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Free-Ranging Rhesus Monkeys Spontaneously Individuate and Enumerate Small Numbers of Non-Solid Portions

Justin N. Wood, Marc D. Hauser, David D. Glynn, and David Barner

Harvard University
Abstract

Fundamental questions in cognitive science concern the origins and nature of the units that compose visual experience. Here, we investigate the capacity to individuate and store information about non-solid portions, asking in particular whether free-ranging rhesus monkeys (*Macaca mulatta*) quantify portions of a non-solid substance presented in discrete pouring actions. When presented with portions of carrot pieces poured from a cup into opaque boxes, rhesus picked the box with the greatest number of portions for comparisons of 1 vs. 2, 2 vs. 3, and 3 vs. 4, but not for comparisons of 4 vs. 5 and 3 vs. 6. Additional experiments indicate that rhesus based their decisions on both the number of portions and the total amount of food. These results show that the capacity to individuate non-solid portions is not unique to humans, and does not depend on structures of natural language. Further, the fact that rhesus’ ability to represent non-solid portions is constrained by the same 4-item limit typically ascribed to the system of parallel individuation that operates over solid objects suggests that the visual system recruits common working memory processes for retaining information about solid objects and non-solid portions. We discuss our results with respect to theories of visual processing, as well as to the role that the human language faculty may have played in both the evolution and development of quantification.
Introduction

Our visual experience consists of a wide range of different types of individuals, such as solid objects, collections of individuals, actions, events, and non-solid portions. Thus, fundamental questions in cognitive science concern the origins and nature of the capacities to individuate and store in memory information about different types of individuals. Here, in experiments with free-ranging rhesus monkeys, we investigate the evolutionary origins of the ability to individuate and retain information about non-solid portions.

More than two decades of research reveal that human infants and non-human animals individuate and represent bounded, cohesive objects and trace the numerical identity of represented objects over space and time (Kellman & Spelke, 1983; Munakata, Santos, O’Reilly, Hauser, & Spelke, 2000; Spelke, 1990; Spelke, Kestenbaum, Simons, & Wein, 1995; Van de Walle, Carey, & Prevor, 2000). Further, these non-linguistic animals can represent and track multiple objects simultaneously (Feigenson, Carey, & Hauser, 2002; Hauser, Carey, & Hauser, 2000; West & Young, 2002). In a forced-choice study, for instance, free-ranging rhesus monkeys (Macaca mulatta) watched as an experimenter sequentially added a different number of apple slices into each of two containers. Monkeys preferentially picked the container with more apple slices provided that each box contained 4 or fewer slices (e.g., success in comparisons of 1 vs. 2, 2 vs. 3, and 3 vs. 4, but failure in comparisons of 3 vs. 6, 4 vs. 8, and 3 vs. 8; Hauser et al., 2000). A similar pattern has been reported in studies of human infants, who exhibit an upper limit of 3 objects (e.g., Feigenson et al., 2002; Feigenson & Carey, 2005), and in studies of visual working memory and object based attention in human adults, who exhibit a set limit of 3–4 objects (e.g., Luck & Vogel, 1997; Pylyshyn & Storm, 1988).

This set limit of 3 or 4 objects, when coupled with studies of numerical representation in
rhesus (Brannon & Terrace, 1998; Flombaum, Junge, & Hauser, 2005), provides evidence that rhesus monkeys deploy at least two distinct mechanisms that represent quantity: (1) an approximate number system for computing the cardinal value of a set (where numerical discrimination is limited by the ratio between the quantities), and (2) a parallel individuation system\(^1\) for tracking individuals through space and time and storing information about those individuals, with a storage capacity of 4 items per set.

In striking contrast to these findings, human infants and non-human primates appear unable to quantify static piles of non-solid substances. In experiments using the expectancy violation looking-time method, for example, infants in the first year of life maintain representations of bounded, cohesive objects over occlusion, but fail to maintain representations of perceptually-identical non-cohesive collections (Chiang & Wynn, 2000) or piles of sand over occlusion (Huntley-Fenner, Carey, & Solimando, 2002). A similar pattern has been reported for adult, non-human primates (Santos, Barnes, Mahajan, & Blanco, submitted for publication). Brown lemurs (*Eulemur fulvus*) watched as an experimenter placed a pile of sand on a stage, concealed the pile with a screen, and then poured a second pile behind the screen. Lemurs did not look longer when the screen was removed to reveal 1 pile of sand (numerically inconsistent) compared to 2 piles of sand (numerically consistent), despite looking longer at numerically inconsistent trials in \(1 + 1\) events with cohesive objects.

