

Comparison of discrete ratios by rhesus macaques (*Macaca mulatta*)

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Abstract Perceiving and comparing ratios are crucial skills for humans. Little is known about whether other animals can compare ratios. We trained two rhesus macaques (*Macaca mulatta*) to choose arrays that contained the greater ratio of positive to negative stimuli, regardless of the absolute number of stimuli in each of the two choice arrays. Subjects learned this task, and their performance generalized to novel ratios. Moreover, performance was modulated by the ratio between ratios; subjects responded more quickly and accurately when the ratio between ratios was higher. Control conditions ruled out the possibility that subjects were relying on surface area, although the ratio between ratios of surface area did seem to influence their choices. Our results demonstrate that rhesus monkeys can compare discrete ratios, demonstrating not only proportional reasoning ability but also the ability to reason about relations between relations.

Keywords Ratios · Proportion · Numerical cognition · Rhesus macaques · Monkeys · Relations between relations

Introduction

We interpret proportions frequently in our everyday lives, such as when we are doubling a recipe, determining how much an item will cost after a discount, or computing a tip. We are also capable of comparing ratios. For instance, what is the relative generosity of a poverty-stricken mother of three who gives \$10 faithfully to a charity each Sunday versus a much wealthier member of the community who gives a little more money? Other typical situations calling on proportional reasoning include comparing the concentration of two solutions in a chemistry experiment or two batting averages of baseball players. Unfortunately, many children have trouble learning about proportions and their symbolic counterpart, fractions (Hartnett and Gelman 1998; Siegler et al. 2013). Thus, an important question is whether and how the mind represents proportions prior to formal education.

One way to address this issue is to investigate the proportional reasoning abilities of individuals in other cultures that lack formal education. Fontanari et al. (2014) tested various aspects of probabilistic cognition in preliterate and prenumerate adults from two indigenous Mayan groups. In one experiment, they asked participants to bet on which of two sets, each composed of a different ratio of winning to non-winning chips, was more likely to produce a winning chip. The Mayan adults tended to choose the set with a greater proportion of winning chips, even when the quantities were varied such that the correct set actually contained the smaller absolute number of winning chips. Those findings suggest that proportional reasoning does not depend on formal math education.

Another line of research has demonstrated that preverbal infants attend to proportion. Denison and Xu (2010) showed 12- to 14-month-old infants two cups: one with 40

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pink and 10 black lollipops, and the other with 10 pink and 40 black lollipops. The experimenter then drew a lollipop from each cup such that infants could not see its color, and placed it in another container. The majority of infants crawled to the container corresponding to the cup with the larger proportion of their preferred color. In a sequence of follow-up experiments, they ruled out a number of different heuristics that the infants might have used, such as preferring the cup with the greater absolute quantity of the preferred color, avoiding the cup with the greater absolute quantity of the non-preferred color, or attending only to whether each individual cup had more of the preferred or non-preferred color (Denison and Xu 2014). These studies demonstrate that infants behave in accordance with probabilistic expectations based on proportions.

Even younger babies appear to extract information about proportions from a visual display. After viewing habituation displays that contained yellow and blue shapes at a particular ratio, 6-month-old infants looked longer to displays that contained yellow and blue shapes with a novel ratio when the two ratios differed by a factor of two, but not when they differed by a factor of 1.5 (McCrink and Wynn 2007). These results indicate not only that preverbal infants are sensitive to ratios but also that their ability to discriminate between ratios depends on the difference between the ratios. Thus, Weber's law (see, e.g., Pica et al. 2004) well characterizes infants' ability to compare sets based on their ratio.

A variety of experimental paradigms have been used with non-human animals to test for proportional reasoning. When foraging competitively, birds and fish distribute themselves among patches according to the ratio of patch profitabilities (Harper 1982; Godin and Keenleyside 1984; Gallistel 1990). The rate of pecking in pigeons is proportional to the ratio of positive to negative items in a stimulus array (Honig and Stewart 1989, 1993; Emmerton 2001). Bonobos, chimpanzees, gorillas, and orangutans make statistical inferences based on proportions (Rakoczy et al. 2014). In that study, apes were shown two containers with mixtures of a preferred and non-preferred food item. An experimenter drew one item from each container and placed the items in opaque cups. When the apes were given a choice between the two opaque cups, individuals of all four ape species tested tended to choose the cup corresponding to the container with a more favorable ratio of preferred to non-preferred food items, even when the absolute quantities favored the other container (Rakoczy et al. 2014), see also Woodruff and Premack (1981).

Finally, Vallentin and Nieder (2008) demonstrated proportional reasoning in rhesus monkeys by training them to match pairs of lines based on the ratio of the two lines within each pair. Monkeys were shown a sample stimulus

composed of two lines. The ratio of the length of the lower line to the upper line was 1:4, 2:4, 3:4, or 4:4 during training, or 3:8 and 5:8 during testing. After a delay, the monkeys were shown a second pair of lines. They were to release a lever if the ratio of the length of the lower line to upper line was the same as during the sample, and to continue holding the lever if the ratio was different. Monkeys transferred to novel ratios and performed this task with accuracies similar to human subjects.

Here, we ask whether the proportional reasoning skills of rhesus monkeys extend beyond those demonstrated by Vallentin and Nieder (2008) in two ways. First, can monkeys decide which of two ratios is more favorable? Most real-world proportional decisions require a judgment to be made about which is greater or less, not about the equivalence or non-equivalence of two ratios. Second, can monkeys make this decision when stimuli are composed of discrete elements rather than continuous quantities?

Our research questions also touch upon another debate that has percolated in the field of animal cognition. How and when can animals reason about relations between relations? This capacity may be the foundation for analogical reasoning (Flemming and Washburn 2012). Some authors have argued that understanding second-order relations requires language (Premack 1983) and may be an ability unique to great apes (Thompson and Oden 2000) or humans (Penn et al. 2008). However, there are reports that other species, including monkeys and birds, succeed at relational matching-to-sample tasks: They can categorize individual arrays as containing all-same or all-different elements and then report whether the types of arrays are the same (both all-same or both all-different) or different (one all-same and the other all-different) (Cook and Wasserman 2007; Flemming et al. 2008, 2011; Truppa et al. 2011; Fagot and Maugard 2013; Smirnova et al. 2015). Similarly, when comparing two ratios, subjects must apprehend the first-order relation between elements within each stimulus array, as well as the second-order relation between the ratios in the two arrays. Determining which of two arrays has the more favorable ratio is therefore an example of understanding relations between relations.

We presented monkeys with two arrays that were each composed of S+ (positive rewarded stimulus) and S− (negative rewarded stimulus) items. We rewarded the monkeys for selecting the array with the higher ratio of S+ to S− items. Following training, we tested monkeys on probe trials with novel numerosities and novel ratios between the ratios in each array. Finally, we tested the monkeys on a variety of control conditions to tease out the relative contributions of numerosity and surface area on their decisions.

Methods

Subjects and housing

Subjects were two adult female rhesus macaques (*Macaca mulatta*, Monkey B: 12 years old and Monkey C: 12 years old). Both subjects had previously been trained to use a touch screen and had participated in a study on magnitude bisection. They had also received minimal training on numerical matching and ordering. They were pair-housed together in a vivarium at Duke University and were separated each day to participate in the experiment. Fresh fruit and Purina monkey chow were provided daily, and additional treats such as dried fruit or nuts were also provided daily. Water consumption was restricted during some periods of this study for unrelated experiments.

