Psychophysically measured task strategy for disparity discrimination is reflected in V2 neurons

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In perceptual tasks, subjects attempt to rely on their most informative cues. Such strategic choices should be reflected in the types of sensory neurons that are used. We investigated this in a binocular-disparity discrimination task. Using psychophysical reverse-correlation, also known as image classification, we identified the perceptual strategies of two macaques (*Macaca mulatta*). Correlations between reported disparity signs and disparity noise samples for each trial yielded detection 'filters'. Filter amplitude was greater at near disparities than at far disparities, indicating that the subjects relied more on near disparities. Recordings from both macaques' disparity-selective V2 neurons showed a correlation between neuronal responses and perceptual judgment in near-preferring, but not far-preferring, units, mirroring the psychophysically measured strategy. After one monkey learned to weight near and far disparities equally, activity in its far-preferring neurons correlated with choice. Thus, the pattern of correlations between neuronal activity and perceptual reports indicates how subjects use their neuronal signals.

Visual perception is an active process, and subjects usually learn to exploit their most useful signals for a given perceptual task. Perceptual signals (carried by neurons) should therefore be used differently in different tasks, depending on the subject's strategy. One technique that has been widely used to evaluate whether signals from particular neurons contribute to a given perceptual decision combines threshold psychophysics with single-unit recordings. A trial-to-trial correlation between neuronal activity and perceptual judgment, which cannot be explained by the visual stimulus, is taken as evidence that neuronal signals contribute to a decision[1–7]. Such a correlation, often quantified by 'choice probability', should then also depend on the task strategy employed by the subject[6]. Only those neurons providing signals that a subject chooses to exploit in a particular strategy should show substantial choice probabilities. It is natural that subjects usually rely on those signals that are most statistically suitable for the task at hand. Several studies have found that neurons carrying higher-precision signals for a given task show stronger correlations with perceptual judgment[2,3,5,8,9].

It should be noted that this sort of relationship would be expected in almost any system that makes optimal use of a set of variable input signals, and so this stronger correlation with perceptual judgment for higher precision neurons does not clearly identify a relationship with a subject's strategy. Consequently, these relationships would be observed even if considerable 'hard-wired' processing modified the signals before they were used for decision-making. Situations where subjects adopt suboptimal strategies are potentially more informative. Suppose that a subject ignores some useful signals, but not others, and that substantial choice probabilities are seen only for those neurons whose signal is included by this subject's strategy. This would indicate a substantially

more specific connection between neuronal activity and the individual subject's perceptual decisions than has been previously shown.

Here we explore this possibility by combining measures of choice probability (in area V2) with psychophysical reverse-correlation[10–12], which is an objective measure of the two macaque monkeys' strategy. In our disparity discrimination task, this method produced psychophysical kernels that quantify how disparities in the stimulus contribute to the subjects' decisions. A similarity emerged. The psychophysical kernels showed that the animals gave considerably less weight to far disparity signals. The neurophysiological data revealed that neurons carrying far disparity signals did not have significant choice probability ($P = 0.43$), unlike neurons with near disparity signals ($P < 0.001$), and despite having similar statistical reliability for the task. Subsequently, one of the two animals learned to give equal weight to near and far disparity signals. Once its strategy had been changed, highly significant choice probabilities ($P < 0.001$) were measured in both this monkey's far-preferring and near-preferring V2 neurons. Combining these techniques allowed us to demonstrate a neurophysiological signature of the strategy that subjects apply to perceptual tasks.

RESULTS

Two macaque monkeys were trained on a disparity discrimination task in weakly correlated random dot–stereograms (RDSs, **Fig. 1**). In a forced-choice task, they reported whether they perceived a central circular patch in front of (near) or behind (far) a surrounding annulus. The central patch contained dots at one of two signal disparities (one disparity was always near and the other was always far) that were masked by 'noise dots', whose disparity was chosen at random from a discrete distribution ($-1.2°$, $-1.0°$, … $1.0°$, $1.2°$). Note that we define

