ANIMAL BEHAVIOUR, 2008, **75**, 1793–1802
doi:10.1016/j.anbehav.2007.10.035

Perception of food amounts by chimpanzees based on the number, size, contour length and visibility of items

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(Received 16 May 2007; initial acceptance 14 July 2007; final acceptance 29 October 2007; published online 1 April 2008; MS. number: A10772R)

Nonhuman animals reliably select the largest of two or more sets of discrete items, particularly if those items are food items. However, many studies of these numerousness judgements fail to control for confounds between amount of food (e.g. mass or volume) and number of food items. Stimulus dimensions other than number of items also may influence how animals perceive sets and make choices. Four chimpanzees, *Pan troglodytes*, completed a variety of tasks that involved comparisons of food items (graham crackers) that varied in number, size and orientation. In experiment 1, chimpanzees chose between two alternative sets of visible cracker pieces. In experiment 2, the experimenters presented one set of crackers in a vertical orientation (stacked) and the other in a horizontal orientation. In experiment 3, the experimenters presented all food items one at a time by dropping them into opaque containers. Chimpanzees succeeded overall in choosing the largest amount of food. They did not rely on number or contour length as cues when making these judgements but instead primarily responded to the total amount of food in the sets. However, some errors reflected choices of the set with the smaller total amount of food but the individually largest single food item. Thus, responses were not optimal because of biases that were not related to the total amount of food in the sets.

Keywords: chimpanzee; numerosity; *Pan troglodytes*; perception; quantity judgement; representation

Many nonhuman animals perceive and respond to the quantitative properties of stimulus sets (e.g. Pepperberg 1994; Emmerton et al. 1997; Brannon & Terrace 2000; Roberts et al. 2000; Call 2000; Hauser et al. 2003; Beran & Beran 2004). In some cases, animals encode the ordinal properties of stimulus sets and make judgements between two or more sets on the basis of the quantity of stimuli in each set (e.g. Boysen et al. 1993; Olthof et al. 1997; Brannon & Terrace 2000; Biro & Matsuzawa 2001; Beran et al. 2005; Brannon et al. 2006; Pepperberg 2006). In nature, a variety of animals may use this capacity to choose among food patches composed of different quantities of food items, or to assess the relative quantity of allies and competitors in a potentially aggressive encounter (Wilson, et al. 2001; Kitchen 2004). Although the primates are well studied, crows (Smirnova et al. 2000), dogs (West & Young 2002; Ward & Smuts 2007), salamanders (Uller et al. 2003), lions (McComb et al. 1994), ferrets (Davis 1996), dolphins (Jaakkola et al. 2005) and fish (Agrillo et al. 2007) all make quantity judgements.

In the laboratory, animals are tested for these abilities in different situations. Some tests involve spontaneous judgements of quantity, while others involve trained responses. Typically, animals choose between alternative sets of food items or other naturally relevant stimuli (e.g. Rumbaugh et al. 1987; Hauser et al. 2000; Call 2000; Beran 2001, 2004; Uller et al. 2003). Often, in these scenarios, animals select the greater of two quantities, because they realize naturally that 'more' is better than 'less' (especially with respect to food items). Conversely, judgements between alternative sets of less naturally relevant stimuli (e.g. plastic blocks or digital arrays) require some degree of training, because animals have no inherent reason to discriminate between such items. However, when investigators train an animal to respond to arbitrary stimuli, they can control the rule that the animals must use to profit from a response (e.g. 'choose more', 'choose less', 'choose three'; Brannon & Terrace 2000; Judge et al. 2005; Beran 2007).

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0003–3472/08/$34.00/0

Depending on the test situation, the quantity judgement of interest may not necessarily be a numerical judgement. Several nonnumeric stimulus dimensions covary with number, and these include surface area, mass, volume, density or contour length (Davis & Perusse 1988; Clearfield & Mix 1999, 2001). For example, if an animal is given a choice between two sets of uniformly sized food items, the overall mass of food in each set will correlate with the number of individual items in each set. To investigate the use of number as the sole cue in quantity judgements, researchers use artificial stimulus arrays to control for other influential dimensions (e.g. Brannon & Terrace 2000; Judge et al. 2005; Beran 2007).

