Neuronal population coding of continuous and discrete quantity in the primate posterior parietal cortex

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Quantitative knowledge guides vital decisions in the life of animals and humans alike. The posterior parietal cortex in primates has been implicated in representing abstract quantity, both continuous (extent) and discrete (number of items), supporting the idea of a putative generalized magnitude system in this brain area. Whether or not single neurons encode different types of quantity, or how quantitative information is represented in the neuronal responses, however, is unknown. We show that length and numerosity are encoded by functionally overlapping groups of parietal neurons. Using a statistical classifier, we found that the activity of populations of quantity-selective neurons contained accurate information about continuous and discrete quantity. Unexpectedly, even neurons that were nonselective according to classical spike-count measures conveyed robust categorical information that predicted the monkeys' quantity judgments. Thus, different information-carrying processes of partly intermingled neuronal networks in the parietal lobe seem to encode various forms of abstract quantity.

monkey | single-unit recording | statistical classifier

The questions "how many?" and "how much?" refer to two different types of quantity. Abstract quantity may be discrete and enumerable, thus referring to the number of elements, as opposed to continuous and uncountable quantity such as spatial extent (1). Behavior based on abstract quantitative parameters is clearly adaptive; for instance, understanding how much drinking water is around (2, 3) or how many individuals belong to an opponent party (4, 5) guide vital decisions in the life of animals and humans alike.

The conceptual similarity between discrete and continuous quantity is perceptually reflected by behavioral interference phenomena. In a number comparison task, for example, choosing the numerically larger number takes significantly longer if the numeral is smaller in size compared with the numerically smaller number (e.g., in the comparison 2 versus 7) (6, 7). This number-size interference implies interactions on the neuronal level when discrete and continuous quantities are processed. The parietal cortex has recently been implicated in the representation of different types of quantity information (8–10). Functional imaging studies in humans suggest that anatomical vicinity (7, 11–13) or even a common magnitude system (14) for the representation of numerical (discrete) and spatial (continuous) quantity in the parietal cortex might be responsible for behavioral interference phenomena between numerical and spatial quantity (15, 16).

How continuous quantity is encoded by single nerve cells, and how it relates to numerosity representations, however, remains unknown. We analyzed the response properties of individual neurons in the fundus of the intraparietal sulcus (IPS) of monkeys simultaneously engaged in numerosity and length discrimination tasks. Using a neural network classification technique, we investigated to what extent the responses of small populations of neurons can account for the monkeys' performance across the entire range of tested quantities. This approach also revealed different behaviorally meaningful types of information in the neuronal discharges.

Results

Behavior. We trained rhesus monkeys in a delayed match-to-sample task (17) to discriminate different types of quantity randomly alternating within each session. In the "length protocol" (Fig. 1A) the length of a line (of four different lengths) needed to be discriminated (continuous spatial quantity). In the "numerosity protocol" (Fig. 1B) the number of (one to four) items in multiple-dot displays (discrete numerical quantity) was the relevant stimulus dimension. While maintaining fixation, monkeys viewed a sample stimulus (800 ms) followed by a delay (1,000 ms) and a test stimulus (1,200 ms). To receive a reward, the monkeys had to release a lever if the test had the same length as the sample in the length protocol or the same numerosity as the sample in the numerosity protocol. Monkeys had to maintain the lever if the first test was showing a different length in the length protocol or a different set size in the numerosity protocol, respectively. To ensure that the monkeys solved the task based on the relevant quantitative information (length or numerosity, respectively), other covarying features of the stimuli (i.e., the total area for the line stimuli, and the total area, thus also luminance and contrast, total circumference, the density, and the geometrical configuration for the numerosity stimuli) were controlled, and the positions of the dots and lines were greatly varied (17) [see supporting information (SI) *Methods*].

During the initial behavioral training, the monkeys discriminated up to nine different line lengths in one session (Fig. 2A), which demonstrates that the animals treated line lengths as continuous dimension. For recording, however, we restricted the quantity dimensions to four lengths and numerosities 1–4, respectively, to obtain a sufficient number of trial repetitions for each stimulus condition. Both monkeys solved 81–99% of the trials correctly for both the length and the numerosity protocols ($P < 0.001$ compared with chance, binomial test) (Fig. 2 B and C) regardless of the controls used (Fig. 2D and SI Fig. 7). Transfer tests ensured that putative associations between ordinal quantitative information in the numerosity and length protocol (e.g., by associating the largest displayed numerosity 4 with the longest presented line) were absent (see SI Methods and SI Fig. 8). Thus, the animal treated continuous and discrete quantities as independent variables.