Why do human infants and non-human primates fail to quantify and maintain representations of static non-solid piles? To a human adult, keeping track of quantities of non-solid portions seems trivial. For example, natural language supplies measure phrases or

\(^1\) We use “parallel individuation” to be consistent with the previous literature. However, a more appropriate term in the present context might be “parallel representation,” since we refer to the number of individuals that can be stored in working memory simultaneously, rather than to the number of individuals that can be individuated simultaneously.
classifiers (as in Chinese) to designate precise portions of nonsolid stuff (e.g., pile of/cup of/piece of rice). For instance, if rice is poured twice into one glass, we can say either that we have one glass of rice or two pours of rice, depending on the criteria used to individuate the portions. The criteria we use are not inherent to the rice, but are specified by the measure word we use. In certain cases, we can also use count syntax to designate individual portions. Expressions like a coffee or a chocolate refer to individual portions of stuff. Even very young children can quantify portions of novel non-solid stuff on the basis of number when the piles of stuff are labeled with count syntax (e.g., these are some blickets), but not when count syntax is absent (e.g., this is some blicket; Barner & Snedeker, 2005, 2006; see also Chierchia, 1998).

Thus, one possibility is that language is required for specifying portions when quantifying non-solid stuff, and that non-linguistic creatures are limited to individuating solid things with stable boundaries (Spelke, 1990). If specifically linguistic parameters are necessary, then pre-linguistic infants and non-linguistic animals should fail to quantify non-solid substances regardless of the experimental context. An alternative possibility is that the capacity to quantify non-solid portions is present in pre- and non-linguistic organisms and thus, depends on non-linguistic capacities, but is only observed in situations in which there are salient criteria for individuation.

Recent findings provide suggestive evidence for the second, non-linguistic account. In one set of studies, vanMarle and colleagues (vanMarle, Aw, McCrink, & Santos, 2006), asked whether capuchin monkeys (Cebus apella) discriminate between cups that have received different numbers of scoops of banana puree. In a within-subject design involving repeated presentations to the same sample of subjects, monkeys successfully chose the cup that received the greater number of scoops in contrasts of 1 vs. 4, 1 vs. 2, 2 vs. 3, and 3 vs. 4. These results are
significant, because they suggest that non-human animals can individuate and represent non-solid portions over occlusion. However, because subjects were only tested with comparisons involving small numbers (i.e. 1, 2, 3, and 4), the data cannot determine whether performance depended on mechanisms of parallel individuation, approximate number, or some other mechanism all together. To differentiate between these mechanisms, it is necessary to test subjects with numerical contrasts that are within and beyond the 4-item limit of parallel individuation. On a related note, each subject was tested in multiple trials, leaving unanswered whether, and by what mechanism, non-human animals spontaneously individuate, represent, and track non-solid portions in the absence of repeated test trials.\(^2\) Finally, the capuchins could have succeeded simply by choosing the container towards which the experimenter directed the greater amount of attention, without individuating or representing the non-solid portions at all. To control for this possibility, it would have been necessary to either equate the number of portions poured in each container or to add control actions, such as pouring nonfood items that, if recognized, should not enter into the computation.

