to more foraging opportunities and would demonstrate a negative cognitive bias during the reduced forage phase when there would have been less enrichment available to them.

Results

One-sample t-tests indicated that, during the limited forage phase, the gorillas, as a group, selected the ambiguous stimulus (indicating positive interpretation) at a level greater than chance ($M = 0.67$, $SD = 0.069$; $t(2) = 4.25$, $p = 0.051$, 95% CI [-0.002, 0.342]). T-tests for the first baseline phase ($M = 0.67$, $SD = 0.312$, $t(2) = 0.944$, $p = 0.445$, 95% CI [-0.605, 0.945]), the elevated forage phase ($M = 0.627$, $SD = 0.125$, $t(2) = 1.755$, $p = 0.221$, 95% CI [-0.184, 0.437]) and the final baseline phase ($M = 0.42$, $SD = 0.193$, $t(2) = -0.717$, $p = 0.548$, 95% CI [-0.559, 0.399]) were non-significant. However, it should be noted that, with three subjects, there was limited power to detect effects. Over the course of this experiment, there was also substantial variability between phases as well as between individuals, as can be seen in Figure 4.

Additionally, as can be seen in Figure 4, Chip chose the ambiguous cue 100% of the time for the first baseline phase. Looking back at Chip’s training data (Figure 5), it becomes clear that this is not a clear indication of optimism given his clear bias for the ambiguous cue (in this particular phase, a blue circle) during training. He selected the ambiguous cue on NA pairings 100% of the time, whereas, on the PA trials, he exhibited difficulty inhibiting that preference for the blue circle (A), choosing the positive cue correctly only 56% of the time.

Binomial tests indicated that for the training pairs (PA & NA), Chip performed above chance (50%) on his NA pair for phase 1 ($p < 0.001$), on both his PA ($p < 0.01$) and NA ($p < 0.05$) pairs for the limited forage phase as well as on his PA pair for phase 4 ($p < 0.05$). Binomial tests also indicated that Kongo performed above chance on his PA pair for phase 1 ($p < 0.05$). All other pairs for all of the gorillas were not above chance – with Pende performing at chance for all pairings (see Figure 5).