Tuning of Single Neurons. We analyzed the activity of 400 single units from the depth of the IPS (SI Fig. 9) from two monkeys
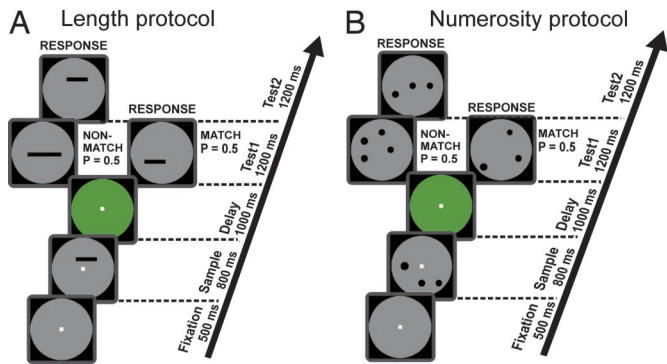
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Fig. 1. Delayed match-to-sample protocols and behavioral performance. (A) Length protocol. A trial started when the monkey grasped a lever and maintained fixation. The monkey had to release the lever if the lines in the sample and test displays had the same length and had to continue holding it if they did not (P = 0.5). Nonmatch stimuli consisted of lines that were longer or shorter than the sample line, respectively. (B) Numerosity protocol. Task conditions were identical to the length protocol, but here the monkeys had to match the number of items in the sample and test displays. The physical appearance of the displays varied widely for the same numerosities (see Methods). Nonmatch stimuli showed lower or higher numerosities than the sample numerosity, respectively.

while they performed the delayed match-to-sample task. Many neurons were quantity-selective, showing maximum discharge to one of the four tested numerosities, lengths, or both. Fig. 3 shows the activity of three neurons selectively tuned to quantity in the sample period. The neuron in Fig. 3A was tuned only to numerosity (with numerosity 3 as the preferred one) and did not respond to variations of the length of a line, whereas the cell in Fig. 3B responded as a function of the line length (with the third longest line preferred) but did not encode numerical quantity. Yet another type of neuron (Fig. 3C) was activated by variations in both discrete numerical and continuous spatial quantity.

The discharge rates were analyzed for the numerosity and length protocol separately during the sample and delay periods by using a two-way ANOVA [$P < 0.01$, with quantity (numerosities or line lengths) and stimulus type (standard or control) as factors]. We found that 72 neurons (18% of the total sample; 60 and 42 neurons early and late response, respectively) were significantly selective to quantity during the sample period (only significant quantity effect, no other significances). Of those quantity-selective neurons, 46 cells (64%) responded differently to one of the four possible numerosities, and 40 neurons (55%) responded differently to one of the four lengths in the length protocol. Interestingly, 14 quantity-selective neurons (19%) were tuned in both the numerosity and the length protocol (see also the example neuron in Fig. 3C).

Similar results were found for the delay period, when the monkeys had to keep the quantitative information in mind (SI Fig. 10). Of a total of 59 quantity-selective neurons (15% of the total sample; 19 and 51 neurons early and late response, respectively), 49 cells (83%) were selectively tuned to numerosity, whereas 22 neurons (37%) responded to length. Twelve neurons (20%) discharged as a function of both discrete and continuous quantity. Thus, our single unit data suggest that two partly overlapping populations of neurons represent quantity information in the depth of the IPS. The overlap neurons, however, did not display any larger–smaller congruity; that is, the magnitude of the preferred numerosity did not correlate with the magnitude of the preferred length [correlation coefficient $r = 0.22$, $P = 0.25$, $n = 14$ (sample period); $r = 0.10$, $P = 0.61$, $n = 12$ (delay period)].