Figure 1 Methods. (**a**) The sequence of events in the task carried out by the monkeys. Once the animal fixated, the stimulus was presented on the screen for 2 s, and then two choice targets appeared above and below the fixation marker. Only saccades made within 500 ms to the correct choice target were rewarded. (**b**) Schematic views of the stimulus at different levels of interocular correlation (100%, 50% and 0%). Upper row, front view. Red and yellow dots were shown to the right and left eye only, respectively. Bottom, schematic view from above. The subject fixated and the stimulus appeared as a disc at the signal disparity (orange dots, 100% correlation), as a 'cloud' extending in depth (cyan dots, 0% correlation) or as a mixture of both (50% correlation). (**c**) A schematic showing how the psychophysical kernels are calculated. The distributions of noise dots (number of dots at each disparity) on each trial were sorted according to the subject's choices. For both kinds of choices, the detection kernel is the average dot distribution minus the average number of dots per disparity across all trials (μ). The number of near-choice trials and far-choice trials are n_{near} and n_{far}. Because of the obligatory symmetry up to a scaling factor between the near- and far-choice detection kernels, they can be summarized by their difference (near-choice detection kernel – far-choice detection kernel).
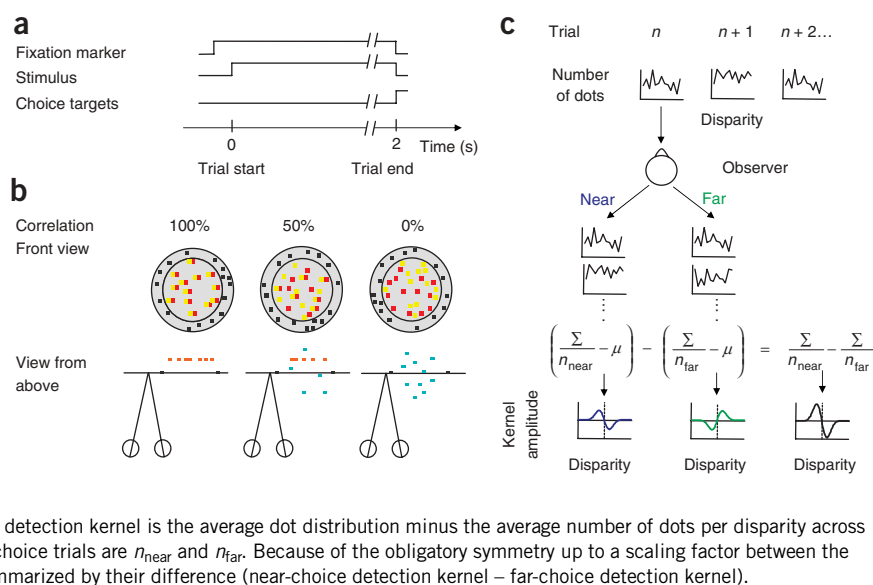
negative disparities as near disparities. The surrounding annulus was presented at 0° disparity and was 100% correlated. We controlled task difficulty by the percentage of signal dots. When there were no signal dots, subjects were rewarded randomly. Within each trial, the distribution of noise dots was fixed and recorded, although the position of every dot was reassigned on each video frame. A different distribution of noise dots was chosen randomly for every trial. If a subject's strategy places more weight on some disparities than others, these disparities will dominate the perceptual decisions. We measured this by calculating the average number of dots at each disparity for all stimuli that elicited a near choice and by calculating a separate average for stimuli eliciting a far choice. The resulting averages constituted 'detection kernels' (**Supplementary Fig. 1** online) and could be summarized by their difference (see Methods, **Fig. 1c**), which we termed the psychophysical kernel. These kernels were calculated for all trials on which the stimulus only included noise dots.

We determined the psychophysical kernel for monkey 1 (**Fig. 2a**). The signal disparities of the stimulus in this experiment were –0.2° and 0.2°. The kernel amplitude showed a clear peak at –0.2°. Kernel modulation was much weaker for all other disparities. In particular, the amplitude at 0.2° was much smaller than that at –0.2°. This pattern was similar for monkey 2 (**Fig. 2b**). For both monkeys, the kernels were more strongly modulated at –0.2° than they were at 0.2°, even though both disparity values were equally useful in the task. The amplitude at the near disparities was significantly larger than that at the far

disparities in all conditions for monkey 1, and in three out of the four conditions for monkey 2 ($P < 0.05$, by resampling). This suggests that the monkeys relied more strongly on the near disparities than they did on the far disparities. The psychophysical kernels were similar in all task conditions (**Fig. 3a,b**), despite the changes in signal disparities. The similarity between kernels for different signal disparities allowed us to summarize all of the data with a single kernel for each monkey (**Fig. 3c,d**), confirming that the subjects' perceptual decisions were most strongly influenced by near-disparity dots at about –0.2°. (The peak kernel amplitude at the near disparities in this average was significantly larger than that at the far disparities, $P < 0.0001$ for both monkey 1 and monkey 2).

