Current Biology *18*, 1420–1425, September 23, 2008 ©2008 Elsevier Ltd All rights reserved DOI 10.1016/j.cub.2008.08.042

Report

Behavioral and Prefrontal Representation of Spatial Proportions in the Monkey

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Summary

Primate brains are equipped with evolutionarily old and dedicated neural circuits so that they can grasp absolute quantities, such as the number of items or the length of a line [1–8]. Absolute magnitude, however, is often not informative enough to guide decisions in conflicting social and foraging situations [9, 10] that require an assessment of quantity ratios. We report that rhesus monkeys can discriminate proportions (1:4, 2:4, 3:4, and 4:4) specified by bars differing in lengths and that they can do so at a precision comparable to that shown by humans; the monkeys thus demonstrate an abstract understanding of proportionality. Moreover, neurons in the lateral prefrontal cortex selectively responded to preferred proportions regardless of the exact physical appearance of the stimuli. These results support the hypothesis that nonhuman primates can judge proportions and utilize the underlying information in behaviorally relevant situations.

Results

Several behavioral studies have shown that humans and animals share an intrinsic understanding of numerical information. Innumerate adults [2, 6], human infants [11, 12], and animals [1, 4, 13, 14] can assess quantitative information without number symbols. Monkeys, for example, are able to judge absolute discrete quantities (such as numerosity) [1, 5, 13, 15, 16] as well as absolute continuous magnitude (e.g., length) [8]. This understanding of absolute quantity in human [17–19] and nonhuman primates [4, 5, 16, 20] is processed in fronto-parietal cortical networks. Neurons in the prefrontal and posterior parietal cortices are selectively tuned to abstract quantity, and the cellular response characteristics can explain basic psychophysical phenomena in dealing with them [8, 21, 22]. Although neurons in the fundus of the intraparietal sulcus convey numerosity earlier, PFC neurons operate on a higher level and integrate different sources of information to gain cognitive control [23, 24]. For instance, only PFC neurons establish long-term numerical associations and relate visual signs with numerical values [25]. This suggests that PFC neurons may primarily become engaged in situations in which not only absolute quantity but also relations between quantities have to be represented. So far, however, it remains unknown whether nonhuman primates understand proportions and, if so, where and how in the brain proportions might be represented.

Evidence from field studies has suggested that animals could use proportional reasoning to guide behavior [9]. For instance, mallards distribute themselves between resource patches in the ratio of the patch profitabilities in foraging situations [10]. Experiments in a controlled laboratory environment, however, were less successful at demonstrating an understanding of proportionality. When chimpanzees were tested on discriminating proportions in a match-to-sample protocol, they failed at this task, except for an ape that had received intensive language-like training [26]. Thus, it was concluded that prior practice with symbol-like labels might be a prerequisite to understanding abstract relations.

Behavior

To scrutinize the potential capability of nonhuman primates to grasp proportionality, we designed a proportion-discrimination task with controlled-quantity ratio stimuli and investigated the behavioral and neuronal representations of abstract relations between two quantities in rhesus macaques. We trained two rhesus monkeys to judge the length ratio (proportion) between two lines, a reference and a test line. They had to briefly memorize a sample proportion over a delay period and match it to the same length proportion shown in a subsequent display (Figure 1A). The length ratios between the test and reference lines were 1:4, 2:4, 3:4, and 4:4.

To determine whether the monkeys solved the task by judging proportionality rather than attending to the absolute length of either the reference or test line, we randomly varied the length of both lines (Figure 1B, upper panel, see Experimental Procedures). In addition, we used control stimuli that showed the same four proportions and in which, first, the reference line was constant while the test line changed in length (Figure 1B, middle panel) and, second, the test line length was constant but the length of the reference line varied (Figure 1B, lower panel). In any given session, the monkeys were confronted with all three (one standard and two control) proportion displays presented in a randomized order.