The distribution of selective cells preferring one of the eight quantities is shown in Fig. 4 A and B. The tuning behavior of numerosity and length-selective neurons was very similar (Fig. 4 C–F), showing a drop in activity for the quantities more remote
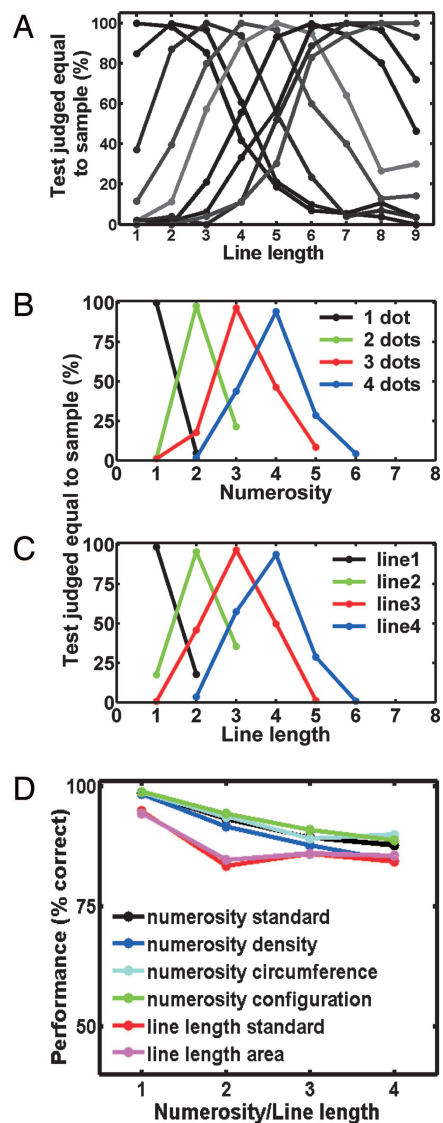

Fig. 2. Performance data. (A) Average performance on nine line lengths in purely behavioral sessions. The functions indicate the probability that a monkey judged displays in the test period as containing the same line length as the sample quantity. Line lengths ranged from 0.58° of visual angle in multiples of 0.58° up to 5.22°. The peak of each performance distribution indicates sample length. (B and C) Behavioral performance of both monkeys during recordings for the two types of quantities (B, discrete; C, continuous). Four line lengths (multiples of 0.85° of visual angle) were used during the recording sessions. The color-coded functions indicate the probability that a monkey judged displays in the test period as containing the same quantity as the sample quantity. (D) Average performance of both monkeys in the numerosity and line-length discrimination tasks (standard and control conditions) during the recording sessions. Chance level is 50%.

from the preferred one. Plotting the normalized tuning curve as a function of the distance from the preferred quantity revealed a clear distance effect for both the sample and the delay phases. Similarly sharp tuning functions were obtained for the continuous as well as for the discrete quantities in both phases (Fig. 4 G and H). More than half of the quantity-selective neurons were also tuned to motion direction in flow-field stimuli (see SI Methods for details).

Population Coding Using a Classifier. Individual tuned neurons alone cannot account for the monkeys' behavior across the entire range of tested stimuli, particularly if some of them respond ambiguously
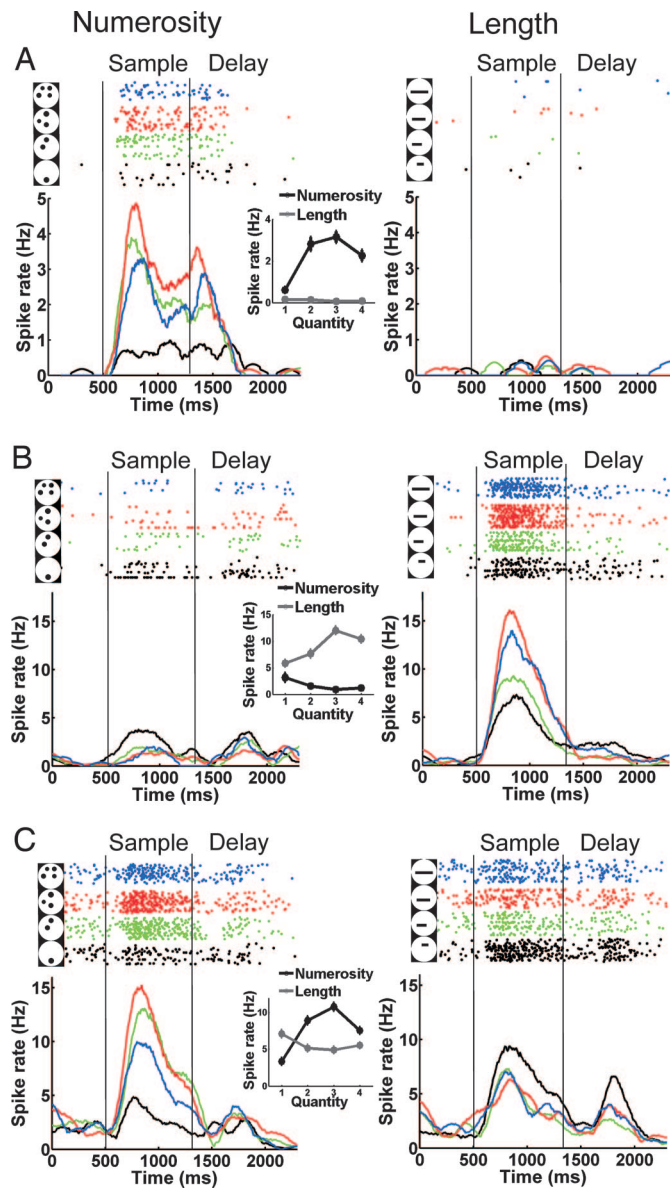
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Fig. 3. Example neurons exhibiting selectivity for quantity in the sample period. (*A*) Neuron tuned to numerosity, but not to length. *Left* and *Right* illustrate the discharge rates of the same neuron in the numerosity and length protocol, respectively. At the top, the neuronal responses are plotted as dot-raster histograms (each dot represents an action potential in response to the quantity as illustrated by example stimuli to the left and is color-coded accordingly); corresponding averaged spike density functions are shown below (activity to a given quantity averaged over all trials and smoothed by a Gaussian kernel). The first 500 ms represent the fixation period. The area between the two black vertical bars represents the sample stimulus presentation, and the following 1,000 ms indicate the delay phase. Colors correspond to the quantity dimensions. (*Inset*) Tuning functions of the neuron to numerosity and length in the sample period. (*B*) Neuron tuned to the third longest line, but not to any tested numerosity (same layout as in *A*). (*C*) Example neuron encoding both discrete and continuous quantity (same layout as in *A*).