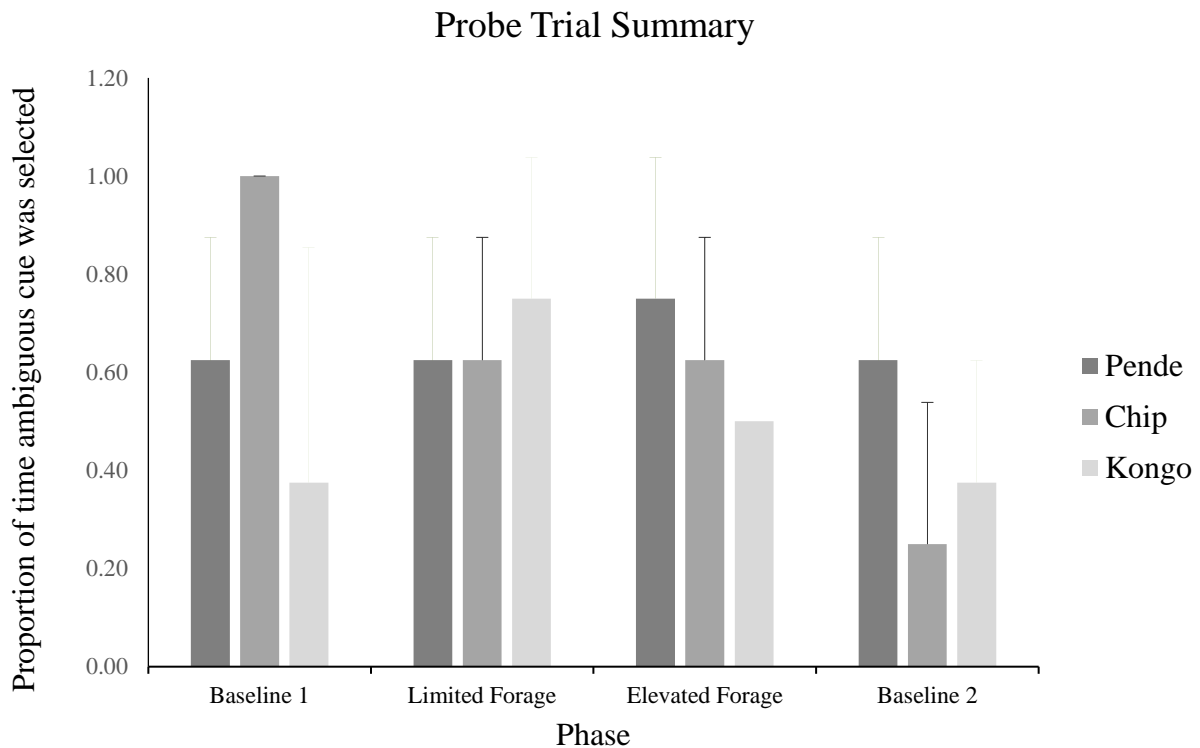


Figure 4. Proportion of trials on which ambiguous stimulus was selected on probe trials during each phase by each gorilla.

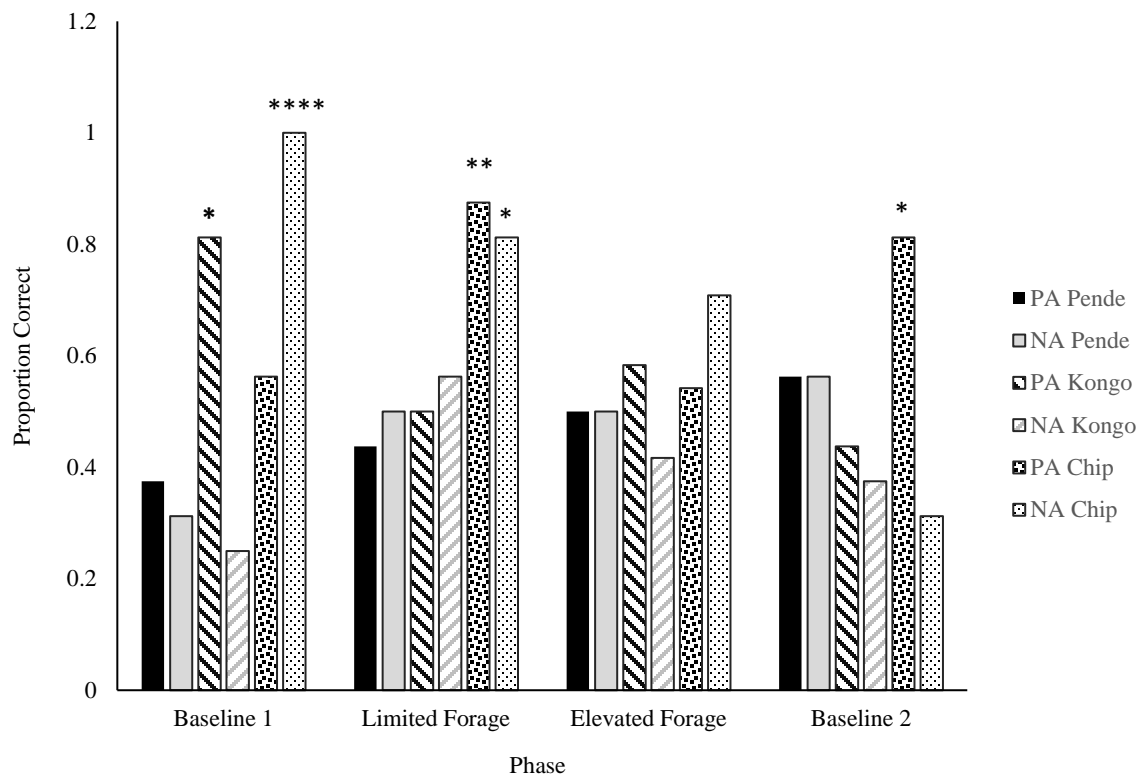


Figure 5. Proportion of trials on which the correct stimulus was chosen for pairs (NA and PA) across phases by gorilla (* $p < 0.05$, ** $p < 0.01$, **** $p < 0.001$).