These results demonstrate that both monkeys based their decisions primarily on the presence or absence of dots with near disparities and placed less weight on dots with far disparities. But these results do not explain why subjects chose this strategy, which is suboptimal in terms of stimulus content, although not necessarily relative to the information content of the set of disparity-tuned neurons by which the monkeys determine their decision. We speculate that the use of this suboptimal strategy was related to the appearance of the uncorrelated stimulus when surrounded by a zero-disparity annulus. The segmentation of the uncorrelated stimulus and its correlated surround at zero disparity yields a clear sensation of depth in some subjects (for additional results in humans, see **Supplementary Figs. 2–4**, **Supplementary Methods** and **Supplementary Discussion** online). Initial responses during training suggest that this was also the case for the animals used here. Both monkeys had previously been extensively
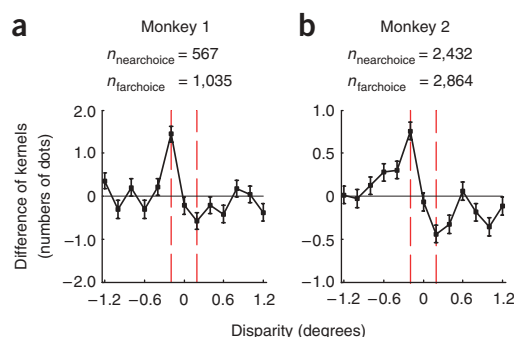
Figure 2 The psychophysical kernels for one experimental condition. (**a,b**) The psychophysical kernels for monkey 1 (obtained from $n = 1,602$ trials, $n_{nearchoice} = 567$ and $n_{farchoice} = 1,035$) and monkey 2 ($n = 5,296$ trials, $n_{nearchoice} = 2,432$ and $n_{farrchoice} = 2,864$), respectively, for the experimental condition in which the signal disparities corresponded to –0.2° and 0.2° (red lines). Across all correlation levels, monkey 1 made $n = 4,974$ near choices and $n = 6,070$ far choices, and monkey 2 made $n = 11,785$ near choices and $n = 13,252$ far choices. Error bars show s.d. of the resampled distributions. In both monkeys, the peak amplitude for near disparities was significantly larger than that for far disparities (by resampling, $P < 0.02$). On average, the stimuli contained 16 dots at each disparity.
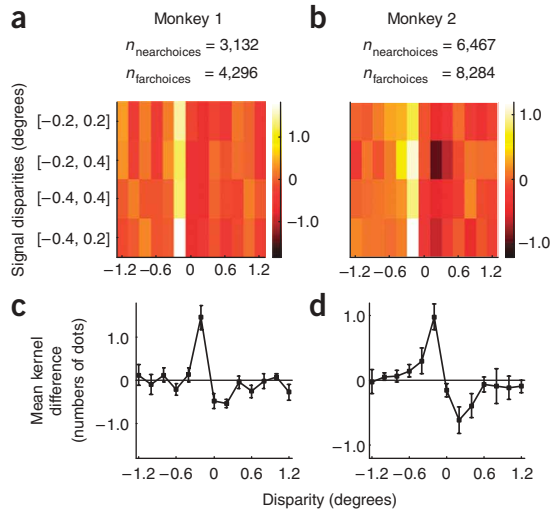
Figure 3 Psychophysical kernels for all experimental conditions. Each column displays data for one monkey. (**a**,**b**) The kernels for all conditions. Each row corresponds to one experimental condition (condition 1, [–0.2°, 0.2°]; condition 2, [–0.2°, 0.4°]; condition 3, [–0.4°, 0.4°]; condition 4, [–0.4°, 0.2°]). The abscissa plots disparity in degrees; color represents kernel amplitude (number of dots). The total number of trials from which the kernels were calculated for each monkey were $n = 7,428$ (monkey 1) and $n = 14,751$ (monkey 2). Across all correlation levels and conditions, monkey 1 made $n = 24,468$ near choices and $n = 26,405$ far choices, and monkey 2 made $n = 30,237$ near choices and $n = 33,702$ far choices. (**c**,**d**) Plots of the means of the kernels across experimental conditions. Error bars are s.d., indicating the degree of similarity across conditions (statistical testing is based on resampling the raw data, see Methods).

trained on a stereoacuity task with similar RDSs. When they first attempted a task in which binocular correlation was varied, they readily detected high correlations, but showed a bias for far-disparity judgments at low correlation. This suggests that these two animals perceived uncorrelated dots as far disparity. The monkeys subsequently underwent extensive training to eliminate this bias in responses using a staircase procedure[13]. It seems that learning not to give a far-disparity response at low correlation led to the monkeys using a perceptual strategy in which dots with far disparities were weighted less than dots with near disparities (see **Supplementary Discussion**).

Why the monkeys relied on dots with disparities close to –0.2°, even when the signal disparity had a different value, is less clear. However, it should be noted that during the recording experiments, the signal disparities were always chosen to approximately match the preferred and the null disparity of the recorded neuron. When recording successively from more than one neuron in a session, the signal disparities could change within a single recording session. The monkeys' reliance on disparities that were close to –0.2° may reflect a strategy that they adopted to deal with changing signal disparities.