by encoding both discrete and continuous quantity. Therefore, we applied a population decoding technique (18–21) based on a self-organizing map classifier, which is an artificial neuronal network using unsupervised learning (22), to assess the discriminative power of small populations of neurons (23). The classifier was trained with neuronal responses (SI Fig. 11), i.e., preprocessed spike trains (24, 25), of a set of neurons recorded while the monkeys
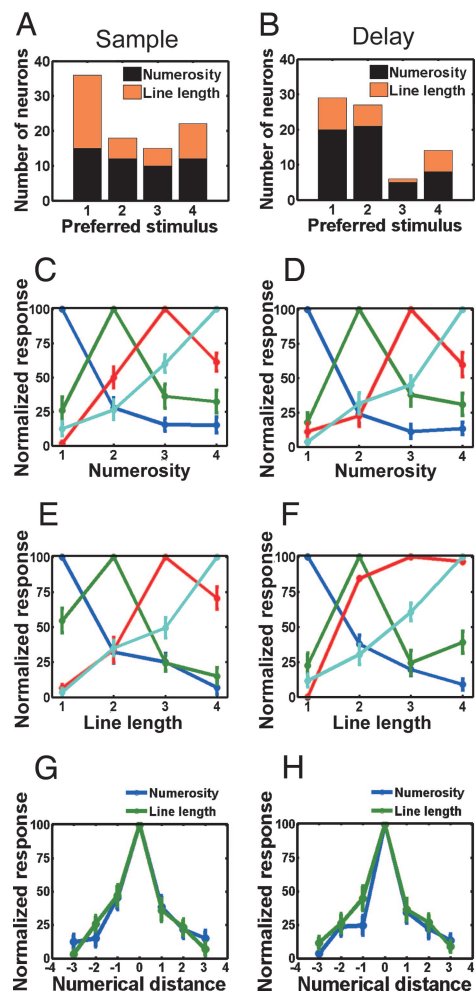

Fig. 4. Frequency and characteristics of quantity-selective neurons. (*A* and *B*) Frequency distribution of quantity-tuned cells in the sample (*A*) and delay (*B*) phases. The absolute number of neurons is plotted for each preferred quantity (from 1 to 4) separately. The colors represent the two types of quantities, continuous (orange) and discrete (black). (*C–F*) The normalized responses averaged for neurons with the same preferred quantity are plotted separately for discrete (*C*, sample; *D*, delay) and continuous (*E*, sample; *F*, delay) quantities. All neurons showed a progressive drop-off of the response with increasing distances from the preferred numerosity or line length, resulting in averaged tuning functions that were comparable for neurons tuned to discrete or to continuous quantities. (*G* and *H*) Normalized activity for the discrete quantities (in blue) and continuous quantity (in green) as a function of distance from the preferred quantity, for both sample (*G*) and delay (*H*).

judged each of the eight quantity categories; at this stage, the classifier was informed about the stimulus configuration and learned the neuronal features that were best suited for identifying a given category. In the subsequent test phase, the classifier predicted the categories from novel neuronal responses of the same pool of neurons, i.e., from data it had not used for learning.