Monkeys made more errors when the proportions were adjacent and performed progressively better as the distance in proportion between two displays increased (distance effect), resulting in performance distributions that could be described with Gauss functions (Figure 2A). The average performance of both monkeys was 85.56% correct (monkey M, 86.69%; monkey H, 84.65%) and, thus, was significantly better than chance for all tested proportions and protocols (binomial test, $p < 0.001$) (Figure 2B). The monkeys readily generalized what they had learned and applied it to the control displays with similar performance (Figure 2B). This shows that the monkeys were indeed judging proportions.

To investigate whether the monkeys could apply what they had learned to novel stimuli, we occasionally introduced transfer tests (probability = 0.12, or two transfers in blocks of 17 trials) requiring the monkey to discriminate proportions 3:8 and 5:8, which it had never seen before. Because the animals were randomly rewarded for their responses in transfer tests, any learning of the "correct" response was impossible. Both monkeys reliably discriminated the novel proportions 3:8 and 5:8 (binomial test, $p < 0.001$) (Figure 2C). We fitted Gauss

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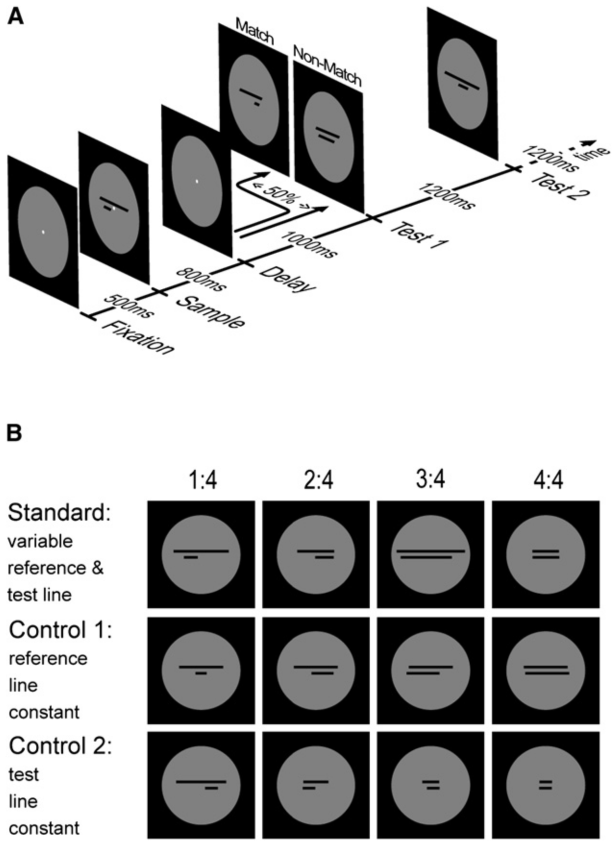

Figure 1. Task Protocol and Stimuli

(A) Delayed match-to-proportion task. To start a trial, the monkey had to grasp a lever and maintain fixation. If the sample and test display showed the same proportion, i.e., the same length ratio between a reference and test line, the monkey had to release the lever. The monkey had to continue holding the lever until the second test appeared (which was always a match) if the sample and test display showed different proportions (probability of match/nonmatch condition = 0.5).

(B) Stimulus examples for the standard protocol (upper panel) and the two control protocols (middle and bottom panels) showing the quantity ratios between the reference (upper line in each display) and the test line (lower line). The proportions were 1:4, 2:4, 3:4, and 4:4. The horizontal position of the reference line was constant, whereas the horizontal position of the test line varied across displays and trials. The edge of the test line could laterally exceed the reference line by up to 0.1° of visual angle so that symmetry was avoided. Moreover, the absolute line length of the reference line (and, consequently, that of the test line) varied considerably in the standard protocol (see Experimental Procedures). In "Control 1" stimuli, the length of the reference line was constant while the test line varied in length. Finally, the length of the test line was held constant, allowing the length of the reference line to change in the "Control 2" stimuli. We presented the different proportions in a pseudo-randomized fashion.

functions to the performance distributions and derived the standard deviation, sigma (σ), to quantify the discrimination precision. The σ values and thus the precisions for both the trained baseline proportions (1:4, 2:4, 3:4, and 4:4) and the transfer proportions (3:8 and 5:8) were comparable (Figure 2F), suggesting that the macaques had a conceptual understanding of length proportions.