Apparatus

A 15-inch touch-sensitive computer monitor (Elo TouchSystems, Menlo Park, CA) and a food pellet reward delivery system (Med Associates, St. Albans, VT) were attached to the front of the subjects' home cage. Stimulus presentation, reward delivery, data collection, and data analysis were performed via custom-written programs in MATLAB (Mathworks, Natick, MA) with the Psychophysics Toolbox add-on (Brainard 1997; Kleiner et al. 2007) (<https://psychtoolbox.org>).

Training

Training progressed through two main phases: shape training and ratio training. In shape training, monkeys learned to associate one of two shapes (black circle and white diamond) with reward, making it S+ while the other shape was S−. For Monkey B, the black circle was S+ while the white diamond was S−, and for Monkey C these contingencies were reversed. During shape training, subjects initiated trials by touching a red rectangle at the bottom center of the screen (Fig. 1). The two shapes then appeared on a gray background, one on the left and one on the right side of the monitor (side randomized). If the subject touched S+, the screen turned the color of that shape for a 1-s inter-trial interval (ITI), a pleasant “ding” sound played, and a candy (either a mini Reese’s Pieces or a mini M&M) was delivered. If she touched S−, the screen turned the color of that shape for a 2-s ITI, a “buzz” sound played, and no candy was delivered. Each session consisted of at least 100 trials. The performance criterion to advance from shape training to ratio training was 80 % accuracy (selecting S+ on at least 80 % of trials) in a single session.

Ratio training was designed to train the monkeys to select the array that had a more favorable ratio of S+ to S−. Monkeys were presented with two intermixed arrays of S+ and S− items with a red circle surrounding each array (Fig. 2). All items had the same width and height. The physical arrangement of S+ and S− items within each red circle was trial-unique and randomly generated such that exact stimulus configurations could not be memorized. The side on which the correct array was displayed was also determined randomly on each trial, with equal probability given to the left and the right. When the subject touched one of the arrays, the circle around that array turned blue for 0.25 s. If the subject chose the array with the higher ratio of S+ to S−, a “ding” sound played, the screen turned the color of the S+ for 1 s, and a candy was delivered. If she chose the array with the lower ratio, a “buzz” sound played, the screen turned the color of the S− for 2–5 s, and no candy was delivered.

We defined the ratio-of-ratios on a given trial as the ratio of S+ to S− on the correct side, divided by the ratio of S+ to S− on the incorrect side. During training, all trials had a ratio-of-ratios of 2 or 4 with 16 different absolute values, as given in Table 1. We constructed these sets such that on half of the trials, the array with the greater absolute numbers of S+ and S− (and thus the greater absolute number of items) was also the array with the greater ratio of S+ to S− (*congruent*), while on the other half of the trials, the greater absolute number of items occurred in the array with the lesser ratio of S+ to S− (*incongruent*). In this way, subjects could not perform above chance expectations if they relied on a strategy of choosing the array with the greater number of S+ . Instead, the structure required that monkeys consider the relative numbers of S+ to S−. A second consideration in stimulus control was to ensure that monkeys needed to compare ratios between the two arrays in order to perform successfully, rather than only considering a single array. Thus, in addition to *unfavorable–favorable* (UF) trials in which one array had more S− than S+ while the other had more S+ than S−, we also included *favorable–favorable* (FF) trials in which both arrays had a greater number of S+ than S− and *unfavorable–unfavorable* (UU) trials in which both arrays had a greater number of S− than S+. In this way, subjects could not be successful by examining just one array, deciding if there were more S+ than S− in that array, then choosing it if the decision were “yes” and choosing the other if the decision were “no.” This yielded a 2×3 design for training trial conditions: Each trial was either congruent or incongruent, and either UF, FF, or UU.

The relative frequency of each trial type within each session was varied according to subjects' performance (for example, including a larger proportion of any trial

Fig. 1 General task structure and shape training. Subjects started each trial by touching a *red rectangle* at the *bottom* of the screen (*left*). Then, the decision stimuli appeared (*middle*). If the subject chose S+ (in this case, the *black circle*), the screen changed *color* for a short inter-trial interval (*top-right*), a positive sound played, and a candy was delivered. If she chose S− (in this case, the *white diamond*), the screen changed *color* for a longer inter-trial interval (*bottom-right*), a negative sound played, and no candy was delivered (color figure online)

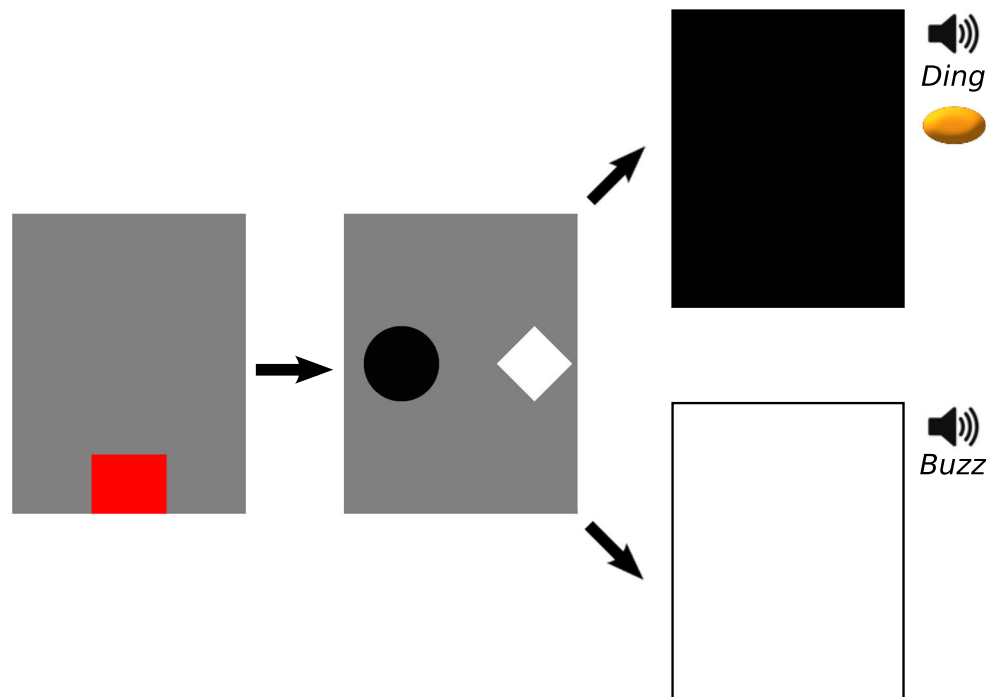


Fig. 2 Example stimuli presented during ratio training. In these examples, S+ is the *black circle*, and the correct array is on the *left*. One example pair of arrays is shown for each of the six congruence X favorability conditions (color figure online)

