LETTERS

Experience-dependent representation of visual categories in parietal cortex

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Categorization is a process by which the brain assigns meaning to sensory stimuli. Through experience, we learn to group stimuli into categories, such as 'chair', 'table' and 'vehicle', which are critical for rapidly and appropriately selecting behavioural responses[1,2]. Although much is known about the neural representation of simple visual stimulus features (for example, orientation, direction and colour), relatively little is known about how the brain learns and encodes the meaning of stimuli. We trained monkeys to classify 360° of visual motion directions into two discrete categories, and compared neuronal activity in the lateral intraparietal (LIP) and middle temporal (MT) areas, two interconnected brain regions[3] known to be involved in visual motion processing[4–6]. Here we show that neurons in LIP—an area known to be centrally involved in visuo-spatial attention[7–9], motor planning[10–13] and decision-making[14–16]—robustly reflect the category of motion direction as a result of learning. The activity of LIP neurons encoded directions of motion according to their category membership, and that encoding shifted after the monkeys were retrained to group the same stimuli into two new categories. In contrast, neurons in area MT were strongly direction selective but carried little, if any, explicit category information. This indicates that LIP might be an important nexus for the transformation of visual direction selectivity to more abstract representations that encode the behavioural relevance, or meaning, of stimuli.

Monkeys were trained to group 12 directions of motion into two categories that were separated by a learned 'category boundary' (Fig. 1a, black dotted line). Monkeys performed a delayed-match-to-category (DMC) task (Fig. 1b) in which they viewed a sample stimulus (650 ms) followed by a delay (1,000 ms) and a test stimulus (650 ms). On a given trial, the sample and test could each be any one of the 12 directions of motion (see Methods). To receive a reward, the monkeys had to release a lever if the test was in the same category as the sample. If the test was a non-match, another delay (150–250 ms) occurred; this was followed by an additional test (650 ms), which was always a match to the sample (and required a lever release). By using this task design, lever releases signalled 'match' and were not directly linked to either category.

After training, the monkeys correctly categorized sample stimuli that were 75° or 45° from the category boundary with greater than 90% average accuracy, and performed at more than 70% correct for stimuli closest to (15°) the boundary (Fig. 1c).

We recorded from a total of 156 LIP neurons from two monkeys (monkey S, $n = 92$; monkey H, $n = 64$) during DMC task performance. A striking number of these neurons were category selective: their activity reliably grouped the 12 motion directions according to their category membership. Figure 2 shows the activity of three category-selective LIP neurons. The 12 traces correspond to the 12 motion directions used as samples, and are coloured red or blue according to their category membership. The pale red and blue traces indicate the four directions closest to (15°) the category boundary. The neuron in Fig. 2a responded more strongly, during the delay, to directions in category 2. The neuron in Fig. 2b preferred sample directions in category 2 during the sample, delay and test, whereas the neuron in Fig. 2c preferred directions in category 1 during the sample, delay and test. Note that each of these neurons showed sharper (that is, binary-like) category selectivity during the delay than during the sample.

For quantitative analyses of neuronal activity, we focused on three time epochs, the 'sample', 'delay' and 'test'. The sample epoch (675 ms duration) began 75 ms after sample onset and ended 100 ms after sample offset. The delay epoch (800 ms duration) began 500 ms after the beginning of the delay (to exclude responses related to sample offset) and included the first 300 ms of the test epoch (because many LIP neurons carried information about the sample stimulus even during the test epoch; see below). Selectivity for the test stimulus