When considering the training trials presented during testing, Pende failed to show a difference in learning on either PA or NA trials across phases (see Figure 4), but Kongo did display a trend of better learning of PA ($M = 81\%$) compared to NA trials ($M = 25\%$) in the baseline 1, and elevated forage phase (PA $M = 58\%$, NA $M = 42\%$) with no visible difference in the other two phases. Chip, on the other hand, displayed better performance on NA ($M = 100\%$) than PA ($M = 56\%$) in baseline 1, although there was some indication that this was a result of an inherent stimulus preference. Additionally, Chip displayed better performance on NA ($M = 71\%$) than PA ($M = 54\%$) in the elevated browse condition but the opposite pattern in baseline 2 (PA $M = 81\%$, NA $M = 31\%$). Thus, he may have either learned to attend to different cues by the end of testing, or been affected by his mood state.

Discussion

Unlike other species that have been trained on the ambiguous cue task, overall, the gorillas in this study failed to exhibit learning across the four phases. Across most phases and pairing types, the gorillas failed to perform above chance on the discriminations. Only Chip performed above chance on both pairings at any time during this study (during the limited forage phase). Aside from Chip's performance during the limited forage phase, there were only three other instances of above chance performance, one of which must be disregarded due to Chip's clear preference for the ambiguous stimulus (during baseline 1). In all, the gorillas reached above chance performance three times on PA pairings (Chip during limited forage and baseline 2; Kongo during baseline 1) and only once on an NA pairing (Chip during limited forage). The fact that they learned the PA pair on three separate occasions and the NA pair only once suggests that, like macaques (Fletcher & Woodruff, 1966) and unlike European starlings (Vasconcelos & Monteiro, 2014), gorillas may find it easier to learn the PA pairing compared to the NA pairing.

This paradigm has its challenges when it comes to assessing cognitive bias. Traditionally NA trials are learned much faster than PA trials (Vasconcelos & Monteiro, 2014) possibly due to the fact that the motivation to touch P conflicts with the motivation to touch A, whereas the motivation to avoid N would align with the motivation to touch A. Looking at the performance of the gorillas on the trained pairings (Figure 5) it is clear that the gorillas displayed significant variability in learning both between individuals and between the various sets of cues. When considering these differences there was not a clear pattern of learning (see also Boyer & Polidora, 1972). These differences were especially problematic in this study given the small sample size.

However, differential performance on NA and PA trials could provide some clues to overall optimism or pessimism. For example, faster learning of the NA pairings may indicate that the gorillas attended to which stimuli were reinforced, whereas faster learning of the PA pairings may indicate that the gorillas attended to which stimuli were not reinforced. A tendency to perform better on the PA pairing than the NA pairing could be interpreted as pessimism, as they may have been attending to non-reinforcement information. Unfortunately, as the gorillas displayed poor learning overall it is difficult to draw strong conclusions. With a longer training period it may be possible for trends in learning speed across the pairing types to be investigated further.

There are a few limitations to the current study that may explain the apparent null results. Most importantly, over the course of this study it became apparent that the duration of the phases (two weeks or approximately 60 sessions), while necessary at the time due to management and husbandry practices, was an insufficient amount of time for the gorillas to reach a level of performance indicative of having learned the discrimination before tests were presented. To put it in perspective, European starlings required approximately 6,500 trials to learn NA and PA pairs (Vasconcelos & Monteiro, 2014). In contrast, our gorillas completed approximately 600 trials for each phase. For future studies, we would recommend training to a set performance criterion before administering the test sessions in order to ensure that subjects have adequately learned the discrimination.

It is also possible that the group's social dynamics may have impacted the performance of the gorillas on a day to day basis. As a group of three young adult males, there may have been tension in the group as the three vied for dominance. Shifts in the social hierarchy may have influenced each individual's motivation to receive rewards in the study on a day to day basis. With only one presentation of each experimental phase, it is possible that the forage manipulation was confounded with possible changes in the gorillas' social dynamic during those time periods.

It is also possible, that with a sample size of three individuals, differences in personality may have had an impact on the results. It may be that individuals that display certain personality traits may be more inclined to react optimistically or pessimistically when faced with uncertainty. For instance, D'Ettorre et al. (2016) found that carpenter ants that displayed more exploratory activity (a trait they attributed to personality) also displayed negative judgment biases on a cognitive bias assessment compared to ants that were less explorative. It may be that the results in this case could have also been skewed by the personality traits of the gorillas, especially as there were only three individuals. It is possible that certain personality traits, such as boldness or shyness, may make an individual more or less willing to investigate novelty.