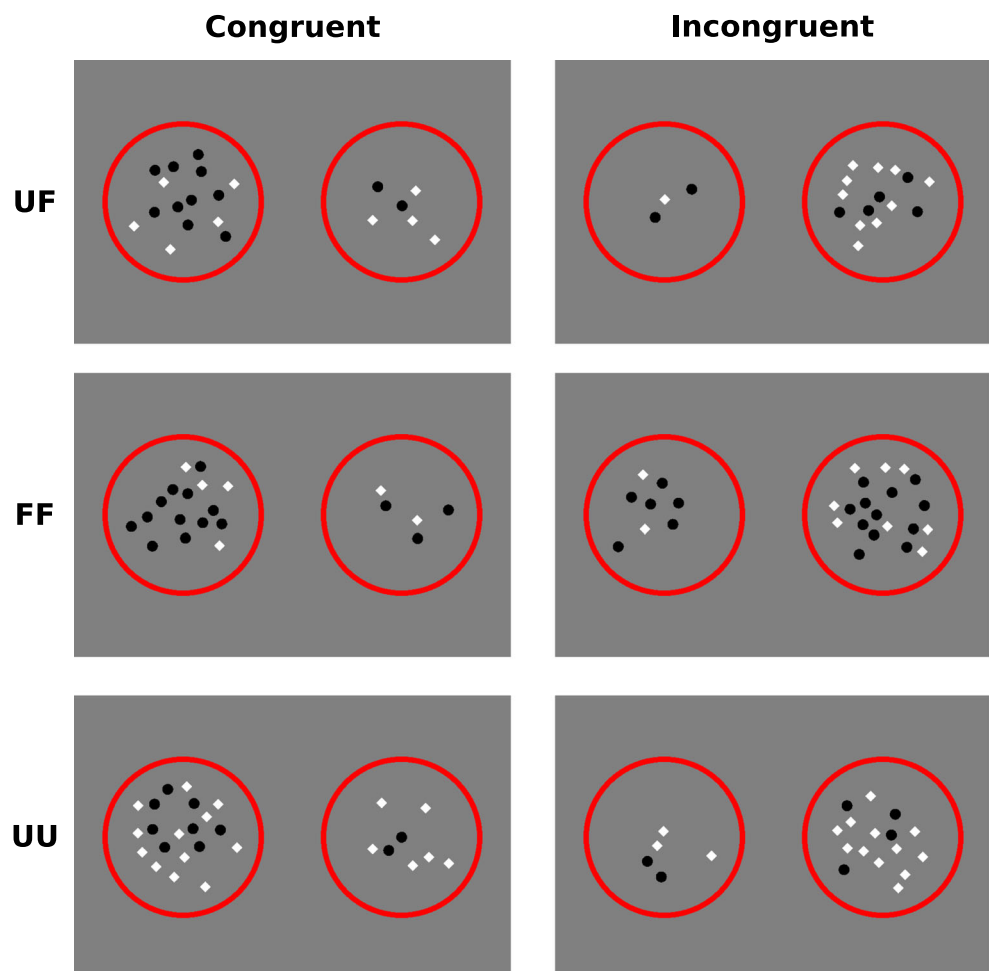


Table 1 Ratio training stimulus array numerosities

Correct, S+	Correct, S−	Incorrect, S+	Incorrect, S−	Congruence condition	Favorability condition	Ratio-of-ratios
8	4	1	2	Congruent	UF	4
10	5	2	4	Congruent	UF	4
16	8	3	6	Congruent	UF	4
18	9	4	8	Congruent	UF	4
18	6	6	4	Congruent	FF	2
12	4	3	2	Congruent	FF	2
6	9	1	3	Congruent	UU	2
8	12	2	6	Congruent	UU	2
2	1	5	10	Incongruent	UF	4
4	2	6	12	Incongruent	UF	4
6	3	9	18	Incongruent	UF	4
4	2	8	16	Incongruent	UF	4
3	1	9	6	Incongruent	FF	2
6	2	12	8	Incongruent	FF	2
4	6	6	18	Incongruent	UU	2
2	3	4	12	Incongruent	UU	2

type for which the monkey was not performing well) until the last 21 sessions, at which point each of the six trial types was presented with equal frequency in an order determined randomly each day. Each 120-trial training session was conducted on a separate day and lasted until the subject completed all trials or did not interact with the screen for 5 min. Training continued for approximately 180 days and accuracy surpassed 75 %.

Probe test session structure

Test sessions included standard trials, which were differentially reinforced and consisted of the training values described above ($n = 120$), and probe trials, which were non-differentially reinforced ($n = 32$ or 36). On probe trials, regardless of which array the subject selected, the positive sound, shorter ITI, and candy reinforcement were delivered. Thus, subjects could not learn which probe arrays were correct over the course of testing. Probe trials were randomly intermixed with standard (training) trials, except that the first 10 trials of every session were standard trials. Four different categories of probe trials were included in separate sessions, detailed below: numerical ratio-of-ratios, surface-area-only, numerosity-only, and surface area versus numerosity. We considered a test session complete if the subject completed at least 90 % of the trials, except for the final session of surface area versus numerosity testing, when a technical malfunction resulted in the presentation of only 104 total trials to each subject, which they both completed.

Numerical ratio-of-ratios probe trials

To test whether the monkeys would generalize what they had learned in training to stimulus arrays with novel numerosities and novel ratios-of-ratios among the numerosities, we introduced probe trials with each of six novel ratios-of-ratios: 1.5, 2.5, 3, 3.5, 6, and 10. We divided these into two stimulus sets (see Table 2) and ran five testing sessions with each stimulus set for each subject. Each session included two exemplars of each of the array sets in Table 2 (the correct array appeared on the left once and on the right once).

Control 1: surface-area-only

During training and numerical ratio-of-ratios probe trials, all S+ and S− items were the same size, such that total surface area covaried with numerosity. To test whether subjects were exclusively relying on the relative surface area of the S+ and S− items, we introduced probe trials in which monkeys were presented with a single S+ and a single S− on each side of the monitor as shown in Fig. 3. In this way, numerical ratio-of-ratios could not serve as a cue. Crucially, we varied the size of the shapes so that the ratio-of-ratios of total surface areas between the array with the more favorable ratio of surface area of the S+ to surface area of S− (the “correct” array) and the array with the less favorable ratio of surface areas (the “incorrect” array) was 1.5, 3, or 6, as given in Table 3. Each set of surface areas was presented twice in a session (the correct array appeared on the left once and on the right once), yielding

Table 2 Numerical ratio-of-ratios probe stimulus array numerosities

Correct, S+	Correct, S−	Incorrect, S+	Incorrect, S−	Congruence condition	Favorability condition	Ratio-of-ratios	Stimulus set
12	10	4	5	Congruent	UF	1.5	2
6	5	12	15	Incongruent	UF	1.5	2
15	6	5	3	Congruent	FF	1.5	2
5	2	10	6	Incongruent	FF	1.5	2
6	16	2	8	Congruent	UU	1.5	2
3	8	5	20	Incongruent	UU	1.5	2
28	8	7	5	Congruent	UF	2.5	2
21	6	21	15	Incongruent	UF	2.5	2
20	2	4	1	Congruent	FF	2.5	2
10	1	12	3	Incongruent	FF	2.5	2
10	22	2	11	Congruent	UU	2.5	2
5	11	6	33	Incongruent	UU	2.5	2
20	12	5	9	Congruent	UF	3	1
5	3	10	18	Incongruent	UF	3	1
14	4	7	6	Congruent	FF	3	1
7	2	14	12	Incongruent	FF	3	1
9	21	1	7	Congruent	UU	3	1
3	7	2	14	Incongruent	UU	3	1
21	15	4	10	Congruent	UF	3.5	2
7	5	8	20	Incongruent	UF	3.5	2
28	6	4	3	Congruent	FF	3.5	2
14	3	20	15	Incongruent	FF	3.5	2
14	22	2	11	Congruent	UU	3.5	2
7	11	4	22	Incongruent	UU	3.5	2
16	12	2	9	Congruent	UF	6	1
4	3	6	27	Incongruent	UF	6	1
27	3	6	4	Congruent	FF	6	1
9	1	12	8	Incongruent	FF	6	1
16	20	2	15	Congruent	UU	6	1
8	10	4	30	Incongruent	UU	6	1
24	6	2	5	Congruent	UF	10	1
4	1	6	15	Incongruent	UF	10	1
24	2	6	5	Congruent	FF	10	1
12	1	18	15	Incongruent	FF	10	1
15	21	1	14	Congruent	UU	10	1
5	7	2	28	Incongruent	UU	10	1