The present study had three goals. First, we asked whether an Old World primate, the rhesus monkey, can spontaneously individuate portions of a non-solid substance defined by discrete pouring actions, maintain representations over occlusion, and choose the box with the most food (i.e. by number of pours, amount of substance, or some combination of these factors). One possibility is that the capacity to individuate portions of non-solid stuff is unique to humans,\(^2\) There is a trend in the existing literature that non-human subjects who are tested with multiple trials show the ratio limit of approximate number representation (Beran & Beran, 2004; Brannon & Terrace, 1998; Hauser, Tsao, Garcia, & Spelke, 2003; Lewis, Jaffe, & Brannon, 2005) whereas subjects that are tested with a single trial show the 4-item limit of parallel individuation (e.g., Hauser et al., 2000). One possibility is that subjects who are tested in multiple trials learn that more than one object will be presented in each trial and thus focus on the objects as belonging to sets. In contrast, subjects who are tested in a single trial cannot form an expectation of multiple objects and thus attempt to represent and track each individual object.
and relies on properties of natural language such as count syntax or measure words. Evidence that non-human animals can track individual portions when provided with external criteria for individuating them (e.g., pouring actions) would support the hypothesis that natural language is not responsible for this capacity, but merely makes it explicit. Second, we asked whether the pattern of performance observed in rhesus is consistent with the 3- to 4-item limit of parallel individuation (Hauser et al., 2000) observed for bounded objects. Finally, we examined whether rhesus base their decisions on number, total amount of food, or both.

**Experiment 1**

In Experiment 1, we adapted the forced-choice method used in previous studies with non-human animals (Beran, 2001; Hauser et al., 2000; Washburn & Rumbaugh, 1991) and human infants (Feigenson et al., 2002) to explore whether rhesus monkeys spontaneously individuate and quantify non-solid portions presented in discrete pouring actions. In this first experiment, we tested individuals with a comparison of 1 vs. 2 non-solid portions.

**Method**

**Subjects.** We conducted all of the present studies on free-ranging rhesus macaques (*M. mulatta*) living on the island of Cayo Santiago, Puerto Rico (Rawlings & Kessler, 1987). At present, the population consists of six social groups. Each individual can be identified by chest and leg tattoos, as well as by distinctive ear notches. We successfully tested 20 adult subjects in this experiment. Across all conditions, an average of 40% of all attempted trials were aborted; see below for criteria used to abort a trial.

**Design and procedure.** A single experimenter approached lone monkeys who were not engaged in any activities such as eating, grooming, or fighting, and stopped approximately 2–3 meters away. The experimenter then presented two large, opaque containers (12 in. in diameter,
10 in. in height), showing that they were empty, and simultaneously placed them on the ground, 2 m apart. The experimenter then removed a small transparent cup (5 in. in diameter, 3 in. in height) from a plastic bucket (11 in. in length, 8 in. in width, 10 in. in height), lowered the cup into the bucket, filled up the cup entirely with carrot pieces (.3 in. in length, width, and height), and then poured the food into one of the containers. All of the pours were sequential, each one taking approximately 2 s to complete. The presentation can be seen at http://www.people.fas.harvard.edu/~jnwood/. After the presentation, the experimenter stood up, turned 180°, and walked away (see Fig. 1). If the subject did not approach within 10 s, we aborted the trial. The experimenter ensured that the subject watched the entire presentation. Subjects were excluded from the final analysis if they (1) failed to look during the entire duration of the presentation (approximately 60% of aborts), (2) were distracted by another individual during the presentation or choice period (approximately 30% of aborts), or (3) moved away before the choice period began (approximately 10% of aborts). In parallel with prior work using

![Fig. 1. Sample frames from the subject’s point of view for the comparison of 1 vs. 2. The experimenter presents the opaque containers to the subject (Frame 1), and then sequentially pours two scoops of carrot pieces into one container (Frames 2–5). He then pours one scoop of carrot pieces into the other container (Frames 6–7) and walks away (Frame 8), allowing the subject to choose one of the two containers.](image-url)
the two-item forced choice method (Hauser et al., 2000; Santos, Hauser, & Spelke, 2001; Sulkowski & Hauser, 2001), we defined a choice as the first container approached and touched. The 2 m separation between the two containers forced subjects to pick one of the containers as opposed to approaching the mid-point in an attempt to feed from both at the same time; thus, there was no ambiguity in identifying the subject’s selection. We counterbalanced across subjects the container receiving the greater number of portions (larger number on the left or the right) and the order of presentation (larger number placed first or second). Each subject received only one trial, and thus all analyses are based on a between-subjects design. In previous studies, this method has produced consistent and reliable results with these subjects (Hauser et al., 2000; Santos et al., 2001; Sulkowski & Hauser, 2001).