Based on the recorded population data, the classifier was able to assign the novel spike trains to one of the eight quantity categories with high accuracy. For the 72 sample quantity-selective neurons together, the average accuracy (percentage of correct class assignments) was 63.7% (chance level is 12.5%), with entropy of 1.65 bits (Fig. 5*A*). Importantly, each of the eight quantity categories was classified reliably, as indicated by the high probability values on the diagonal of the confusion matrix in Fig. 5*A*. There were barely any misclassifications of quantity categories. The accuracy values averaged along the main diagonal and all secondary diagonals resulted
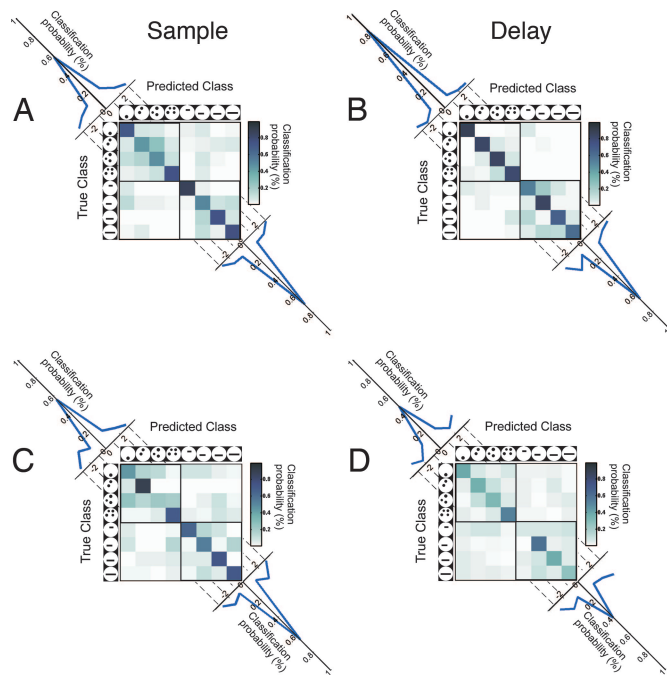
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Fig. 5. Classification performance across the neuronal population. Shown are confusion matrices describing the pattern of quantity classification performed on four different neuronal populations. The rows in each confusion matrix represent the true classes the monkey had seen, and the columns correspond to the output of the classifier. Color codes the classification probability. The eight classes correspond to the eight stimulus quantities: numerosity 1–4 and line length 1 to line length 4, where length 1 is the shortest line (0.85° of visual angle). Thus, the main diagonal shows how often the classifier correctly assigned quantity stimuli to their real category (i.e., accuracy). Averaging the classification probabilities over each diagonal parallel to the main diagonal results in the average performance of the classifier as a function of distance from the real quantity, which is plotted, separately for each stimulus type (length and numerosity, respectively), as a tuning function at each end of the main diagonal (the data points resulting from the misclassifications across stimulus types are not included in the computation of the tuning functions, where only data from within-category classifications, marked in the confusion matrix by a solid black frame, were used). (*A*) Classification performance on the population of 72 quantity-selective neurons during the sample phase. (*B*) Classification performance on the population of 59 quantity-selective neurons during the delay period. (*C* and *D*) Classification performance based on untuned, task-related neurons. The number of untuned neurons tested in the sample (*C*) and delay (*D*) phases was matched to the populations of tuned neurons (*A* and *B*).

in a tuning function showing a distance effect (i.e., more erroneous classifications occurred for adjacent quantities), very reminiscent of single-cell tuning curves (see Fig. 3). An even higher classification performance (accuracy of 74.3% and entropy of 1.99 bits) was derived from the 59 neurons tuned to quantity in the delay phase (Fig. 5*B*). When tested on average spike rates alone, performance for the quantity-tuned sample and delay neurons dropped to 42% (*SI Methods* and SI Fig. 12 *A* and *B*); this indicates that the spike rate in tuned neurons played a major role for classification but was not sufficient to explain the superior classification based on the full spike train information.