However, in scenarios in which stimulus sets are not controlled with regard to these nonnumeric properties, we do not know whether animals use number as a cue. After all, when animals choose between two food sources that are composed of different quantities of identical items, number and amount will correlate perfectly (e.g. Beran 2001, 2004). In this situation, we do not know whether the animal makes a quantity judgement based on the difference in number, the difference in some estimate of amount, or some combination of numeric and nonnumeric properties. Furthermore, we do not know how animals respond in spontaneous judgement tasks when number and one of these other properties conflict (e.g. in a situation in which one set of items is greater in number and, at the same time, smaller in overall amount than the other set). If the choice is between alternative sets of food items, animals should attend mostly to differential amount, because animals naturally prefer more food compared to less food. However, investigators have not thoroughly studied cues relevant to spontaneous quantity judgements of this type in the laboratory.

Contour length may contribute to judgements of quantity. Contour length is defined as the amount of edge or perimeter that is visible around an item, and this property sometimes plays a prominent role in the responses of children (e.g. Clearfield & Mix 1999, 2001; Feigenson et al. 2002). The contour length of a stimulus set is simply the contour length of every item in the set added together. When alternative sets contain different sized items, individual item size may also influence the responses of animals. Thus, we must account for these properties when we present nonhuman animals with choice tasks using discrete food items if we want to understand the basis for the responses made by animals.

We provided chimpanzees, *Pan troglodytes*, with several food-choice scenarios, in which number, contour length and amount (i.e. mass) varied systematically across trials. We tested how chimpanzees would respond when nonnumeric dimensions were presented in conflict with the numeric dimension. We presented chimpanzees with the choice between two sets of the same food (graham cracker pieces) across three experiments. In experiment 1 and experiment 2, we presented choices between static visible sets of different sized cracker pieces in both horizontal and vertical arrangements. In experiment 3, we provided the chimpanzees with similar choices between sets of cracker pieces, but we used a sequential presentation method (i.e. one-by-one addition of items to an opaque container). We hypothesized that the chimpanzees would respond on the basis of amount when amount, number and contour length were presented in conflict. However, we did not know how strongly each of these stimulus dimensions (contour length, number of items, size of items and the visibility of items) might contribute to chimpanzees' responding. Our hypothesis was that none of these other dimensions would strongly distract the chimpanzees from maximizing intake (i.e. using amount of food as a guide) given how well chimpanzees usually perform in comparing slight differences in food amount (e.g. Menzel 1961; Menzel & Davenport 1962). However, we expected that the number of food items and the presentation of individual food pieces that were larger than all other items in the two sets might slightly affect chimpanzees' ability to choose the larger amount of food.

We based our last prediction on data from a previous study in which chimpanzees showed an overall bias to point to sets of food items that had the larger individually sized items, even when those items were not in the set containing the larger amount of food (Boysen et al. 2001). This finding suggested that item size produced a strong response bias for chimpanzees. In addition, the first author of the present study (Beran) once observed a chimpanzee repeatedly choose to receive a whole banana instead of three halves of bananas, suggesting that individual element size might affect choice responding. In that case, the chimpanzee failed to maximize its intake because of this bias to choose the whole item. Thus, we wanted to assess whether presenting comparisons between alternative sets, in which items within each set could vary in size, would bias chimpanzees towards selecting the set with the largest individual item. We predicted that item size would contribute to responding.

EXPERIMENT 1: JUDGEMENTS OF VISIBLE AMOUNTS

Methods

Participants

Four chimpanzees, Lana (female, 35 years of age), Sherman (male, 32 years of age), Panzee (female, 20 years of age) and Mercury (male, 19 years of age) participated in the experiment. These chimpanzees had extensive testing histories in a variety of cognitive tasks including tests relevant to quantity judgement (e.g. Rumbaugh et al. 1987; Beran 2001, 2004; Beran & Beran 2004; Beran et al. 2005).

Apparatus

We positioned food arrays at opposite ends of a wooden bench (48 cm high, 67 cm wide and 36 cm deep). An experimenter pushed forward a shelf that was mounted on a drawer slide at the top of the bench. This movement presented both sets of food items to the chimpanzee at the same time.

Design and procedure

At the start of each trial, we placed an opaque barrier between the chimpanzee and the experimental apparatus.