In many domains of numerical competence, humans vastly outperform animals by using number symbols to precisely represent absolute or relational quantity. However, if the monkeys' discrimination of proportions constitutes a nonverbal (nonsymbolic) precursor of processing relational quantity, humans should show a similar behavior when simply estimating proportions. Therefore, we tested 18 human subjects with an identical protocol and explicitly avoided a verbalization of the proportions as number fractions. Supporting our hypothesis, the humans' nonverbal behavioral performance was only mildly better than the monkeys' performance (Figure 2E). On average, humans made 7% fewer errors when comparing sample proportions to nonmatch proportions (paired t test, $p < 0.05$), thus showing steeper flanks of the performance curves (Figures 2A and 2D). Humans also showed a distance effect (Figure 2D) with discriminating precision resembling that of monkeys (Figure 2E). The σ values as a measure of discrimination precision were comparable for both humans and monkeys (Figure 2F). The higher accuracy at both end points of the tested proportions (Figures 2B and 2E) might be attributed to a "guessing end effect" [27], which has also been observed for numerosity discriminations [16].

Single-Cell Responses in PFC

After having established that monkeys can discriminate spatial proportions, we investigated this capacity's neuronal underpinning and recorded from 526 randomly selected neurons of the prefrontal cortex (PFC) (Figures 3A and 3B) from both monkeys while they performed the proportion-discrimination task (Figure 1A). During sample presentation, many of the tested neurons (131/526, or 25 %) were significantly tuned only to proportion, irrespective of the absolute lengths of the test and reference bars (two-way ANOVA, with factors [sample proportion] × [stimulus protocol] $p < 0.01$; only main effect of proportion, no other significant effects or interactions). Each of the selective neurons preferred one of the four tested proportions. Neurons preferring 1:4 were most frequent (Figure 3C), possibly because 1:4 constitutes the fundamental proportion from which all higher proportions could be derived. A further 16 % (83/526) of the total set of recorded neurons were tuned to proportions during the sample period but additionally showed a significant protocol and/or interaction effect; those neurons were not regarded as pure proportion-selective cells and were excluded from further analysis.

In the delay during which the monkeys had to remember the length ratios, a similar fraction of only proportion-selective neurons (126/526, or 24 %) was found (only main effect of proportion, no other significant effects or interactions). Again, neurons preferring 1:4 were most frequent (Figure 3C). Nine percent of the total sample neurons (47/526) were tuned to proportions but additionally showed a significant protocol and/or interaction effect and, thus, were excluded. This indicates that most of the PFC neurons that showed a main effect in response to proportions generalized across changes in the exact appearance of the displays. Overall, we found 38 neurons that were proportion selective during both sample presentation and delay phase; typically, neural preference was similar for both epochs (Pearson's correlation coefficient, $r = 0.54$, $p < 0.001$). Proportion preferences of these 38 neurons (39% with preferred proportion 1:4; 16% with 2:4; 24% with 3:4; and 21% with 4:4) were almost identical to the overall frequency distribution of proportionality selective neurons (see Figure 3C).

Figures 3D–3G show the neuronal activity of four example neurons tuned to proportions in the sample (Figures 3D and 3E) and delay (Figures 3F and 3G) periods. The tuning function of the neuron in Figure 3D showed peak activity for the smallest proportion, 1:4, which was its preferred proportion, and a systematic drop-off of activity as the proportions in the