These psychophysical kernels demonstrate a suboptimal strategy that was employed by the monkeys: far choices largely reflected an absence of near dots, rather than the presence of far dots. Although we can only speculate as to why the monkeys adopted this strategy, the important point is that the psychophysical kernels document the fact that they were using this strategy. This then allowed us to investigate whether this perceptual strategy was reflected in the neuronal response in disparity-selective V2 neurons. For this, we re-examined previously reported data[14].
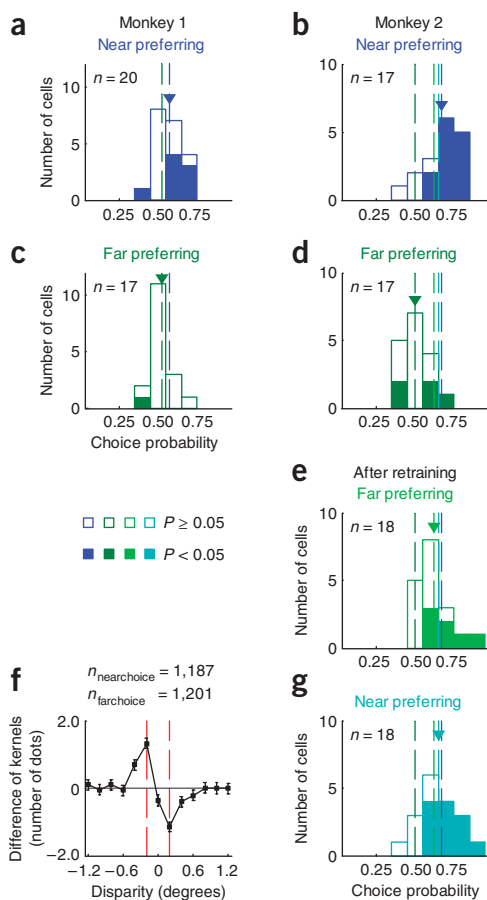
Choice-related neuronal response reflects task strategy

We recorded responses from 71 disparity-selective V2 units (significant modulation of mean response with disparity in a one-way ANOVA, $P < 0.01$) in the same two macaque monkeys as they performed an almost identical disparity discrimination task in weakly correlated RDSs. The only difference between the stimuli was that the positions of the noise dots in the two eyes' images were completely uncorrelated. To appreciate the similarity of the two stimuli, note that in the psychophysical stimulus, if the total range of disparities used was equal to the stimulus width, the horizontal dot locations were uncorrelated in the two eyes' images. The values for the two signal disparities corresponded approximately to the preferred and null disparity of the

neuron. We quantified the trial-to-trial correlation of the neuronal response with the perceptual judgment as choice probabilities using receiver-operating characteristic analysis[3]. This metric describes the probability with which an ideal observer would be able to predict the subject's response on a given trial, knowing only the firing rate on this trial and the distributions of firing rates for the choices to both targets. We recently reported that disparity-selective V2 neurons showed significant choice probabilities in this task, with the mean choice probability in the population being 0.57, which was significantly larger than chance ($P < 0.001$). Here, we separated the neurons according to the sign of their peak disparity (near-preferring neurons have a peak disparity $< 0°$ and far-preferring neurons have a peak disparity $> 0°$) for both monkeys (**Fig. 4**). This revealed that the mean choice probability was significantly larger than chance for near-preferring neurons (mean choice probability was 0.62, $n = 37$, above 0.5, $P < 0.001$, by resampling), but not for far-preferring neurons (mean choice probability was 0.51, $n = 34$, not significantly different from 0.5, $P = 0.43$). The same pattern holds in each monkey individually (**Fig. 5**): the choice probabilities were significant for the near-preferring units (0.58, $n = 20$ and 0.67, $n = 17$ for monkey 1 and monkey 2; significantly different from 0.5, $P < 0.001$ for both, by resampling; **Fig. 5a,b**) and were not significantly different from chance for the far-preferring neurons (0.52, $n = 17$, $P = 0.17$ and 0.5, $n = 17$, $P = 0.98$ for monkey 1 and monkey 2, both by resampling, respectively; **Fig. 5c,d**). For both monkeys, the difference in mean choice probability between the two groups was significant ($P < 0.05$ for monkey 1 and $P < 0.0001$ for monkey 2, t-test).
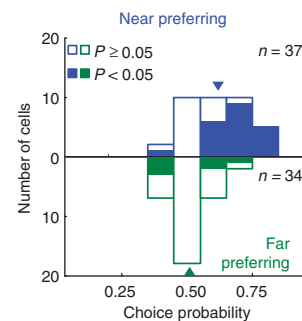
Figure 4 Distribution of choice probabilities in V2, separated for near- and far-preferring neurons. Filled and open bars depict cells with significant ($P < 0.05$) and nonsignificant choice probabilities, respectively ($n = 71$, overall mean choice probability = 0.57). The distribution of choice probabilities for near- and far-preferring neurons are plotted in the top (blue) and bottom (green) half of the panel, respectively. Note that the distribution for near-preferring neurons is shifted toward higher values. The mean choice probability for near-preferring units was 0.62 (blue triangle), and for far-preferring units the mean choice probability was 0.51 (green triangle).