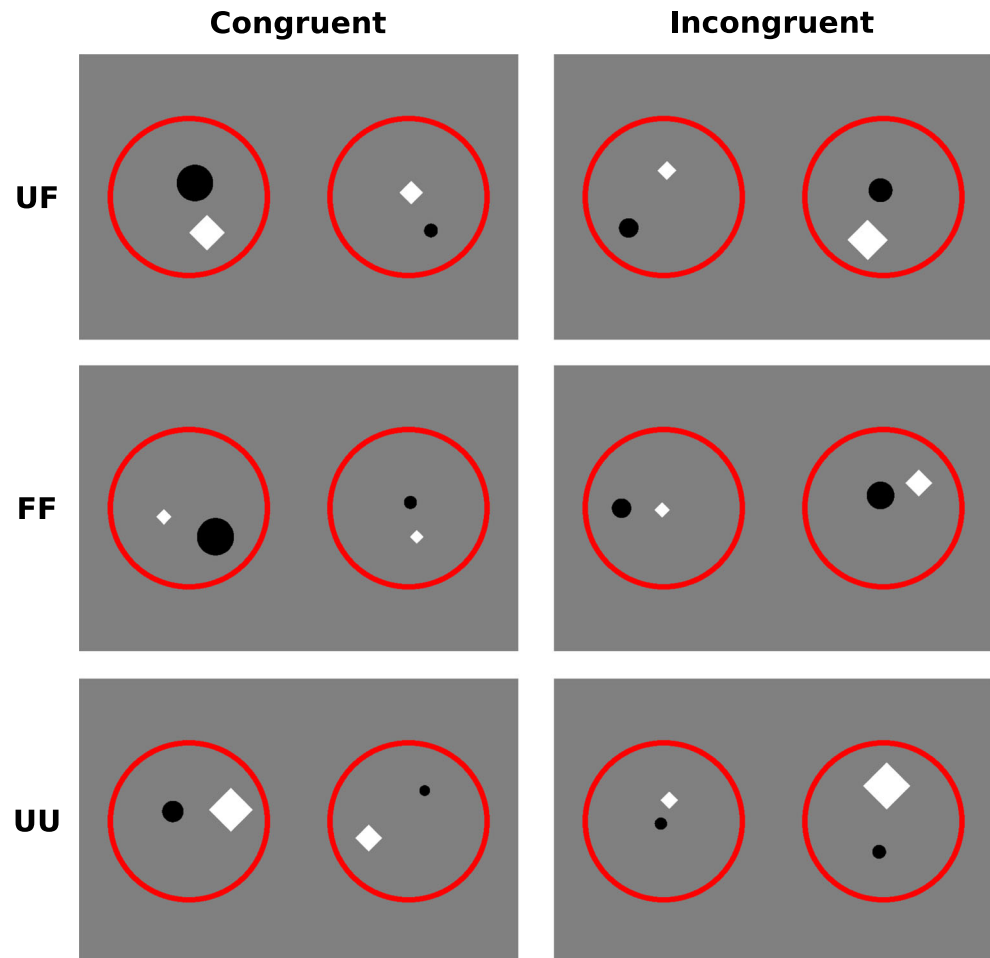
36 probe trials per session. Subjects were given three sessions of this control condition.

Control 2: numerosity-only

To test whether subjects would select the array with the greater numerical ratio-of-ratios in the absence of surface area cues, we introduced probe trials in which total surface area was equated for S+ and S− within each array and across the two arrays. Specifically, we

altered individual item size so that the total surface area of S+ on the correct side, total surface area of S− on the correct side, total surface area of S+ on the incorrect side, and total surface area of S− on the incorrect side were all equal (Fig. 4). Numerosities in these probe trials were the same as in training (see Table 1), with each numerosity set appearing twice in a session as a probe trial, yielding 32 probe trials per session. Subjects were given three sessions of this control condition.

Fig. 3 Example stimuli presented during surface-area-only probe testing. In these examples, S+ is the *black circle*, and the correct array is on the *left*. One example pair of arrays is shown for each of the six congruence X favorability conditions. *Note* that here congruence and favorability refer to surface area rather than numerosity



Control 3: surface area versus numerosity

To further investigate the potential contributions of numerosity and surface area in guiding subjects' decisions, we introduced probe trials in which numerical ratio-of-ratios and surface area ratio-of-ratios would lead to opposite choices. On these trials, the numerical ratio-of-ratios between the left and the right array was 4 (or 0.25), while the surface area ratio-of-ratios between the left and the right array was 0.25 (or 4, respectively) (Fig. 5). Thus, the array with the greater numerical ratio was the array with the lesser surface area ratio, and vice versa. We included six different numerical sets (one for each of the congruence X favorability categories; Table 4) and presented each one six times according to six different surface area sets (again, one for each of the congruence X favorability categories; Table 5), yielding 36 total probe trials, which were each presented once in a session. Subjects were given three sessions of this control condition.

Results

Shape training

Both subjects quickly learned to select S+. By the second training session, they each exceeded the 80 % accuracy criterion for advancing to ratio training.

Ratio training

Subjects successfully learned to perform the ratio comparison task over many training sessions (180 for Monkey C and 179 for Monkey B). Over the final 10 training sessions, during which each monkey completed all 120 trials per session, Monkey B had a mean accuracy of 82.4 % correct per session (SEM = 0.8 %), and Monkey C had a mean accuracy of 77.6 % correct per session (SEM = 1.4 %). Given a binomial distribution with a success probability of 50 %, a two-tailed *P* value of 0.05,

Table 3 Surface-area-only probe stimulus array surface areas (given in pixels)

Correct, S+	Correct, S−	Incorrect, S+	Incorrect, S−	Congruence condition	Favorability condition	Ratio-of-ratios
3000	2500	1200	1500	Congruent	UF	1.5
1200	1000	1600	2000	Incongruent	UF	1.5
2500	1000	1500	900	Congruent	FF	1.5
1000	400	2000	1200	Incongruent	FF	1.5
1200	3200	300	1200	Congruent	UU	1.5
600	1600	800	3200	Incongruent	UU	1.5
3500	2100	500	900	Congruent	UF	3
1000	600	1500	2700	Incongruent	UF	3
2800	800	700	600	Congruent	FF	3
1400	400	2100	1800	Incongruent	FF	3
1200	2800	300	2100	Congruent	UU	3
300	700	500	3500	Incongruent	UU	3
2000	1500	300	1350	Congruent	UF	6
600	450	800	3600	Incongruent	UF	6
3600	400	450	300	Congruent	FF	6
1800	200	2100	1400	Incongruent	FF	6
1600	2000	200	1500	Congruent	UU	6
400	500	500	3750	Incongruent	UU	6

and a 120-trial session, performance worse than 40.8 % or greater than 59.2 % exceeds chance expectations. Both subjects performed above that level on each of the final 21 days of training, when the six trial types were presented with equal frequency.