Additionally, as the gorillas were housed in a zoological park rather than a laboratory setting, there were constraints with regard to controlling their diets and testing intervals. It was not possible to food adjust the gorillas or to offer them more highly valued food items (due to dietary restrictions) as a means of increasing their motivation to obtain food. As a result, it is presumed that they may not have been motivated to perform at high levels of accuracy (although they always participated in the tasks). Another artifact of these gorillas living at a zoo and not in a laboratory setting is that it was not possible to completely ensure a total lack of environmental distractions. Measures were taken to minimize as many possible distractions as possible, such as separating the gorillas prior to testing and testing them in their off-exhibit enclosures, away from the public and from enrichment in their public enclosure. Even so, it was impossible to completely isolate the gorillas from the vocalizations of the other species that share the building (chimpanzees) or from visual and auditory contact with each other (their off-exhibit enclosures are separated by mesh doorways, which prevent physical contact but not visual or auditory contact).

Although there is potential for the ambiguous cue paradigm to be a useful tool for measuring cognitive bias given the time to learn the initial discrimination and the appropriate motivating forces, there are still several limitations inherent in the design such as the fact that the ambiguous stimulus can be presented for only a limited number of times before it loses its ambiguity for the subject. In this study, we attempted to minimize the risk of losing ambiguity by presenting probe trials only four times in a single phase. To further prevent learning and interference, we used unique sets of stimuli for each phase. However, this also posed a problem as each set required substantial training before the subject was able to pass criteria for learning.

These findings suggest that, if given adequate training, western lowland gorillas are capable of learning the ambiguous cue paradigm. Further, it may be possible to manipulate the ambiguous cue paradigm for use as a measure of cognitive bias. In this case, the individual differences in learning shown by the three gorillas prevented a clear assessment of cognitive bias across the phases, but, as can be seen in Figure 5, Chip was able to learn both the NA and PA pairings for the limited forage phase (the phase for which the gorillas displayed optimism). It is possible that the optimism displayed by the gorillas in the limited forage condition stemmed from a greater motivation to seek food rewards due to a lack of foraging opportunities in this phase. Unpublished behavioral data collected by the Detroit Zoological Society during this study suggest that increasing browse availability did have some positive impacts, such as a lack of regurgitation and reingestion, an undesirable behavior found in only captive gorillas (Lukas, 1999) in the elevated forage condition alone. This behavioral difference would also suggest that in the limited forage condition, the gorillas may have been especially motivated to seek out food and foraging opportunities.

Unexpected results are not uncommon in studies of cognitive bias. For instance, Briefer and McElligott (2013) found that goats previously housed in poor welfare conditions showed shorter latencies of approach (suggesting increased optimism) than the control group, which had experienced only good welfare conditions. These findings contradicted the authors' predictions, that goats with a history of neglect would display greater pessimism than their non-neglected counterparts. They interpreted these results as suggesting that the goats from the poor welfare conditions may have been experiencing positive cognitive biases due to relief from stress. Cognitive bias studies could be improved by using physiological or biological indicators alongside the behavioral indicators as a way to strengthen interpretations. For instance, Doyle, Fisher, Hinch, Boissy, and Lee (2010) demonstrated that release from a restraint resulted in a positive bias in sheep and they were able to verify their results through a combination of behavioral data as well as hormonal data (i.e., cortisol levels). During the course of this study, salivary and fecal cortisol samples were collected for analysis. The results of these hormonal studies are still pending but they may lend further insight into the effects of forage availability on the welfare of the gorillas (Fuller et al., 2015).