Figure 5 Distribution of choice probabilities separated by monkeys and preferred disparity sign. (a–d) The near-preferring neurons are summarized in the top row ($n = 20$, mean $= 0.58$ and $n = 17$, mean $= 0.67$ for monkeys 1 and 2, respectively), and far-preferring neurons are shown in the second row ($n = 17$, mean $= 0.52$ and $n = 17$, mean $= 0.50$ for monkeys 1 and 2, respectively). (e–g) The psychophysical kernel and choice probabilities for monkey 2 after retraining (symbols as in **Fig. 2**). The peak amplitudes of the physical kernel for near and far disparities were no longer statistically different ($P = 0.38$, **f**). The changed strategy in monkey 2 is mirrored by significant choice probabilities in far-preferring neurons after retraining (**e**, $n = 18$, mean choice probability $= 0.61$, significantly larger than 0.5, $P < 0.001$, and different from the mean choice probability for far-preferring neurons before retraining, $P < 0.002$). The mean choice probabilities for near-preferring neurons remained unchanged (**g**, $n = 18$, mean choice probability $= 0.65$, larger than 0.5, $P < 0.001$, not significantly different from the mean choice probability preceding pretraining, $P = 0.62$). Vertical dashed lines in **a**–**e** and **g** show distribution means (blue, near preferring; green, far preferring; light green, far preferring after retraining; cyan, near preferring after retraining) to facilitate comparison.

phase[15] to quantify symmetry of disparity tuning: the disparity-tuning curves were fit by Gabor functions (required to explain 65% of the variance, $n = 69$). The extent to which this fitted curve was even or odd symmetric (about zero disparity) was then expressed as a phase angle between $-90°$ and $90°$. The distributions of the absolute values of symmetry phase for near and far-preferring neurons were not significantly different ($P = 0.49$, Kolmogorov-Smirnov test). We quantified the neuronal thresholds as described previously[5,16] (see ref. 14). The mean neuronal threshold for the task was even slightly lower for the far-preferring neurons (mean threshold, $36\% \pm 17\%$) than for the near-preferring neurons (mean threshold, $44\% \pm 19\%$), although this difference was not statistically significant ($P = 0.14$, t-test). Differences in disparity symmetry or neuronal thresholds between near- and far-preferring V2 neurons are therefore unlikely to explain the lack of significant choice probabilities in far-preferring neurons.

Instead, choice probability depended on the preferred disparity of the neuron, with a negative correlation existing between the two (**Fig. 6a**; Spearman's rank correlation, $r_s = -0.43$, $P < 0.001$). This correlation was significant in both monkeys individually ($r_s = -0.34$ and $P < 0.05$, and $r_s = -0.49$ and $P < 0.005$ for monkey 1 and monkey 2, respectively). The effect on responses over a range of disparities can be seen from a population-mean disparity-tuning curve (**Fig. 6b**), in which the contribution from each neuron is weighted by w, where $w =$ choice probability -0.5. Note that this difference ensures that for neurons in which firing is unrelated to choice, random deviations of choice probability from 0.5 average to a weight of zero. This average weighted tuning curve showed a peak at about $-0.5°$ and a trough for disparities $> 0°$ (far disparities). To control for any sampling bias, we
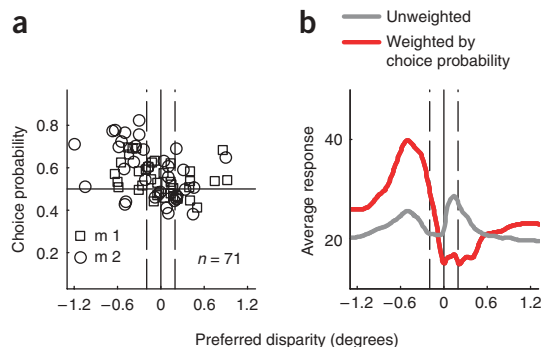
A previous study of choice probability in disparity-selective neurons in middle temporal cortex using an almost identical task reported that two neuronal properties were associated with choice probabilities[5]: (i) the more asymmetrical a neuron's tuning curve was about $0°$, the higher its choice probability, and (ii) a neuron's choice probability was negatively correlated with its disparity correlation threshold (neuronal threshold) for the task. If one of these properties were more prominent for the near-preferring than for the far-preferring neurons in our V2 data, the discrepancy in choice probability might simply be a reflection of this. We therefore investigated the distribution of these two properties in our V2 neurons. In the middle temporal cortex study, disparity-tuning symmetry was quantified as the phase of the Gabor fit to the disparity-tuning curve whose mean was constrained to $0°$. For many disparity-tuning functions in V2, this constraint on the mean led to poor fits. We therefore used a slight modification of the symmetry

Figure 6 Choice probability depends on preferred disparity. Squares correspond to data from monkey 1, circles to data from monkey 2. (**a**) A comparison of preferred disparity (degrees) with choice probability showed a negative correlation ($r_s = -0.43$, $P < 0.001$, $n = 71$). Dashed lines mark the disparities of $-0.2°$ and $0.2°$, solid black lines mark the disparity of $0°$ and the choice probability of 0.5. (**b**) The average disparity-tuning curve, weighted by the choice probability $- 0.5$, is shown in red. Superimposed is the unweighted average disparity-tuning curve in gray. In contrast to the unweighted average, the weighted average has a peak at disparities $< 0°$ and a trough at disparities $> 0°$. The trough arises because the weighted curve is dominated by near-preferring neurons, which often show a trough in their response at small far disparities. The black solid line marks the disparity of $0°$ and black dashed line marks the disparities of $-0.2°$ and $0.2°$.