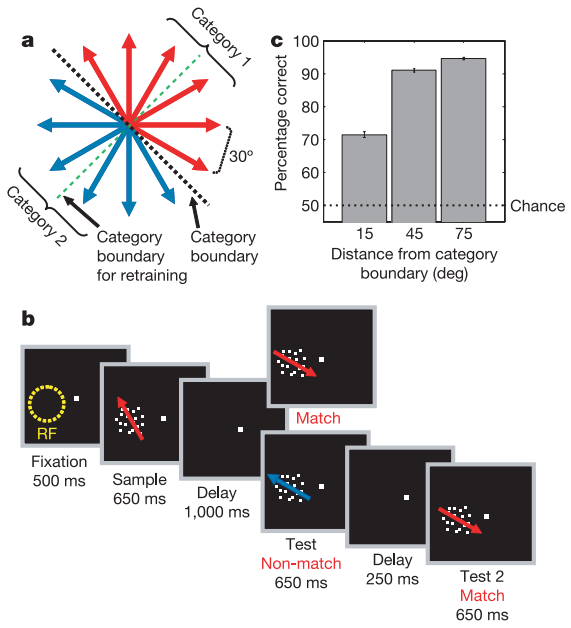

Figure 1 | Behavioural task. a, Monkeys grouped 12 motion directions into two categories (the red and blue arrows) separated by a 'category boundary' (black dotted line). The green dotted line is the boundary used for retraining with the new categories. **b**, Delayed match-to-category (DMC) task. A sample stimulus was followed by a delay and test. If the sample and test were in the same category, monkeys were required to release a lever before the test disappeared. If the test was a non-match, there was a second delay followed by a match (which required a lever release). **c**, Monkeys' average DMC task performance across all recording sessions was greater than chance (50%) for sample stimuli that were close to (15°) and farther from (45° or 75°) the boundary. Error bars are s.e.m.

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and match/non-match effects were analysed over an interval of 275 ms beginning 75 ms after test stimulus onset (Supplementary Information).

A majority of LIP neurons (122 of 156; 78%) showed activity that differed across the 12 motion directions during the sample ($n = 115$) and/or delay ($n = 61$; one-way analysis of variance (ANOVA) across 12 directions, $P < 0.01$). However, this direction selectivity was closely related to the distinction between categories. To evaluate whether individual neurons responded more similarly to directions within than between categories, we computed two parameters: a within-category difference (WCD) and a between-category difference (BCD) in average firing rates to the 12 sample directions (Methods, and Supplementary Information). Across the entire LIP population ($n = 156$), responses to directions in the same category were more similar than to directions in different categories. This was evident during both the sample (Fig. 3a: WCD, 6.22 Hz; BCD, 8.72 Hz; paired t-test, $P \approx 10^{-9}$) and delay (Fig. 3b: WCD, 2.62 Hz; BCD, 4.42 Hz; $P \approx 10^{-11}$).

We also recorded from 67 middle temporal (MT) neurons (monkey S, $n = 40$; monkey H, $n = 27$) during DMC task performance. During the sample, nearly all (66 of 67; 99%) MT neurons distinguished between the 12 directions (one-way ANOVA, $P < 0.01$). However, MT responses did not systematically discriminate between categories (Supplementary Fig. 1). Across the entire MT population, WCD and BCD values were not significantly different during the sample (WCD, 21.49 Hz; BCD, 22.66 Hz; paired t-test, $P = 0.61$; Supplementary Fig. 2a). During the delay, no MT neurons (0 of 67) were selective for the direction of the previously presented sample, and WCD and BCD did not differ from one another (WCD, 2.92 Hz; BCD, 2.93 Hz; paired t-test, $P = 0.93$; Supplementary Fig. 2b).

To measure the strength of neuronal category selectivity, we constructed a category-tuning index by taking the difference between BCD and WCD and dividing by their sum. Category-index values can vary from −1.0 to 1.0, where positive values indicate larger differences for directions in different categories and negative values larger differences within each category (Methods and Supplementary Information). The distributions of category-tuning indices across the entire LIP population ($n = 156$) are shown in Fig. 3c, d. During both epochs, the mean category indices were shifted towards positive values (sample: mean 0.125, t-test, $P \approx 10^{-11}$; delay: mean 0.180, $P \approx 10^{-15}$), with stronger category tuning during the delay than sample (paired t-test, $P = 0.019$). The positive shift of LIP category indices indicates that the distribution of preferred directions became highly non-uniform as a result of training in the categorization task (see below and Methods). In addition, we did not detect an obvious relationship between LIP activity and reward probability (Supplementary Information).