Numerical ratio-of-ratios testing

To determine whether subjects' decisions were based on ratio-of-ratios or instead whether they had memorized the training sets, we presented non-differentially reinforced trials with novel ratio-of-ratios values ("probe trials") mixed in with standard training trials that were differentially reinforced ("standard trials"). Subjects continued to perform above chance expectations on the standard trials during these test sessions (see Fig. 6; $P < 0.001$ for both binomial tests). Importantly, subjects also performed above chance expectations on probe trials with novel ratio-of-ratio values (mean = 83.5 %, SEM = 1.4 %, binomial $P < 0.0001$). This was true for each of the novel ratio-of-ratio values (see Fig. 6; $P < 0.001$ for all binomial tests).

As shown in Fig. 6, performance increased as the ratio-of-ratios increased. A generalized linear model (GzLM) following a binomial distribution predicting whether a given probe trial was correct from the four factors subject, ratio-of-ratios, congruence condition, and favorable condition confirmed that accuracy increased with the ratio-of-ratios and thus followed Weber's law (beta weight for ratio-of-ratios: 0.244, $P < 0.0001$). The overall model was

significantly different from the constant model ($\chi^2_{709} = 116$, $P < 0.0001$). There was a marginal effect of subject ($\beta = -0.417$, $P = 0.0614$), due to the fact that Monkey C (mean = 81.1 %, SEM = 2.1 %) was less accurate than Monkey B (mean = 85.9 %, SEM = 1.9 %). There was an effect of congruency ($\beta = 1.65$, $P < 0.0001$), indicating that subjects performed better on congruent (mean = 92.7 %, SEM = 1.4 %) than incongruent (mean = 74.3 %, SEM = 2.3 %) trials. Finally, there was an effect of favorability condition, with subjects performing best on UU trials (mean = 91.1 %, SEM = 1.9 %), slightly less well on UF trials (mean = 87.5 %, SEM = 2.1 %), and least well on FF trials (mean = 71.9 %, SEM = 2.9 %). The difference between UU and UF was significant ($\beta = -1.59$, $P < 0.0001$), as was the difference between UU and FF ($\beta = 1.17$, $P < 0.0001$), while the difference between UF and FF was not ($\beta = -0.845$, $P = 0.18$). Within each of these favorability categories, however, performance was still significantly above chance expectations ($P < 0.0001$ for all binomial tests).

In order to determine whether subjects selectively attended to certain aspects of the stimulus arrays—for instance, only looking at one side of the screen, or only taking S+ or S− into account—we fit a GzLM that predicted a left-side array choice based on the following factors: number of S+ on the left, number of S− on the left, number of S+ on the right, number of S− on the right, and subject. We found that each of the four quantities of

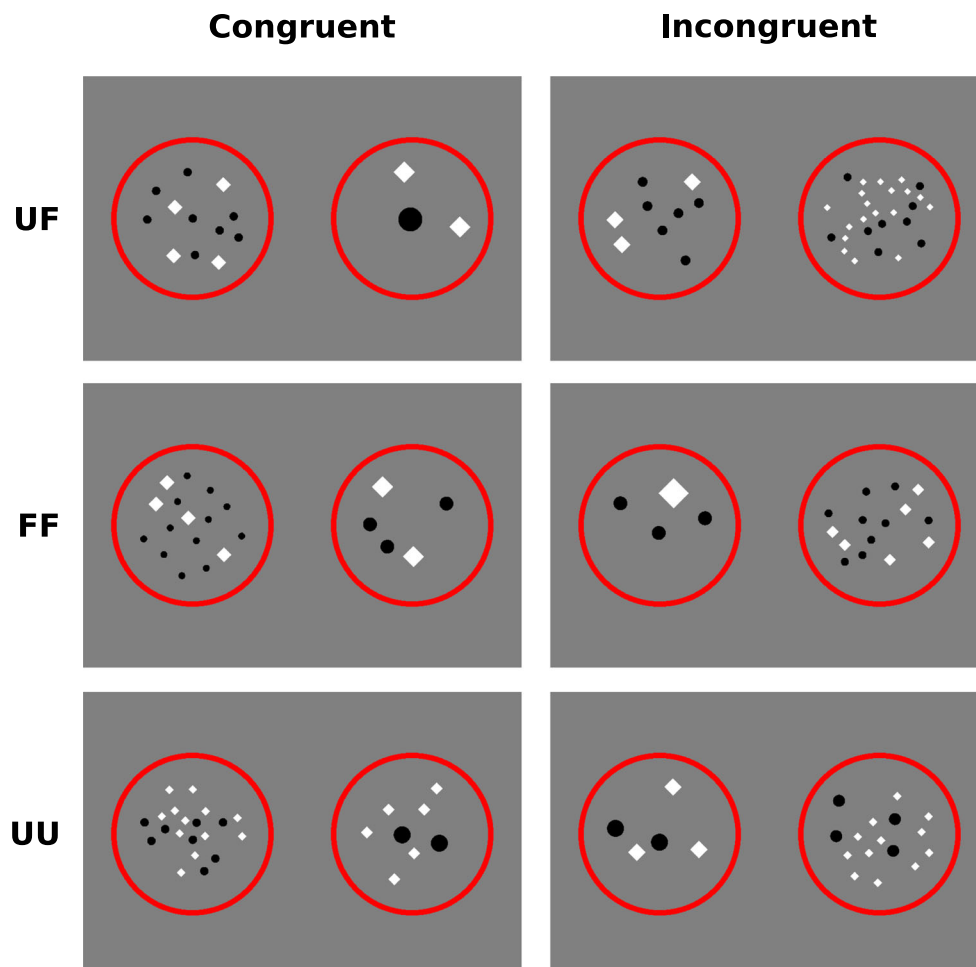


Fig. 4 Example stimuli presented during numerosity-only probe testing. In these examples, S+ is the black circle, and the correct array is on the left. One example pair of arrays is shown for each of the six congruence X favorability conditions

interest contributed significantly to the subjects' decisions (beta for number of S+ on the left: 0.342, $P < 0.0001$, β for number of S- on the left: -0.156, $P < 0.0001$, β for number of S+ on the right: -0.251, $P < 0.0001$, β for number of S- on the right: 0.142, $P < 0.0001$). The overall model was significantly different from the constant model ($\chi^2_{709} = 493$, $P < 0.0001$). There was no significant effect of subject ($\beta = 0.315$, $P = 0.16$). These results indicate that both subjects considered the relations between all the quantities on the screen when making their decisions.