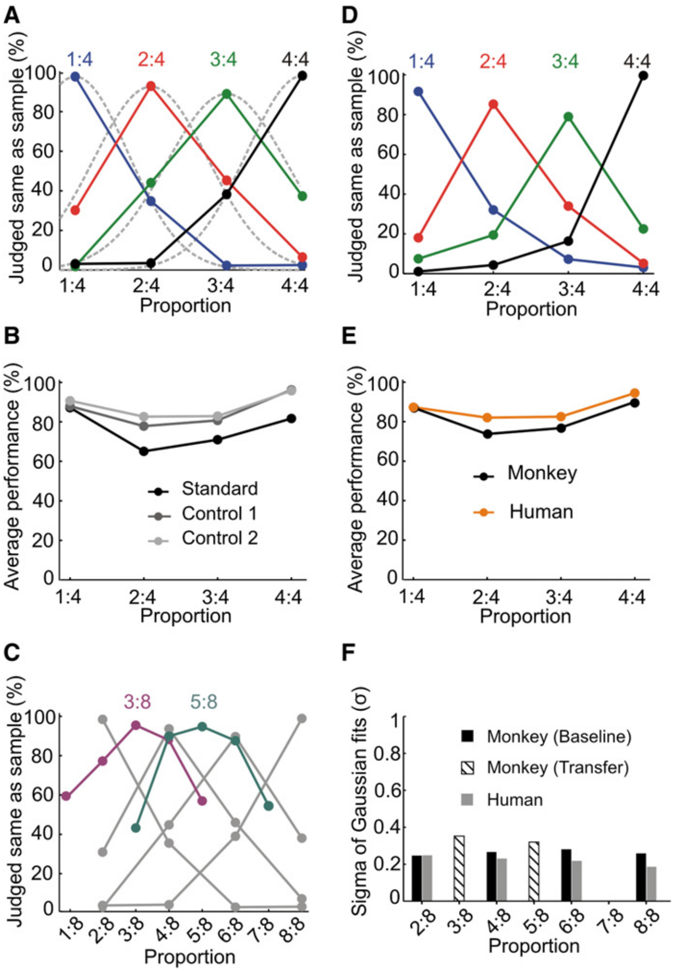

Figure 2. Behavioral Performance

(A) Behavioral performance averaged during the recording sessions and fitted with Gaussians (dotted gray lines). The functions indicate the percentage of trials in which a monkey judged displays in the test period as containing the same proportion as the sample display. The peak of each colored function indicates the correct performance in the match trials for the four sample proportions. The data points to the left and the right of the peak indicate the probability that the monkeys judged smaller or larger proportions as equal to the sample proportion. Each nonmatch data point (i.e., data points at the flanks of the peak functions) consists of a minimum of 955 and a maximum of 1386 trials.

(B) Average performance of both monkeys in the standard and control protocols. Chance = 50%.

(C) Monkeys' performance in transfer trials with novel proportions 3:8 and 5:8. Each nonmatch data point of transfer tests is based on at least 84 trials (maximum 94).

(D) Humans' proportion discrimination performance (minimum nonmatch trials, 72; maximum nonmatch trials, 84).

(E) Average performance of 18 humans and the two monkeys.

(F) Half-bandwidth (σ) of the Gaussian functions fitted to the behavioral performance curves for monkeys and humans.

sample period varied from the preferred value. This was true even if the visual appearance of the sample display changed substantially across standard and control protocols (see tuning functions in Figure 3D, bottom panel), indicating an abstract representation of the length ratio between the bars. A neuron with preferred sample proportion 2:4 is plotted in Figure 3E. Figures 3F and 3G illustrate two neurons tuned during the memory delay to preferred proportions 3:4 and 1:4.

Behavioral Relevance of Cellular Responses

To evaluate the proportion selectivity for the population of neurons, we averaged the normalized tuning curves for all neurons that preferred a given proportion. Neural activity formed overlapping tuning functions with progressively decaying activity as the distance from the preferred proportion increased (Figures 4A and 4B). The standard deviations (σ) of the Gauss fits were used as a measure of precision (Figures 4A and 4B, bottom panel). The standard deviations of both the performance functions and the neuronal tuning functions were almost constant across the tested proportions, suggesting that the neuronal tuning functions were the basis for behavioral discrimination. The overlapping neural tuning functions can explain the distance effect found in the behavioral tests because the ability of two proportions to be discriminated increases as the overlap between the tuning functions of neurons preferring the respective proportions decreases.

More direct evidence that the activity of proportion-selective neurons contributed to behavior came from an examination of error trials. When the monkeys made judgment errors, neuronal activity for the preferred proportion was significantly reduced, to 85% and 88% of that observed on correct trials (100 %) for the sample and delay periods, respectively (Wilcoxon signed-rank test, two-tailed, $p < 0.01$) (Figures 4C and 4D). The population tuning function, generated by normalizing the activity of each proportion-selective neuron and plotting its activity as a function of distance from its preferred proportion, was degraded on error trials.