In contrast, category tuning was not observed across the MT population ($n = 67$ neurons; Supplementary Fig. 1). Mean category-

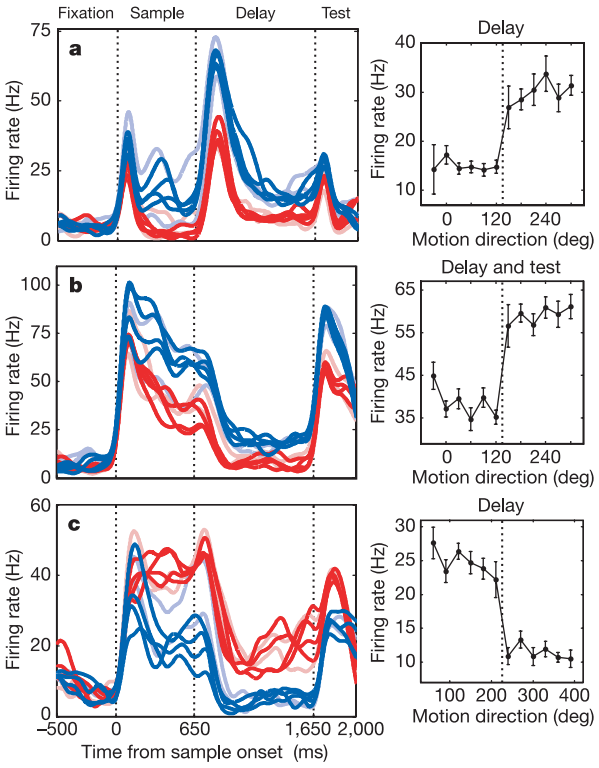

Figure 2 | Examples of three category-selective LIP neurons. Average activity to the 12 sample directions for three LIP neurons is shown. The red and blue traces correspond to directions in the two categories (red, category 1; blue, category 2), and pale traces indicate the directions closest to (15°) the boundary. The three vertical dotted lines indicate (from left to right) the timing of sample onset, the sample offset and the test-stimulus onset. The neurons in **a** and **b** were recorded with the original category boundary. The neuron in **c** was recorded after the monkey had been retrained on the new categories. The plots at the right of each peri-stimulus time histogram (PSTH) show activity (means ± s.e.m.) for the 12 directions during the delay (**a**), delay and test (**b**) and delay (**c**).

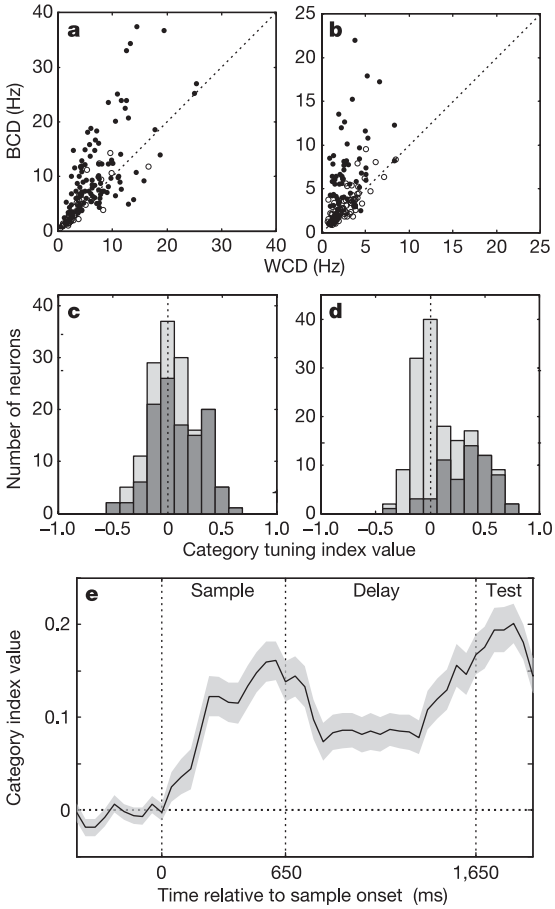

Figure 3 | Category effects across the LIP population. **a**, **b**, For each neuron, BCD and WCD values are shown for the sample (**a**) and delay (**b**). The filled and open circles indicate direction-selective and non-direction-selective neurons, respectively. **c**, **d**, A category index was computed from the BCD and WCD values. Positive index values indicate greater selectivity between categories and/or more similar activity within categories. The light grey bars show index values across all neurons ($n = 156$). The dark grey bars show index values for direction-selective neurons during sample (**c**) and delay (**d**). **e**, The time course of average category indices across 122 direction-selective neurons (during sample and/or delay).

tuning indices during both the sample (mean index 0.015) and delay (mean index 0.008) were not significantly different from zero (*t*-tests; sample, $P = 0.73$; delay, $P = 0.61$; Supplementary Fig. 2c, d).