Classification Based on Untuned Neurons. To investigate whether the spike trains would carry additional information besides the averaged spike rate, we tested the quantity classification performance of neurons that were not quantity-tuned ($P > 0.12$ on the two-way ANOVA). The size of the respective populations of neurons for each period tested was matched (72 and 59 neurons in the sample and delay periods, respectively), as was the mean firing rate ($P >$

0.05, paired t test). Surprisingly, these untuned neurons carried sufficient information to achieve a remarkable classification performance of 61.0% (1.54 bits) in the sample (Fig. 5*C*) and 43.8% (1.02 bits) in the delay period (Fig. 5*D*) but still worse than the performance of the quantity-selective neurons in both sample and delay ($P < 0.001$, t test). When tested on average spike rates alone, the classifier performance for untuned neurons was only slightly (but significantly) better (24% and 22% in the sample and delay, respectively; see *SI Methods* and SI Fig. 12 *C* and *D*) than chance (12.5%). This indicates that only in few cases the ANOVA might have been too conservative in detecting tuning based on spike rate. Thus, only some 10% of the performance in untuned neurons can be explained by spike rate information.

To further demonstrate that temporal pattern information was important, we performed a multivariate ANOVA using the wavelet coefficients extracted by the feature extraction algorithm as dependent variables. This allowed us to compare the number of neurons that would be significant provided that the temporal information in the spike trains were taken in to account, to the number of neurons significant when the temporal information was ignored (as was done with ANOVA). The results showed that the untuned neurons mainly relay information based on the temporal spike train pattern (see *SI Methods* and SI Fig. 13).

Is the information extracted by the classifier from discharges of task-related, untuned neurons really relevant for the monkeys' judgment behavior? To test this hypothesis, we compared for the same set of neurons the classification performance in correct trials with the performance in trials when the monkeys made judgment errors (*SI Methods*). In both the sample and delay phases, performance on correct trials was better than on error trials ($P < 0.001$, t test). (Note that the reduced classification performance for the correct trials is caused by fewer neurons with sufficient error trials as well as fewer trials for each class.) As shown in Fig. 6, the classification performance based on error trials was not different from chance ($P > 0.05$, one sample t test). In other words, whenever the monkeys made discrimination errors, the information that could have been used by the classifier was absent. This finding strongly argues that the monkeys exploited this type of information extracted by the classifier when performing correctly.

Discussion

We analyzed the responses of single neurons in the fundus of the IPS of monkeys simultaneously engaged in numerosity and length discrimination tasks, presented in random fashion. This allowed us to investigate an individual neuron's responses to both quantity types in an unbiased way. We found that anatomically intermingled single neurons in the monkey IPS encode continuous spatial, discrete numerical, or both types of quantities. Similar to previous findings about numerosity encoding (9, 10, 17, 26, 27), length-selective neurons exhibited a maximum discharge to one of the four displayed line lengths and a progressive drop-off for more remote lengths, resulting in peaked tuning functions that together formed a bank of overlapping band-pass filters, a coding scheme that might be optimal for abstract categories in explicit tasks (28).

Our results are in agreement with the notion that the quantity system in the parietal lobe might be part of a broader network of areas that are involved in nonnumerical magnitude representation (11–13). Recently, Pinel *et al.* (7) measured parietal activation in response to three tasks that involved judgment of brightness, size, and numerical magnitudes. With task difficulty equated across all three tasks for each individual, functional MRI revealed a network of areas that were activated in each of the three tasks. Interestingly, number and size activations overlapped within the horizontal segment of the IPS, and those dimensions interfered in behavioral response time measures. We speculate that parts of the horizontal segment of the IPS might be an equivalent structure to the one we recorded from in monkeys.
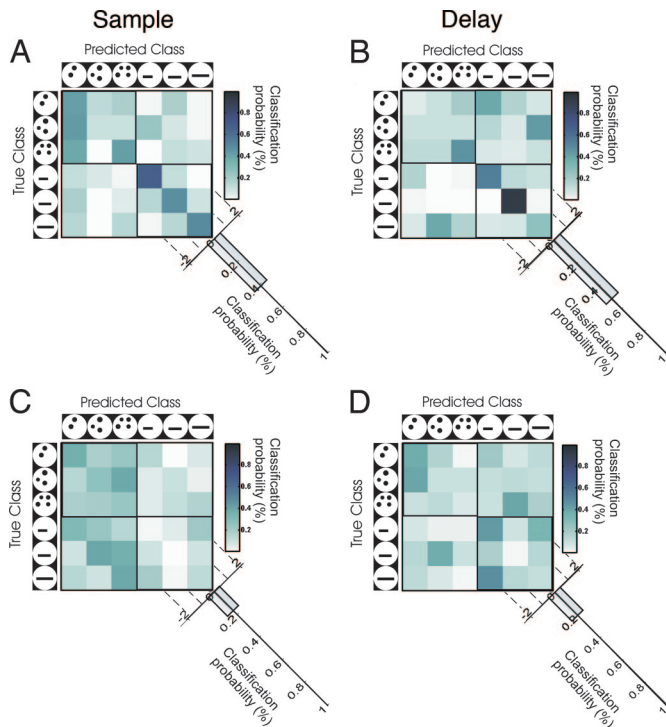
Fig. 6. Comparison of classification performance based on untuned neurons for correct and error trials (same layout as in Fig. 5). Because of an insufficient number of errors the monkeys made for the smallest line length and numerosity 1, the error trial analysis had to be restricted to the six remaining quantities, resulting in a 6-×-6 confusion matrix with fewer neurons. The classification performance on the main diagonal is represented by the column at the bottom right corner of each confusion matrix. (*A* and *C*) Classification performance on the population of 30 untuned neurons during the sample phase whenever the monkeys responded correctly (*A*) or made judgment errors (*C*). (*A*) The classifier's tuning functions show a clear peak along the diagonal for correct trials, indicating significant quantity classification. However, tuning was absent for the same population of neurons whenever the monkeys made errors (*C*). (*B* and *D*) A similar result was found for the 34 neurons in the delay phase; the classifier predicted quantities significantly better than chance based on data from correct trials but failed for those from error trials.