also determined the unweighted average disparity-tuning curve (**Fig. 6b**), which was more balanced, with one peak for near disparities and one for far disparities. The single peak at near disparities for the weighted average is therefore a reflection of the fact that the monkeys relied more strongly on near disparities. That this average peaks at disparities of $-0.5°$, even though the psychophysical kernels suggest that the animal most strongly relied on disparities around $-0.2°$, is surprising if one supposes that neurons that carry the most weight in the decision have the highest choice probabilities. However, this assumption ignores the effect of interneuronal noise correlation. If noise was equally correlated between all near-preferring neurons, then choice probability should be similar in all near-preferring neurons, regardless of which neurons carry the most weight for the decision[17]. This would produce a weighted tuning curve which would reflect the unweighted mean across all near-preferring neurons (as can be seen in **Fig. 6b**). This is similar to a previous observation[17], in which the correlation between choice probability and neuronal thresholds could not be achieved by weighting more precise neurons more strongly, but could be explained by supposing that more precise neurons showed stronger interneuronal noise correlations than less precise neurons did.

A different explanation for the discrepancy between the peak in **Figure 6b** and the peak of the monkeys' psychophysical kernel would be to suggest that choice probability has a top-down origin. If the top-down signal is sent back to all near-preferring neurons, then choice probability would be present in all these neurons, giving rise to a weighted average resembling that shown in **Figure 6b**. Nonetheless, we do not claim that these explanations are correct—we merely point out that the shape of the weighted tuning curve and the psychophysical kernel do not necessarily have to match.

A changed strategy yields choice probabilities in far neurons

Both monkeys subsequently carried out the discrimination task for several months with a modified stimulus. In this RDS, all of the dots had the same disparity on any given frame, but the disparity value was changed randomly from frame to frame (96-Hz frame rate). The appearance of the RDS was that of a central disc whose depth changed from frame to frame, surrounded by a zero-disparity annulus. Because the frame rate exceeded the temporal resolution for disparity modulation[18,19], successive disparities 'blurred' together, producing a transparent percept, with the near and far components being visible. Therefore, this stimulus did not have a near or far appearance at 0% correlation. As a consequence of training with this stimulus, monkey 2 learned to rely equally on near and far disparities, even when retested with the stimulus used to measure psychophysical kernels above. The kernel measured after this retraining at signal disparities $(-0.2°, 0.2°)$ is shown in **Figure 5f**. Here, however, the amplitudes at near and far disparities were not significantly different from each other ($P = 0.38$; compare with **Fig. 2b**). Note that, despite the same amount of retraining, monkey 1 persisted to rely more strongly on near disparities, as indicated by significantly different kernel amplitudes ($P < 0.05$, $n = 520$; **Supplementary Fig. 5** online). We subsequently recorded additional data from 36 units (18 near preferring and 18 far preferring) in monkey 2. The mean choice probability in the population of far-preferring neurons was 0.61, which was significantly larger than 0.5 ($P < 0.001$, by resampling; **Fig. 5e**), and was significantly different from the mean choice probability in the far neurons before retraining ($P < 0.002$, t-test). After retraining, mean choice probability in far-preferring neurons no longer differed from the mean choice probability in near-preferring units ($P = 0.36$, t-test), whereas the mean choice probability in near-preferring neurons remained unchanged with this training ($P = 0.62$, t-test, pre- versus post-retraining; mean choice

probability after retraining was 0.65, significantly larger than 0.5, $P < 0.001$, by resampling; **Fig. 5g**). This change in choice probability for far-preferring units following the change in perceptual strategy strengthens our conclusion that choice probability reflects task strategy.

DISCUSSION

Here we combined neurophysiological measures of choice probability with psychophysical reverse-correlation, which quantifies how information is used by observers when carrying out a task, in the same subjects. The results manifest a compelling similarity; that is, in our task, the monkeys appeared to rely predominantly on dots with near disparities, and choice probabilities were substantially larger in neurons signaling near disparities (0.62) than in those signaling far disparities (0.51). This occurs despite the fact that, in purely informational terms, the near-preferring and far-preferring neurons provided equally reliable signals. After one monkey's strategy changed to giving similar weight to near and far disparities, its far-preferring V2 neurons showed significant choice probabilities (0.61). This demonstrates that for neurons in a given brain area to show substantial choice probability, not only must they provide information that is relevant to the task, but they must also provide information that is exploited by the subject's perceptual strategy. This is, to our knowledge, the first demonstration that a measured task strategy is reflected in activity at the level of individual neurons, and that changing this strategy changes choice probability in the relevant neuronal population. Although it has been suggested before that patterns in observed choice probability reflect subjects' perceptual strategies[5], such proposals have been interpretations of neurophysiological data and have lacked behavioral evidence that any particular strategy was employed.