To assess the time course of LIP category tuning in more detail, we computed a 'sliding' category-tuning index (window width 100 ms, step size 50 ms). Figure 3e shows the time course for 122 neurons that were direction-selective during the sample and/or delay. Category effects were evident within 100 ms of sample onset and persisted throughout the sample. After sample offset, category tuning waned somewhat but became progressively stronger across the delay, reaching peak values during the late delay and early test, when the monkey presumably prepared to compare the test category with that of the previously presented sample. It is notable that information about the category of the previously presented sample stimulus was strongest during the early test epoch, although the sample was presented 1 s earlier and the monkey was currently viewing the test stimulus.

Stronger category-tuning indices during the delay were apparently due to tighter clustering of responses to directions within each category and larger differences between categories. To confirm this, for each neuron we computed two separate one-way ANOVAs ($P < 0.01$, with Bonferroni correction) that compared responses to the six directions in each category. For the 115 LIP neurons that were direction selective across all 12 directions during the sample, the majority (92 of 115; 80%) also distinguished between the six directions within one or both of the two categories. However, for the 61 direction-selective neurons during the delay, a significantly smaller proportion (26 of 61, or 43%) differentiated between the six directions within either category (χ^2 test, sample versus delay, $P = 0.02$). Thus the responses tended to become more 'binary' during the delay, reflecting category membership. This trend is evident in the example neurons in Fig. 2a–c. In contrast, nearly all MT neurons (66 of 67; 99%) were selective between the six directions in either category during the sample epoch.

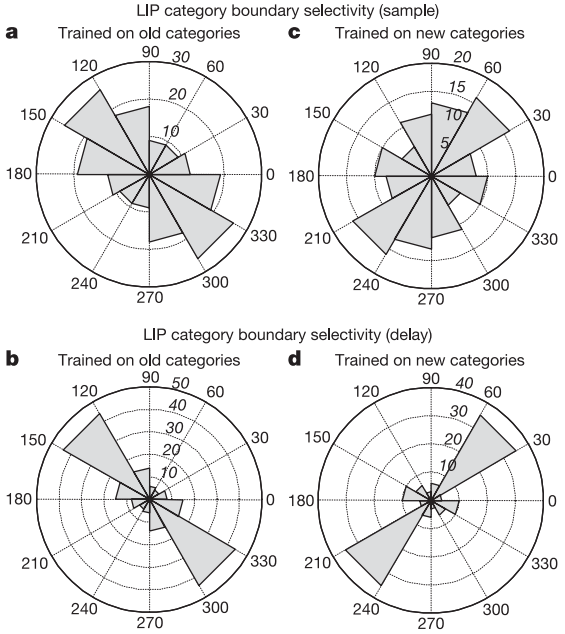

Figure 4 | LIP category selectivity followed retraining. After the recording of 92 neurons with the original category boundary, monkeys were retrained to categorize the same stimuli with a boundary perpendicular to the original one; we then recorded an additional 64 neurons. For each neuron we determined which of six possible boundaries (that is, the 'new' and 'old' boundaries, plus the four boundaries that we did not use) gave the largest difference in average activity among directions on either side of the boundary. **a**, **b**, Polar distribution of the best boundary for the sample (**a**) and delay (**b**) activity of all neurons with monkeys trained on the original boundary. The number of neurons that preferred each boundary (measured on the concentric scale with numbers in italics) corresponds to the radius of either of the two opposite 'bowtie' segments (but the two should not be added). **c**, **d**, Distribution of the best boundary for the activity of all neurons after retraining on the new categories.

To ensure that LIP category effects were due to learning the DMC task, we retrained both monkeys to group the same 12 directions into two new categories separated by a category boundary perpendicular to the original boundary (Fig. 1a, green dotted line). LIP selectivity shifted markedly with retraining. After retraining, neurons reflected the new categories and not the old (now irrelevant) categories. To quantify this effect, we determined which of six possible category boundaries (which divided the 12 directions into two equal groups) resulted in the greatest difference between average neuronal activity among the six directions on each side of the boundary. Among neurons recorded with the original boundary (92 neurons from both monkeys), sample and delay activity for most neurons was best classified by the actual category boundary that the monkeys were using and not the other five 'irrelevant' boundaries (Fig. 4a, b). After retraining the monkeys on the new categories, neuronal activity (across 64 neurons tested with the new category boundary) no longer reflected the old category boundary but was best divided by the new, now relevant, boundary (Fig. 4c, d).