The fact that we found single neurons that encode spatial and/or numerical quantity anatomically intermingled in a restricted area of the IPS could at least partly explain the behavioral interference found between number and size in comparison tasks (6, 7). Such interference effects are thought to arise through the influence of a task-irrelevant but automatically processed stimulus dimension. We speculate that automatic but undesired "cross-talk" between quantity-selective neurons might occur because of the anatomical vicinity of these two populations. In humans, this overlap might favor the cultural emergence of automatic spatial–numerical associations that have been observed in many behavioral investigations (15).

Single neurons tuned to quantity can provide information about only a restricted range of magnitudes. Moreover, some individual neurons respond ambiguously by encoding both discrete and continuous quantity. Thus, only the population of selective neurons together can account for the monkeys' behavior across the entire range of tested stimuli. We therefore applied a population decoding technique to assess the discriminative power of small populations of neurons (18–21, 29). Our quantitative results based on a statistical classifier demonstrate that the relatively small population of quantity-selective neurons carried most of the categorical information. Already by exploiting the classical spike-rate measure alone resulting in quantity-tuning functions (9, 10, 17, 30, 31), the classifier was able to accurately and robustly discriminate both continuous and discrete quantity classes. The spike-rate measure is in fact behaviorally meaningful, because it has been demonstrated several times that the discharge rate of quantity-selective neurons correlates with the monkeys' judgment performance; compared with trials in which subjects performed correctly, the spike rate at the preferred numerosity was significantly reduced whenever the monkeys made discrimination errors (9, 10, 17).

Surprisingly, however, even an equally sized population of neurons that were untuned, according to classical spike-count measures, had a remarkable and significant quantity-coding ability, although worse than that of the tuned neurons. Relative to the population of quantity-selective neurons, average classification probability dropped by 2.7% in the sample and by 30.5% in the delay for the nonselective neurons. Because firing-rate information alone resulted in classification performance that was barely above chance in untuned neurons, the good performance can be explained only by additional information in the spike trains. This extra information is most likely conveyed by the fine temporal structure of the spike trains, which was preserved in the classification input by the wavelet-based feature extraction algorithm (24). Abstract category information thus seems to be encoded by both firing rate and temporal pattern information.

The comparison between the monkeys' neuronal and behavioral responses suggests that the brain does use temporal information extracted from spike trains; neuronal responses recorded whenever the monkeys failed to discriminate the quantity categories prevented the classifier from predicting the correct classes. In addition, however, target brain areas of the parietal lobe could decode information, using inputs from relatively small populations of fewer than a hundred neurons. The prefrontal cortex is a putative candidate structure for such a following readout stage because it is functionally interconnected with the posterior parietal cortex (32–35) and responsible for cognitive control (36). In addition, functional imaging studies in humans show that the frontal lobe represents aspects of nonverbal quantity representations even in the absence of task demands (37). Interestingly, quantity activation in the frontal lobe is particularly prominent in children (38, 39). Future single-cell studies are needed to clarify whether complex quantity judgements require an interplay with, or readout by, more executive structures, such as the prefrontal cortex (36).