**Results and discussion**

Based on approaches to the container receiving the greater number of portions, rhesus showed statistically significant discrimination for the 1 vs. 2 comparison (Fig. 2: 1 vs. 2 (16/20), \( p < .02 \), two-tailed sign test). Thus, rhesus successfully individuate and quantify non-solid portions when the units are presented in distinct pouring actions. This raises the possibility that human infants and non-human primates failed to quantify piles of non-solid substances in previous studies because subjects were unable to individuate the substances into countable units given the available information. Support for this claim comes from studies showing that when infants are presented with two non-solid portions on plates, which are then poured into separate containers, infants choose the container that received the greater quantity of food (vanmarle, 2004). Thus, both infants and the rhesus monkeys tested here represent non-solid portions presented in discrete pouring actions.
Fig. 2. Percentage of subjects choosing the greater number in Experiments 1 and 2. The dashed line indicates chance performance.

Experiment 2

To investigate whether performance depended on the system of parallel individuation (Feigenson et al., 2002; Hauser et al., 2000), we presented subjects with comparisons of 2 vs. 3, 3 vs. 4, 4 vs. 5, and 3 vs. 6 portions of carrot pieces. Previous studies reveal that, when tracking bounded, cohesive objects, rhesus monkeys successfully discriminate between comparisons of 2 vs. 3 and 3 vs. 4, but not 4 vs. 5 and 3 vs. 6 (Hauser et al., 2000). Thus, if rhesus represent non-solid portions using parallel individuation (Feigenson et al., 2002; Hauser et al., 2000), then they should succeed at comparisons of 2 vs. 3 and 3 vs. 4 and fail to discriminate between 4 vs. 5 and 3 vs. 6 as 5 and 6 fall outside the 4-item limit.

Method

The methods were identical to Experiment 1 except we tested subjects on comparisons of 2 vs. 3, 3 vs. 4, 4 vs. 5, and 3 vs. 6. Using a between-subjects design, we successfully tested a total of 120 male and female adult monkeys (20 subjects in each comparison).
Results and discussion

Rhesus approached the container with the greater number of portions and showed statistically significant discrimination for two contrasts (Fig. 2: 2 vs. 3 (15/20), $p < .05$, two-tailed sign test), and 3 vs. 4 (15/20, $p < .05$).

Rhesus’ performance in the smaller number comparisons (1 vs. 2: Experiment 1, 2 vs. 3, 3 vs. 4) differed from their performance when one of the sets exceeded the 4-item limit of parallel individuation: 4 vs. 5 (10/20) and 3 vs. 6 (14/20, $p = .12$).

Given the non-significant trend towards success for 3 vs. 6, we re-ran this condition as well as 2 vs. 3 to test for the stability of these patterns with a new set of subjects. If our subjects’ performance depends on the set-size limit of parallel individuation, then they should succeed in a comparison of 2 vs. 3 but not 3 vs. 6, even though the ratio in the former is less favorable.

Rhesus successfully chose the container with more pours in the comparison of 2 vs. 3 (15/20) but not 3 vs. 6 (9/20). Pooling across replicates, subjects picked the container with 3 pours over 2 pours in 30 out of 40 trials ($p < .005$), while picking the container with 6 pours over 3 pours in 23 out of 40 trials ($p = .43$). Subjects were more likely to choose the container receiving the larger number of portions in the 2 vs. 3 comparison relative to the 3 vs. 6 comparison $\chi^2(1) = 2.74, p = .049$ (one-tailed test, Fig. 3).

Pooling across the two conditions in which we failed to find successful discrimination (4 vs. 5 and 3 vs. 6), subjects tended to choose the container in which the food was last presented (41/60; $p < .01$, two-tailed sign test). This order effect was not observed for the other conditions (47/80, $p = .15$).
Fig. 3. Percentage of subjects choosing the greater number (Experiment 3a, 3b, and 3d) and the greater amount of food (Experiment 3c) in Experiment 3. All comparisons contained 20 subjects.