Together these results indicate that training monkeys to perform a motion-categorization task causes neurons in LIP to strongly and robustly reflect the category membership of visual motion direction. LIP neurons responded more similarly to motion directions of the same category even when those directions were visually dissimilar, and they discriminated sharply between visually similar directions of different categories. In contrast, neurons in area MT, an important stage of visual motion processing[4] that provides input to LIP[3], were highly direction selective but did not group directions according to their category membership.

After retraining the monkeys to group the same stimuli into two new categories, LIP selectivity shifted markedly to encode the motion directions according to the newly learned categories. This demonstrates a profound learning-based plasticity of visual representations in LIP, beyond that typically seen in striate or extrastriate visual cortex[17], and indicates that LIP is probably important in encoding the behavioural relevance, or meaning, of visual-motion stimuli. The exact nature of the role of LIP during learning, and whether changes in the directional representations of LIP are stable or vary dynamically with the demands of the task, remain to be determined.

Whereas recent studies found categorical representations in the prefrontal cortex[18,19], a frontal lobe area involved in more 'executive' functions[20], it has been unclear whether neurons in brain areas considered to be more involved in sensory processing could encode category information. For example, studies of shape categorization in inferior temporal cortex found enhanced selectivity for task-relevant features or shapes[21,22] as a result of learning, but did not show more explicit signals about category membership[23,24]. Because area LIP is known to be involved in both sensory[25] and cognitive functions[26–28], it is well positioned for a function in transforming sensory information to more abstract, and meaningful, representations of visual stimuli.

METHODS

Physiological techniques. Two male rhesus monkeys (*Macaca mulatta*, weighing about 14 kg) were implanted with a head post, scleral search coil and recording chamber. Recording chambers were implanted in accordance with coordinates (approximate centres at P3, L10) determined by magnetic resonance imaging, and allowed access to both the intraparietal sulcus (IPS) and superior temporal sulcus by means of a dorsal approach. All surgical and experimental procedures followed Harvard Medical School and National Institutes of Health guidelines.

During LIP recordings, electrode penetrations sequentially encountered both the medial and lateral banks of the IPS. Most IPS neurons were tested with a memory-saccade task and a passive viewing flash-mapping task to generate detailed spatial maps of neuronal response fields (RF). Neurons were considered

to be in LIP if they showed spatially selective delay activity during the memory saccade task or were located between such neurons in that electrode penetration. LIP neurons were not prescreened for direction selectivity. Area MT neurons were distinguished by direction-selective responses to moving spots and bars, and RF sizes that were roughly proportional to their eccentricity[4].

DMC task. Monkeys were trained to indicate whether a test stimulus was in the same category as a previously presented sample stimulus. The monkeys could not predict whether a given trial would require a release to the first test stimulus. Monkeys' average reaction times on correct match trials were 349 ms (monkey S) and 368 ms (monkey H).

Stimuli were circular patches (9.0° in diameter) of high-contrast square dots that moved in 1 of 12 evenly spaced directions (30° apart) with 100% motion coherence and at a speed of 12.0° s^{-1}. Stimuli were always centred in the RF of the neuron under study. Trials began with the onset of a 0.25° spot, which monkeys were required to fixate within ±1.5° for the duration of the trial. During recordings from monkey H we excluded the four test stimuli closest to (15°) the category boundary where the monkey made the greatest number of errors.

Data analysis. All analyses (except error trial analyses) were conducted across correct trials. The pattern of behavioural and neuronal results was similar, and all main effects were observed in both monkeys. The precise timing of analysis windows was not critical; similar results were obtained with a variety of window widths and starting points.

The strength of neuronal category selectivity was estimated by a category-tuning index. It was determined for each neuron by computing two values: the average WCD in firing rates between pairs of directions in the same category, and the average BCD in firing rates between pairs of directions in different categories (Supplementary Information). The index was computed with the formula (BCD − WCD)/(BCD + WCD) and could vary from −1.0 to 1.0. The index was computed according to the currently relevant category boundary, allowing the data sets with each category boundary to be combined and analysed together.

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