To appreciate why the monkeys may have adopted this suboptimal strategy, it is helpful to consider their initial bias: reporting far in response to the uncorrelated stimulus. From the reports of human observers, it seems likely that this bias is perceptual; that is, an uncorrelated stimulus appears to be far to the monkeys. We do not know the origin of this perceptual bias, and its direction and strength differed between human subjects (see **Supplementary Results** and **Discussion** online). In response to an uncorrelated stimulus, the rewards were randomized and the monkeys therefore saw the stimulus as far, but were rewarded on only 50% of the trials. Conversely, the monkeys only perceived the stimulus as near when the stimulus contained a sufficient proportion of signal dots at the near disparity, and therefore always received a reward. Consequently, the sensation of near is a more reliable predictor of reward than the far sensation. The optimal method to compensate for this perceptual bias would be to integrate all of the sensory information and simply apply a decision criterion (incorporate a response bias) that maximizes rewards. The monkeys' failure to do this is demonstrated by our psychophysical kernels. It should be noted that this demonstration that the animals are using the signals in this manner holds, regardless of our speculation as to why the monkeys developed this suboptimal strategy. This suggests that adjustments to the perceptual decision criterion interact with the processing of the perceptual signals themselves. That these changes are also reflected in the choice probabilities of V2 neurons indicates that this interaction occurs early in visual processing.

If this interpretation is correct, the interaction between response criterion and sensory signals could be important in many situations. It may be that experimental manipulations of the psychophysical responses, for example, by changing reward regimens or target salience, produce similar changes in the representation of the sensory inputs. Combining psychophysical reverse-correlation with measures of choice probability allows one to examine this possibility directly.

The above interpretation also supports early selection theories of attention (for example, see ref. 20). These theories suggest that selection for further cognitive processing occurs early in and affects sensory processing, as opposed to late selection theories (for example, see refs. 21,22), which in their extreme position propose that sensory processing is unaffected by attention and that selective processing only occurs at a later stage. A number of physiological studies that manipulate attention (for example, see refs. 23–27) have likewise supported early selection.

Two general schemes by which task strategy could be reflected in the choice-related activity of sensory neurons have been put forward: bottom-up and top-down[28]. In the bottom-up scheme, it has been suggested that during training the monkey's strategy causes relevant neurons to become more strongly connected to the decision process[5,29]. Detailed computational simulations[17] of the bottom-up scheme have quantitatively explained empirical findings of choice probabilities and psychophysical performance for motion discrimination in middle temporal cortex by assuming that there are two pools of sensory neurons, each supporting one alternative perceptual decision. Adapted to our disparity discrimination task, one pool of neurons would consist of near-preferring neurons, and the other would consist of far-preferring neurons. The stronger connectivity developed to support task strategy could be implemented in this scheme as a higher weight being given to the activity of the near-preferring pool, generating higher choice probabilities for this group. However, all of our results are also readily explained in a top-down scheme. If the perceptual decision is formed elsewhere in the brain (compare ref. 30), it would be unsurprising that this signal be fed back more strongly into those neurons used in the task, as has been shown for neurons at higher stages of processing, such as MST[31] or VIP[32]. Feature-based attention[23,25,33] is an alternative top-down mechanism that could give rise to significant choice probabilities. Findings of task-dependent changes of interneuronal noise correlations, which are closely coupled to choice probability[17], in middle temporal cortex (M.R. Cohen & W.T. Newsome, *Soc. Neurosci. Abstr.* 16.6, 2005) are difficult to reconcile with a purely bottom-up explanation. It therefore seems likely that a component of choice probability is produced by a top-down mechanism.

Combining psychophysical reverse-correlation with measurements of choice probabilities in the same animals refines our understanding of how the activity of a single neuron is linked to perceptual decisions. These links depend not only on the information carried by single neurons, but also on just how that information is exploited in forming a decision.

METHODS

Animals. Two male macaque monkeys (*Macaca mulatta*) were implanted with scleral search coils in both eyes[34], with head-fixation posts and with a recording chamber under general anesthesia. All procedures were in agreement with the Public Health Service policy on the humane care and use of laboratory animals and all protocols were approved by the National Eye Institute Animal Care and Use Committee.

Task. The subjects carried out a disparity discrimination task (near versus far). Stimuli were circular dynamic RDSs, consisting of a circular central region and a surrounding annulus. On each trial, the central patch contained one of two disparities. For the neurophysiological experiments (average psychophysical functions in **Supplementary Fig. 6** online), the disparities were chosen to be close to the preferred and null disparities of the unit. The disparity values were not necessarily symmetrical about zero, but one disparity always had to be negative and the other always had to be positive. The percentage of the dots correlated between the two monocular images varied from trial to trial (typical percentages were 0%, 6.25%, 12.5%, 25% and 50%). For the 0% correlation condition, the disparity became undefined and subjects were rewarded randomly. The dots in the surrounding annulus were always 100% correlated at zero disparity. The monkeys had to maintain fixation during the 2-s stimulus presentation and indicate their choice by making a vertical saccade (3° above or below the fixation marker) to one of the choice targets within 500 ms of the end of the stimulus presentation (**Fig. 1a**).