These results show that rhesus monkeys’ ability to spontaneously represent, track, and quantify non-solid portions reveals the 4-item limit of parallel individuation: subjects chose the container that received the greater number of non-solid portions only in comparisons in which each container received 4 portions or less (1 vs. 2, 2 vs. 3, 3 vs. 4, but not 4 vs. 5 or 3 vs. 6).

Representations of approximate number (see Dehaene & Changeux, 1993; Meck & Church, 1983; Xu & Spelke, 2000) cannot explain this pattern of results because performance did not depend on the ratio between the quantities. Rhesus chose at chance in the comparison of 3 vs. 6 despite succeeding with the less favorable ratios of 2 vs. 3 and 3 vs. 4. Based on this pattern, we suggest that rhesus tap the system of parallel individuation when quantifying and discriminating between portions of nonsolid substances, showing a set size limitation of 4; this account does not rule out the possibility that rhesus can discriminate between large numbers of
non-solid portions that exceed the 4-item limit (e.g., 6 vs. 12). Rhesus’ performance when comparing cohesive, bounded objects (Hauser et al., 2000) is identical to their performance when comparing the non-cohesive, unbounded portions presented here: with both types of entities, they successfully represent up to four individuals per set. This suggests that a common mechanism underlies performance in both tasks.

Although the results of Experiment 1 are consistent with the hypothesis that subjects represent and track non-solid portions, it is also possible that the upper limit found in this task reflects a limit in the number of pouring actions that can be represented simultaneously, independent of the non-solid portions presented in each action. This claim is consistent with studies showing that non-human primates, human infants, and human adults can retain about three actions in memory at one time (Wood, 2005; Wood, submitted for publication). Therefore, in Experiment 3 we ran four further conditions to explore the nature of the representations underlying rhesus’ behavior in Experiments 1 and 2.

**Experiment 3**

**Methods**

In each comparison we tested 20 subjects. The method was identical to Experiments 1 and 2 except in the following ways.

Experiment 3a was designed to test for continuous variables. In all of the conditions from Experiments 1 and 2 the amount of food was correlated with the number of portions placed in each container. Thus, rhesus might have based their decisions on either of these variables. Experiment 3a asked whether rhesus resolve comparisons of 1 vs. 2 when the total amount of food in the container that received 2 portions is equal to the amount of food in the container that received 1 portion. Rhesus saw the experimenter pour a full cup of food into one container and
two half-full cups of food (equal in total amount of food to the one full cup) into the other container. A small line on the cup marked when it was half full.

In Experiment 3b we asked whether the rhesus monkeys’ behavior in Experiments 1 and 2 was based on representations of non-solid portions or on representations of the number of pouring actions. If their response was based solely on the number of actions, then they should fail to distinguish between two portions that contain different amounts of non-solid material. In Experiment 3b, we presented rhesus with a comparison of 1 large portion (1 full cup) vs. 1 small portion (1/3 full cup). Subjects were only presented with one portion at a time; thus, to succeed in this task they would need to compare quantities stored in memory.

In Experiment 3c we controlled the number of actions directed towards each box, by presenting comparisons of 2 portions of carrot pieces versus 1 portion of carrot pieces and 1 portion of sand. If the pattern of responses observed in the previous conditions was based solely on the number of actions directed towards each box, independent of the properties of the presented portions, then we should fail to observe a selective preference to approach the box with more food portions. In parallel with prior work using solid objects (Hauser et al., 2000), this experiment sought to distinguish between discrimination based on actions as opposed to either actions and substances or substance kind alone.

Finally, one potential explanation of the results from Experiments 1 and 2 is that subjects perceived the non-solid portions as solid, bounded objects. That is, since the pouring cup was transparent, subjects may have created initial representations of solid, bounded, cup-shaped food objects and failed to update these representations as non-solid as they poured from the cup to the container. If so, this reduces the experiment to a replication of earlier work on solid, bounded pieces of apple (Hauser et al., 2000). To test for this possibility, we ran Experiment 3d, involving
only one modification to the method from Experiments 1 and 2: we used an opaque pouring cup as opposed to a transparent one. Under these conditions, subjects’ only experience with food occurred when the experimenter tilted the cup and began pouring the food into the test containers.