Discussion

We investigated the behavioral and neuronal representations of proportions in rhesus monkeys trained to judge length ratios. We found that monkeys grasped the concept of proportionality, and their discrimination performance was comparable to the nonsymbolic capability of humans. Neurons in the monkeys' PFC encoded abstract proportions irrespective of varying sensory features of the stimulus, and the cells' activity was directly related to the monkeys' performance. Even if there is no direct evidence, these data suggest that the perception of relational quantity is represented by the same neural network and magnitude code as absolute quantity in the primate brain.

Our experiments in trained monkeys demonstrate that nonhuman primates (and probably other animals) can explicitly exploit ratios to guide behavior. Just as for numerosity or other absolute quantities, the representation of proportions is approximate and characterized by a distance effect. Interestingly, our human subjects who were prevented from using symbolic notations of fractions also showed a clear distance effect, almost identical to the one seen in nonhuman primates. Thus, humans without symbolic representations of fractions perform on par with nonhuman primates. The distance effect suggests a nonverbal capacity to operate with analog magnitude representations that have been demonstrated repeatedly in animals [1, 5, 8, 13, 21, 22] and innumerate humans [2, 6]. These striking qualitative and quantitative similarities between the performance of adult humans and that of monkeys indicate an evolutionarily ancient cognitive system for proportional understanding that is already present in preverbal infants [28] and little children [29–31]. This system approximates ratios