Reaction time (RT) also decreased as ratio-of-ratios increased on probe trials (Fig. 7). A GzLM predicting RT from the factors subject, ratio-of-ratios, congruence condition, and favorable condition was fit to the data after all RTs that exceeded the 97.5th percentile (1.23 s, two standard deviations above the mean) were excluded. The overall model was significantly different from the constant model ($F_{690} = 24.6$, $P < 0.0001$). Each of the four factors had a significant effect on RT: subject ($\beta = -0.291$,

$P < 0.0001$), indicating that Monkey B (mean = 0.573 s, SEM = 0.008) responded more quickly overall than Monkey C (mean = 0.682 s, SEM = 0.010); ratio-of-ratios ($\beta = 0.011$, $P = 0.043$), indicating that RT decreased as ratio-of-ratios increased (note that beta weight sign is opposite to the direction of the effect due to the use of a gamma distribution with a reciprocal link function); congruence condition ($\beta = 0.091$, $P = 0.0031$), indicating that subjects responded more quickly on congruent (mean = 0.611 s, SEM = 0.009) than incongruent (mean = 0.648 s, SEM = 0.010) trials; and favorability condition (between UF and FF: $\beta = 0.140$, $P = 0.00015$; between UF and UU: $\beta = 0.153$, $P < 0.0001$; between UU and FF: $\beta = -0.013$, $P = 0.74$), indicating that subjects responded more quickly on UU trials (mean = 0.608, SEM = 0.011) and FF trials (mean = 0.612 s, SEM = 0.011) with no significant difference between them, and significantly more slowly on UF trials (mean = 0.670, SEM = 0.013). The finding that subjects responded more quickly to higher ratios-of-ratios even

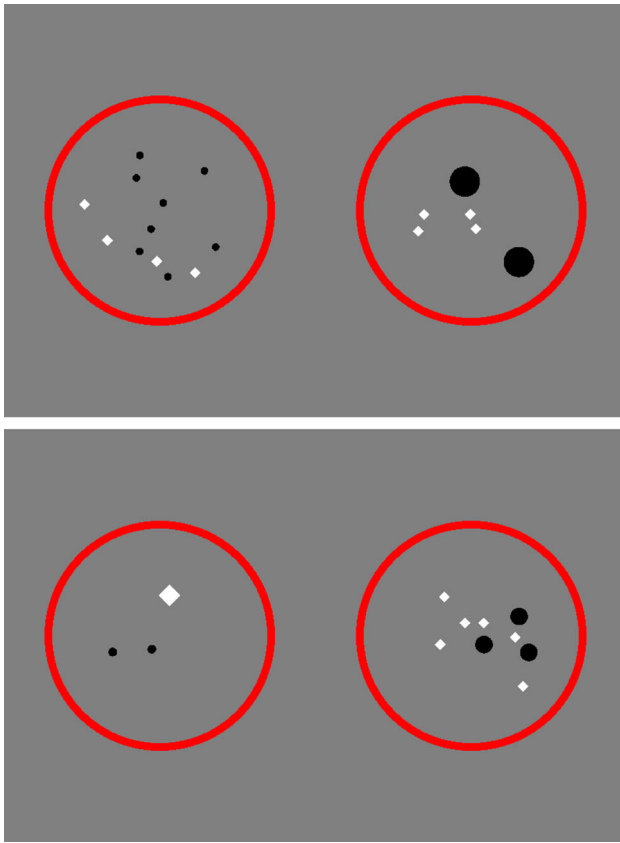


Fig. 5 Example stimuli presented during surface area versus numerosity probe testing. In these examples, S+ is the *black circle*, the array with the greater numerical ratio of S+ to S- is on the *left*, and the array with the greater surface area ratio of S+ to S- is on the *right*

when controlling for individual differences (subject) and the effects of congruence and favorability conditions supports the hypothesis that subjects attended to and made decisions based on ratio-of-ratios values, with their behavior conforming to Weber's law.

Control 1: surface-area-only

During training and numerical ratio-of-ratios testing, both S+ and S- items were held constant in size, such that the

ratio-of-ratios of total surface areas varied systematically with the ratio-of-ratios of numerosities. To determine the degree to which subjects relied on the ratio between total surface area of S+ to S- to make their decisions, we tested the monkeys in three control conditions described in the Methods. In the first of these, as shown in Fig. 3, we presented only one of each shape on each side so that the numerical ratio-of-ratios was 1 (i.e., 1:1/1:1). Crucially, we varied the size of each shape such that the surface area ratio-of-ratios were equal to 1.5, 3, or 6, which were values the monkeys succeeded at in the numerical ratio-of-ratio probes. If subjects used ratios of total surface area rather than numerosity, they should have chosen the side with the more favorable surface area ratio-of-ratios in these probe trials. However, subjects performed near the 50 % chance level on these trials. Monkeys chose the side with the more favorable surface area ratio-of-ratios on 49.5 % of trials (SEM = 3.5 %, binomial $P = 0.53$). This held true at each of the three surface area ratio-of-ratio values (see Fig. 8), with performance close to exceeding chance level only for the easiest ratio-of-ratios value of 6 (mean accuracy = 58.3 %, SEM = 5.9 %, binomial $P = 0.063$). A GzLM predicting whether a given probe trial was correct from the factors subject, surface area ratio-of-ratios, surface area congruence condition, and surface area favorability condition revealed that accuracy was modulated by surface area ratio-of-ratios ($\beta = 0.178$, $P = 0.034$) and congruence condition ($\beta = 1.67$, $P < 0.0001$), and by favorability condition (between UF and FF: $\beta = 0.848$, $P = 0.028$; between UF and UU: $\beta = 0.713$, $P = 0.064$; between UU and FF, $\beta = 0.135$, $P = 0.71$), but not by subject ($\beta = 0.329$, $P = 0.28$). The overall model was significantly different from the constant model ($\chi^2_{202} = 40.6$, $P < 0.0001$). RT was not significantly modulated by surface area ratio-of-ratios on these probe trials; a GzLM with factors subject, surface area ratio-of-ratios, surface area congruence condition, and surface area favorable condition revealed that none of these factors had a significant impact on RT: The model was not significantly different from the constant model ($F_{198} = 0.51$, $P = 0.77$, and all beta P 's > 0.1). These results indicate that subjects did not exclusively use total surface area ratio-of-ratios to guide

Table 4 Surface area versus numerosity probe stimulus array numerosities

Correct, S+	Correct, S-	Incorrect, S+	Incorrect, S-	Congruence condition	Favorability condition	Ratio-of-ratios
8	4	2	4	Congruent	UF	4
6	9	1	6	Congruent	UU	4
8	1	2	1	Congruent	FF	4
2	1	3	6	Incongruent	UF	4
2	3	2	12	Incongruent	UU	4
8	1	8	4	Incongruent	FF	4

Table 5 Surface area versus numerosity probe stimulus array surface areas, in pixels

Correct, S+	Correct, S−	Incorrect, S+	Incorrect, S−	Congruence condition	Favorability condition	Ratio-of-ratios
1200	600	200	400	Congruent	UF	4
800	1600	200	1600	Congruent	UU	4
2400	400	600	400	Congruent	FF	4
800	400	800	1600	Incongruent	UF	4
200	400	200	1600	Incongruent	UU	4
1200	200	1800	1200	Incongruent	FF	4

Here, “correct” refers to the array with the greater surface area ratio-of-ratios, and congruence and favorability conditions relate to surface area