**Results and Discussion**

In Experiment 3a, rhesus reliably chose the container that received two portions over the one that received 1 portion with an equal volume (16/20; $p < .02$). This suggests that when the total amount of food is equated, rhesus base their decision on the number of portions in each container.

In Experiment 3b, 16 of the 20 subjects ($p < .02$) successfully chose the container that received the larger amount containing three times as many carrot pieces as the smaller portion. This suggests that rhesus represent the amount of food in each portion in addition to the number of pouring actions. While the number of portions may be used as a proxy for amount of food under conditions where total amount is not discriminable, it is abandoned when the amount of food in each container differ by a highly discriminable ratio (i.e. 1:3 ratio).

In Experiment 3c, 15 out of 20 subjects ($p < .05$) chose the container that received two portions of carrot pieces over one portion of carrot pieces and one portion of sand. This shows that performance in Experiment 1 was not based only on the number of pouring actions directed towards each box.

In Experiment 3d, 15 out of 20 subjects ($p < .05$) chose the container that received two portions from an opaque cup over one portion, showing that their performance in Experiment 1 did not depend on prior experience with the food in a resting (non-pouring) state.

In summary, our results show that for each of the two containers, rhesus can retain
information about up to 4 non-solid portions. Further, rhesus can perform at least two computations over those representations. When the total amount of food poured into each container is equal, rhesus base their decision on the number of portions. However, when the amount of food in each container differs by a highly discriminable ratio, as in Experiment 3b, rhesus base their decision on total amount. It is worth noting that the capacity to perform multiple computations over a set of representations in this sense might be a developmental achievement. For instance, although human infants can represent up to 3 objects per container, they base their decision entirely on the amount of food rather than on the number of food items in each container (Feigenson et al., 2002; Feigenson & Carey, 2005).

**General discussion**

The present studies explored whether, and by what mechanism, rhesus monkeys spontaneously individuate and quantify non-solid portions. Rhesus successfully chose the container that received more portions in comparisons of 1 vs. 2, 2 vs. 3, and 3 vs. 4. However, they failed to choose the container that received more portions in comparisons of 4 vs. 5 and 3 vs. 6. These data show that rhesus represent multiple non-solid portions simultaneously over occlusion, and that their performance is constrained by the same 4-item limit typically ascribed to object representation. This pattern provides evidence that the system of parallel individuation is capacity-limited, but capable of operating over a wide range of inputs. These results further suggest that within the constraints of the experimental methods we used, rhesus do not distinguish between solid objects and non-solid substances in the context of quantification. Rhesus monkeys do, however, distinguish between objects and substances in other ways, such as when reasoning about physical constraints and possible transformations of objects and substances (Santos & Hauser, 2002; Hauser, unpublished data). For example, when rhesus watch
as sand is poured behind an occluder onto a table with a hole in the middle (shown before occlusion), they look longer when the sand appears, magically, on top of the table, than below the table. Finally, rhesus differentiated portions containing carrot pieces and sand, showing that they were able to represent property/kind information bound to portions of non-solid substances. This is important, because it shows that kind representations can be bound to both object representations (Santos, Sulkowski, Spaepen, & Hauser, 2002; Webb & Santos, 2007) and substance representations in the absence of natural language.

It is of interest that rhesus can spontaneously represent the same number of unbounded, non-cohesive portions as bounded, cohesive objects (4 entities per set for both; Hauser et al., 2000), given results that human adults can track four discrete objects that move from one location to another, but fail to track four entities that “pour” from one location to another (vanMarle & Scholl, 2003). These results are consistent with the view that visual processing is composed of a series of capacity-limited operations (i.e., stimulus selection, stimulus identification, and memory storage), and that some factors influence these operations in different ways (see Alvarez & Cavanagh, 2005; Delvenne, 2005). The type of entity being processed (e.g., cohesive, bounded versus non-cohesive, unbounded) might be one of these factors. Stimulus selection picks out items in the visual field for attention and is primarily concerned with the spatial location of the items (which is critical for tracking tasks). From a visual perspective, this is precisely the way in which non-solid portions differ from bounded, cohesive objects. In motion, non-solid portions do not move in a connected and bounded way, but rather “extend and contract” from one position to another, making it difficult to assign a specific location to the non-solid portion. This ambiguity in location might overload the stimulus selection operation, leading to impairments in tracking non-solid portions (vanMarle & Scholl, 2003). Once the
portion is successfully selected, however, there is no reason to expect further operations, such as stimulus identification or memory storage, to be affected. In the present task subjects only tracked one non-solid portion at any given time, after which that entity was stored in memory. It is unlikely that stimulus selection reaches capacity under these circumstances, as it does when multiple portions need to be tracked simultaneously (vanMarle & Scholl, 2003). Rather, the present task more likely overloads memory storage, resulting in the 4-item limit found here and in previous studies using discrete objects (Hauser et al., 2000).