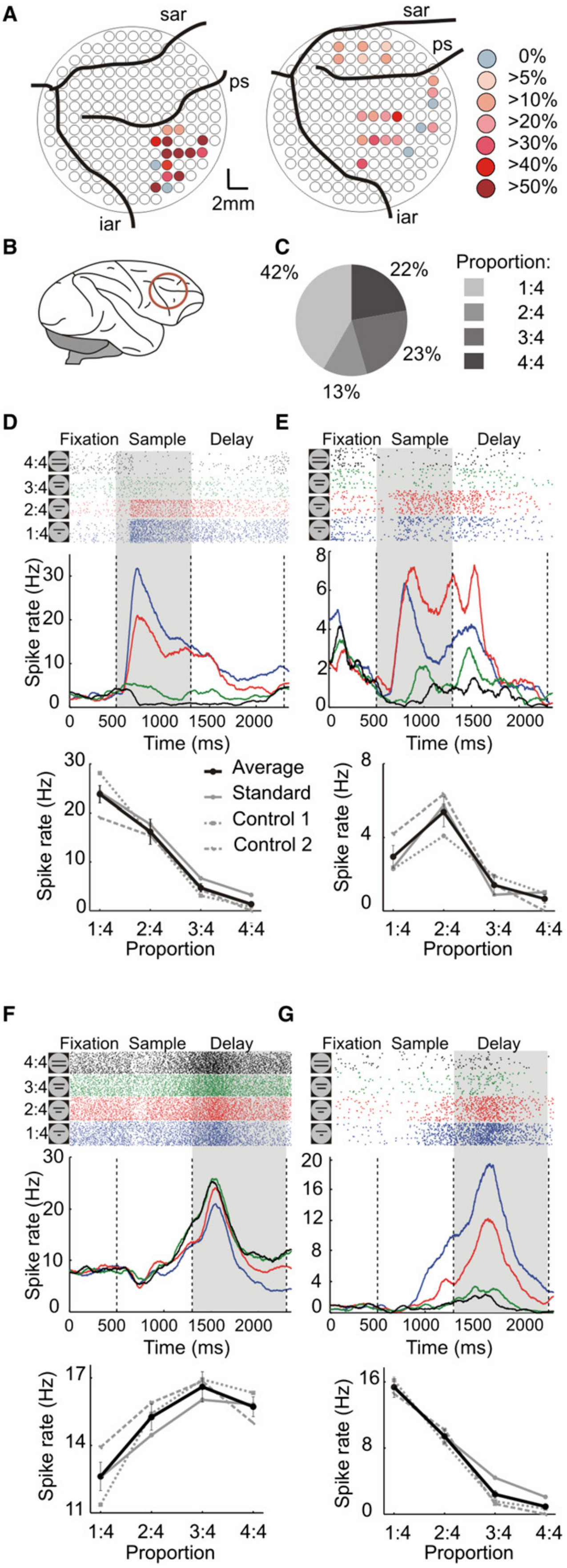

Figure 3. Single-Cell Recordings

(A) Location of recording sites in the PFC of the two monkeys. Abbreviations are as follows: iar, inferior arcuate sulcus; sar, superior arcuate sulcus; ps, principal sulcus. The percentage of proportion-selective units found at each recording site is color coded.

(B) Lateral view of a rhesus monkey brain. The circle indicates the location of the recording chamber.

(C) Frequency-distribution of proportionality-selective neurons.

(D–G) Responses of four example neurons during the fixation, sample, and delay periods. Neurons were proportion selective during the sample (D and E) or delay (F and G) period (marked in gray). In the top panel, the neuronal responses are plotted as dot-raster histograms (each dot represents an action potential, spike trains are sorted and color-coded according to the sample proportion illustrated by example stimuli on the left). Middle panels show spike density functions (activity to a given proportion averaged over all trials and smoothed by a 150 ms Gaussian kernel). The first 500 ms represent the fixation period, which is followed by a 800 ms sample and a 1000 ms delay phase (separated by vertical dotted lines). Bottom panels depict the tuning functions of the respective neurons for each of the three stimulus protocols derived from the periods of maximum proportion selectivity (error bars represent SEM).

before symbolic notations endow us with precise mental representations of fractions and relations.

Our findings in rhesus monkeys are in contrast to previous claims in apes. Woodruff and Premack [26] taught five chimpanzees (four naive, juvenile animals, and chimpanzee Sarah, who had received intensive language-like training) to match proportions made of naturalistic materials. For instance, the apes had to match one-quarter of an apple to one-quarter of another apple, as opposed to three-quarters of another apple. They did the same with liquid in a jar, filled either one-quarter or three-quarters full, and ultimately combined these two types of materials (i.e., apples and liquid). It was found that all four naive chimpanzees failed at this task; only Sarah passed. Based on these results, the authors argued that language-like training might constitute a prerequisite to understanding abstract relations. Our data in rhesus macaques, however, demonstrate that quantity ratios, similar to basic arithmetic [32], can readily be derived in the absence of symbolic labels.

In addition to the behavioral demonstration of an understanding of proportionality, we also present a neuronal correlate for this capacity in the frontal lobe. Previous electrophysiological recordings from nonhuman primates identified individual neurons sensitive to changes in absolute spatial or numerical quantity in prefrontal and intra-parietal cortices [4, 5, 8, 16, 20–23, 33]; these neurons were comparable to a fronto-parietal network activated in humans processing quantities [17, 18, 34, 35]. Our results together with a recent fMRI adaptation study (Jacob and A.N., unpublished data) now suggest that proportion, a relational and derived quantity category, is represented in a partly overlapping magnitude-coding network. We found a relatively high percentage of PFC neurons that discharged as a function of the displayed lengths ratios. Different populations of neurons coded proportions during sample presentation and maintained this derived quantitative information during the memory period. Importantly, the responses of selective neurons were unaffected by the absolute magnitude of the stimulus components and responded irrespective of length variations of the test and reference lines. The proportion-selective neurons showed maximum discharge in response to one of the four displayed length ratios (a neuron's preferred proportion) and a systematic drop-off of activity as the proportion in the sample period varied from the preferred value, resulting in peaked tuning functions.