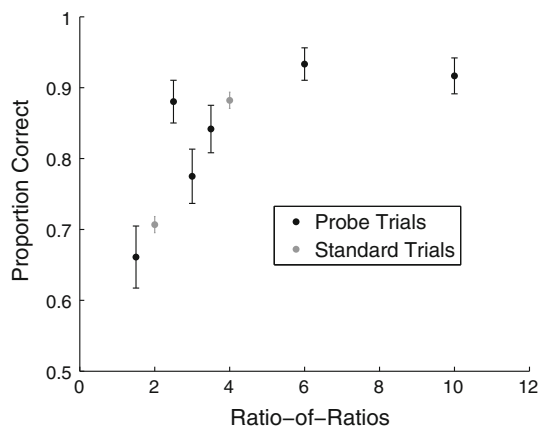


Fig. 6 Performance during numerical ratio-of-ratios testing. Error bars are standard error of the mean. Black points show the non-differentially reinforced probe trials; gray points show the differentially reinforced standard trials

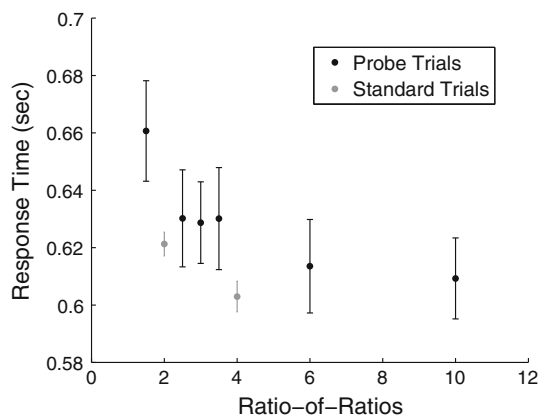


Fig. 7 Response time during numerical ratio-of-ratios testing. Error bars are standard error of the mean. Black points show the non-differentially reinforced probe trials; gray points show the differentially reinforced standard trials

their decisions during training or in the numerical ratio-of-ratios probe trials; however, the analysis also revealed some sensitivity to the surface area ratio-of-ratios.

Control 2: numerosity-only

To further explore the monkeys' use of numerical ratio-of-ratios versus other visual cues, we removed total surface area as a cue by equating the total surface area of each of the four sets of shapes such that surface area ratio-of-ratios was equal to 1 (see Fig. 4). The numerosities and numerical ratio-of-ratios were identical to those used in training and given in Table 1. Surprisingly, subjects were unsuccessful at these probe trials, choosing the correct numerical ratio-of-ratios on only 51.0 % of trials (SEM = 3.6 %, binomial $P = 0.36$). To assess whether individual item size controlled performance, we fit a GzLM predicting whether subjects chose the left-side array based on the following factors: radius of S+ on the left, radius of S− on the left, radius of S+ on the right, radius of S− on the right, and subject. We found that radius of S+ on the left ($\beta = 0.089$, $P = 0.045$) and on the right ($\beta = -0.108$, $P = 0.017$) was significant predictors of choosing the left side and that radius of S− on the left ($\beta = 0.074$, $P = 0.066$) was marginally significant, while radius of S− on the right ($\beta = -0.056$, $P = 0.21$) was not significant. There was no effect of subject ($\beta = -0.066$, $P = 0.23$). The overall model was significantly different from the constant model ($\chi^2_{186} = 51.7$, $P < 0.0001$). In a GzLM on response latency with the same factors, the overall model was again significantly different from the constant model ($F_{179} = 12.4$, $P < 0.0001$). There was a significant effect of subject ($\beta = -0.298$, $P < 0.0001$) and of S− radius on the left side ($\beta = -0.010$, $P = 0.049$; all other P 's > 0.1). These results suggest that subjects' decisions were strongly modulated by individual item size. Monkeys tended to choose the side with the larger individual shapes, particularly for the S+, though the trend was similar for S− (see Fig. 9). It is important to note that since all items had the same radius during training and numerical ratio-of-ratios probe testing, subjects could not have used this strategy in those conditions.

Fig. 8 Subjects' performance during surface-area-only probe trials. The *left plot* shows mean accuracy at each surface area ratio-of-ratios, and the *right plot* shows mean response time at each surface area ratio-of-ratios (*error bars* are standard error of the mean)

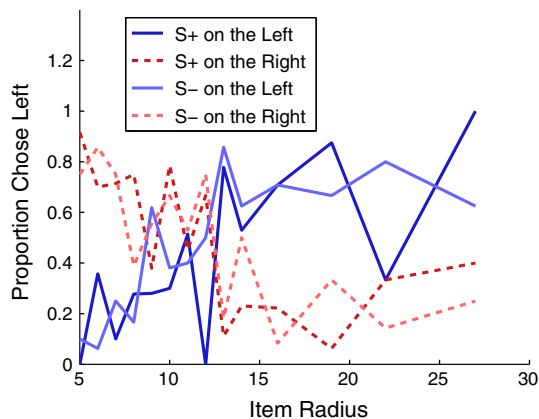
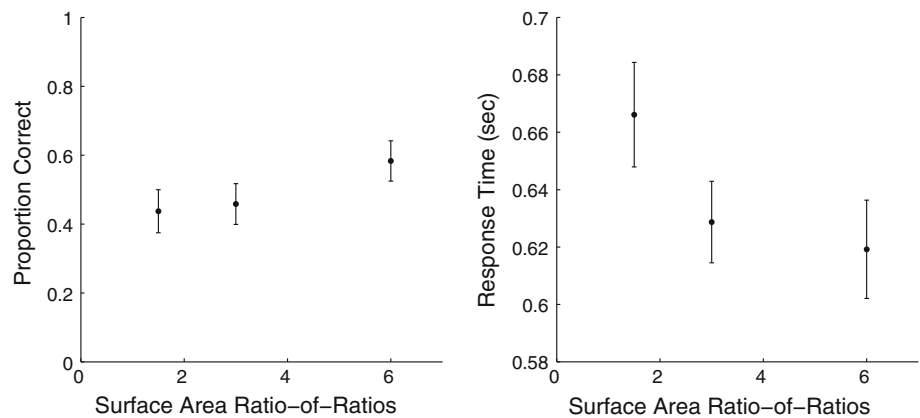


Fig. 9 Impact of individual item size on subjects' choices during numerosity-only probe trials. *Solid lines* represent items on the *left side*, and *dashed lines* represent items on the *right side*. *Darker shades* represent S+ and *lighter shades* represent S-. As item radius on the *left* increases for either S+ or S- (*solid lines*), the proportion of *leftward* choices increases. Conversely, as item radius on the *right* increases for either S+ or S- (*dashed lines*), the proportion of *leftward* choices decreases, and consequently the proportion of *rightward* choices increases

Control 3: surface area versus numerosity

In the final control condition, we directly pitted surface area and numerosity against each other. On probe trials, the numerical ratio-of-ratios between the left and right arrays was either 4 or 0.25, while the surface area ratio-of-ratios was 0.25 or 4, respectively. Thus, the side with the more favorable numerical ratio-of-ratios was also the side with the less favorable surface area ratio-of-ratios, and vice versa (see Fig. 5). In these probe trials, subjects chose the side with the more favorable surface area ratio-of-ratios on 59.5 % of trials (SEM = 3.5 %), which was significantly above chance level (binomial $P = 0.0032$). However, this performance still fell well below subjects' performance during numerical ratio-of-ratios probes where subjects could have used both numerosity and surface area (83.5 %, $\chi^2 = 52.1$, $P < 0.0001$), suggesting that they were not solely using surface area ratio-of-ratios during those trials. Moreover, performance was once again strongly modulated by item size, according to a GzLM predicting a left-side array choice from the factors subject ($\beta = -0.246$, $P = 0.61$), radius of S+ on the left ($\beta = 0.32$, $P < 0.0001$), radius of S- on the left ($\beta = 0.145$, $P = 0.0002$), radius of S+ on the right ($\beta = -0.307$, $P < 0.0001$), and radius of S- on the right ($\beta = -0.184$, $P < 0.0001$). The model was significantly different from the constant model ($\chi^2_{189} = 141$, $P < 0.0001$). Together with the other control conditions, these results suggest that subjects' choices were influenced by changing item radius and total surface area, but also suggest that the monkeys did not solely rely on these factors during training or numerical ratio-of-ratios probe testing.