Methods

Stimuli. Numerosity stimuli were black dots (diameter range 0.5–1.1° of visual angle) randomly placed on a circular gray background (6° of visual angle in diameter) presented in the center of the monitor. The size, total area, and position of the dots varied randomly from trial to trial. Line-length stimuli consisted of one horizontal black line displayed at random locations on a gray background circle (6° diameter, centered on the screen). The lengths of the lines were multiples of 0.85° of visual angle (line 1, 0.85°; line 2, 1.7°; and so on). The thickness of the lines varied randomly across trials from 0.06° to 0.36° of visual angle. To prevent the memorization of the patterns of visual displays, the monkeys were tested with different displays for each trial, and the displays were generated randomly each day by shuffling relevant item features (e.g., position and size). In each trial, sample and test displays never showed the identical images. Trials were randomized and balanced across all relevant features (line length versus numerosity, match versus nonmatch, standard versus control, etc.).

Recordings. Recordings were made from one left and one right hemisphere in the depth (9–13 mm below the cortical surface) of the IPS of two rhesus monkeys (*Macaca mulatta*) while they performed the delayed match-to-sample task. This area was chosen because it contains the highest proportion of visual numerosity-selective neurons in the parietal cortex (40) and is specifically activated by quantity information in humans (41, 42). All procedures were done in accordance with the guidelines for animal

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experimentation approved by the Regierungspräsidium (Tübingen, Germany). Recordings were localized by using stereotaxic reconstructions from magnetic resonance images. Neurons were randomly sampled, with no attempt to select them based on task selectivity. Both monkeys are still engaged in quantity discrimination studies. Separation of single-unit waveforms was performed off-line applying mainly principal component analysis (Plexon Systems, Dallas, TX). The monkeys maintained their gaze within 1.75° of the central fixation spot (measured by using an infrared eye-monitoring system, ISCAN, Burlington, MA).

Data Analysis. Sample activity was derived from an 800-ms interval after stimulus onset shifted by a cell's individual response latency, which was defined as the time when the activity varied by at least two standard deviations from the baseline activity measured in the 400 ms preceding the stimulus onset. Delay activity was derived from a 900-ms interval after stimulus offset shifted by 200 ms. Both sample and delay activity was analyzed in two windows of 400 ms (sample) and 450 ms (delay), respectively, to account for early and late response. A two-way ANOVA ($P < 0.01$) was calculated separately for the numerosity and length protocol for each neuron. Factors were quantity (numerosities 1–4, or line with lengths of 0.85°, 1.7°, 2.55°, or 3.4° of visual angle, respectively) and stimulus type (standard or control). The putative relationship between preferred numerosity and line length of neurons tuned to both quantities was quantified with a simple regression technique ($y = a + b \times x$), where y is the preferred numerosity of a neuron, x is the preferred line length, a is the intercept, and b is the slope of the x–y relationship.

For the neuronal population analysis, we applied a statistical classifier (21) based on the learning vector quantization algorithm developed by Kohonen (22) for the self-organizing feature maps. The classifier received as input the preprocessed activity of neurons. We assumed independent firing because putative correlations among neurons could add only a small amount of information in our small populations of neurons ($n \leq 72$) (43). The preprocessing

step consisted of extracting the feature vectors from the spike trains of 10 trials per stimulus condition from the total number of trials of each neuron (3.5 features per neuron on average). A wavelet method based on the Daubechies four-point mother wavelet decomposed the smoothed spike trains and extracted feature vectors. A self-organizing map trained on these preprocessed neuronal responses predicted the quantity corresponding to each trial from this pool of neurons by performing classifications in a 10-fold cross-validation design. This process was repeated 100 times, ensuring a reliable estimate of the average classification performance. The output was the averaged accuracy and entropy obtained for each of the classes. Over the runs performed on each population, we computed the average accuracy of trial assignment to each class to construct an 8-by-8 confusion matrix with all of the average class assignments, thus obtaining the correct classifications per class on the main diagonal. To estimate a putative classification bias, the procedure was also performed on shuffled trials (neuronal responses randomly assigned to one of the eight classes); discrimination accuracy on shuffled trials was 12% (theoretical chance level was 12.5%) and therefore negligible.

To evaluate behavioral significance of the derived information, the network was also trained and tested with spike trains recorded during error trials. Because the monkeys hardly made errors for line length 1 and numerosity 1, the quantitative categories had to be restricted to three numerosities and three line lengths (i.e., six classes). All relevant parameters (population size, number of classes, and repetitions per stimulus condition) were adjusted for the comparison error versus correct trial classification.

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