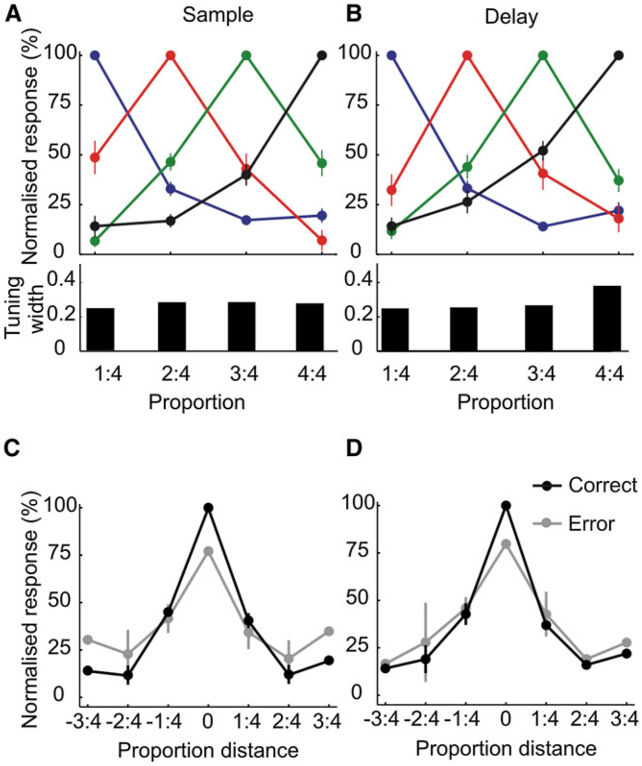

Figure 4. Neuronal Population Tuning Properties

(A and B) Normalized responses averaged for neurons preferring the same proportion during the sample (A) and delay (B) phases. Bottom panels show the tuning curves' standard deviation values (half-bandwidth) across preferred proportions.

(C and D) Normalized tuning functions plotted relative to the preferred proportion for correct trials (black line) and error trials (gray line) during the sample (C) and the delay phase (D).

Error bars represent SEM.

This labeled-line coding was analogous to the previously described coding scheme of quantity-selective neurons found in animals trained to explicitly discriminate numerical and spatial absolute magnitudes [5, 8, 21, 22]. It suggests that abstract quantity in general may be coded by peak-tuned neurons whenever magnitudes are stored as distinct magnitude categories.

The neural activity in the PFC correlated well with the behavioral performance of the monkeys. Both the behavioral and neural discrimination curves showed similar tuning selectivity. An analysis of trials in which the monkeys made judgment errors further emphasizes the significance of proportion-tuned neurons for behavioral responses. The spike rates at the neurons' preferred proportion were significantly reduced whenever the animals made a wrong decision. In other words, whenever the proportion detectors did not properly encode the preferred proportion by maximum discharges, the animals tended to fail. This observation argues for a direct relationship between the neurons' peaked proportion selectivity and task performance.

Our data emphasize the importance of PFC for integrating different sources of quantity information and for ultimately understanding derived quantities, such as fractions. Because the PFC is particularly rich in anatomical connections with other cortical and subcortical areas [24, 36], it is possible that it receives already highly processed ratio information from presynaptic brain areas, such as the parietal lobe. Neurons in lateral intraparietal sulcus (area LIP) have been shown to add probabilities (i.e., the proportion of times a stimulus delivers a reward), a kind of proportional reasoning in the temporal domain [37]. Future studies will have to elucidate whether other brain areas also play a major role in representing relations between quantities.

Experimental Procedures

Behavioral Protocol and Stimuli

Two monkeys (Macaca mulatta, weighing 6 and 7.5 kg) were trained to indicate whether a test stimulus showed the same proportion as a previously presented sample stimulus (Figure 1A). They had to keep their gaze within 1.75° of the fixation point during sample presentation and the memory delay (gaze was monitored with an infrared eye-tracking system, ISCAN). Length-ratio stimuli consisted of two horizontal lines placed 0.5° of visual angle above and below the center of a circular gray background (12° of visual angle in diameter) (Figure 1B). In the standard protocol, the length of the reference line changed between 1.5° of visual angle (1.5 cm) (50 Pixel, on a 17 inch monitor with a resolution of 1024 × 768 pixels) and 6° (6 cm) (200 pixel), and the test line varied in accordance with one of four proportions. So that the appearance of the stimuli was further altered, the horizontal position of the test line within the gray background circle varied randomly. In one of the control protocols, the length of the reference line was held constant (2.5° of visual angle) while the test line was adjusted to 0.625° (1:4), 1.25° (2:4), 1.875° (3:4), and 2.5° (4:4) of visual angle. In the other control protocol, the length of the test line length was fixed at 1.5° of visual angle while the length of the reference line changed between 1.5° and 6° of visual angle. To prevent memorization of patterns in the visual displays, we tested the monkeys with many different stimuli during each recording session, and shuffling relevant item features (e.g., position and size) every day ensured random displays. Sample and test images were never identical. Trials were randomized and balanced across all relevant features (match versus nonmatch, standard versus controls). A 1.5 s timeout was inserted whenever the monkeys made an error. Probe-trial probability in transfer tests was set to p = 0.118; that is, on average two novel and not reinforced transfer proportions appeared in each block of 17 trials.