Discussion

The findings presented here demonstrate proportional reasoning abilities in rhesus macaques. First, we showed that monkeys could learn to choose between two intermixed arrays of positive and negative stimuli based on which array had a higher ratio of positive to negative stimuli. In novel, non-differentially reinforced probe trials, subjects continued to choose the more favorable array. Importantly, monkeys exhibited above chance performance even when the absolute quantity of positive stimuli was lower in the array with the higher ratio, showing that they were attending to relative quantity. Their performance improved as the ratio between ratios increased, indicating that ratio discrimination follows Weber's law.

Continued probe testing with controls for surface area, however, suggested that the monkeys relied on a combination of cues. The stimuli were discrete arrays of positive and negative items that were homogeneous in size, so numerical ratio and surface area ratio were confounded

throughout training and novel ratio-of-ratios probe testing. Thus, monkeys could have attended to numerical ratio-of-ratios, surface area ratio-of-ratios, or both. Our three control conditions reveal that subjects used both numerical and surface area cues and did not exclusively use one or the other. Specifically, monkeys failed to perform above chance expectations in the first control condition, which completely removed numerosity ratio-of-ratios as a potential choice dimension. This demonstrates that monkeys could not solve the problem when required to attend only to the surface area ratio-of-ratios and thus that they were unlikely to have been solely attending to the surface area ratio-of-ratios in training and probe testing. In the second control condition, when the stimuli were designed such that monkeys could not use the surface area ratio-of-ratios, they again performed poorly, suggesting that they were unable to attend to the pure numerosity ratio-of-ratios information. Moreover, there was also clear evidence that the size of the items influenced performance. Finally, in the third control condition when surface area and numerosity ratio-of-ratios were pitted against each other, monkeys showed a small but significant bias to use surface area over numerosity.

The data are consistent with the idea that surface area and number served as redundant cues and that the monkeys did not exclusively rely on either cue. This finding parallels data from infants in which the ordinal relationship between quantities was detected when surface area and numerosity were redundant cues but not when either dimension was presented in isolation (Suanda et al. 2008). Results in fish also suggest that providing multiple cues to magnitude—i.e., both number and continuous quantities like surface area—can facilitate performance in a numerosity comparison task (Agrillo et al. 2011). Indeed, continuous visual variables influence human adults' perception of non-symbolic number (DeWind et al. 2015; Gebuis and Reynvoet 2012a, b), perhaps because such variables are often confounded with numerosity in daily life. Thus, it may be unsurprising that monkeys integrated information from multiple sources to aid performance in our task.

The small bias exhibited by the monkeys for surface area over numerosity in the third control condition was unexpected in light of prior evidence that monkeys attend more to number than surface area during a match-to-sample task (Cantlon and Brannon 2007). It could be that it is more natural for animals to consider ratios of continuous quantities and magnitudes of discrete quantities. However, it is also possible that features of our experimental design—such as the order of the control conditions—produced the greater reliance on surface area we observed. Subjects may have learned to rely on or ignore certain cues during the numerosity-only and surface-area-only probe

trials which later influenced their performance during surface area versus numerosity testing.

An important point, however, is that the monkeys in our study were trained with stimuli that confounded number and surface area. It is an open question whether monkeys could make pure numerical ratio judgments if their initial training was with numerosity stimuli that controlled for surface area. However, training in our task already required many months, likely due to the complex nature of the stimuli in which many different features could have been relevant. Based on our findings, we would predict that monkeys could ultimately succeed at ratio comparison when surface area and other continuous visual variables are controlled during training, but such a task—made more difficult by removing helpful cues—may take even longer for them to learn.

Our study nevertheless demonstrates that monkeys are able to make decisions about ratios of visually discrete items, as opposed to continuous quantities like line length. This is the first time such a skill has been demonstrated in monkeys and thus extends prior work, showing that monkeys can make ratio judgments about continuous quantities (Vallentin and Nieder 2008; Hayden et al. 2010). The distinction between continuous and discrete quantities is important because children struggle with non-symbolic proportions involving discrete quantities more than they do with continuous quantities (Spinillo and Bryant 1999; Jeong et al. 2007; Boyer et al. 2008). One explanation for children's increased difficulty with discrete ratios is that learned explicit mathematical processes with whole numbers, such as counting, interfere with correct intuitive processes, such as relative visual comparison (Boyer et al. 2008; Thompson and Opfer 2008; Vamvakoussi 2015). Monkeys' success at comparing ratios of discrete items suggests that similar tasks can be solved by intuitive processes in humans. Moreover, accuracy in a non-symbolic fraction magnitude comparison task correlated with overall math achievement in fifth-grade children (Fazio et al. 2014). This evidence supports the notion that intuitive strategies should be encouraged while explicit strategies like counting should be discouraged when children are learning about discrete proportions and fractions.

Our results also demonstrate that rhesus macaques can reason about relations between relations. They made decisions based not only on the first-order relation between S+ and S− within each array, but also on the second-order relation between the ratios of S+ to S− in the two arrays. This finding adds to the recent literature that animals other than apes can reason analogically (Cook and Wasserman 2007; Flemming et al. 2008, 2011; Truppa et al. 2011; Fagot and Maugard 2013; Smirnova et al. 2015), and argues against the hypotheses that such skills require language or symbol training (Premack 1983; Thompson and

Oden 2000), or may be unique to humans (Penn et al. 2008). However, our results do not speak to whether monkeys can match relations, nor to whether they spontaneously reason analogically, as has been found in apes (Vonk 2003) and crows (Smirnova et al. 2015). Whether rhesus macaques identify relations between relations without explicit training remains an open question.

In conclusion, we demonstrate that rhesus macaques are able to compare arrays of discrete items based on the ratio of the items within each array, with performance following Weber's law. These findings extend prior work, demonstrating that rhesus monkeys can match ratios of continuous line lengths (Vallentin and Nieder 2008) and that human infants are sensitive to the equivalence or non-equivalence between arrays based on the ratios of discrete items (McCrink and Wynn 2007). Proportional reasoning clearly does not require language or formal education. An important question is how we can harness these primitive nonverbal capacities to facilitate proportional reasoning in children.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted. All procedures were approved by Duke University's Institutional Animal Care and Use Committee.

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