Cognitive bias testing is a useful measure of well-being as it allows researchers to tap into emotional valence (especially positive emotions that are often difficult to measure in animal species) as opposed to general arousal levels indicated by many of the existing behavioral and physiological measures of welfare (Mendl, Burman, Parker, & Paul, 2009). Yet even though cognitive bias has been closely correlated with reported subjective emotions in people (Mendl et al., 2009) and with other welfare measures in animals (Destrez, Deiss, Belzung, Lee, & Boissy, 2012; Mendl, Burman et al., 2010; Pomerantz et al., 2012), there are still potential problems inherent to cognitive bias paradigms. One of the fundamental issues with these tasks is that animal emotions may be very different from human emotions. Given this, researchers need to be careful in their interpretations of cognitive bias test results. Brydges and Braithwaite (2008) argue that researchers must recognize that even if animals perform similarly to their human counterparts under similar conditions, it does not necessarily follow that their experience is the same as a human's would be. Researchers must keep this in mind when interpreting their results, and they could strengthen their interpretations by incorporating some of the other measures of welfare (such as hormonal assays, measures of stereotypic behavior, or other behavioral measures etc.) into their experimental designs.

Future cognitive bias studies may benefit from focusing on newer methods of assessment that require less training. Recently, there has been success in assessing cognitive bias using reaction times alone (Bethell, Holmes, MacLarnon, & Semple, 2016). In this study, rhesus macaques were trained to touch a neutral stimulus, a grey square, on a touch-screen computer. Researchers then introduced either neutral

faces of unfamiliar macaques or threatening faces of unfamiliar macaques into the training stimulus during a testing phase. Researchers found that after having undergone veterinary procedures assumed to be aversive, that macaques were slower to touch the threatening faces compared to macaques that had not undergone these procedures. They interpreted this slowing of reaction time as an indicator of negative emotion; a form of “cognitive freezing.” Similarly, Allritz, Call, and Borkenau (2016) found that chimpanzees reacted more pessimistically (displaying slower response times) on a modified Stroop task after having undergone a recent anesthetization experience.

Testing novel methods for assessing cognitive biases is an important step in establishing methodology that will provide insight into the emotional states of nonverbal beings. Although the ambiguous cue paradigm may not have been the ideal assessment tool in the current setting, we would encourage researchers to continue to apply other tests of cognitive bias in combination with enrichment manipulations. Indeed, we are continuing to assess cognitive bias in gorillas using several unique techniques, which will contribute to knowledge of both the gorillas’ cognitive abilities and stability of cognitive biases.

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References

- Allritz, M., Call, J., & Borkenau, P. (2016). How chimpanzees (*Pan troglodytes*) perform in a modified emotional stroop task. *Animal Cognition*, *19*, 435–449.
- Bateson, M., Desire, S., Gartside, S. E., & Wright, G. A. (2011). Agitated honeybees exhibit pessimistic cognitive biases. *Current Biology*, *21*, 1070–1073. <http://doi.org/10.1016/j.cub.2011.05.017>
- Bateson, M., & Matheson, S. M. (2007). Performance on a categorisation task suggests that removal of environmental enrichment induces “pessimism” in captive European starlings (*Sturnus vulgaris*). *Animal Welfare*, *16*, 33–36.
- Bethell, E., Holmes, A., Maclarnon, A., & Semple, S. (2012). Cognitive bias in a non-human primate: Husbandry procedures influence cognitive indicators of psychological well-being in captive rhesus macaques. *Animal Welfare*, *21*, 185–195. <http://doi.org/10.7120/09627286.21.2.185>
- Bethell, E. J., Holmes, A., MacLarnon, A., & Semple, S. (2016). Emotion evaluation and response slowing in a non-human primate: New directions for cognitive bias measures of animal emotion? *Behavioral Sciences*, *6*, 2. doi:10.3390/bs6010002
- Boyer, W. N., & Polidora, V. J. (1972). An analysis of the solution of PAN ambiguous-cue problems by rhesus monkeys. *Learning and Motivation*, *3*, 325–333.
- Briefer, E. F., & McElligott, A. G. (2013). Rescued goats at a sanctuary display positive mood after former neglect. *Applied Animal Behaviour Science*, *146*, 45–55. doi.org/10.1016/j.applanim.2013.03.007
- Briefer Freymond, S., Briefer, E. F., Zollinger, A., Gindrat-von Allmen, Y., Wyss, C., & Bachmann, I. (2014). Behaviour of horses in a judgment bias test associated with positive or negative reinforcement. *Applied Animal Behaviour Science*, *158*, 34–45. doi.org/10.1016/j.applanim.2014.06.006
- Brilot, B. O., Asher, L., & Bateson, M. (2010). Stereotyping starlings are more “pessimistic.” *Animal Cognition*, *13*, 721–731. doi.org/10.1007/s10071-010-0323-z
- Brydges, N. M., & Braithwaite, V. A. (2008). Measuring animal welfare: What can cognition contribute? *Annual Review of Biomedical Sciences*, *10*, 91–103. doi.org/10.5016/1806-8774.2008.v10pT91
- Brydges, N. M., Leach, M., Nicol, K., Wright, R., & Bateson, M. (2011). Environmental enrichment induces optimistic cognitive bias in rats. *Animal Behaviour*, *81*, 169–175. doi.org/10.1016/j.anbehav.2010.09.030
- Burman, O., McGowan, R., Mendl, M., Norling, Y., Paul, E., ...Keeling, L. (2011). Using judgement bias to measure positive affective state in dogs. *Applied Animal Behaviour Science*, *132*, 160–168. doi.org/10.1016/j.applanim.2011.04.001
- Burman, O. H. P., Parker, R., Paul, E. S., & Mendl, M. (2008). A spatial judgement task to determine background