Animal Training

Monkeys were first trained to discriminate the lengths of single lines in a match-to-sample protocol. Next, two proportions (1:4 and 4:4) were introduced. After one month, the animals reliably discriminated 1:4 and 4:4 at 80% correct. The proportions 2:4 and 3:4 were added, and the monkeys were trained for two more months. Recordings started after the monkeys reached a constant accuracy level of >80% for all proportions. The behavioral and neurophysiological data presented in the current study were derived from 31 recording sessions in monkey M and 32 recording sessions in monkey H. Monkey M and monkey H, on average, performed 581 and 594 trials per session, respectively.

Electrophysiological Techniques

Recordings were made from the ventrolateral prefrontal cortex (Figure 2B) from the two monkeys in accordance with the guidelines for animal experimentation approved by the Regierungspräsidium Tübingen. Arrays of up to eight tungsten microelectrodes (1 MOhm impedance) were inserted via a grid with 1 mm spacing. Recording sites were localized with stereotaxic reconstructions from magnetic resonance images. Neurons were selected at random; no attempt was made to search for any task-related activity. Separation of single-unit waveforms was performed offline with mainly principal component analysis (Plexon Systems).

Data Analysis

We fitted the behavioral data with Gaussian functions. For all proportions, the goodness of fit (r^2) of the Gauss distributions was determined (mean $r^2 = 0.97$), and the standard deviation (σ) was derived. All analyses of neuronal responses (except error-trial analyses) were conducted for correct trials only. Cells from which activity was recorded during at least eight trials of each proportion and protocol (standard, control 1 and 2) were included in the analysis. Sample activity was derived from an 800 ms interval that began once the individual response latency of the cell was taken into account after stimulus onset. To measure neuronal response latency, we generated average spike-density histograms (at 1 ms resolution and smoothed by a sliding window; kernel bin width, 10 ms) for a neuron's responses to all sample stimuli. Response latency was defined by the first time bin that reached a value higher than any value before sample onset. A default latency of 100 ms was used if no measure based on these criteria could be derived. For the delay period, activity was summed in an 800 ms interval starting 200 ms after delay onset. We analyzed both sample and delay activity in two windows of 400 ms to account for early and late responses. To determine the selectivity of a neuron, we performed a two-way ANOVA ($p < 0.01$) for each cell in the sample and delay period with proportion (1:4, 2:4, 3:4, 4:4) and stimulus type (standard, control 1, control 2) as factors. Only cells showing a significant main effect of proportion ($p < 0.01$) but no significant main effect of stimulus type (standard, control 1, control 2) or interaction were classified as "proportion selective," and the proportion eliciting the largest spike rate was defined as the "preferred proportion." To derive averaged proportion tuning functions, we normalized activity rates by setting the maximum activity to the preferred proportion to 100% and the activity to the least preferred ratio to 0%. Qualitatively similar functions were obtained when the tuning functions were normalized only by the maximum.

Acknowledgments

We thank S. Jacob for critical reading of the manuscript. This work was supported by a junior research group grant (C11/SFB 550) from the German research foundation Deutsche Forschungsgemeinschaft (DFG) and a Career Development Award from the International Human Frontier Science Program Organization (HFSP) to A.N.

Received: May 7, 2008
Revised: July 23, 2008
Accepted: August 4, 2008

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