Stimulus for psychophysical reverse-correlation. The manner by which uncorrelated dots were added to the display differed slightly for the two parts of the study. For physiological recordings, noise dots were given completely independent locations in the two eyes' images (and this was done independently on each video frame). For the psychophysical work, to produce sufficient disparity variation to permit reverse-correlation analysis, each noise dot was given a random disparity from a discrete distribution of 13 disparity values (−1.2°, −1.0°, …1.0°, 1.2°). Dot density was 20%, stimulus diameter (center) was 3°, the width of the surrounding annulus was 1° and eccentricity was 4.2°. The total number of dots was the same on each trial. For the duration of a single trial, the distribution of dot disparities was the same on every frame and these values were stored, but the dot locations were randomly assigned anew on each frame (that is, the stimulus was a dynamic RDS). Although one frame contains many false matches, averaging these over many frames of the dynamic stimulus reduces their impact relative to the signal dots. It should also be noted that the difference between this stimulus and a truly uncorrelated stimulus is small. If the disparity range had been −1.5° to 1.5° (range equal to stimulus diameter), then the horizontal dot locations would have been uncorrelated in the two eyes.

Psychophysical reverse-correlation analysis. Only trials in which the stimuli consisted entirely of noise dots (defined as 0% correlation) were used to calculate the psychophysical kernels. To obtain the detection kernels for the near and far choices, we calculated the mean disparity distribution for near and far choices, respectively. The average number of dots per disparity for all trials was subtracted from each mean distribution, so that kernel amplitude was represented in units of numbers of dots (above or below average). The average number of dots at each disparity in the 0% correlated stimulus was 16. There is an obligatory symmetry between the near detection kernel and the far detection kernel up to a scaling factor, as they were obtained by splitting a single distribution. For this reason, the two kernels are summarized by their difference (k_i):

$$k_i = \bar{s}_{\text{near},i} - \bar{s}_{\text{far},i} = \frac{1}{n_{\text{near}}} \sum_{j=1}^{n_{\text{near}}} s_{\text{near},j,i} - \frac{1}{n_{\text{far}}} \sum_{j=1}^{n_{\text{far}}} s_{\text{far},j,i}$$

The vector k_i corresponds to the amplitude of the psychophysical kernel as a function of disparity (i), $\bar{s}_{\text{near},i}$ and $\bar{s}_{\text{far},i}$ are the mean stimulus vectors preceding near and far choices, n_{near} and n_{far} are the numbers of near and far choices, and $s_{\text{near},j,i}$ and $s_{\text{far},j,i}$ are the stimulus vectors preceding the near and far choices on each trial (j), respectively.

We tested whether the monkeys relied predominantly on near or far disparities by resampling[35]. For each resampled kernel, we compared the peak amplitude for all near disparities with that for all far disparities, and *P* values were obtained from these comparisons. This procedure was carried out for each signal-disparity condition individually and on the combined dataset for each monkey.

Recording and stimulus presentation for electrophysiology. Two thirds of the physiological data presented here are further analyses of data for which the recording procedure was fully described[14]. Briefly, we recorded extracellular activity from disparity-selective single units in V2. The horizontal and vertical positions of both eyes were measured with a magnetic scleral search system and digitized at 800 Hz. The monkeys viewed the stimuli on CRT monitors in a Wheatstone stereoscope configuration. All stimuli were dynamic RDSs (2–5° center diameter, 1–2° width of surround, 50% black and 50% white dots of 99% contrast, dot density was generally 40%, and dot size was generally 0.09 × 0.09°).

Analysis of choice probabilities. Trial-to-trial correlations between neuronal firing and perceptual choice were quantified as choice probabilities[3] based on

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signal detection theory. Data for correlation levels of 25% and below and for which the monkey had made at least five near choices and five far choices were included. For each trial, the mean firing rate was obtained. The firing rates at each disparity and correlation level were z-scored to remove the stimulus-evoked mean response and variance. The z-scores were then divided into two groups determined by the monkeys' choices. From the distributions of the z-scores for all near and far choices, we calculated a receiver-operating characteristic curve. The choice probability is defined as the area under the receiver-operating characteristic curve. In a permutation test[3,13] (1,000 permutations), we determined whether the choice probability was significantly different from chance. Choice probabilities that lay outside of the 95% interval of the distribution of permuted choice probabilities were considered to be significant.

Stimulus that altered the perceptual strategy. The monkeys subsequently carried out the disparity discrimination task with a modified stimulus as part of another study. The RDSs were changed such that on each frame all of the dots of the central region had the same disparity, but this disparity value changed randomly from frame to frame (the frame rate was 96 Hz). For the 0% correlation condition, the disparity value on each frame was drawn from a uniform distribution of discrete disparity values (usually $-0.6°$, $-0.5°$, ... $0.5°$, $0.6°$). Disparity signal was introduced by increasing the probability for this disparity value on a given frame. This stimulus looked different from an uncorrelated stimulus and yielded a more transparent percept with near and far disparities being visible.

Note: Supplementary information is available on the Nature Neuroscience website.

AUTHOR CONTRIBUTIONS
H.N. conducted the experiments and the data analysis and wrote the paper. B.G.C. supervised the project.

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