- emotional state in laboratory rats, *Rattus norvegicus*. *Animal Behaviour*, 76, 801–809. doi.org/10.1016/j.anbehav.2008.02.014
- Chapman, D. P., Whitfield, C. L., Felitti, V. J., Dube, S. R., Edwards, V. J., & Anda, R. F. (2004). Adverse childhood experiences and the risk of depressive disorders in adulthood. *Journal of Affective Disorders*, 82, 217–225. doi.org/10.1016/j.jad.2003.12.013
- D’Ettorre, P., Carere, C., Demora, L., Le Quinquis, P., Signorotti, L., & Bovet, D. (2016). Individual differences in exploratory activity relate to cognitive judgement bias in carpenter ants. *Behavioural Processes*, epub ahead of print. <http://dx.doi.org/10.1016/j.beproc.2016.09.008>
- Destrez, A., Deiss, V., Belzung, C., Lee, C., & Boissy, A. (2012). Does reduction of fearfulness tend to reduce pessimistic-like judgment in lambs? *Applied Animal Behaviour Science*, 139, 233–241. <http://doi.org/10.1016/j.applanim.2012.04.006>
- Douglas, C., Bateson, M., Walsh, C., Bédoué, A., & Edwards, S. A. (2012). Environmental enrichment induces optimistic cognitive biases in pigs. *Applied Animal Behaviour Science*, 139, 65–73. <http://doi.org/10.1016/j.applanim.2012.02.018>
- Doyle, R. E., Fisher, A. D., Hinch, G. N., Boissy, A., & Lee, C. (2010). Release from restraint generates a positive judgement bias in sheep. *Applied Animal Behaviour Science*, 122, 28–34. <http://doi.org/10.1016/j.applanim.2009.11.003>
- Doyle, R. E., Lee, C., Deiss, V., Fisher, A. D., Hinch, G. N., & Boissy, A. (2011). Measuring judgement bias and emotional reactivity in sheep following long-term exposure to unpredictable and aversive events. *Physiology & Behavior*, 102, 503–510. <http://doi.org/10.1016/j.physbeh.2011.01.001>
- Fletcher, H. J., & Woodruff, A. N. D. B. (1966). Monkeys’ performance on ambiguous-cue problems. *Perceptual and Motor Skills*, 22, 883–888.
- Fuller, G. A., Vonk, J., McGuire, M., Murray, A., & Allard, S. (2015). The influence of browse availability on behavior and cognitive bias in captive Western lowland gorillas (*Gorilla gorilla gorilla*). Conference Proceeding, *American Journal of Primatology*, 77, 139.
- Günther, V., Dannlowski, U., Kersting, A., & Suslow, T. (2015). Associations between childhood maltreatment and emotion processing biases in major depression: Results from a dot-probe task. *BMC Psychiatry*, 15, 123. <http://doi.org/10.1186/s12888-015-0501-2>
- Hallion, L. S., & Ruscio, A. M. (2011). A meta-analysis of the effect of cognitive bias modification on anxiety and depression. *Psychological Bulletin*, 137, 940–958. <http://doi.org/10.1037/a0024355>
- Harding, E. J., Paul, E. S., & Mendl, M. (2004). Animal behaviour: Cognitive bias and affective state. *Nature*, 427, 312.
- Katz, R., & Chauvin, R. (2016). Animal model and human depressive disorders animal models and human depressive disorders, 76, 34. [http://doi.org/10.1016/0149-7634\(81\)90004-X](http://doi.org/10.1016/0149-7634(81)90004-X)
- Kleim, B., Thörn, H. A., & Ehlert, U. (2014). Positive interpretation bias predicts well-being in medical interns. *Frontiers in Psychology*, 5, 6.
- Lukas, K. E. (1999). A review of nutritional and motivational factors contributing to the performance of regurgitation and reingestion in captive lowland gorillas *Gorilla gorilla gorilla*, *Applied Animal Behaviour Science*, 63, 237–249.
- Masi, S., Cipolletta, C., & Robbins, M. M. (2009). Western lowland gorillas (*Gorilla gorilla gorilla*) change their activity patterns in response to frugivory. *American Journal of Primatology*, 71, 91–100. <http://doi.org/10.1002/ajp.20629>
- Matheson, S. M., Asher, L., & Bateson, M. (2008). Larger, enriched cages are associated with “optimistic” response biases in captive European starlings (*Sturnus vulgaris*). *Applied Animal Behaviour Science*, 109, 374–383. <http://doi.org/10.1016/j.applanim.2007.03.007>
- Mendl, M., Brooks, J., Basse, C., Burman, O., Paul, E., ... Casey, R. (2010). Dogs showing separation-related behaviour exhibit a “pessimistic” cognitive bias. *Current Biology*, 20, R839–R840. <http://doi.org/10.1016/j.cub.2010.08.030>
- Mendl, M., Burman, O. H. P., Parker, R. M. A., & Paul, E. S. (2009). Cognitive bias as an indicator of animal emotion and welfare: Emerging evidence and underlying mechanisms. *Applied Animal Behaviour Science*, 118, 161–181. <http://doi.org/10.1016/j.applanim.2009.02.023>
- Mendl, M., Burman, O. H. P., & Paul, E. S. (2010). An integrative and functional framework for the study of animal emotion and mood. *Proceedings of the Royal Society B: Biological Sciences*, 277, 2895–2904. <http://doi.org/10.1098/rspb.2010.0303>
- Najm-Briscoe, R. G., Thomas, D. G., & Overton, S. (2000). The impact of stimulus ‘value’ in infant novelty preference. *Developmental Psychobiology*, 37, 176–185.