As mentioned in the introduction, prior to the work presented here, studies of pre-linguistic infants and non-linguistic primates suggested that subjects fail to quantify substances in contexts in which they readily quantify objects (Chiang & Wynn, 2000; Huntley-Fenner et al., 2002; Santos et al., submitted for publication). One interpretation of these results is that in the absence of linguistic operators that enable a distinction between mass and count nouns, or measure words like *piece* and *pile*, it is not possible to individuate non-solid portions. An alternative possibility, supported by the present studies, is that the failure to show quantification over portions results from methodologies that fail to make information for individuation sufficiently salient. Specifically, static piles of non-solid substances do not provide sufficient criteria for individuation for human infants and non-human primates. In contrast, the pouring actions presented here provide information that can be used to delineate individuals (see also vanmarle, 2004). On this view, non-linguistic animals, pre-linguistic infants, and linguistic adults are all capable of quantifying over portions of stuff, and do so in the absence of natural language. This view leaves intact the fact that adults use language to represent individuals, portions, and continuous quantities of stuff, but suggests that these representations may be grounded in distinctions that exist prior to language. For instance, the present studies show that rhesus store
non-solid portions in working memory as numerically distinct units, with a working memory capacity of about 4 units per set. Further, property information, such as amount of stuff, appears to be bound to these units. Thus, one role of language might be to explicitly select the type of information to be processed from the representations stored in working memory. When non-solid portions are presented in count syntax then numerical information is computed, whereas when non-solid portions are presented in mass syntax then amount information is computed. This claim is supported by studies showing that when presented with non-solid portions, 3-year-old children and adults quantify by number when the portions are presented in count syntax but by volume when the portions are presented in mass syntax (Barner & Snedeker, 2005, 2006).

Future studies will investigate how rhesus individuate non-solid portions on the basis of action information. For instance, is merely observing non-solid substances in a pouring state sufficient to maintain an enduring representation of an individual, or is individuation from action information transient, applying only when the portion is viewed in a pouring state and thus discarded when the portion is visible as a static pile? Previous research with human infants (Huntley-Fenner et al., 2002) and lemurs (Santos et al., submitted for publication) provides preliminary evidence for the latter possibility, because subjects do not notice a numerical mismatch when portions of non-solid substances are poured behind a screen into discrete piles. Thus, action information might only provide sufficient criteria for individuation when the non-solid portions are perceived exclusively in a pouring state, as in the present studies, but not when the portions are poured into visible stationary piles. Specifying the pattern of individuation will allow further explorations into the role of language in individuating non-solid substances; language, for instance, might allow observers to maintain enduring representations of non-solid individuals (thereby permitting inferences from numbers of pours to numbers of piles) through
the tagging of spatially defined static piles with count nouns, classifiers, and measure phrases.

In sum, our results show that although animals reason about perceptual units such as solid objects and non-solid portions in different ways, the visual system may nonetheless recruit common perceptual and cognitive processes for retaining information about these units. Thus, a complete description of a given capacity requires not only an understanding of how that capacity differs from other capacities, but also an understanding of how it is the same.
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References


Santos, L. R., Barnes, J. L., Mahajan, N., & Blanco, M. Enumeration of objects and substances in nonhuman primates: experiments with brown lemurs (*Eulemur fulvus*). Manuscript submitted for publication.