- Overstreet, D. H. (1993). The flinders sensitive line rats: A genetic animal model of depression. *Neuroscience and Biobehavioral Reviews*, *17*, 51–68.
- Parron, C., & Call, J. (2008). Behavioural responses to photographs by pictorially naïve baboons (*Papio anubis*), gorillas (*Gorilla gorilla*) and chimpanzees (*Pan troglodytes*), *78*, 351–357. <http://doi.org/10.1016/j.beproc.2008.01.019>
- Pomerantz, O., Terkel, J., & Suomi, S. J. (2012). Stereotypic head twirls, but not pacing, are related to a “pessimistic”-like judgment bias among captive tufted capuchins (*Cebus apella*), *Animal Cognition*, *15*, 689–698. <http://doi.org/10.1007/s10071-012-0497-7>
- Vasconcelos, M., & Monteiro, T. (2014). European starlings unriddle the ambiguous-cue problem. *Frontiers in Psychology*, *5*, 1–8. <http://doi.org/10.3389/fpsyg.2014.00944>
- Vonk, J., Torgerson-White, L., McGuire, M., Thueme, M., Thomas, J., & Beran, M. J. (2014). Quantity estimation and comparison in western lowland gorillas (*Gorilla gorilla gorilla*). *Animal Cognition*, *17*, 755–765. <http://doi.org/10.1007/s10071-013-0707-y>
- Widom, C. S., DuMont, K., & Czaja, S. J. (2007). A prospective investigation of major depressive disorder and comorbidity in abused and neglected children grown up. *Archives of General Psychiatry*, *64*, 49–56. <http://doi.org/10.1001/archpsyc.64.1.49>